RESTORATION
ECOLOGY

To
Heleen and *Arieke*
Thibaud and *Perrine*

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RESTORATION ECOLOGY

THE NEW FRONTIER

Second edition

Edited by Jelte van Andel and James Aronson

with the assistance of
Christelle Fontaine and Bérengère Merlot

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Ongoing restoration along the Wemmershoek River in the Western Cape, South Africa. (Photographs: D.M. Richardson)

Top (1985). Invasive Australian wattles (*Acacia longifolia* and *A. mearnsii*) and cluster pine (*Pinus pinaster*), from the Mediterranean region, dominate the landscape.

Bottom (2011). Following clearing of invasive trees by the government-funded Working for Water Programme natural regeneration of native plants has helped bring the ecosystem to a healthy condition and water once again flows in the streams. Remaining non-native trees on the left are Casuarinas that serve as a windbreak for fruit orchards.

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- "For this second edition of *Restoration Ecology: The New Frontier*, editors Jelte van Andel and James Aronson have organized a world-class group of authors to create the most comprehensive restoration ecology textbook currently available. I believe *Restoration Ecology: The New Frontier* is a substantial contribution to the science of restoration ecology and will contribute to our ability to create an improved future."

  From the Foreword to this book by Professor Steven Whisenant, Texas A&M University and Chair of the Society for Ecological Restoration.

- "This newly revised and fully updated edition should be on the shelf of every restoration ecologist. Not a 'how-to' book, but a fine overview of many of the conceptual and interdisciplinary issues involved."

  Truman Young, University of California at Davis

- The editors of Restoration Ecology provide a prompt and adequate response to the challenge of our era: to reconcile the link between humanity and nature. Jelte van Andel and James Aronson broaden their work to include New Frontiers and a global perspective in the second edition, supporting a paradigm shift in decision making which is unavoidable if we are to cope with the global environmental crisis. The reader is convinced that ecological restoration is vital to maintain biodiversity and their services, the basis of our life. This fundamental book will certainly contribute to the global effort of restoring 15% of degraded land by 2020, as expressed in the Aichi Biodiversity Targets. It offers clear concepts and practical knowledge at the level of biomes to train scientists and practitioners and to provide knowledge to bridge the gap in the science–policy interface. I recommend the book to use in restoration planning, for the training of students and in science communication."

  Katalin Török, Centre for Ecological Research, Hungary and
  SER Europe Board member

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FOREWORD

By some estimates, nearly two-thirds of all ecosystems have been degraded by human activities. This depletion of our global 'natural capital trust fund' makes it less likely we can sustain current levels of ecosystem services. Ecosystem degradation that diminishes biological diversity or alters nutrient and hydrologic processes has serious impacts that can no longer be ignored. Direct economic losses to agriculture, livestock production, forestry, and recreation are well-known consequences of ecosystem degradation. Less understood, yet equally important, are the implications for food security and poverty. Providing for future human populations, currently over seven billion and rising toward nine billion by 2050, will be increasingly difficult. You probably wouldn't be reading this if you weren't troubled by these trends and committed to improving our collective future.

The practice of ecological restoration is a proactive approach to addressing the real-world challenges of ecosystem degradation. Our ultimate goal is to understand ecosystem functioning and apply science-based practices that solve these significant environmental problems. It is increasingly clear that ecosystem degradation has social, economic, and biophysical causes that interact at multiple spatial and temporal scales. Thus, effective restoration strategies must address this complexity in ways that vary considerably with each unique set of circumstances. This has proven to be a significant and ongoing challenge for the evolving discipline of restoration ecology. Fortunately, I believe the book you hold in your hands will be a seminal contribution toward those lofty goals.

For this second edition of *Restoration Ecology: The New Frontier*, editors Jelte van Andel and James Aronson have organized a world-class group of authors to create the most comprehensive restoration ecology textbook currently available. Significantly, the book begins by developing a robust conceptual framework linking ecosystem damage to the primary causes of degradation and potential restoration strategies. Subsequent chapters provide numerous ecosystem-specific examples selected to illustrate and reinforce those concepts and provide a framework for future endeavors. I found these chapters to be both interesting as individual case studies and effective at illustrating the book's conceptual framework. The book concludes with discussions of uncertainties associated with climatic, evolutionary, and community processes and how to incorporate those ideas into sustainable restoration strategies. I believe *Restoration Ecology: The New Frontier* is a substantial contribution to the science of restoration ecology and will contribute to our ability to create an improved future.

Steven G. Whisenant
College Station, Texas
January 2012

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PREFACE

At the turn of the twenty-first century, some 15 years ago, conservation biology and restoration ecology were clearly identified by some as vital 'hopes for the future' (Dobson *et al.* 1997). E.O. Wilson (1998) went further: given the current state of affairs, he said, a forward-looking, global society committed to a better future would devote much energy and resources, throughout this century, to restoration. But why, 'all of a sudden', do thoughtful scientists like Wilson, and many others, urge society to devote a century to ecological restoration?

Throughout human history, that is for the last hundred thousand years or so, people have explored and exploited natural resources to meet their needs for food, fresh water, timber, fibre, medicines and fuel. While recognizing that this has contributed to substantial gains in human well-being, over the millennia, the rapidly increasing 'ecological footprint' of humans, during the last two centuries in particular, has resulted in a substantial and largely irreversible loss in the diversity of life, the resilience of ecosystems and the quality of our own collective habitat on this Earth. Some say we are moving towards a precipice. Unquestionably, we have set off the first human-caused extinction crisis in the history of the planet; we have also set off climate change processes the consequences of which we cannot predict let alone control.

One hundred and ten years ago, we were one billion. Now the situation is radically different: we have a population of seven billion, adding another billion every 12 years or so, and about a fifth of humankind is consuming far more resources per capita than anyone but kings and queens had ever dreamt of before. Conclusion: we need a new *modus operandi* if we wish to move away from the precipice. We now have to work hard, and together, to 'restore towards the future', to borrow a phrase from the Society for Ecological Restoration (SER), which is the major international nongovernmental organization (NGO) in this field since 1987. We also need to shift paradigms and move towards sustainability. And justice. In short, towards a sustainable and desirable future for our children and grandchildren

By the last quarter of the twentieth century CE[1], many could see that traditional nature protection and management techniques, aimed at stopping further degradation of threatened ecosystems and landscapes, and preserving what was still more or less intact in set-asides or 'protected' areas, were no longer going to be enough. Whether the primary goal of conservationists was to safeguard perspectives for well-functioning, evolving 'nature', including biodiversity in all its forms, and to insure what is currently called the flow of ecosystem goods and services to people, restoration of degraded ecosystems was going to be necessary as well. An important trailblazer in this area was the late Anthony Bradshaw, who initiated research in the United Kingdom to learn how to reconstruct ecosystems on what he called derelict lands, left behind at the end after closure of mining sites (Bradshaw 1983).

Today, ecological restoration is a fast-growing and increasingly important component in the business, politics and applications of biodiversity conservation, ecosystem management, societal adaptation to climate change and legislated mitigation for ecological and environmental damage related to economic development. Restoration ecology as a science has come a long way too: as part of a dynamic feedback loop, the practice of ecological restoration calls for, and stimulates, ongoing development of concepts and theories, as well as short- and long-term field studies and experimentation providing scientific validation and underpinning for the practice. At the same time, it is providing much

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insight into the fundamental questions of biology and ecology at all levels of resolution, from landscapes and ecosystems to communities and populations. In other words, restoration ecology, at 30, is truly coming of age, in dozens of countries around the world. Scientists from different disciplines, along with engineers, technicians and other professionals, not to mention the thousands of amateurs and volunteers engaged in restoration, should all embrace the challenge to explore, test and, where appropriate, apply the theories, models and concepts coming from ecology, even though many of them were not conceived or developed in view of direct applications to restoration. Not all restoration practitioners may recognize the need for this, so let us explain why we say that.

In our approach towards restoration ecology, we consider a few elements essential. First of all, understanding of ecosystem structure and functioning is the central level of interest, even in cases where the reintegration of a disrupted landscape, or the rescue of biodiversity, is the main goal of a restoration project. For effective, long-lasting ecological restoration of an ecosystem, the first condition is to have as much knowledge as possible about its historic development, including human use and management, as well as misuse and mismanagement. The second condition is to analyse the causes of degradation and of current threats by applying scientific tools. The latter requires an interest both in fundamental ecological theories and models and in exploring their applicability. Techniques and approaches from the social sciences may be necessary as well, depending on the context. Last but not least, restoration ecology is intrinsically transdisciplinary, and has a huge role to play in the further development of both inter- and transdisciplinarity. Indeed, the reconstruction of earlier existing 'nature' or ecosystems, or the development of 'new nature', cannot be realized in isolation from societal and political will and impact. These elements are reflected in the structuring and the contents of this book.

In the first of four chapters in Part 1, which is intended to set the scene for all that follows, we briefly consider the historic situation of terrestrial and aquatic ecosystems in today's changing world. Next, we discuss key concepts in current restoration ecology, emphasizing the hot topics as seen from inter- and transdisciplinary perspectives. We have done our utmost to be consistent in the core concepts, and the terminology used throughout, and all general terms that appear in two or more chapters are defined in the detailed and original glossary provided near the back of the book. In the chapter texts, we have marked certain words in places where they can be useful to help the readers find their way to textbooks and scientific journals. All words and terms printed in italics appear in the index; terms in bold are defined in the glossary and included in the index.

In view of future requirements for the development of restoration ecology, the third, invited, chapter in Part 1 is devoted to implications for ecological restoration of climate change and other global changes, one of the most intriguing and complex problems we must cope with. And finally, in the last chapter of this part, planning and implementing successful restoration are discussed by two distinguished veterans in this field.

In the four interrelated chapters of Part 2, the basics of ecology and genetics are discussed in search of concepts and theories – at the levels of landscapes, ecosystems, communities and populations – that can or could be made applicable to ecological restoration in general, or some specific situations. Particular attention is paid to the problems and prospects related to the reinforcement and reintroduction of populations of animals or plants within a restoration context.

We then move on to Part 3, where the reader will find 11 chapters by invited sets of distinguished authors who discuss the problems and perspectives of ecological restoration as they have experienced them personally across a broad range of ecosystems and biomes. We here use the classic biome-by-biome approach to help readers quickly find the specific settings they are most interested in, and compare the barriers and options existing between biomes. These specialists and recognized experts in the science and the practice of ecological restoration provide a solid scientific background to evaluate the consequences of different human interventions and management measures aiming at restoration in a very wide range of biophysical and bioclimatic contexts. All the chapters in this part follow a similar approach, which should help students and other general readers get the most from them. In each of them, the authors discuss what we can learn from restoration successes and failures in the past.

In the fourth and final part of the book, the concepts and approaches mentioned in the first part are recalled, and the reader is invited to reflect upon the consequences, and help identify the perspectives, for ecological restoration in the coming years. How to cope with uncertainties, for example, is a key question. Particular

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attention is paid to evolutionary and community dynamics related to dramatic changes in the environmental conditions, and to coping with associated invasions of alien species. The ultimate goal of ecological restoration is to achieve sustainable, resilient and interconnected ecosystems, and socio-ecological systems, providing goods and services to humans and habitat and well-being for nonhuman creatures as well.

The present book is an enlarged, enhanced and updated edition of the first university-level textbook to have appeared on restoration ecology in any language (van Andel & Aronson 2006). While working on the updates of those chapters that appeared in the first edition of this book, six short years ago, we discovered how much new information has become available. Not only have new results from long-term field experiments become available, but also these results have given rise to new insights, and slowly shifting paradigms. The notion of 'restoring to the future' is a good example.

As before, the book is designed for senior undergraduate- and graduate-level courses in all disciplines related to fundamental and applied ecology, environmental studies, conservation and development. We think it will be useful especially in Europe, North America, Australia and New Zealand, but have in mind also students, researchers, teachers and others in the tropics and developing countries as well. It should provide a solid scientific background for managers and professionals involved in protected area, park or nature reserve management where restoration is being practised or contemplated, as well as practitioners of ecological restoration in governmental and nongovernmental organizations. Ecological restoration is one of the best bridges available to reconcile the seemingly opposing imperatives of nature conservation and economic development. As such, it constitutes one of the key components of the increasingly urgent search for sustainability — hence the use of 'New Frontier' in the title of the book. We hope that readers will find that this volume is helpful in their efforts to pave the way towards the future. Today's students, after all, are tomorrow's decision makers.

ACKNOWLEDGEMENTS

The editors are indebted to the team of enthusiastic chapter authors, all international experts in their fields, who bring to this book a huge amount of knowledge and expertise, while agreeing to respect a certain format and basic terminology. We are also very grateful to dozens of colleagues who reviewed manuscripts of chapters in this book, and who are acknowledged by the various authors. A special song of appreciation goes to Christelle Fontaine and Bérengère Merlot for their careful coordination and fine-tuning of all our editorial work. They contributed in particular through the verification and quality assessment for bibliographic references, figures, photos, and tables, and handled obtaining the reproduction permissions for the figures borrowed from other publications.

As for the first edition, in 2006, we dedicate this book to our children, those cherished and respected representatives of the upcoming generation who will inherit this beautiful, beleaguered and precious planet, and must shoulder the task of working for sustainability, environmental ethics and social justice in the twenty-first century CE.

Jelte van Andel and *James Aronson*
Groningen and Montpellier, January 2012

NOTE

1. The abbreviation CE refers to Common Era, a secular alternative to AD, while BCE stands for Before Common Era, substituting for BC. We will use these abbreviations throughout the book.

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Plate 4.1 Restorationists measuring a simple indicator (ground cover) along a transect on a minesite. (Photograph by David Tongway.)

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Plate 13.1 Forest conditions prior to treatment, and after combined thinning and burning treatments, as recorded from permanent photograph points in ponderosa pine forest in the Upper South Platte Watershed Protection and Restoration Project, western United States. (a) Dense ponderosa pine forest before mechanical thinning treatments. (b) Condition of this same site following thinning and prescribed burning. Prescribed burning reduces woody fuels created as a result of logging and helps maintain an open canopy similar to historic conditions. Additional prescribed burns are planned for every 10–30 years to maintain forest health. (Photographs by USDA Forest Service.)

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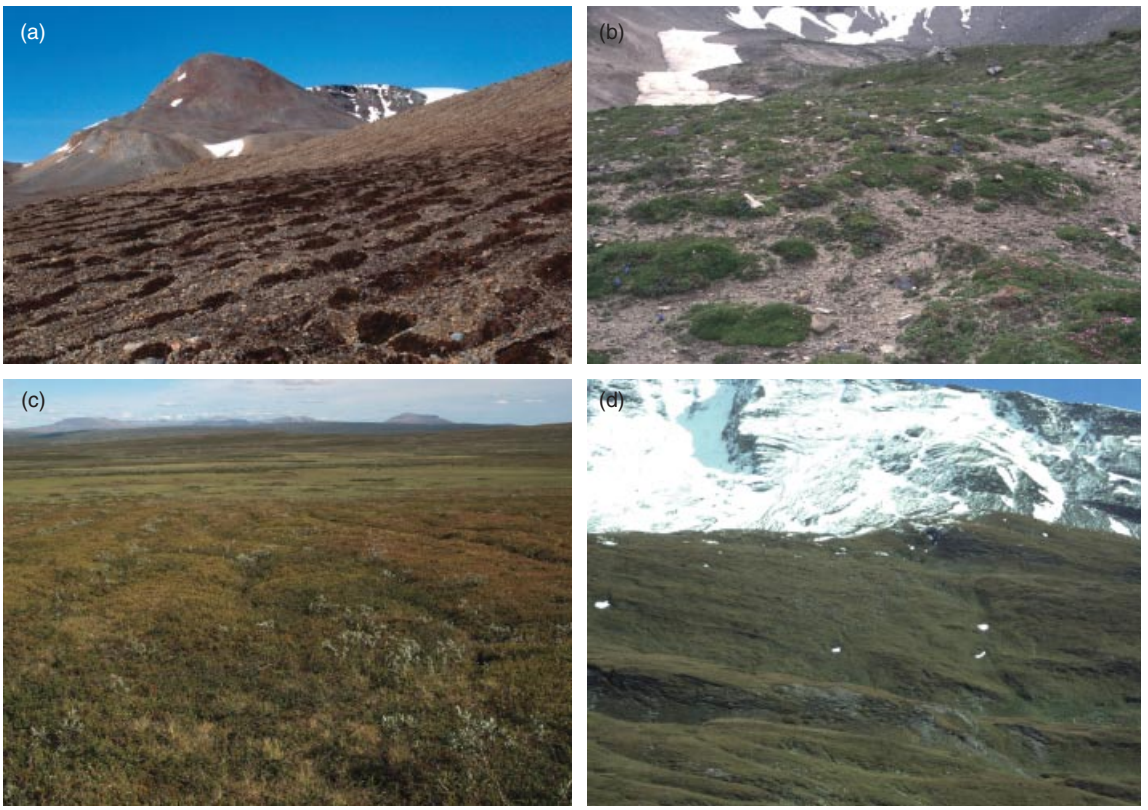


Plate 15.1 Figurative comparisons of analogous Arctic-alpine zones. (a) high Arctic zone, (b) alpine nivale zone, (c) middle Arctic zone, (d) alpine zone, (e) low Arctic zone, (f) low alpine zone, (g) subarctic zone, (h) subalpine zone. (Photos by C. Uhlig, B. Krautzer and W. Graiss).

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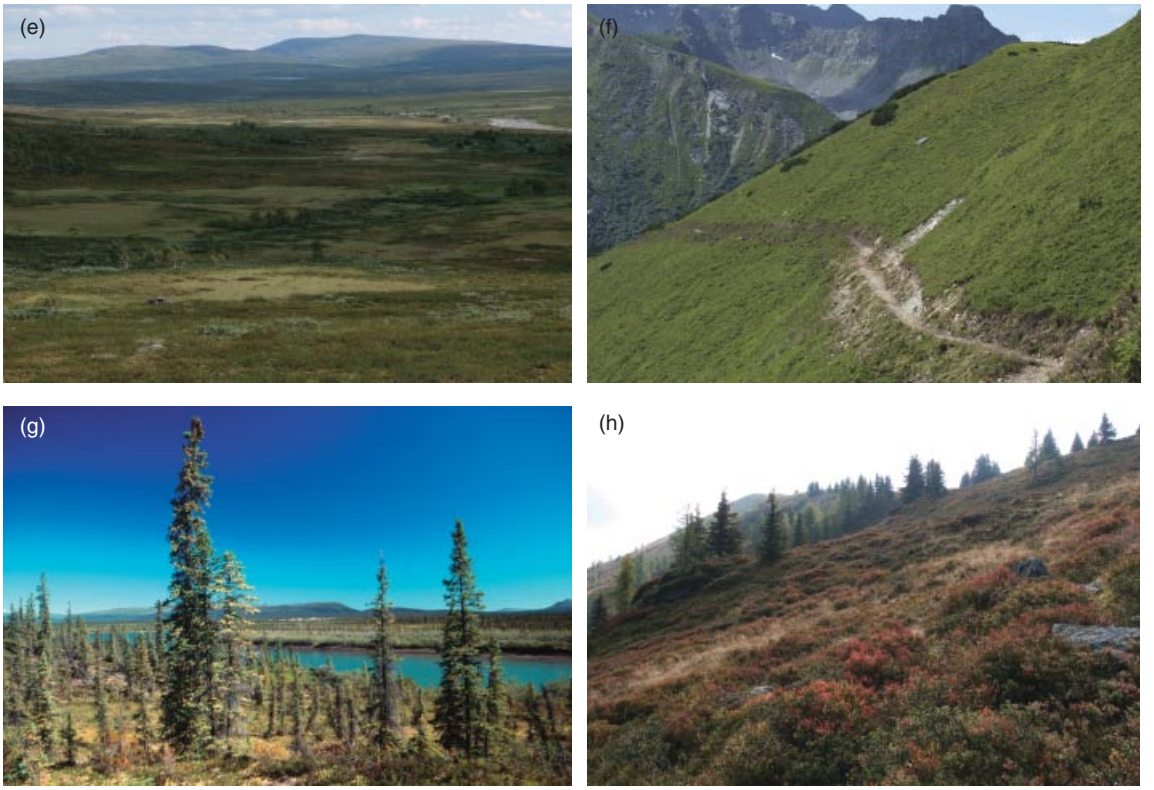


Plate 15.1 *Continued*

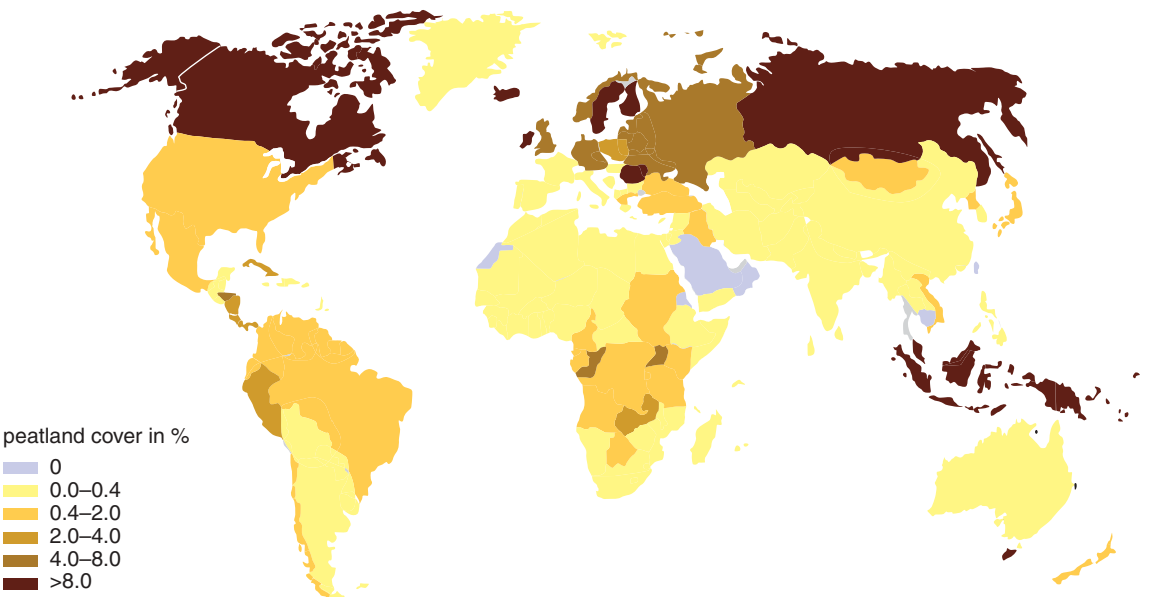


Plate 16.1 Peatland cover per country. (From Joosten 2009b.)

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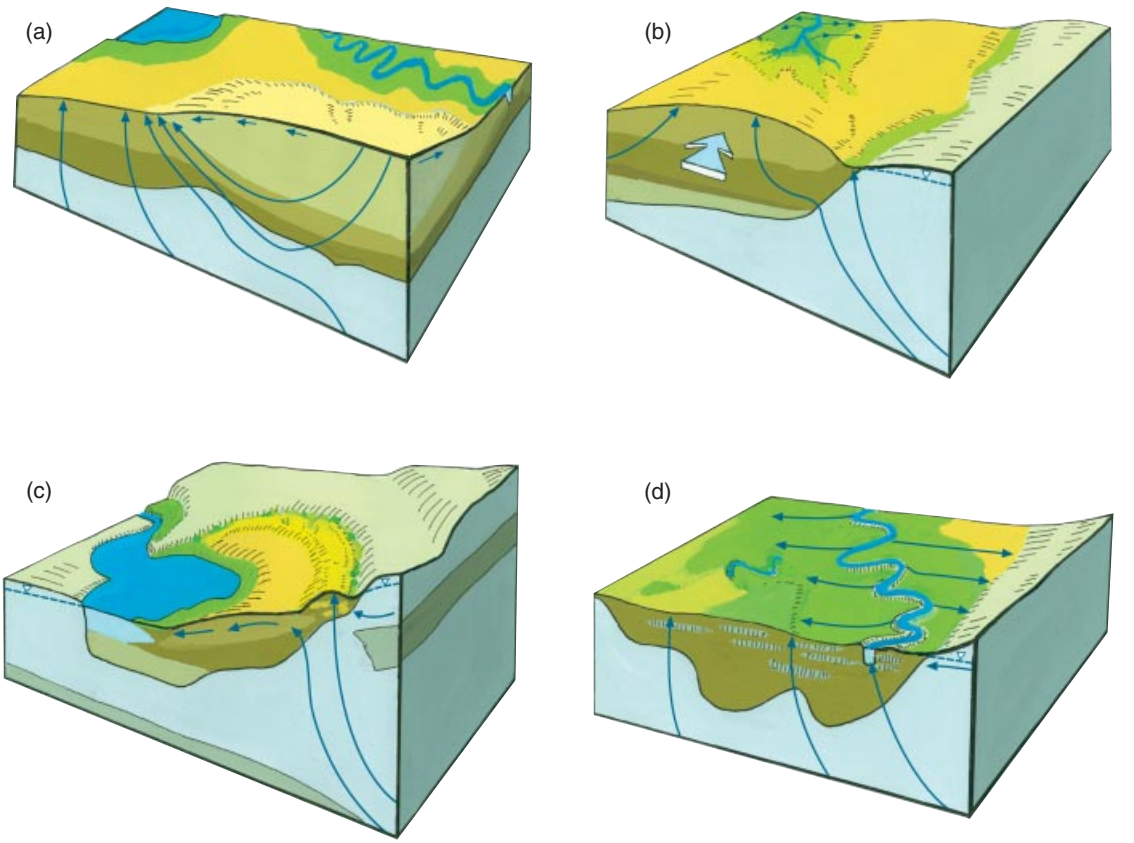


Plate 16.2 Natural mire types in a pristine landscape (i.e. relatively unaltered by humans). (a) Nutrient-poor bog system (yellow), surrounded by fens, rivers and lakes. (b) Nutrient-poor percolating mire with through-flow of groundwater in the very flexible peat layer. (c) Combination of nutrient-poor spring mire, percolating mire and terrestrialization mire along a lake. (d) Nutrient-rich floodplain mire with regular flooding of surface water and sedimentation of sand and clay.

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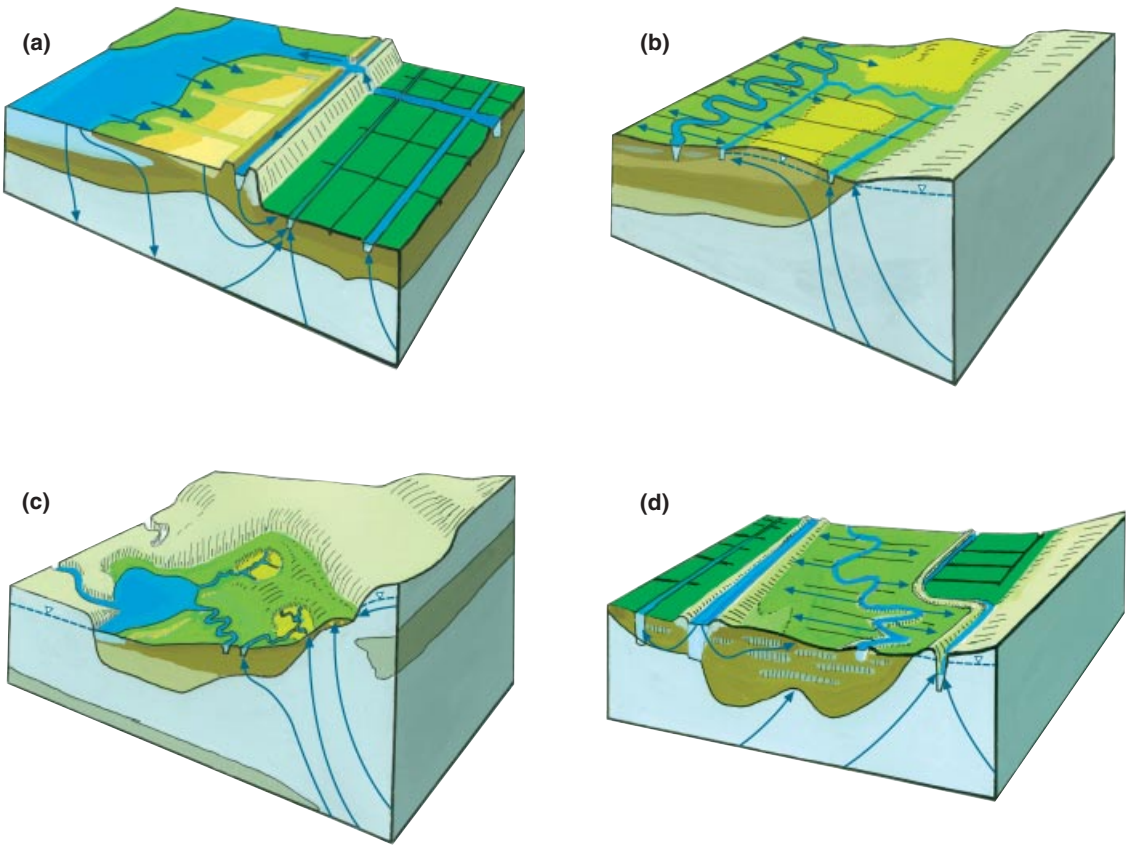


Plate 16.3 Mire types within a human-influenced ('seminatural') landscape. (a) Terrestrialization mires in lakes developed after large-scale peat cutting. The mires are surrounded by deeply drained agricultural areas. (b) Fen meadows and remnants of fens in a slightly drained brook valley. (c) Erosive spring–mire system, which developed after lowering of the lake levels. The spring rivulets erode and drain the remnants of a former percolation mire. (d) Floodplain meadows along the remnants of a river system, which is surrounded by deeply drained agricultural areas.

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Plate 19.1 Aerial photograph of an island salt marsh with natural drainage by creeks on Schiermonnikoog, the Netherlands. The marsh is bordered by dunes and part of an artificial sand dike in the north. The part east of the creek in the centre is natural, the part west of the central creek towards the seawall is seminatural (i.e. grazed by cattle). (From Google Earth).

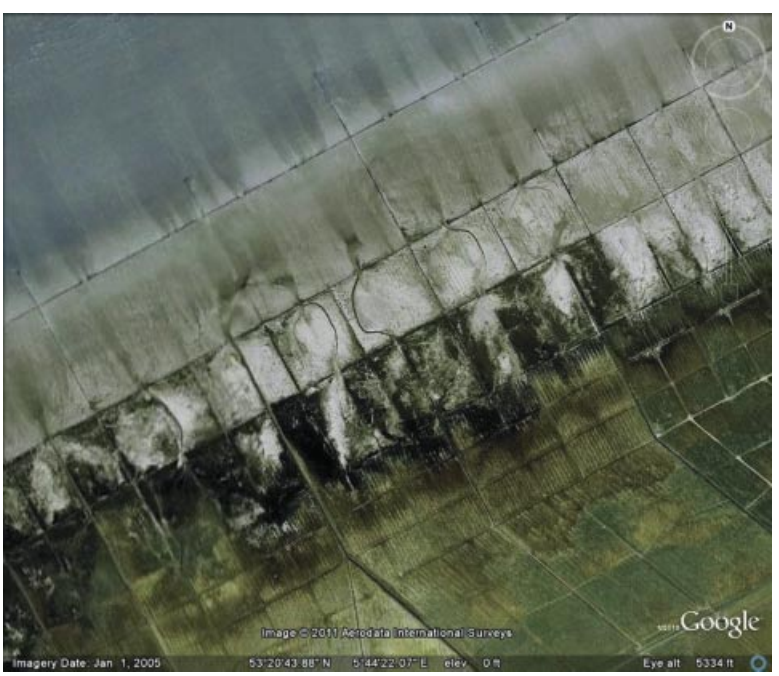


Plate 19.2 Aerial photograph of a mainland salt marsh with artificial drainage by large and small ditches in the 200 m × 200 m sedimentation field surrounded by brushwood groynes in Noard Fryslân Bûtendyks, the Netherlands. The marsh is seminatural (i.e. grazed by cattle). Note the development of creeks in unvegetated sedimentation fields where ditching has been abandoned. Ditches maintain once vegetation has established. (From Google Earth.)

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Plate 20.1 Impacts of invasive Australian woody legume trees on ecosystems of the Western Cape, South Africa. The pictures show (clockwise from top left): seedlings of *Acacia implexa* near Stellenbosch (photograph by H. van Zyl); a dense stand of *A. mearnsii* along the Wemmershoek River (photograph by D.M. Richardson); a cleared stand of *A. mearnsii* at Wildcliff Nature Reserve (photograph by P. Pebsworth), and a dense stand of *Paraserianthes lophantha* in the understorey of a eucalyptus stand near Gansbaai (photograph by D.M. Richardson).

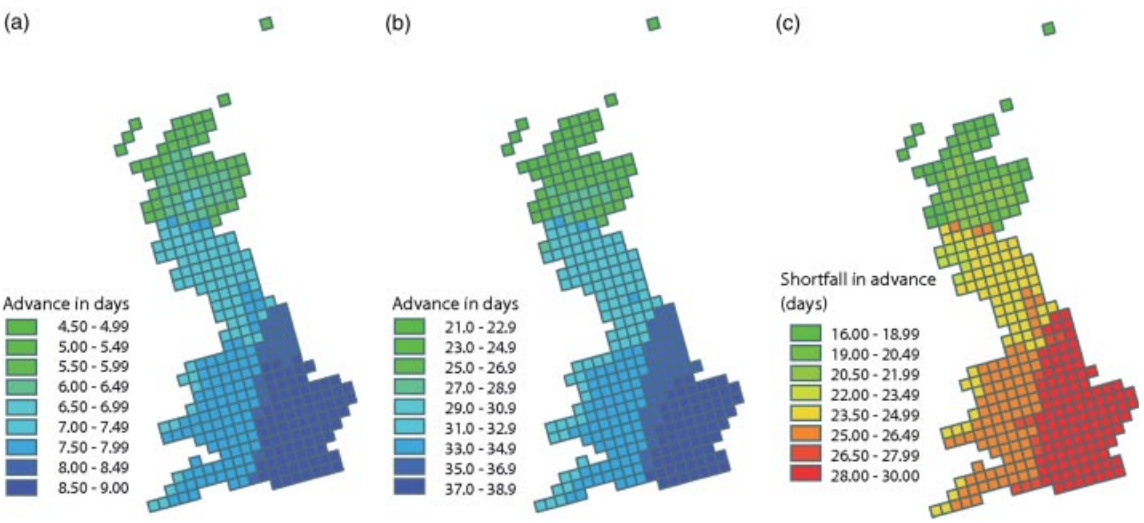


Plate 21.1 Estimates of (a) current levels of phenotypic plasticity in first spawning date in natural populations of *Rana temporaria*, (b) likely change in phenology necessary to remain locally adapted under climate change scenarios and (c) the number of days change that cannot be addressed with phenotypic plasticity. Adaptive evolution would need to occur for populations to remain in similar phenological sync with their environment. (From Phillimore *et al.* 2010.)

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Part 1

Setting the Scene

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EDITORS' INTRODUCTION

Rather than being just concerned and conservative about remains of 'wild nature', ecological restoration requires a dynamic, adaptive approach to problem solving and resource management, especially in this era of rapid and irreversible change in climate, land use and species assemblages. Indeed, evolutionary and environmental dynamics, such as invasions of species outside their recent biographical ranges, and anthropogenic climate change, can no longer be denied or ignored, as was often the case when ecological restoration was associated solely with nature conservation concerns. However, as we think about potential future developments in ecological restoration, we must respect the historic roots of our human societies, and the relationship between them and nonhuman nature as well. Evolution of species has been a natural phenomenon throughout the history of life on Earth, but the direction and speed for some species have been strongly influenced by human activities, such as plant and animal breeding, and also indirectly affected by our growing impact on global, regional and local environments. Similarly, climate change has been a natural phenomenon since the very beginning of the Earth's existence, but the recent rate of change is recognized by all experts as being largely due to human impact. This is one of the main reasons why humanity must accept responsibility for its actions, and include nature management in the decision-making process of planning towards a sustainable and desirable future – especially as we climb from the current 7 billion people to an estimated 9–10 billion in the next 25 years.

Not only does nature alter in response to changes in environmental conditions, but also human societies change and adapt to new conditions. Wilderness, earlier considered as areas to be exploited for human well-being, is nowadays valued as near-natural ecosystems to be cherished and protected. Similarly, what was earlier considered as 'wastelands' may now be called seminatural ecosystems; if financing is provided, even derelict and devastated post-mining areas may effectively be revegetated, rehabilitated and 'recycled' into the mainstream of society. However, for ecological restoration to be successful, a firm agreement is required between all the stakeholders. Opportunities have to be valued in terms of scientific validation, societal needs and available budgets for execution and monitoring.

We start our book by giving a brief overview of changing points of view on nature and on the goals of nature management, along with changes in the human society (Chapter 1). In brief, this implies a change from human dependence on nature towards nature's dependence on human management. In Chapter 2, we present some of the key concepts in the field of restoration ecology where for example we explain how to distinguish between the reintegration of disrupted and dysfunctional landscapes, the restoration of degraded ecosystems, and the rescue of biodiversity through the reinforcement or reintroduction of species populations. We also discuss such concepts as stability, the functional role of biodiversity, reference systems and how stocks of natural capital allow the flow of ecosystem services. However, we note that despite recent progress huge uncertainties and unknowns remain in our field.

In Chapter 3, our colleague Richard Hobbs pays explicit attention to this problem, helping the reader focus on the challenge of coping with ongoing changes in climate even as we set about the restoration of degraded ecosystems in the context of highly modified landscapes. Indeed, an intriguing and important question is to what extent historical knowledge and perspective can continue to be applicable if we are restoring now 'towards the future', as we put it in the preface. Finally, David Tongway and John Ludwig describe an approach to landscape-scale restoration that emphasizes the need for understanding how ecosystem processes are affected by disturbances, causing landscapes to be dysfunctional (Chapter 4). This knowledge can then be used by practitioners to set achievable goals, and to design and implement restoration technologies to achieve their goals.

In summary, this first part of our book sets the scene for all that follows. Rather than giving a complete overview, we aim at highlighting topics that we consider to be necessary elements for the reader who will here discover the rapidly growing, and evolving, field of restoration ecology; we hope it will give you an appetite to carry on reading the book and at least some of the references cited and, above all, to start thinking about concepts and strategies for differing biophysical and sociocultural contexts where ecological restoration is needed.

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Chapter 1

GETTING STARTED

Jelte van Andel and *James Aronson*

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1.1 INTRODUCTION

Increasing and unrelenting human impact on the biosphere – in particular since the industrial revolution began in the late eighteenth century – has brought us to the threshold of what Paul Crutzen dubbed the 'Anthropocene Era', that is an unprecedented geological era in which humans dominate all ecosystems and the global environment as a whole. However, the widespread recognition of the need to regulate the human 'footprint' dates back only a few decades, in most parts of the world. Pioneer nature conservation organizations began to be formed over a century ago, it is true, in western and central Europe in particular – including the German Nature and Biodiversity Conservation Union, founded in 1899, and the Dutch organization known as *Natuurmonumenten* that was founded by an elementary school teacher in Amsterdam in 1905. Today, there are literally thousands of conservation NGOs around the world, and gradually, over the past 50 years, they have found increasing support from the public and the scientific community. Although started as recently as the 1960s, 'in response to the devastation of our natural habitats', the network of Wildlife Trusts in the United Kingdom now has more than 800 000 members. This is just one example among many, and ecological restoration – under many different names – is gaining an increasing share of attention in conservation activities all around the world, and in international treaties as well.

In this introductory chapter, we start using the terminology related to the subject without defining the terms; the definitions will be given and discussed in the next chapter. Throughout the book we draw the reader's attention to the Glossary in this book by marking terms in bold.

Restoration ecology is the field of study and experimentation that provides the scientific background and underpinnings for practical **ecological restoration**, rooted in the early developments and visionary work of a few individuals and programmes in the nineteenth and twentieth centuries. It has grown to a respectable 'size' and volume only in the last few decades, since Bradshaw's (1983) pioneering work, but as mentioned already, is now gaining momentum and attention as never before. Restoration ecology has also begun to command much more attention from scientists in the last 25–30 years, especially since the Society for Ecological Restoration has got underway in the late 1980s. Twelve years ago, ecologist Truman Young suggested that 'restoration ecology is the future of conservation biology' (Young 2000). By that he surely meant that in today's crowded, much-transformed world, conservation – in the sense of preservation or setting-aside – will not be adequate to meet the goals of conservation – and sustainability. Instead, restoration of damage will be required on both scores. In terms of the sciences, at any rate, a clear convergence between the three fields is taking place, conservation biology, restoration ecology and the overarching, inter- and transdisciplinary field of **sustainability science** that is barely a decade old. Why include the latter in this introductory chapter? Because ecological restoration does not only aim at the repair of degenerated ecosystems, including their structure and functioning and their biodiversity. For ecological restoration to be effective, we must consider not only the biophysical context, but also the socio-economic and political matrix in which a restoration project must be planned, financed and carried out. That is why there is a clear need for a broader interdisciplinarity, and **transdisciplinarity** as well, which means forging interprofessional partnerships and coalitions, as well as good communication and indeed collaboration with nonprofessional stakeholders and neighbours. Jackson *et al.* (1995) portrayed ecological restoration as having four main components to consider – ecological, social, cultural and economic (see Figure 1.1). In the last few years, however, it is also becoming clear that political and legislative components are needed as well (Aronson 2010) and will also be an important part of restoration in coming years.

Ecological restoration aims at the safeguarding and the repair of what is commonly called 'nature' (i.e. **ecosystems** and **biodiversity**) and what ecological

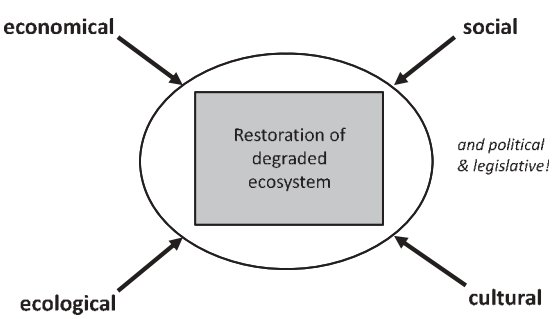


Figure 1.1 Five main components of ecological restoration. Modified from Aronson (2010).

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economists, and a growing number of ecologists, call humanity's stock of **natural capital** (i.e. renewable and nonrenewable resources from 'nature') that assure the flow of **ecosystem goods and services** to society (Aronson *et al.* 2007a). Thus, many motivations and justifications for ecological restoration exist (see Clewell & Aronson 2006, and Chapter 2), yet a financial – and perhaps also a social or political – cost is inevitably involved. Increasingly, it is obvious – at least to us – that all societies everywhere should be devoting resources to this activity to insure and enhance the supply of ecosystem services as well. However, what may seem like a clear gain for some, can be perceived as a loss or waste of resources for others. Trade-offs, negotiation and, above all, good communication are a *sine qua non* in this realm of human endeavour that require both ecological and environmental as well as socio-economic and even political criteria for monitoring and evaluation (Blignaut *et al.* 2007; Aronson 2010).

Needless to say, points of view in most situations will differ among **stakeholders**, and they will also change over time, in any heterogeneous society, and even among specialized scientists. To illustrate this, let us consider the concept of steady states and disturbance, a key notion in all discussions of conservation, management and restoration of ecosystems.

1.2 VIEWS ON STEADY STATES AND DISTURBANCE

Disturbance, though it may sound negative, is basically a neutral term in science. The term is widely used in **ecology**, and we will also use it in this book, but the neutral term 'transformation' is often a better choice for indicating a change of a complex system from one state to another one. What we call a **disturbance factor** causes a change or transformation in an ecosystem's steady state, in terms of its standing biomass, productivity or biodiversity, which may be followed by either *recovery* to the former state (through **resilience** or **resistance**) or a change to another state, following the crossing of a so-called **threshold of irreversibility** (see Figure 1.2); then the system is disturbed. In the latter case, the system may shift to another steady state, or not; in the ecological literature, this new state is referred to as an **alternative stable state**.

Depending on your point of view, State C, the alternative steady state, can be a gain or improvement, or else a loss or example of degradation. For example, if a farmer clears a piece of woodland and then cultivates the land, he or she will naturally consider the change as a gain. Yet, from the point of view of a bird watcher, or local authority in charge of nature conservation, such a transformation may be considered as a loss of **habitat** for birds, or a **degradation** of the woodland ecosystem at the landscape scale. Similarly, local communities dependent on woodlands for various services (for example watershed protection and outdoor recreation) will consider it as negatively impacting their welfare and well-being. Thus, especially if the farmer eventually abandons production, for reasons of changing markets for example, there may be a good argument that ecological restoration should be attempted, in order to restore the woodland that once was there. However, the farmer may instead seek other crops or land uses that raise income to his or her family or corporation. In Chapter 2, we will return to the concept of **disturbance**, and the related one of **stability**. Here we will consider points of view on 'nature' as related to the qualification of 'disturbance'.

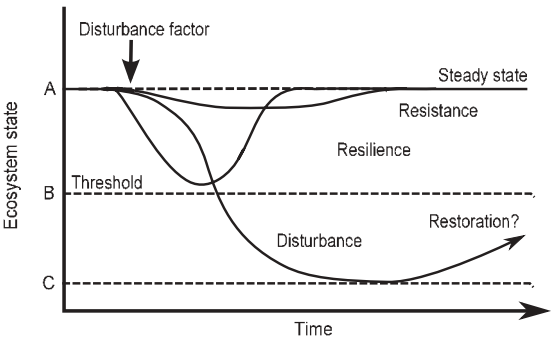


Figure 1.2 Model of three types of system response to a disturbance factor: resistance, resilience and disturbance. State A is the starting or 'initial' steady state, State C is a new, alternative steady state. As long as the system state does not pass a 'threshold of irreversibility' (State B), the system remains stable. Restoration of the ecosystem from State C towards the starting state A is affected by hysteresis and by the nature and number of the threshold(s) it has crossed.

1.3 VIEWS ON NATURE AND NATURE CONSERVATION

Just as views on what constitutes a disturbance differ, the same is true for notions of 'nature', 'nature

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conservation' and 'ecological restoration', and points of view may even change over time. In large parts of northern and central Europe and indeed the entire northern hemisphere, the **forests** and **woodlands** that developed after the last Ice Age ended, approximately 11 000 years ago, have repeatedly been exploited or even clear-cut for timber, and the lands they formerly occupied cleared and burnt to make way for agricultural production systems. Though this disturbance, or transformation, from forest or woodland to farmland and pasture sometimes resulted in heavy soil erosion, it was generally considered as a gain for the farmers, and for the entire society. From the Middle Ages up to the beginning of the twentieth century, the prevailing land use in Europe was low-intensity farming, resulting in agro-ecosystems such as species-rich meadows and open **heathlands**, currently known as seminatural ecosystems. In Figure 1.3, we illustrate this notion schematically, in the broader context of the range of anthropogenic disturbances to ecosystems and the alternative states or conditions presented already in Figure 1.2.

After the introduction of artificial fertilizers in the early twentieth century, the application of which enables intensive production of food, these less intensively used farmlands were no longer considered as a gain; instead they were called 'non-use lands' or even 'wastelands' that should, logically, be 'reclaimed' for production. Large-scale fertilizer application resulted in a new change of the ecosystem state, from low-intensity farmlands to increasingly high-input, high-production systems. Again, this change was appreciated by most farmers, but not by all members of society, especially those concerned with **sustainability**. The high level of nutrient supply to the soil resulted in a steep decline in **biodiversity**, not only in the cultivated areas, but also in adjacent landscapes. Nature conservationists, who had taken initiatives to establish formal nongovernmental institutions to counteract the ongoing process of what they considered as degradation of the environment, were gradually supported by scientists from universities and research institutions who conducted detailed studies and provided quantitative data on the impacts. Increasingly, points of view

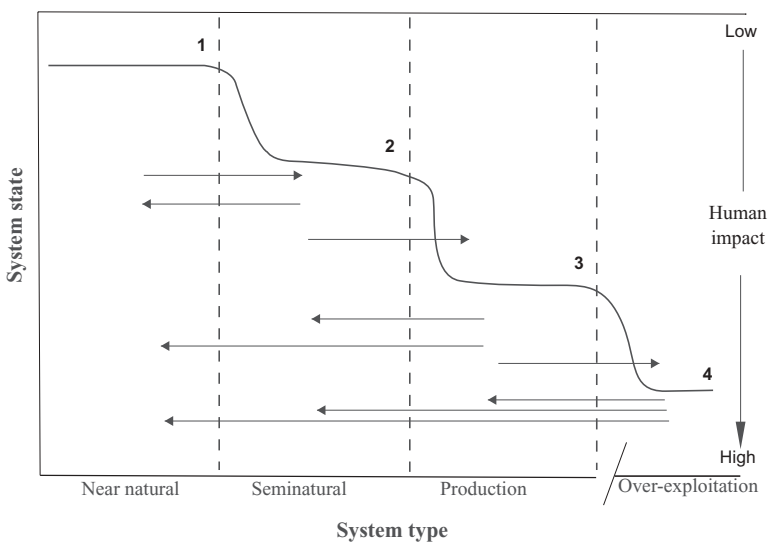


Figure 1.3 Schematic representation of common transformations of ecosystems. Arrows from left to right indicate anthropogenic disturbances; arrows from right to left indicate options for ecological restoration or rehabilitation, or, alternatively, reclamation to some type of sustainable system. Note that the route to recovery or restoration of an ecosystem after prolonged disturbance and profound transformation often takes much longer than, and differs from, the initial route of degradation. This discrepancy is known as hysteresis. It is important that restorationists and restoration scientists not forget or underestimate this factor of unpredictability, which generally increases in correlation to the degree of human impact.

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about the aims of nature conservation became under debate, mainly related to the degree of desired or allowed human **intervention**. In 1945, for example, the Royal Dutch Society for Natural History (KNNV) organized a conference to identify and agree on the choices for aims of nature conservation and management (van der Windt 1995). The dilemmas were discussed among landscape architects, nature conservationists and managers, and scientists. A choice was made for **seminatural ecosystems and landscapes** as a primary goal of nature conservation and management. The most important conclusion was that the principle of including human interventions in nature was no longer questioned, thus leaving room for different options. Currently, it is common use to recognize three archetypes of 'nature', dependent on the degree of naturalness (see Swart *et al*. 2001): (1) **wilderness**, or self-regulating near-natural ecosystems, (2) **Arcadian or seminatural ecosystems**, based on a long history of extensive human interference, and (3) intensively managed **production systems**. The intensity of human impact may be strong or moderate or even zero, depending on the view of nature applied to different sites, ranging from production systems to some kind of wilderness. In Figure 1.3 we used these three categories, and added the notion of *over-exploitation* as a fourth step in the disturbance of a system to an alternative state; the latter state can no longer be considered part of 'nature'. In the next section we will present views on various options for the repair of different disturbed states.

1.4 VIEWS ON RESTORATION

The focus of nature conservation has been on the preservation of near-natural and seminatural ecosystems through preventing them from being degraded. Ecological restoration has much broader perspectives, aiming at the repair of damage, now including the ecological restoration or rehabilitation of production and exploitation systems (see Figure 1.3). And again, there are often difficult choices to be made, even when the general goal of ecological restoration has been agreed upon. Indeed, in most situations a broad range of targets can be distinguished, from spontaneous or assisted recovery to the former state, to a state that one could call a halfway condition with respect to the former state. Currently, different options for restoration are recognized: (1) **near-natural restoration**, aiming at almost non-assisted natural recovery, (2) **ecological restoration**, that is, the return to some historic **reference system**, representing pre-disturbance conditions, be it natural or seminatural, (3) **ecological rehabilitation**, that is, the improvement of **ecosystem functions** without necessarily a return to pre-disturbance conditions, and (4) **reclamation**, that is, conversion of heavily degraded land such as post-mining areas to a productive condition.

However, new problems continually pop up. Nature management, as agreed upon, and the restoration of abandoned production systems, may result in successes and failures. Sometimes the return to past ecosystem types simply can not be achieved by re-applying the former management measures. Irreversible environmental conditions, for example due to severe drainage of peat soil or high soil-nutrient loads, could prevent or severely retard a return to the past, and this raises the need to consider other options. Currently in the field of restoration ecology, it is generally accepted that a return to past ecosystems, indeed a return to the past in general is, strictly speaking, not possible; history can not be repeated. This implies that the notion of **reference systems** should no longer be conceived of in a narrow fashion, or restricted to an idealized situation of the past. Instead, it can be conceived, and then utilized, in many different ways. A reference system may change over time and may in fact be developed as a series of successive reference states or systems (Figure 1.4).

There is also a need to recognize uncertainties involved in restoration, and the reality that many ecosystems today are in fact **emerging ecosystems** (see Part 4), since the world has changed so radically, from a biologist's point of view, and will continue to change, as a result of climate change, land use change, biological invasions and so on. In Chapter 3, we will also encounter the notion of **novel ecosystems** that have entirely altered from historical ranges. There the main aim of restoration might be to ensure the maintenance or optimization of the flow of material ecosystem goods and services with less concern for cultural services or biodiversity or any spiritual or cultural ties with the past. Several chapters in Part 3 will deal with this theme, and we will reflect on the different options available in the three concluding chapters of Part 4. Now, at the beginning of our journey through this book, we would like to emphasize that ecologists' primary job is to provide as much information as possible to make predictions, and effective applications in ecological restoration projects, based on historical, analytical, and experimental

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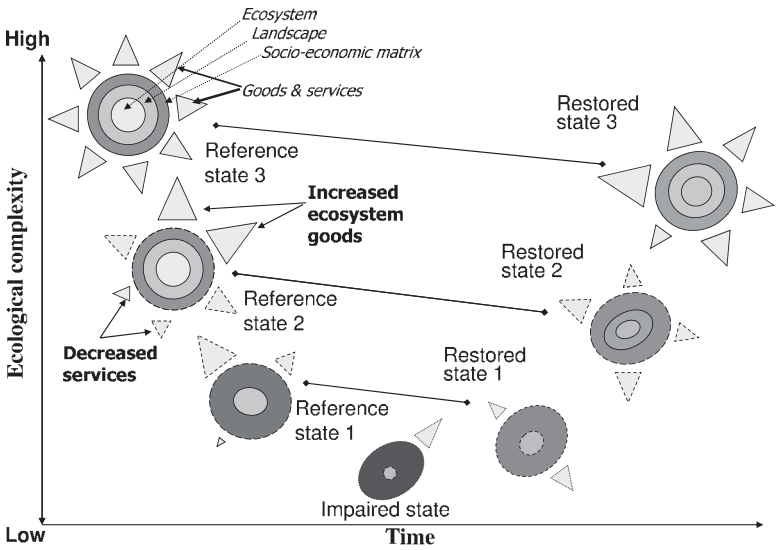


Figure 1.4 Sequential references in ecological restoration. Dashed lines represent degraded conditions as compared to an intact, undisturbed system. The inner circles in each 'sun' on the figure represent the ecosystem. The outer concentric circles of each 'sun' represent the landscape (biophysical matrix of the ecosystem), and the socio-economic matrix, in which the ecosystem is embedded. The triangular 'rays' of each 'sun' represent various goods and services that flow from the 'natural capital' that is an intact ecosystem with its native biodiversity. From Clewell and Aronson (2007); reproduced with permission from Island Press.

knowledge of patterns and processes of 'nature' (i.e. ecosystems and biodiversity at all relevant scales and levels of organization). We recall that restoration ecology is essentially a branch of applied ecology (see Freckleton *et al.* 2005) – that is, ecological research that informs management practice to be used by society as a whole.

In this first chapter, we have indicated the starting place for our project. As mentioned, several of the concepts that we introduced here will be elaborated on in Chapter 2 as part of a set of what we consider the unifying concepts for restoration ecology, indispensable for appreciating the chapters that will follow.

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Chapter 2

UNIFYING CONCEPTS

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2.1 INTRODUCTION

Restoration ecology is an applied natural science that lies at the intersection with the social sciences, but can also help us leap from that broad platform into the realm of transdisciplinary science and problem solving, which we will discuss below. Restoration ecology is thus truly a 'new frontier', as first noted by one of the most notable and prolific pioneers in the field, in the introduction to the book he edited (Cairns 1988), which was one of the very first books to appear on this topic.

In this book, we focus on the ecological foundations of restoration ecology. We feel strongly that restoration efforts must aim to restore entire ecosystems, and not just focus on parts of them, or other derivative goals. Increasingly, we hear and read about the need to 'restore' **biodiversity**, or **ecosystem services**, but these goals are ultimately vain if we do not succeed in restoring living, dynamic ecosystems, and figuring out how to help them be self-sustaining. It is difficult or impossible to 'restore' or rather **reintroduce** species populations in a given site, without 'restoring' the abiotic environment necessary for the persistence and reproduction of those species, including the networks of interactions with many other species that occur in a well-functioning **ecosystem**. Conversely, **biotic communities** strongly influence the abiotic environment, and without a full complement of native species, autogenic or self-sustaining ecosystems – the ultimate goal of ecological restoration – will not be attained (MacMahon & Holl 2001). Thus, we endorse the definition given in the *SER Primer for Ecological Restoration* we cited already, namely, that **ecological restoration** is 'the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed' (SER 2004).

Note the emphasis in that definition on the idea of assisting the recovery of an ecosystem, and not just a species. The definition explicitly assumes that something has been lost, or gone wrong at the level of a system, and, secondly, it implies that we can and should try to understand how ecosystems respond to interventions of all sorts, including efforts to help them recover. Ecological restoration is interventionist and systems-oriented by nature, as opposed to traditional conservation, that was about reducing human pressure or 'keeping our hands off' certain areas of land or wetland set aside for protection of one or an assembly of species. It is hands on, and is, by definition, applied at the level of whole ecosystems.

The corresponding field of science called restoration ecology can take various approaches to the task of providing knowledge that will help put ecosystem recovery in motion. New theories and syntheses, predictive models and the testing of hypotheses through experiments and careful monitoring and evaluation of ongoing projects are the primary means to achieve that end. Additionally, outreach and collaboration with people from other academic disciplines, in both the natural sciences (e.g. conservation biology and landscape ecology) and the social sciences, including economics, as well with nonscientists and professionals, is essential. That will require engaging in the 'entire restoration process' (Cairns & Heckman 1996). In this chapter, then, we focus on the major unifying concepts relevant to both fundamental and applied ecology, but start with the notions of inter- and transdisciplinarity.

2.2 INTER- AND TRANSDISCIPLINARITY

Restoration ecology draws knowledge, ideas and data from disciplines as diverse as landscape ecology (including geomorphology and hydrology), community ecology along with soil and water physics, and chemistry at the ecosystem scale, as well as physiology and genetics at the level of organisms and populations. But as mentioned, to address and engage the 'entire restoration process', we must incorporate the socio-economic sciences (e.g. Mascia *et al*. 2003). This implies cross- or *interdisciplinarity*, which is what happens when concepts, models, methods and findings of different scientific disciplines are merged together and integrated to address an idea, or to solve a societal problem (Schoot Uiterkamp & Vlek 2007).

Scientists need to cross traditional lines and work together in the essential arena of environmental amelioration and management. The word 'transversal' – which means cross-cutting – is rarely used in English as an adjective, and yet it beautifully describes what is needed: not just a summing of skills, but also an actual breaking of new ground, thanks to original or 'lateral' thinking, resulting from a new juxtaposition and combination of approaches. In order to help **stakeholders**, and society as a whole, in the urgent task of

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restoring, repairing and rehabilitating the natural and **socio-ecological ecosystems** on which we all depend, new synergies of this kind are clearly called for. All of the categories of 'nature' referred to in Chapter 1 – 'wilderness' or near natural systems, semi-natural ecosystems and production systems – not to mention the fourth category in Figure 1.3, namely, over-exploited systems – can all be approached from ecological, economic, social, cultural and political perspectives, as per Figure 1.1. Of course, the intensity of human impact in each category may be strong, moderate or close to nil, and of course such a simplistic typology can distract from the tremendous complexity of landscapes (and seascapes) that occur around the world. Yet for now, it can help advance discussion, especially in an interdisciplinary setting.

Making interdisciplinarity 'work' is actually a huge achievement, but **transdisciplinarity** takes us several steps further. We appreciate, by the way, that the term transdisciplinarity can seem daunting, especially when you learn that common synonyms or related terms and expressions are being used in the academic literature such as 'post-normal science', 'mode-2 knowledge', 'integration and implementation sciences' and 'interdisciplinary and interprofessional problem solving' (see e.g. Scholz *et al.* 2000). Following Max-Neef (2005), who provided an approach that we adopt here, transdisciplinarity implies that we must cross not only traditional boundaries between scientific fields and engineering, design or management professions, but also the unofficial but deeply entrenched frontiers between scientific and nonscientific habits, techniques and social communities. Indeed, the goal is to get professionals, scientists, public officials, landowners, businesspeople and leaders of local people – in brief, all relevant stakeholders – involved in the restoration process and the transition to **sustainability**.

We will now illustrate the importance of inter- and transdisciplinarity in ecological restoration with a brief introduction regarding values followed by a presentation of the key notions of **natural capital** – a stock or asset, and **ecosystem services** – the dividends which flow to human society from natural capital. Thereafter, we discuss a core group of fundamental ecological concepts related to three different levels of interest in restoration ecology, respectively focusing on the reintegration of **landscapes**, the repair of degraded or impaired **ecosystems** and finally the salvation and protection of endangered **biodiversity**.

2.2.1 Determining values of nature

When it comes to determining how people value 'nature', it is important to recall that 'monetary value' is just one among many options, or proxies in economic terms, that can be applied. But it is an important and convenient one, however, for two reasons. Firstly, money is something that everyone understands, and which therefore facilitates communication. Secondly, money – and the postulates of economists and economic pundits – plays a huge role in our lives as citizens today, whether we approve of this state of affairs or not. The good news from conservationists' perspective is that in recent years there is a new school of thought in economics called **ecological economics** (Daly & Farley 2010). This approach is helping to mainstream nature conservation and restoration objectives into political decision-making and negotiation processes at national and international levels. Costanza and Daly (1992), and many others since, have argued that 'natural capital' has become a limiting factor for both human well-being and economic sustainability (elaborated in Aronson *et al.* 2006, 2007a; Blignaut *et al.* 2007). De Groot *et al.* (2002) developed a framework to help integrate values of **ecosystem goods and services** in the process of decision making.

2.2.2 Ecosystem goods and services, natural capital

The *Millennium Ecosystem Assessment* (MA 2005) defined ecosystem goods and services as natural products and processes generated by ecosystems that sustain and fulfil human life (cf. Daily 1997). We prefer, however, to adopt the typology provided by the interdisciplinary, UN- and EU-funded project called *The Economics of Ecosystems and Biodiversity* (TEEB), that distinguishes between **ecosystem processes and functions**, **ecosystem services** and **human well-being** in terms of the benefits and values people perceive or assign to those services (de Groot 2010). This becomes still more clearly interdisciplinary when we see that the term **natural capital** is used as an economic metaphor for **ecosystems** and **biodiversity** (Neßhöver *et al.* 2011). Natural capital is in fact a broad concept indicating the limited stocks of both physical and biological natural resources found on Earth (Aronson *et al.* 2007a).

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According to the MA (2005) and TEEB (2010, 2011), there are four, partially overlapping types: (1) renewable natural capital (the restoration of ecosystems), (2) nonrenewable natural capital (subsoil assets, e.g. petroleum, coal and diamonds), (3) replenishable natural capital (e.g. the atmosphere, potable water and fertile soils) and (4) cultivated natural capital (e.g. crops and forest plantations). To help show how this notion provides a clear and usable model of the relationship between ecosystems and society, we quote from Aronson *et al*. (2007b):

> The restoration of natural capital is any activity that integrates investment in and replenishment of natural capital stocks to improve the flow of ecosystem services, which enhances all aspects of human well-being. In common with ecological restoration, natural capital restoration is intended to improve the health, integrity, and self-sustainability of ecosystems for all living organisms. (p. 5)

This statement implies a diversity of rationales, both scientific and nonscientific. It also brings together various kinds of values that are all necessary for an 'entire restoration process' or what Clewell and Aronson (2007) called *holistic restoration*. These include (1) ecological values, based on ecological science and what it can tell us about sustainability at population, community and ecosystem levels, (2) sociocultural values, based on equity, intergenerational justice, and cultural customs and perceptions and (3) economic values, based on efficiency and cost effectiveness combined with the ecological economics caveats that natural capital is the basis of all economies. This approach was adopted in the Millennium Ecosystem Assessment (MA 2005) and further elaborated in the global assessment on the economics of ecosystems and biodiversity (TEEB 2010, 2011).

Weesie and van Andel (2002) modified this model, aiming at explicitly including non-anthropocentric, or biocentric, values in the valuation system. Clewell and Aronson (2007) added personal, psychological and spiritual values, for example those resulting from aesthetic motivations, to this triple valuation, further illustrating the need for transdisciplinarity in the valuation of nature. In the second chapter of the book *Restoring Natural Capital*, Blignaut *et al*. (2007) expressed this same sentiment from a transdisciplinary perspective.

2.2.3 Setting goals of restoration

For the full (i.e. democratic and participatory) restoration process, essential for ecological restoration projects to be successful over time, we need transdisciplinarity. Goal setting and the choice of goals are among the most important decisions to be taken at the interface between science and society. This should come after common values have been discussed by stakeholders and project managers, not before! In other words, before starting to actually 'do' ecological restoration, we need to know 'why' we should try to restore damaged or altered ecosystems and to what state or condition or trajectory we wish to see them move (Higgs 1997; Clewell & Aronson 2006, 2007). Ecologist Margaret Palmer and coworkers (Palmer *et al*. 2005) spoke of a 'guiding vision' to help define what we – as a society – want to achieve in a restoration context. This in turn demands, in our view, insight and discussion among stakeholders on the causes of degradation in an historical perspective. It is the task of the science of restoration ecology to search for laws and general rules, and to develop applicable concepts and theories, including, very simply, how to get from State C 'back to' the State A of Figure 1.2.

In Chapter 1, we distinguished three different levels of ambition in the broad field of ecological restoration, as exemplified by the terms restoration, rehabilitation and reclamation. Here we elaborate a bit more on these terms, to illustrate how goal setting depends on collaboration between parties. As noted already, the term **ecological restoration** is often used in a very broad and rather vague way, to mean bringing a site, or place, or ecosystem 'back' to something called or considered as 'original', 'initial' or, more precisely, 'pre-disturbance' conditions in the sense employed in Chapter 1 (Figures 1.2 and 1.3). **Ecological rehabilitation**, in the broad sense, is the improvement of ecosystem functions without necessarily achieving or even seeking a full return to 'pre-disturbance' conditions. A rehabilitated site will be similar in ecological functioning to the reference system (as discussed in this chapter) and contain similar but not necessarily the same organisms. Emphasis is generally on restoring ecosystem processes and functions so as to increase the flow of services and benefits to people. But, nonhuman members of ecosystems are considered as well, and as in restoration, ecological rehabilitation implies consideration of an ecosystem of reference – a concept we will develop further in what follows. Finally, **reclama-**

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tion is simply about 'improving' a degraded or 'useless' site and making it useful again. The goal is to bring the site to, or back to, a condition considered desirable and sustainable for people, whether the use is for production (e.g. for grazing livestock, for recreation or for something else). In many languages, there is no clear homologue for this word, and terms like 'environmental recuperation or revitalization', 'enhancement' or 'amelioration' are more readily understandable. 'Clean-up' is often a major part of such operations, and new terms exist for this activity as well, such as 'bioremediation' and 'phytoremediation', as applied to oil spills, secondarily salinized areas and other areas that have suffered pollution or massive denaturalization.

It is important to recall that at the scale of whole **landscapes**, where **socio-ecological ecosystems** co-occur and interact with each other, all three activities can be planned and pursued simultaneously. Once the goals for a given landscape unit – restoration, rehabilitation and/or reclamation – have been set, indicator values can be used for diagnostic purposes, as early-warning indicators of deviations, or otherwise in the process of piloting a system along a target **trajectory**. In this book we will not go into monitoring and evaluation of socio-economic, cultural and moral values. Ecological evaluation values are often based on **indicator species**, members of a biotic community that have been shown (by experience or by scientific calibration) to be characteristic of certain environmental conditions and sensitive to changes therein (e.g. Ellenberg *et al*. 1991 for plants; Carignan & Villard 2002 for multiple species; Harris 2003 for microorganisms). They can be used to qualify the direction of changes in an ecosystem, that is, by distinguishing between developing and degrading ecosystems. Note, however, that quantitative indicator values of species that have been asserted in a specific region may not be applicable to, and thus have to be calibrated for their use in, the environmental context of other regions.

2.2.4 Reference ecosystems

Central to the goal-setting process in projects and programmes of ecological restoration is the concept of **reference ecosystems**. The choice or construction of a reference ecosystem, or more simply 'the reference', in restoration ecology consists of identifying one or more natural, or seminatural, ecosystems (or descriptions thereof) which can serve as models or targets for planning and executing an ecological restoration – or rehabilitation – project (SER 2004; Clewell & Aronson 2007). When no such site or system exists, it is necessary to construct a reference from available information and knowledge about what did exist in the past, within the limits of a well-defined so-called *normal functioning* (van Andel *et al*. 1987) and *historical range of variability* (Higgs 2003).

Considerations of natural dynamics and environmental changes imply that reference systems, which we know or construct from past or from present undisturbed areas relevant to our site, can serve as models to orient and inspire us, rather than as a strict objective to be literally reached. The reference serves the role of a 'guiding vision' but also provides a multidimensional yardstick or benchmark, to be used for the comparison of what is happening to the ecosystem undergoing restoration with respect to our prespecified goals for it. It is not a romantic or naive notion of trying to return somehow to the past, something we know is not possible. Inspired by the knowledge of the process of evolution of species – an ongoing process that does not start from scratch, *de novo*, but inevitably has historical roots – a restoration scientist should gather as much information as possible to understand the historical development and, where appropriate, the human transformation of the ecosystems and landscapes to be restored.

For purposes of nature conservation and restoration, in many parts of the world there are often adequate, appropriate and well-documented historical references available, sometimes even *in situ*, dating for example from the late nineteenth or early twentieth century. Often, however, for example within the vast Euro-Mediterranean region, with its intricate tapestries of seminatural and managed ecosystems, the choice or construction of a reference model is quite complicated, and polemical, involving much discussion and negotiation. We are of the opinion, however, that it is a worthwhile endeavour (see Clewell & Aronson 2007).

2.2.5 Zooming in on ecology

After having emphasized the need for inter- and transdisciplinarity, we now zoom in on key ecological topics. In the *SER Primer on Ecological Restoration* (SER 2004), and in Clewell and Aronson (2007), nine *attributes of restored ecosystems* are proposed for consideration. These are (1) a characteristic assemblage of the species

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that occur in the reference ecosystem, (2) the primary presence of indigenous species, (3) the representation of all known functional groups necessary for the continued development and/or stability of the system, (4) the appropriate physical environment to sustain reproducing species populations, (5) the normal functioning, and the absence of signs of dysfunctioning of the system, (6) the suitable integration into a larger ecological matrix or landscape, (7) the elimination or reduction of threats to the health from the surrounding landscape, (8) a sufficient resilience to endure the normal periodic stress events and (9) an ability to be self-sustaining to the same degree as its reference ecosystem. Clewell and Aronson (2007), exploring these 'desirable attributes', consider the formulation of 'standards' a useful 'broad-brush' approach, in each case to be judged in comparison to a reference system. Though they recognize that it may be impossible to meet all these criteria, they consider such standards indispensable for the evaluation of monitoring results during the trajectory towards any goal.

We recall that **ecosystem structure and functioning** are core issues in any ecological restoration project, also in cases of a focus on the reintegration of a landscape or the rescue or reintroduction of a species population. At the same time, we recognize throughout this book that understanding of ecosystem processes requires knowledge of landscape ecology, community ecology and population ecology and genetics. Therefore, each of these subdisciplines of ecology is discussed in Part 2 of this book. Here, we introduce a number of key topics in restoration ecology related to landscapes, ecosystems and biodiversity.

2.3 LANDSCAPES

As mentioned, the focus of ecological restoration in this book is on entire ecosystems, as per the *SER Primer's* definition (SER 2004). In Part 3 of this book, the reader will find no less than 11 applications of this philosophy. However, as we will see in several of these chapters (especially 16–19, dealing with wetlands), and still more explicitly in each of the next three chapters (3–5), a 'landscape perspective' on the restoration of ecosystems is essential. Ecosystems can be defined individually, but they do not function independently of their biotic and abiotic surroundings. Their spatial and ecological relationships at the landscape scale matter a great deal to what happens within them (Thompson 2011). Indeed, 'natural' or 'seminatural' ecosystems are part of a landscape matrix with several interacting systems, including production systems or overexploited systems, as per Figure 1.3.

In Chapter 5, on landscape ecology, the authors propose a new definition of 'landscape', as the initially clear definition, as given by physical geographers, has steadily become blurred after ecologists adopted the term 'landscape ecology' for their studies on the spatial dynamics of individual plant and animals species. Here, we would like to clarify the different positions in the scientific literature. From a human perspective, a **landscape** is commonly defined as a geographical area that can be mapped and interpreted from aerial photographs, forming a mosaic of interacting systems that may include 'natural' ecosystems, agro-ecosystems, villages, and industrial areas (cf. Turner *et al.* 2001). This notion of landscape has ecological, historical, economic and other human dimensions; spatial patterns and transport of matter and organisms are also important aspects. Ecologists studying **metapopulations**, at a landscape or regional scale, have adopted the term 'landscape ecology'. In this approach, a landscape is defined from the perspective of varying kinds of organisms (Wiens 1976), all of which move within and among habitat patches characterized by some degree of connectivity. As an analogy, the term 'landscape genetics' was recently coined to describe a study that aims at mapping how genes flow at the landscape scale (Manel *et al.* 2003). These landscape-scale ecological and genetic studies might, after all, have been better named 'spatial ecology and genetics', to avoid confusion with the geographical approach to 'landscape ecology'.

There is still more to be clarified. The **habitat** of a species may become fragmented in a landscape, resulting in habitat patches with local populations. The logic term **habitat fragmentation** (used in Chapter 7) has then also confusingly been termed 'landscape fragmentation', in Chapter 5 defined by the extent of habitat destruction. Once the reader understands how to interpret the existing literature, including the terminology used, we will have completed this guided tour of fundamental – and hopefully unifying – concepts.

2.4 ECOSYSTEMS

In view of the central task of ecological restoration to restore degraded ecosystems, we must reflect further

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upon the notions of **disturbance** and **stability** introduced already in Chapter 1. Note that these topics are applicable not only to ecosystems (e.g. in terms of nutrient cycling, hydrology etc.) but also to biotic communities (e.g. trophic interactions), populations (e.g. genetic equilibria) and individuals (e.g. health). Also, we need to introduce the reader to notions such as ecosystem functioning, ecosystem services and the functional role of biodiversity.

2.4.1 Disturbance and disturbance factors

The midcontinent population of the lesser snow goose (*Chen caerulescens*), which breeds in the eastern and central Canadian Arctic and sub-Arctic, and winters in the southern United States and northern Mexico, was relatively stable from 1950 to 1970, but it increased fourfold until a peak in 1998 (Abraham *et al.* 2005). This increase was largely because of increased survival in the winter areas in response to an agricultural food subsidy. Due to an expanding and increasingly intensive agriculture, they have adapted their migration pathways and largely graze on food crop residues, rice and wheat, and waste corn in particular (Jefferies & Rockwell 2002). Also, well-meaning nature–conservation managers established an increasing number of wildlife refuges in the winter areas and along the flyway, sometimes alongside agricultural fields. The inadvertent result of these coinciding changes in agriculture and conservation was that with ever greater densities, the geese over-exploited the tundra vegetation of their breeding ground, for example the coastal Hudson Bay salt marshes, which led in turn to irreversible degeneration of this formerly highly stable ecosystem to an **alternative stable state** of exposed sediment. The present pattern of vegetation loss is likely to continue in the foreseeable future (Abraham *et al.* 2005). This is an example of an ecological disturbance, defined as a long-term disordering of a constant or steady state, due to an external event or phenomenon, to which a given system is not capable of responding through its inherent resistance or resilience; the terms are explained below. We call the artificially inflated geese population a **disturbance factor**, and the resulting effect on the salt marsh a **disturbance** (see Figure 1.2). In the case of a serious disturbance of this sort, an ecosystem is often no longer stable in its previous state or condition, but moves instead to an alternative steady state (see also Chapters 6 and 21).

Please note that in this book we avoid the term *perturbation*, which originates from physics where it has a very precise meaning (indicating a small vibration), and is not taken to imply an interruption or disruption in a normal process. By contrast, in ecology, the term is often used either to denote a trigger or cause of severe disturbance or else as a close synonym of disturbance. There is no consistency in the way the two terms are used in the scientific ecology literature, and we do not concur with the two sole efforts at elucidation. To wit, we do not follow the terminology of Rykiel (1985) who proposed to use 'disturbance' to refer to causes, and 'perturbations' to refer to effects. Nor we do not agree with White and Jentsch (2001), who proposed to measure disturbance in absolute terms, for instance by the reduction of biomass of a mown grassland. To wit, the notion of 'disturbance' takes on meaning only once a reference system or state has been defined. In the case of the Arctic tundra, mentioned in this chapter, the reference was the ecosystem state before the disturbance was induced, when grazing by geese was still part of the 'normal functioning' of the vegetation.

To avoid confusion, researchers and authors often distinguish between kind, intensity, frequency and scale of disturbance. The kind of disturbance depends on the environmental factor concerned, whether living or nonliving, and whether human or nonhuman. The degree or intensity of a disturbance is determined by the difference between the new conditions and the previous steady state (or reference) conditions. Frequency is also important because of different effects from isolated, recurrent and continuous disturbing events; they can be irregular or regular and of differing durations. Finally, the scale or extent of disturbance refers to different spatial and temporal patterns, and to different levels of ecological organization: ecosystem, community, population or individual.

2.4.2 Stability and alternative stable states

What does the notion of stability – in other words, a long-standing steady state – imply? Since there are dozens of definitions of stability in the ecological literature, and definitions of resilience and resistance sometimes overlap, we adopt the most useful ones for our purposes when we discuss stability, and resistance and resilience (see Figure 1.2).

- **Stability** is the capacity of a system to return to a starting state following a significant change in its

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environmental conditions as the result of one or more 'disturbance factors'. If the initial or 'starting state' has persisted for a relatively long time, we can refer to it as a 'steady state', and it is kept within boundaries by the system's **resistance** and **resilience**. In ecological systems, a steady state is considered to be a dynamic equilibrium, not truly static or immobile.

- **Resistance** is a characteristic of systems that show relatively little response to a disturbance factor in terms of their structural and functional attributes.
- **Resilience** is a characteristic of systems that can be altered relatively easily by a disturbance factor but then regain their former structural and functional attributes in a relatively short time. The length of time a system requires to return to a former steady state is inversely related to its resilience; the faster the system returns to State A of Figure 1.2, the more resilient it is.

The choice of parameters to measure ecosystem stability is of utmost importance. Seeking to implement the aforementioned definitions of resilience and resistance, Mitchell *et al.* (2000) combined measurements of species attributes with environmental variables, which can represent attributes of either ecosystem structure or functionality. Their multivariate modelling approach, first applied to the conservation management of lowland heaths in Dorset, United Kingdom, helps assess why some ecosystems are more resilient than others.

As mentioned, a disturbed ecosystem is sometimes described as having crossed over **thresholds** or even **thresholds of irreversibility**, indicating that changes or switches have occurred that are severe and difficult to reverse without more or less important human intervention. In Chapter 20 the authors refer to this concept of 'thresholds' as a tool for determining the degree of ecosystem resilience and apply it to evaluate the effects of invading alien species. Once a threshold is passed, the system is considered disturbed. Similarly, a degraded ecosystem itself may remain in the disturbed state, that is, the alternative steady state can also be resilient through internal feedback that constrains restoration (Suding *et al.* 2004; cf. Folke *et al.* 2004). Very often removing a disturbance factor will not result in recovery of components of the pre-existing ecosystem that have been 'lost'. For example, just rewetting a drained wetland will not be sufficient to insure return of the 'original' or pre-existing species of that ecosystem to that site (Chapter 16). Similarly, reduction of nutrient loading in turbid, eutrophied shallow lakes rarely leads to a satisfactory recovery of a condition of clear water, indicative of a restored lake, even if the nutrient level is considerably reduced (Chapter 18). The discrepancy between the route to recovery or restoration and the initial route to degradation is known as **hysteresis**. Current knowledge on alternative stable states, or 'catastrophic shifts', can be helpful to understand and explain both disturbance and restoration processes, and to develop early warning signals for so-called *critical transitions* – also known in the popular literature as 'tipping points' – both in ecosystems and in human societies (Scheffer *et al.* 2009).

2.4.3 Ecosystem health and stress, and landscape integrity

We now consider three useful, but confusing, metaphors, often used to indicate the state of an ecosystem or a landscape as if these systems are a super-organism, which is of course not the case. Although it seems only a small step to elaborate the notion of ecosystem stability towards defining terms such as 'ecosystem health' and 'landscape integrity', these terms may be associated with an improper interpretation of holism. Similarly, the term 'ecosystem stress' is sometimes used metaphorically to describe the state of an ecosystem, as if the physiological state of an ecosystem could be compared to that of an individual organism. As scientists, we may have reservations about metaphors and analogies, but we are obliged to work with useful terms such as *ecosystem health*, *stress* and *integrity*, as they can help in communication and consensus building wherever ecological and socio-economic valuation systems meet (Aronson *et al.* unpubl. MS).

Ecosystem health has been described as 'the state or condition of an ecosystem in which its dynamic attributes are expressed within normal ranges of activity relative to its ecological state of development' (SER 2004). It can be ecologically evaluated in terms of the state of ecosystem functioning at a given time (Winterhalder *et al.* 2004), but socio-economic criteria should also be taken into account (Rapport *et al.* 1998). Rivers, for example, are not just ecosystems, but can also be considered as sources of clean water for drinking and washing, for industrial and agricultural purposes, as conduits for pollutants, and as places for recreation and aesthetic pleasure. **Ecosystem stress** then indicates the state of an unhealthy ecosystem, outside the optimal environmental range, which can be caused by

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disturbance factors such as **acidification** or **eutrophication** of a soil or a water body, or **climate change** in the atmosphere. Note that an ecosystem under stress may reveal to be resilient, resistant, or unstable (see Section 2.4.2). **Landscape integrity** can be indicated the way McIntyre and Hobbs (1999) describe *intact landscapes* as a **reference system** (see also Chapter 5). The degree of human intervention associated with intact landscapes can be extremely low, particularly in reserves managed for conservation, such as in Antarctica, but they can also be intensively managed, such as traditional agricultural landscapes in Europe. Disturbance factors may result in the fragmentation of habitats of particular species, among other disturbances at the landscape scale.

2.4.4 Ecosystem functioning

Before we move on to introduce the concept of 'biodiversity', we must touch upon the relationship between ecosystem stability and the species richness of a biotic community (see e.g. McCann 2000). Ecosystem stability is often measured in terms of **ecological functions**, or functioning or functionality, which includes rate of primary production, rate of decomposition or rate of nutrient cycling. Since the early twentieth century, the application of artificial fertilizers to species-rich seminatural grasslands, in order to increase ecosystem productivity, has caused a large decline in species richness. This in turn has triggered a strong and sustained investment in research on how productivity and species richness are related. Among efforts to explain the relationship between *species richness* and *ecosystem productivity*, we can distinguish two approaches, differing in perspectives on what is the cause and what is the effect: (1) 'How does species richness depend on ecosystem productivity?', a question that is inspired by a primary interest in determinants of biodiversity (see Section 2.5.1), and (2) 'How does ecosystem productivity depend on species richness?' The latter question is at stake here, as it relates to the role of **biodiversity** as contributing to **ecosystem functioning**, for example productivity (see e.g. Naeem *et al*. 2002). Some observations are in support of the *rivet hypothesis* (the majority of species essentially contributing to ecosystem productivity), whereas others favour the *redundant-species hypothesis* (only a few keystone species contribute to the productivity of the ecosystem). For the purpose of this chapter, rather than going into the details of this debate, we prefer to illustrate the unifying concepts of **functional groups**, **keystone species** and **framework species**, which – rather than species richness – play a significant role to explain or restore ecosystem functioning.

Functional groups

Various ecological classifications have been assessed to escape from dealing with individual species lists and to focus on ecological species groupings, for example life forms, strategies, adaptive syndromes and guilds. Currently, the term 'functional groups' is being used to indicate a grouping of individually known species in one particular class of functions (e.g. all the nitrogen-fixing plants in a community). Functional groups have been identified by multivariate techniques (often even without an indication of which type of function is associated with the species group), and by deductive methods that are based on the *a priori* statement of the importance of particular processes or properties in the functioning of an ecosystem (e.g. C_3 or C_4 grasses, and N_2-fixing Fabaceae, also known as Leguminosae). In restoration projects that make use of functional groups, it is often assumed that the effects of increasing species richness on ecosystem productivity work through changes in functional diversity. Indeed, ecosystem functioning in general is probably more related to the number of, and interactions among, the functional groups present at a site than to the overall species number (J. Wright *et al*. 2009).

Keystone species

Since the seminal review of Paine (1980), biotic interactions have been considered as the main underlying mechanism explaining the relationship between species diversity and ecosystem stability. Removal of a weakly interacting – that is, functionally insignificant – species would yield no or slight change, and removal of keystone species may have a cascade of effects on the community composition, transmitted by a chain of strongly interacting links. A keystone species is a member of a food web that has a disproportionally large effect on community structure. A key function can be due to high abundance of a species in a food web (e.g. a prey species) relative to other species, or result from having a large impact relative to the abundance of the species itself (e.g. a top predator).

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Keystone species sometimes play a role in reintroduction programmes, for example in the case of the reintroduction of European beaver (*Castor fiber*) in a river flood plain (see Chapter 8). It is often, however, difficult to know what the true keystone species were or are, if at all, in cases where degradation and transformation have gone very far, especially in species-poor communities.

Framework species

An interesting alternative approach, increasingly applied in projects of ecological restoration in tropical forest areas (see also Chapter 9), is to introduce a subset of species – called 'framework species' – to reorient an ecosystem along a desired or targeted **successional trajectory**, aiming pragmatically for a balance between the competitive exclusion of undesired species (e.g. exotics or invasives) and the facilitation of colonization of desired species. The so-called *Framework Species Method* first developed in Queensland, Australia (Goosem & Tucker 1995), and more recently in northern Thailand (Elliott *et al*. 2003), appears to be a promising approach to restoring tropical forests. In this technique, native 'framework species' (also called **foundation species**) are selected from the reference plant community on the basis of field trials and functional traits such as fast growth, high survival in exposed areas and rapid production of a dense canopy and fleshy fruit. Their relative position in forest succession (e.g. early, intermediate or advanced) can also serve as a selection criterion (Román-Dañobeytia *et al*. 2011). The goal is to assemble a group of species that can rapidly 'capture' or occupy a restoration site and attract seed-dispersing birds and mammals, and other dispersers, that will introduce seeds of additional native plant species, thus catalysing a progression towards a diverse native forest community. At the same time, this approach helps shade out unwanted invasive exotics or rapidly expanding populations of native colonizers, or it prevents their arrival on the site. Whether or not the community will be identical or even close to that of the reference system may take decades to determine. But, given the rapidity with which tropical forests grow, there at least one can hope for significant findings in a reasonably short period, and these results will in turn be of great interest for restoration in other, slower developing ecosystems as well.

2.5 BIODIVERSITY

Thanks to rising concerns about the loss of species richness and genetic variation within species due to human impact, the broad topic of **biodiversity** (biological diversity) has received much attention worldwide since 1992, following the adoption of the Convention on Biological Diversity (CBD), the Rio Declaration on Environment and Development, and Agenda 21 (http://www.un.org). 'Restoring biodiversity', an expression that we will not apply in this book, is obviously a central issue in the field of restoration ecology (see Falk *et al*. 1996, 2006; J. Wright *et al*. 2009). What is of importance here is the **reinforcement** or rescue of populations (Chapter 7) and the **reintroduction** of species (Chapter 8) in specific ecosystems. While species diversity and genetic diversity – measured as numbers or some mathematical formula – are neutral concepts, it is the task of restoration ecologists to value and evaluate both types of diversity in terms of 'naturalness', rarity, or risks. From a socio-economic perspective, biodiversity can be considered as a living, evolving biotic component of the stock of (renewable, and cultivated) natural capital. From an ecological point of view, however, if a species goes extinct, it is not renewable. This implies that not only the current functional aspects of biodiversity but also its evolutionary potential must be taken into account.

In the CBD, biological diversity is described as 'the variability among living organisms within species, between species and of ecosystems'. Though this definition has been adopted worldwide, we consider the inclusion of ecosystem diversity in the definition of biodiversity as confusing, because ecosystems not only are composed of biota but also contain an abiotic component. Here, following SER (2004), we focus on concepts related to restoration of (1) *taxonomic diversity* in biotic communities, among species of plants, animals and/or microorganisms, and (2) *genetic diversity* among individuals and populations within species.

2.5.1 Species diversity in biotic communities

It has been empirically shown in various ecosystems that species richness often exhibits a positive relationship with ecosystem productivity, with peak species

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richness at intermediate productivity (or intermediate disturbance). This unimodel relationship, also known as the 'intermediate disturbance hypothesis' (Connell 1978), or 'humped-back model' (Grime 1979), may result from increasing environmental limitations to the left and increasing interspecific competition to the right of the peak. Mittelbach *et al.* (2001), however, reviewed 171 published studies that revealed positive and negative relationships between the two as well. Probably, the entire productivity gradient is not always covered by the data. Nevertheless, this approach, which implies that species richness can be regulated by ecosystem management, has steadily gained attention in nature conservation (e.g. Bongers *et al.* 2009, and references therein). Application of concepts such as the 'species pool' and 'assembly rules' to ecological restoration help to identify the potential species richness in a region, and to predict the composition and interaction webs of a 'target community' following restoration.

2.5.2 Assembly from a species pool

In an ecosystem, biotic communities develop through a process called community assembly, in which individuals of species invade, persist or become extinct. While it is still an open question whether we can really speak of **assembly rules** as a set of principles or laws that predict the development of specific biological communities, as compared to development that is attributable to random processes, the search for applicability of assembly rules has opened up fruitful perspectives in the practice of ecological restoration (Temperton *et al.* 2004).

We adopt the approach given by Zobel (1997), who defined **species pools** at three different scales, with environmental filters in between, living or nonliving. A 'regional species pool' represents the total of species available for colonization and is defined within a large biogeographic or climatic region, extending over spatial scales many orders of magnitude larger than those of local ecosystems. The 'local species pool' is a selection from the regional pool, defined at the level of a landscape, and a further selection, the 'community species pool', is the set of species in a site to be restored. Assembly rules indicate constraints or environmental filters determining which species can occur in the community and which combinations are irrelevant.

2.5.3 Assembly rules

Which are the environmental filters? The term 'assembly rules' was coined by Diamond (1975), to help explain or elucidate, through experimentation and observation, the dynamic structure of stable and rapidly evolving communities based on niche-related processes. Working with this concept, Weiher and Keddy (1999) proposed to envisage two basic kinds of community patterning, with different causes: (1) environmentally mediated patterns, that is, correlations between species due to their shared or opposite responses to the physical environment, and (2) assembly rules, that is, patterns due to interactions between species, such as competition, allelopathy, facilitation, mutualism and all other biotic interactions that we know about in theory, and actually affect communities in the real world. Currently, all these processes, including the arrival of propagules, their germination and establishment, and their interactions with co-occurring species, are included in the notion of assembly rules.

Cavender-Bares *et al.* (2009) contribute to the clarification of the concept of assembly rules, by distinguishing between three perspectives on the dominant factors that influence community assembly, composition and diversity: (1) the classic perspective that communities are assembled mainly according to niche-related processes, (2) the perspective that community assembly is largely a neutral process in which species are ecologically equivalent and (3) the perspective that emphasizes the role of historical factors in dictating how communities are assembled, with a focus on speciation and dispersal rather than on local processes. Note that these different points of view are not mutually exclusive, and that it is useful to investigate the relative importance of the different hypothetical processes.

The notion of 'assembly rules' implies that the species composition of biotic communities can be explained and predicted. Independent of whether this claim is justified, the advantage of the search for assembly rules is that it helps make ecological knowledge about communities and ecosystems explicit in terms of predictions that can be tested.

2.5.4 Genetic diversity within species

Within-species genetic diversity is increasingly recognized as an important aspect of biodiversity (Falk *et al.* 2006; Chapter 7). It represents the adaptive potential of genotypes and the associated phenotypes to their

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living and nonliving environment, the basis of evolutionary processes such as adaptive differentiation and speciation. In the case of species richness, we have considered neutral and functional approaches. Likewise, genetic diversity can be valued in neutral ways (e.g. immunity to selection, or non-Darwinian evolution by random drift of genes that are not expressed in the phenotype) and by functional approaches (selection and adaptation, survival of the fittest or Darwinian evolution). In order to be applicable to species reintroduction projects pursued as part of ecological restoration (see Chapter 8), it is necessary to identify the ecological relevance of genetic variation.

A large number of techniques have been developed to quantify genetic diversity in populations of species. What is their adaptive value? Most molecular markers are neutral or nearly neutral to natural selection and patterns of variation in these markers primarily reflect the past gene flow and genetic drift. Neutral molecular variation rarely predicts quantitative genetic variation, a critical determinant of a population's *evolutionary potential* (see Chapter 21), and there is no theoretical basis for assuming that the population with the highest genetic diversity in molecular markers will be the best genetic source for restoration (McKay *et al.* 2005; Kramer & Havens 2009). We agree that a combination of molecular studies of large-scale patterns with ecological studies of **local adaptation** is required to assess the adaptive value of genetic variation. In view of application to ecological restoration programmes, McKay *et al.* (2005) raised the following two key questions (see also Chapter 7): (1) 'How will existing populations, adapted to local conditions, be affected by the introduction of novel genes and genotypes in a geographic region?' and (2) 'What is the level of genetic diversity required to ensure the long-term success of restoration projects?' Note that reinforcement or reintroduction of a local population only deals with the problem of introducing genotypes from nonlocal populations of the same species, which the reader should clearly distinguish from the introduction of alien species or even unwanted exotic invaders.

Single populations only seldom live in isolation. Increasing human impact at the level of landscapes may have resulted in **habitat fragmentation** and thus in an increasing risk of isolation of formerly interacting local populations. This has consequences for the genetic diversity and composition of the local populations, such as the risk of reduced gene flow and inbreeding effects or just the opposite (Young *et al.* 1996). As long as there is migration between two or more local populations, they can form a **metapopulation** (Hanski 1999). The body of theory and models concerning metapopulations is developing quickly, and has been applied for example to identify the minimum number of patches required for population persistence (e.g. Bascompte *et al.* 2002). In view of the fact that a metapopulation of any species may interact, in each of the local patches where it occurs, with members of metapopulations of other species, the concept of *metacommunity* has been proposed, described as 'a set of local communities that are linked by dispersal of multiple potentially interacting species' (Hanski 1999; Leibold *et al.* 2004). The development of this concept is still in a theoretical stage and difficult to apply to ecological restoration. We prefer, therefore, to confine the terminology to 'interacting populations', either in biotic communities (within ecosystems) or in metapopulations (within a landscape).

Something new in science and potentially useful in restoration ecology is the study of *phylogenetic similarity* (Cavender-Bares *et al.* 2009; Gerhold *et al.* 2011), and *phylogenetic signatures* (Verdú *et al.* 2009) at the level of biotic communities. Here the mapping and tracking efforts also include the phylogenesis of taxa, and would be applied not only to extant but also to intentionally reintroduced organisms or groups of organisms, and to the possible interactions to be expected among them. One issue of note is how and to what extent 'phylogenetically poor plant communities' respond to or 'receive' incoming species, and how well these newcomers co-exist with existing communities (Gerhold *et al.* 2011).

2.6 CHALLENGES

We close this chapter by referring to some of the key challenges ahead: uncertainty, contingency, chaos and unpredictability, on the one hand, and then transdisciplinary science and problem solving.

2.6.1 Coping with uncertainty

An inspiring essay by Hilderbrand *et al.* (2005), entitled *The Myths of Restoration Ecology*, points to a number of simplified and dogmatic 'beliefs' in ecological restoration. The goal of the authors clearly was not to discredit the field but rather to challenge practition-

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ers and scientists to think about their unconscious assumptions and the inherent limitations of this field of action. A central point in the essay is the need to cope with uncertainty. The authors warned against selecting of restoration goals and endpoints as if there would be a specified climax, for the trajectory as if this would be repeatable in numerous locations, and for the concept of self-organization as if one could confine the restoration measures to recreating the physical variables. Based on their analysis, Hilderbrand and co-authors recommend how to move 'beyond the myths', recognizing and addressing uncertainty and contingencies. For example: (1) restoration requires periodic attention and **adaptive management**, (2) designing for resilience implies planning for surprise and focusing on a diversity of approaches, functions, and taxa, (3) goals should include multiple scientifically defensible endpoints of functional or structural equivalence and (4) invasive species should not *a priori* be ruled out, but considered with respect to their role as compared to native species.

Understanding uncertainty and unpredictability is a scientific goal in itself. In mathematics, **chaos theory** describes the behaviour of certain systems that exhibit dynamics that are highly sensitive to initial conditions. The behaviour of chaotic systems may seem to be random, but as soon as the initial conditions are known, it can be explained deterministically. Chaos theory can help explain incomprehensible observations. For example, Huisman and Weissing (1999), considering the so-called paradox of the plankton – the number of co-existing species far exceeding the number of limiting resources at equilibrium conditions – were able to explain species oscillations and chaos in mixtures of phytoplankton species by experiments and associated models in which they had started with slightly different initial conditions and in which the species had complex competitive interactions. Beninca *et al.* (2008) have experimentally shown that long-term stability is not required for the persistence of complex food webs; interestingly, however, also irregular oscillations appear to remain within certain limits. But, in their observations over 7 years, predictability remained limited to a period of 14 days only.

2.6.2 Science and Society

After considering the irrefutable and implacable reality of uncertainty and unpredictability in nature, we must nevertheless come back to the realm of active interventions, of doing restoration, as best we can. As noted, the holistic approach is transdisciplinary, and requires much outreach and consensus building – network building across professional, ideological and intellectual lines. To quote Cairns and Heckman (1996), 'The field of restoration ecology represents an emerging synthesis of ecological theory and concern about human impact on the natural world' (p. 167).

Let us thus round off this chapter by emphasizing that restoration ecology, which is ultimately the study of ecological restoration, can perhaps help form an alliance between science and society, in the search for a transition to **sustainability**. On the one hand, this interface between science and society opens up new opportunities, and on the other hand it implies risks. Applied sciences, or *science-in-context*, may become politicized when scientific uncertainties and societal interests are both heavily involved (Swart & van Andel 2008; Chapter 22). Looking at the 'scene' in Europe, today, exemplified by the implementation of the nature policy plan Natura 2000, Keulartz (2009) noted that the 'democratization' of nature conservation policy is fraught with problems and pitfalls and requires an adequate and professional organization of communication between the various actors. In Slovakia, for instance, many state-owned nature reserves have been given back to former private owners, which has resulted in much more limited conservation and restoration measures actually being carried out, even though there was no change in the legal protection of the sites. Similar problems could be cited in Albania, Italy, Greece and many other countries.

Kricher (2009) emphasizes that an understanding of the dynamic nature of ecology and evolution is essential to formulating environmental policies based on ethics that can help guide humanity towards a more responsible stewardship of our planet and all its ecosystems. He warns against nonscientific, 'teleological thinking', as if nature would or could have a goal, for example associated with a search for equilibrium or a 'climax'. Humans set goals, not ecosystems, and if the goals are set scientifically, they should include estimates not only of means but also of the transient nature of ecosystems, with all their uncertainties and sudden opening of opportunities. Coping with uncertainty is primarily a scientific task, to try and quantify the risks of deviation from means and equilibria, but this issue should be communicated with all the stakeholders in ecological restoration projects and

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programmes. Restoration ecology is a science, but restoration ecologists need to be competent and proactive when it comes to communications with society at large. Ultimately, restoration ecology, ecological restoration and the restoration of natural capital are all vital components of the emerging, transdisciplinary science and problem-solving paradigm of sustainability, wherein lies humanity's best chance for finding the way towards a sustainable and desirable future for humanity and all other life on our planet as well.

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Chapter 3

ENVIRONMENTAL MANAGEMENT AND RESTORATION IN A CHANGING CLIMATE

Richard J. Hobbs

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3.1 INTRODUCTION

Despite ongoing media and political debate, it is generally accepted scientifically that the Earth's climate is changing and that human activities are, at least in part, implicated in speeding up the rate of change (Intergovernmental Panel on Climate Change (IPCC) 2007a). Carbon dioxide concentrations in the atmosphere are increasing more rapidly and to higher levels than ever before experienced in human history, and climate appears to be changing such that parts of the world are experiencing record temperatures, changing rainfall patterns, more frequent intense storms and so on.

While the existence and effects of a changing climate are increasingly evident, the policy and management responses at global and local levels are still under intense debate. In addition, climate change comes as the latest in a large array of changes being wrought on the earth by human activity – land use change, transport of species around the globe, pollution, land degradation and resource over-use present an interacting set of pressures on the world's ecosystems (Sala *et al.* 2000; Millennium Ecosystem Assessment (MA) 2005). Climate change adds a further factor to this set of interactions. In this chapter, I discuss **climate change** in this context and examine what it means in the context of ecosystem management and restoration. In particular, I focus on coping with uncertainties, the increasing prevalence of **novel ecosystems** and the challenges of devising, and choosing among, effective management interventions.

3.2 THE UNCERTAINTY CASCADE: WHAT WE KNOW AND WHAT WE DON'T KNOW

Clearly there is a lot we still do not know about how climate change will play out, how it will interact with other global changes and how it will impact ecosystems and human society. While levels of understanding are likely to increase as more information becomes available and climate models become more reliable, there will still be considerable uncertainty surrounding all aspects of both the science and how management and policy should respond. Uncertainty can be viewed in many ways and can lead to endless debate, controversy and lack of action. However, it is useful to consider the levels of uncertainty associated with the various aspects of climate change. There are elements

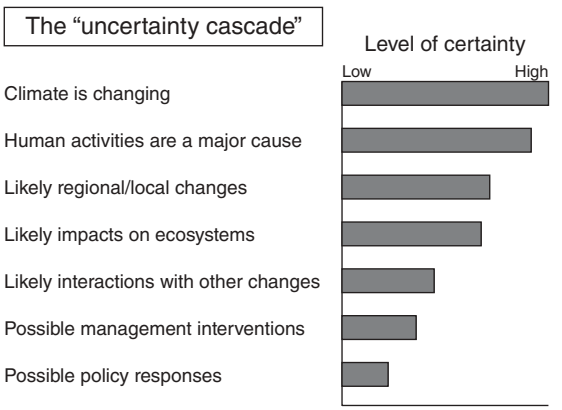


Figure 3.1 The uncertainty cascade.

about which there is increasing consensus and various levels of uncertainty about others. One can view this situation as an *uncertainty cascade* (Figure 3.1).

This schematic cascade starts with the basic premise that climate is changing, and this premise has a high degree of certainty – climates have changed in the past and will continue to do so. It is now agreed that human activities are currently of a magnitude and pervasiveness that it is fairly certain that humans are a causal factor in recent and ongoing climatic change – however, the complexity of the global climate system means that there is still debate around the relative influence of humans compared to other factors. This uncertainty is at the heart of the public and political debate surrounding climate change (Hulme 2009).

While there is near consensus in the scientific community that climate change is occurring, there is still considerable uncertainty about how climate will change in particular places. Climate models are constantly being improved and the spatial resolution has increased greatly over the last few decades, to the extent that regional and local predictions are becoming possible. Despite this, it remains difficult to provide certainty about the direction and magnitude of change in rainfall and other important climatic parameters at regional and local scales. This, in turn, causes considerable uncertainty around what the impacts of climate change will be on particular ecosystems, especially when the potentially interacting effects of other factors such as land use change, invasive species and so on are also taken into account (Chapin *et al.* 2008).

Hence there is increasingly less certainty at local scales and when management responses are consid-

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ered. Particularly since management and policy need to take into account not only biophysical attributes but also social, economic and political factors, considerable uncertainty surrounds the management and policy responses to climate change. How, for instance, do national and state governments devise policies to deal with rapidly changing environmental and socio-economic aspects? And how does a manager of a nature reserve decide on management options that will carry his or her reserve through an uncertain future? Although policy documents may be drafted to portray a relatively certain response, there is always likely to be incomplete knowledge and understanding embedded in the assumptions on which the management and policy rests.

Recognizing that different levels of uncertainty exist can help clarify otherwise confusing debates. On one hand, endless discussion on things for which there is a fair degree of certainty can be short-circuited. On the other hand, dogma or vested interest can be prevented from dominating in arenas where considerable uncertainty persists. For the practice of **restoration ecology**, the uncertainty cascade indicates that climate change definitely needs to be considered in planning and management of restoration projects but that there may be considerable uncertainty surrounding different approaches and likely outcomes. These issues are discussed further in subsequent sections.

3.3 NOVEL ECOSYSTEMS

A feature of the development of ecology over the past few decades has been the incorporation of dynamism and change as a key feature of most ecosystems. From a rather static view of ecosystems as equilibrium entities which stayed the same or had predictable *recovery* patterns from disturbance back to that equilibrium, ecology now recognizes that ecosystems are dynamic at a wide range of spatial and temporal scales (see Chapter 6). Long-term climatic shifts cause ecosystems and their components to shift across landscapes and continents. Disturbances of varying scale and intensity set ecosystems on complex paths of recovery, and sometimes complex feedback mechanisms cause alternative states to form and persist (Botkin 1990; Scheffer 2009).

As humanity's influence on the planet grows, the extent to which human activities modify ecosystem dynamics also grows. The various ways in which humans are changing the planet discussed above lead to complex and profound changes in ecosystems. In the past, ecosystems exhibited a range of characteristic dynamics, mostly within a bounded state space. This state space has been termed the *historic range of variability*, a concept that is frequently used to define conservation and restoration goals and targets (Landres *et al.* 1999). However, human alteration of the abiotic environment and changing biotic composition because of local extinctions and the advent of introduced species can, and does, shift ecosystems into new configurations with respect to what was present historically. These **novel ecosystems** are characterized by new species combinations and/or significantly altered abiotic conditions (Hobbs *et al.* 2006, 2009). While the existence of such ecosystems has been discussed for several decades, they have been relatively little studied, and the implications for management and restoration have only recently been considered (Seastedt *et al.* 2008). Markedly differing dynamics may be apparent in novel systems (Mascaro *et al.* 2008), but in some cases it appears possible to alter assemblages in particular directions through either facilitating natural processes or active management (Abelleira Martínez 2010; Kueffer *et al.* 2010). Particularly where the novel assemblage includes non-native species, there is valid concern that conservation goals may be compromised (Simberloff *et al.* 2011; Vince 2011), although there is also the potential for novel systems to provide useful ecosystem services.

The need to consider how to manage significantly altered ecosystems has become increasingly apparent as recent estimates indicate that about 80% of the Earth's land surface is modified by humans in some way, with perhaps 40% qualifying for description as 'novel' (Ellis & Ramankutty 2008; Marris 2009; Ellis *et al.* 2010). These estimates arise mostly from land use modifications. When climate change is considered, there is the additional likelihood that some areas will experience climate conditions for which there are no current analogues (Williams & Jackson 2007; Williams *et al.* 2007). In addition, as species respond individualistically to climate change, new species assemblages are likely to form (Jackson *et al.* 2009; Stralberg *et al.* 2009). Because it is impossible to model species distribution shifts into climate spaces for which there is no current analogue, it is very difficult to predict with any accuracy the future species combinations in such areas (Fitzpatrick & Hargrove 2009). Equivalent analyses for marine systems also suggest a

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pervasiveness of human influence in the world's oceans, with 41% being classed as experiencing medium–high impact (Halpern *et al.* 2008).

Hence the future holds many challenges for ecosystem management given the rapidity and extent of ecosystem change, the uncertainty surrounding likely redistributions of species, and the formation of novel assemblages that also lead to new sets of interactions among species. The implications of these challenges and potential approaches to dealing with them are outlined in the next section.

3.4 ECOSYSTEM INTERVENTIONS

Deciding if and how to intervene in ecosystems in a rapidly changing world is one of the major challenges facing humanity in the twenty-first century. Clear enunciation of goals, identification of the various options for intervention and successful intervention at key leverage points will be essential for the effective conservation, management and restoration of the world's ecosystems and the services they provide (Hobbs & Cramer 2008; Hobbs *et al.* 2011). Many different management interventions are possible, ranging from no active intervention, through activities such as removing invasive species, to large-scale engineering works such as removing dams from rivers or reinstating hydrologic flows in whole river systems. Deciding on the type and extent of intervention is partially based on the identification and diagnosis of degradation or dysfunction in a system and an accompanying analysis of likely costs, benefits, and likelihoods of success. However, social and value-based judgements are also important, and decisions to intervene in particular ways may be made on the basis of current social norms, valuation of particular species or ecosystem states over others and so on.

3.4.1 Setting goals and targets when everything is changing

Deciding on goals is an important ingredient in the development of effective management and restoration programmes, and yet such goals are often poorly articulated or else are presented in broad terms that have little relevance in any particular situation. Without clear goals and targets, it is impossible to tell management outcomes are being achieved or to decide what to measure in order to check on progress. Much conservation management aims to maintain current assemblages or species populations in particular places, particularly nature reserves, while ecological restoration often takes historic or current **reference systems** as the basis for setting restoration goals (Jackson & Hobbs 2009; Cole & Yung 2010). A key element of the discussions mentioned above on climate change and other environmental changes is that the future may be quite unlike the past or the present.

Currently in the conservation and restoration literatures, there is much debate concerning how rapid environmental change might or should alter how goals are set. Are historical ecosystems still valid points of reference on which to base conservation and restoration goals? Should we focus on past and present species distributions if, in all likelihood, these might be dramatically different in the next few decades? Restoration projects, in particular, are at the forefront of decision-making discussions, and increasingly prominent in the politics and legislation related to attempts to slow and mitigate anthropogenic climate change. How much should project managers aim to maintain or restore systems that are likely to be resilient in future climates rather than systems which mimic past states? Should we even set targets at all, or should we simply let the system take whichever course matches the changing situation? Should species selection be made on the basis of local species and populations or should a mix of species from different environments and locations be used to bet-hedge against future changes? To date, there is a lot of discussion (e.g. Broadhurst *et al.* 2008), but no clear answers to these questions.

3.4.2 Conserving species and assemblages

Heller and Zavaleta (2009) reviewed two decades of scientific literature on recommendations on **biodiversity** management in the face of climate change. They suggested that adaptation to climate change broadly requires improved regional institutional coordination, expanded spatial and temporal perspectives and incorporation of climate change scenarios into all planning and action. In addition, a greater effort is needed to address multiple threats and global change drivers simultaneously in ways that are responsive to and inclusive of human communities. Interestingly, the same recommendations could also be made about making conservation efforts more effective in general.

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Hence climate change in many ways is simply bringing the requirement for improved conservation planning and management into sharper focus. However, Heller and Zavaleta (2009) also found that, for many recommendations, there is little specificity about how, by whom and under what conditions they can be implemented. In other words, most recommendations currently deal in generality rather than providing specific guidance in particular situations. The problem of moving from the general to the specific has been recognized often, and recently there have been attempts to provide general checklists of issues to be considered and adapted in the context of specific systems or situations (Lindenmayer *et al.* 2008). These include recognizing the importance of landscape mosaics (including terrestrial–aquatic linkages), maintaining the capacity to recover from disturbance and managing landscapes in an adaptive framework. These broad considerations are influenced by landscape context, species assemblages and management goals and need to be adapted accordingly for on-the-ground management. Two important requirements are a clearly articulated vision for landscape conservation and quantifiable objectives that offer unambiguous signposts for measuring progress (Lindenmayer *et al.* 2008).

Climate change and the resulting biotic responses provide multiple challenges for conservation. Species ranges are likely to shift and species assemblages are likely to change (see also Chapters 20 and 21). The biotic assemblage will respond to not only the direct climatic changes but also the changed incidence of episodic events, altered fire, flooding and other disturbance regimes, and changes in disease and pest prevalence. Increasingly, active intervention may be required to achieve conservation goals as currently formulated and previous 'hands-off' approaches to reserve management may no longer be sufficient (Hobbs *et al.* 2010). Increasing levels of intervention seem inevitable (Figure 3.2). Particularly in the United States, approaches to reserve and wilderness management based on the 'natural' system are under question – what constitutes 'natural' in a rapidly changing human-dominated world? However, if we abandon existing norms and concepts, what will replace them? The options include utilizing concepts such as **ecosystem integrity** and **resilience** (Cole & Yung 2010; Hobbs *et al.* 2010). Climate change will not lessen the requirement for traditional place-based management (set-aside reserves, etc.) but may render it insufficient. If a reserve has been designated because it contains a particular species or set of species, what happens to that reserve if the species no longer occur there because they have moved elsewhere in response to a changing climate? And where do these species move to? The reserve system worldwide is patchy and unrepresentative, and there is increasing recognition that the surrounding landscape can be very important in determining the overall success of local conservation efforts (Daily *et al.* 2001; Ranganathan *et al.* 2008). This is likely to become even more relevant under climate change.

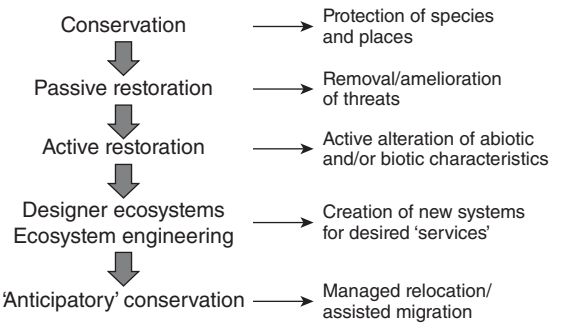


Figure 3.2 Increasing levels of intervention, from traditional 'preservation'-focused conservation through active restoration and design of ecosystems which fulfil specific purposes.

Determining landscape configurations which facilitate movement of species under threat from changing climates will be an important process. However, beyond that, there is also increasing discussion of the desirability and practicality of deliberately moving species in anticipation of changing climates. The process of assisted migration or managed relocation remains controversial, although there have been recent attempts to consider the circumstances under which it might or might not be considered (Hoegh-Guldberg *et al.* 2008; Richardson *et al.* 2009). Given the uncertainty surrounding the rate and direction of climate change at local and regional scales, it will remain difficult to predict future ranges for many species with any degree of certainty. However, some groups are already conducting such relocations: for instance, *Torreya taxifolia* has been relocated by the Torreya Guardians in the south-eastern United States (Shirey & Lamberti 2011). The issues surrounding such activities are as much ethical as ecological, and are forcing a rethink of conservation norms and policy (Minteer & Collin 2010).

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3.4.3 Maintaining productive systems

Provision of a range of **ecosystem services** is essential to continued human existence on the planet, and yet recent analyses suggest that humanity is living beyond its means both by utilizing ecosystem services at a greater rate than they can continue to be provided and by degrading or transforming the ecosystems providing these services (Millennium Ecosystem Assessment (MA) 2005). Food production, in particular, is a key area of concern, with current agricultural practices in developed countries relying on high energy and chemical inputs and often leading to on-site or downstream environmental degradation, despite recognition that a move to more sustainable practices is essential (Kitzes *et al.* 2008; Pretty 2008). Meanwhile in less developed parts of the world, subsistence farming methods cannot supply sufficient food to feed growing populations or deal with climatic vagaries. Similarly, global fisheries are in decline, with over 60% of fish stocks worldwide still requiring rebuilding, and lower exploitation rates needed to reverse the collapse of vulnerable species (Worm *et al.* 2009).

Reversing these trends is essential, even without considering climate change. Often, simple changes in practices can result in dramatic increases in productivity and its reliability. For instance, in arid areas where ongoing degradation occurs, both broad-scale and local actions can result in improved production (Bainbridge 2007a; Reynolds *et al.* 2007). As for conservation objectives mentioned above, current and future climate change accentuates the need to implement policies and practices which can help make ecosystems and human societies more resilient to current and future challenges.

3.4.4 Restoring degraded systems – local and regional

Ecological restoration and **rehabilitation** can be carried out for many reasons, including the return of conservation or production value to systems which have become degraded in some way (Hobbs & Norton 1996; Hobbs & Harris 2001). There was little consideration until relatively recently of how restoration efforts might be affected by climate change and how practitioners might need to modify their goals and approaches in the light of potential climate change (Harris *et al.* 2006). As discussed above, climate change may render it increasingly difficult to carry out traditional restoration which has as its aim the return of a system to some historic state. However, it may still be possible and desirable to do this in some circumstances, particularly where society as a whole or local community groups in particular are strongly motivated and have the resources to do so. For instance, efforts to restore prairie systems in urban remnants in Chicago involve reinstating historic management practices and ongoing removal of non-native plant species, but have inspired both local groups and a city-wide movement, the *Chicago Wilderness* (http://www.chicagowilderness.org). In addition to these efforts, it may also be desirable to try different approaches and aim for more future-focused outcomes (Jackson & Hobbs 2009). A key element in the response to climate change will most likely be the need to actively plan for a varied set of responses both at local and regional levels. Not doing the same thing everywhere seems to be the best bet when faced with an uncertain future. For instance, in a restoration area, it may be useful to use different mixes of species across the area, while such activities as fire management and grazing can be varied across nature reserves.

3.4.5 Managing and restoring resilience

The word **resilience** is increasingly used as an important property of both ecological and socio-ecological systems, particularly in the context of responding to and coping with climate change. But what does it mean, really, and how can it be used in management and restoration? In ecology, the term 'resilience' is used for several purposes, but most commonly in reference to the ability of natural systems to recover from a temporary **degradation** (cf. Holling 1996; Walker *et al.* 2004; see also Chapter 2). A focus on resilience in conservation and ecosystem management may increase our ability to understand and manage **socio-ecological systems** by considering system-level processes and interactions, the integration of multiple biotic and abiotic factors, interactions across spatial and temporal scales and dynamic shifts in ecosystem controls and management needs (e.g. Walker & Salt 2006). It also moves conservation beyond the concept of static targets by explicitly acknowledging the need to accommodate a shifting baseline (see Chapter 21). Elmqvist *et al.* (2003) suggest that 'Resilience is necessary to sustain desirable ecosystem states in variable

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environments and uncertain futures', while Chapin *et al.* (2009) advocate 'resilience-based natural resource management in a changing world' and other authors suggest 'resilience thinking' as an approach likely to assist and inform ecosystem management (Walker & Salt 2006; Fischer *et al.* 2009). However, while resilience thinking is thus seen as a useful concept with policy relevance, it has also been viewed as potentially confusing because it is a conceptual muddle without clear operational utility (Brand & Jax 2007). How to actually maintain or restore resilience in practical terms remains a challenge because of the lack of clear measures or operational guidelines. It appears to be essential that this challenge is tackled effectively, given the increasingly important role resilience is seen to have in allowing ecosystems and human societies to deal with multiple environmental changes. For example, Chapin *et al.* (2006) discussed policy strategies to address sustainability of Alaskan forests in response to a directionally changing climate. A key strategy identified was increasing resilience by strengthening feedbacks that buffer the system from change and increasing options for adaptation through biological, cultural, and economic diversity. A further example is given in Chapter 20, dealing with invasive species.

3.5 PERSPECTIVES

The key take-home message from this chapter is that climate change adds a layer of uncertainty and change over a world already undergoing rapid and pervasive change through human modification of ecosystems. While there is considerable debate on how to factor climate change into policy and ecosystem management, few concrete ways forward have emerged. However, uncertainty cannot be an excuse for inaction, and scientists have a responsibility to (1) try to identify and reduce uncertainties where possible, (2) help develop strategies for dealing with uncertainties where they are known to exist and (3) better equip humanity to anticipate and prepare for future surprises. Repeatedly, the message seems to be that if humanity was able to better implement the policies, strategies and management options that are already recommended and available, this would go a long way to help us respond effectively to the additional challenges arising because of climate change. Humanity faces significant challenges in the stewardship of the planet, even without climate change. As Hobbs *et al.* (2009) suggest, 'In the meantime, it is prudent to respect several delicate balances: between ecosystem services and natural processes, and between ecological integrity and cultural values'.

Another key recommendation is to vary management approaches both locally and regionally, given the uncertainty of what the future holds: putting all eggs in one basket does not seem sensible. For instance, Ravenscroft *et al.* (2010), using a modelling approach to forest restoration in the eastern United States, suggested that 'Given the uncertainty associated with climate change, ensuring a diversity of species and conditions within forested landscapes may be the most effective means of ensuring the future resistance of ecosystems to climate-induced declines in productivity'.

Beyond these overarching themes, the particulars of management approaches such as assisted colonization, large-scale connectivity and resilience all require considerable thought and increased efforts to link theory with practice so that operational and effective approaches can be developed that incorporate the reality of climate change in local and regional restoration and ecosystem management projects and programmes. **Climate change** provides opportunities for restoration as well as challenges. For example, the advent of markets for carbon and the need for **carbon sequestration** have the potential to provide funds for large-scale restoration projects that would otherwise be too costly (e.g. Bekessy & Wintle 2008; Galatowitsch 2009). As another example, in growing cities around the world, communities and local authorities are recognizing the benefits of increasing the numbers of trees in the urban environment, and particularly in the context of a warming world, trees can modulate local climate and temperature (e.g. Million Trees NYC, in New York City http://www.milliontreesnyc.org).

We are at an interesting point in history where we know that we need new approaches to ecosystem management and restoration which complement, rather than replace, the approaches that have developed over the last century. However, there are many questions around these approaches, and as yet no clear answers to these questions. This makes it both an extremely uncertain time in restoration practice and an extremely interesting and crucial time to be working in restoration research.

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Chapter 4

PLANNING AND IMPLEMENTING SUCCESSFUL LANDSCAPE-SCALE RESTORATION

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4.1 INTRODUCTION

Chapter 2 articulated the need for society and science to have an integrated and concerted approach to address restoration of disturbed ecosystems. The authors also identified a range of potential objectives as well as possible barriers to successful restoration. Most of the restoration objectives were defined in terms of particular mindsets or paradigms, which have been of use in a range of activities such as 'restoring' species diversity, improving the provision of ecosystem services, and using reference sites to help specify targets. At one level, these are sound and worthwhile restoration activities, but they also identify a gap in our understanding of how disturbances affect ecosystems, or, more broadly, **landscapes**, defined as a mosaic of connected and interacting ecosystems (Turner *et al*. 2001). Understanding impacts of disturbances is critical to our capacity to plan and implement effective landscape restoration technologies.

In this chapter, we describe an approach to restoration that emphasizes the need for understanding how ecosystem processes, connected in a landscape, are affected by disturbances, causing landscapes to be *dysfunctional*, and how this knowledge can then be used by restorationists to set achievable goals and to design and implement practical restoration technologies to achieve their goals. We also describe how to inexpensively monitor and evaluate progress towards goals by building on the information gained in assessing the causes of landscape dysfunction. This monitoring methodology, discussed in section 4.2.5, is called *Landscape Function Analysis*. It defines and measures **indicators** of landscape processes that are affected by disturbances. Restoring disturbed processes is the key to successful landscape-scale restoration (Tongway & Ludwig 2011).

4.2 A RESTORATION PLANNING APPROACH

To successfully restore, or reintegrate, a disturbed landscape, we recommend that restorationists first take two important steps: (1) explicitly define the goals of their restoration project, and (2) fully understand how disturbances have historically affected the landscape in question (Figure 4.1). We know examples of successful landscape-scale restoration projects where these first two steps were done so well that steps 3, 4 and 5 followed without having to revise technologies (e.g. Spain *et al*. 2009). We are also aware of failed restoration projects where, in a wave of enthusiasm, the first two steps were not carefully considered. We link steps 1 and

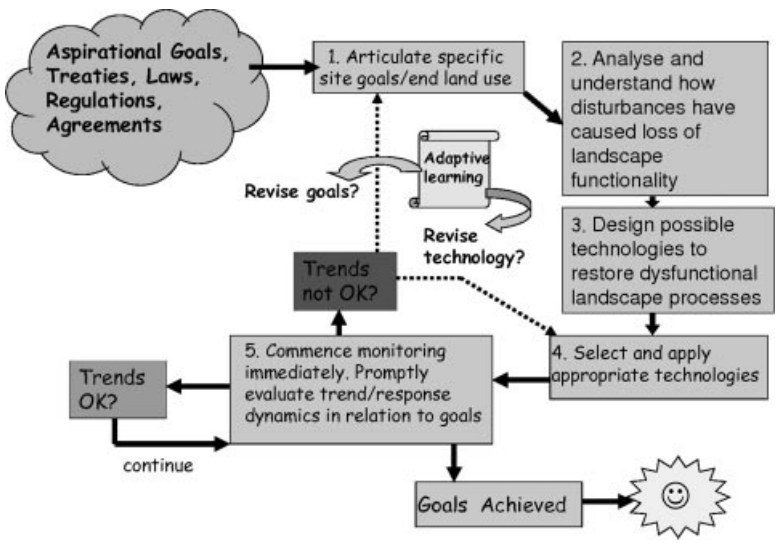


Figure 4.1 A stepwise approach to landscape restoration with regular reviews and evaluations of whether trends in indicators are towards specified goals.

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2 because of the importance of understanding the restoration problem relative to goals before designing, selecting and implementing technologies. A set of 'initial status' data is crucial in step 2, so as to be able to properly understand the nature of the landscape dysfunction that is to be restored. For example, where the goal is to reduce high weed abundance in a disturbed landscape, such as hilly pastureland, we recommend that the services provided by the weedy plants with regard to erosion control in the landscape be carefully analysed before taking control actions. It may not be necessary to eradicate all the weedy species, just the aggressive species – less aggressive weeds may be retained to help protect soil surfaces from erosion. The biology of the weed species needs to be known to decide whether an aggressive **eradication** or a more measured response is appropriate. Taking these preconditions of our approach into account, we will now illustrate and discuss the five steps as presented in Figure 4.1 in more detail, focusing on Landscape Function Analysis (step 5).

4.2.1 Specifying project goals

We propose that restoration goals be specified based on aspirations of **stakeholders** (those with an interest in the landscape being restored) and on existing land use agreements and official regulations (Figure 4.1, step 1). These initial goals should not be viewed as 'set in stone', but rather be kept open to revision following after an analysis of the factors underlying the need for landscape-scale **restoration** (or **rehabilitation**). These goals also need to be stated in ways that are measurable so that they can be regularly and rigorously evaluated in terms of whether restoration trends are acceptable not, and with time whether success has been achieved.

In the process of setting goals, we urge restorationists not to be over-ambitious. Setting realistic goals requires a sober reflection on what is possible technically and what is socially and financially acceptable. For example, restoring a landscape to form a stable, non-eroding, self-sustaining system may be realistic, but re-creating the full species composition and physical conditions of the pre-disturbance landscape is often impossible to achieve because the species composition in reference sites is too dynamic over time. Landscape-scale restoration should aim to achieve self-sustaining systems by repairing dysfunctional processes such as those involved in the retention of resources such as rain water. By repairing damaged landscape processes, vital resources are retained to improve the system's **natural capital** (e.g. goods and services).

4.2.2 Understanding landscape processes

Landscape disturbances may arise from deliberate human actions such as clearing trees, grazing domestic stock and mining, or they may be non-human-mediated events such as floods, windstorms or wildfires. To analyse how such disturbances damage the functioning of landscapes, we need to focus on understanding biophysical processes (Figure 4.1, step 2), before designing, implementing and monitoring restoration technologies (steps 3, 4 and 5).

Over many years, we have developed a conceptual framework that summarizes how human and natural disturbances affect how landscapes function as dynamic, biophysical systems (Tongway & Ludwig 1997, 2002, 2007, 2009). Our framework specifically builds on models of ecosystem behaviour based on the availability and flow of water in space and time. We draw on the work of Noy-Meir (1973, 1981) and, more generally, on approaches analysing disturbed landscapes such as those of Hobbs and Norton (1996), who clearly listed the fundamental information required to restore landscapes. To successfully restore disturbed landscape processes that have become dysfunctional or impaired, we find frameworks are useful for identifying those processes most urgently in need of repair, in order to achieve restoration success.

Our conceptual framework represents a sequence of events and processes (Figure 4.2) that are responsible for gains and losses of resources (reserves) such as water, seeds and soil nutrients. Because of the vital importance of water in ecosystems (Noy-Meir 1973; Le Houérou 1984), we use rainfall as a trigger event, which initiates a series of biophysical processes dynamic in space and time. The scope of this framework can be readily extended to include the dynamics of other vital resources such as soil (containing plant available nutrients) and litter (decomposing to facilitate the cycling of nutrients). A significant rainfall event triggers transfer processes, wherein spatially explicit and time-dependent *infiltration* and ***runoff*/*run-on*** processes (#1 in Figure 4.2) add water to soil reserves within the landscape (run-on patches). Similarly, if *runoff* (#2a) is excessive,

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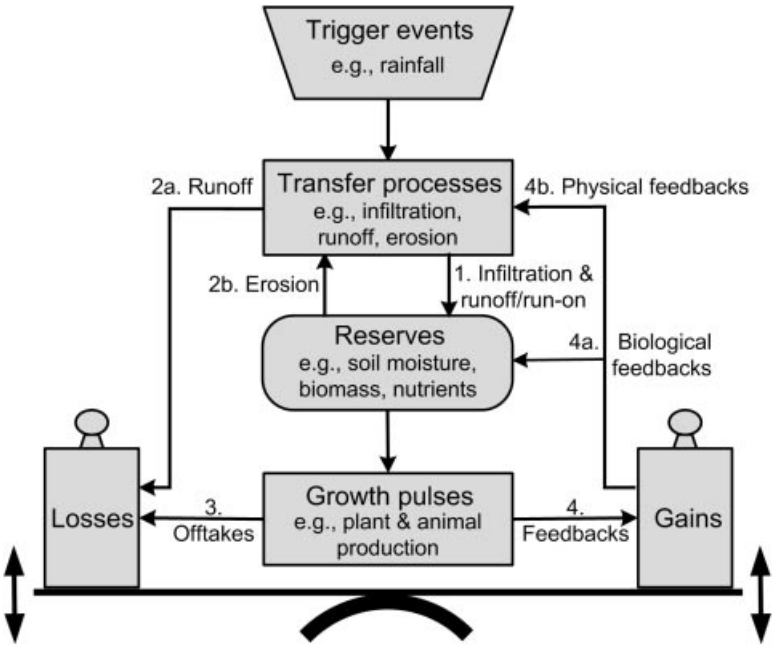


Figure 4.2 A conceptual framework illustrating how landscape systems function in terms of a sequence of events and processes affecting the economy (gains and losses) of vital resources. In healthy systems, these gains and losses fluctuate, but in the long term they are in a dynamic equilibrium.

water is lost and soil erodes (#2b) from the landscape. Broadly, the reserve represents a pool or bank of ecosystem resources such as soil moisture, soil nutrients, seeds and the biomass of plant, animal and decomposer organisms. When water reserves exceed a threshold, organisms experience a pulse of growth. For example, seeds germinate and establish new plants. Such pulses of plant growth provide the resources (food, fiber, firewood and forage) that people the world over utilize. This use of resources is what we call offtake processes (#3) such as the consumption of forage by livestock, which are subsequently locally consumed or taken to markets. Part of the growth pulse also delivers *feedbacks* (#4); these gains can be viewed as being largely biological feedbacks (#4a) or physical feedbacks (#4b). Biological feedbacks include, for example, the rebuilding of soil nutrient reserves by the decomposition of plant biomass produced during growth pulses. Physical feedbacks include, for example, increases in the size and/or density of vegetation patches due to pulses of plant growth, which then enhances the capacity of the landscape to obstruct overland flow and hence infiltrate more water during the next rainfall event.

We all know that ecosystems and landscape systems fluctuate in the short term in their resource gains and losses, which we metaphorically depict as weights that are balanced (Figure 4.2) but fluctuating due to seasonal effects and minor disturbances. However, in 'healthy' landscapes, in the long term, there is an overall balance between gains from feedbacks and losses due to offtakes. This dynamic balance between gains and losses can be greatly affected by disturbances, which in turn may cause excessive offtakes (e.g. fire and grazing). Disturbances reduce biological and physical feedbacks from growth pulses (e.g. the amount of biomass reserves and the size of run-on patches of vegetation).

In 1997, we published the first version of our conceptual framework consisting of a sequence of dynamic landscape processes, and which included the notion of 'out-of-balance' systems because of excessive losses relative to gains (Tongway & Ludwig 1997). Since then, we have updated and refined the original concepts a

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number of times (e.g. Tongway & Ludwig 2002, 2009, 2011), and have coupled it with the use of Landscape Function Analysis monitoring data collection methods (see section 4.2.5). Because the means to the overall goal in the restoration of disturbed landscapes is to repair damaged processes to achieved long-term **stability** and **sustainability** of the restored system, we view our framework as more than just a depiction of landscape system components and connections. We see it as a framework that identifies triggering events, including natural and human-induced disturbances, and sequences of processes where each process is contingent on the efficacy of prior processes. Learning how disturbances affect processes can help us understand why some landscape systems become unbalanced in terms of gains and losses in resources over the long term, and how these systems can be repaired.

4.2.3 Designing restoration technologies

Using the above-described conceptual framework as a tool to analyse how disturbances affect ecological processes at the level of whole systems, restorationists can now use the information and understanding gained from this analysis to address the problems arising from dysfunctional processes by designing restoration technologies (Figure 4.1, step 3). To design effective restoration technologies, we need to consider the following questions:

- Was the disturbance caused by a hurricane, for example, or was it caused by human activity, such as mining?
- Did the disturbance factor(s) have a large impact, such as is the case with strip mining, which requires building new landforms, or did it entail a relatively low impact needing only minor surface adjustments, such as building 'brush-packs' to reduce runoff?
- Was the disturbance a one-off event, such as due to woodland clearing, or is it current and ongoing, such as due to cropping in marginal lands?
- Did the causes of disturbance extend over a long period of time, such as livestock grazing, or was it a brief impact, such as a wildfire?
- Was the disturbance a rare and unpredictable event, such as caused by a one in a hundred year flood, or is it frequent and common, such as due to browsing and grazing?
- Did the disturbance extend over large land areas or was it restricted to small areas?
- Was the disturbance intentionally planned, such as in mining, or was it an unintended consequence, such as dense woody regrowth after clearing woodland to create pasture?

After addressing such questions, especially in terms of an analysis of how disturbances affect landscape processes (Figure 4.2), restorationists will have the knowledge needed to design restoration technologies (Figure 4.1, step 3). Step 3 is still at the 'ecological science' level rather than at the 'engineering' level or implementation stage (step 4). Ecological science involves communicating how to enhance biological and physical feedback processes, for example, by selecting plant species in **revegetation** projects known to be effective for providing litter to enhance nutrient cycles in the developing soils (Box 4.1).

Designing technologies to restore landscapes by repairing processes can be relatively straightforward (see Box 4.1). However, designing technologies can be very challenging, such as where coal mining operations have greatly disturbed landscapes and major land-forming is required to reshape massive spoil heaps. Such projects require teams of restorationists with modelling and engineering skills, and also people with the geotechnical and geochemical knowledge about the properties and quantities of the mine spoil materials available, such as the potential for exposure of saline, sodic or pyritic soil materials. Ecologists are needed for designing ways to establish self-sustaining vegetation on the reformed landscape, and for dealing with unplanned problems. For example, if monitoring shows that **exotic weed species** are providing most of the ground cover on a landscape being restored, then strategies for progressive replacing these weeds with more desirable and permanent **native plant species**, while maintaining some protective ground cover, requires careful design.

4.2.4 Implementing restoration technologies

Once the designing step is complete, appropriate physical or engineering works can be selected and implemented (Figure 4.1, step 4). These technical **interventions** may vary from being difficult and expensive, such as those required when restoring landscapes after coal-mining enterprises, to relatively easy and inexpensive, such as the work needed to reduce the energy of flows of water along trails or tracks in a park.

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Box 4.1 Enhancing landscape processes: selecting species for mine site revegetation

After a site in eastern Australia was mined for sand and gravel, and then regraded with topsoil to reproduce a landform comprised of low rolling rises and ponds, an unknown restorationist undertook a project with a goal to successfully restore self-sustaining vegetation on this disturbed landscape. This restorationist selected *Casuarina* and *Eucalyptus* plantation species to revegetate the landform in a mixture simulating the relative abundance and spatial distribution in reference sites.

We and the body responsible for restoration, who invited Landscape Function Analysis to be deployed, observed that the *Casuarina* species quickly established and commenced dropping leaf litter within a couple of years, forming a dense, interlocked surface mat (Figure 4.3a), which resisted runoff and erosion. The *Eucalyptus* species was slower to establish, permitting a physical crust to develop on the soil surface (Figure 4.3b), which readily shed rainfall. However, after 5 years, the *Eucalyptus* steadily increased its production of coarse woody litter (twigs, branches) so that after 10 years areas with a mix of *Casuarina* and *Eucalyptus* species formed an excellent ground cover of litter (Figure 4.3c). The restorationist used Landscape Function Analysis monitoring methods (see section 4.2.5) to measure indicators of runoff and soil particle movement processes, and found that data trends for these indicators were OK and that restoration goals were being achieved (see Figure 4.1).

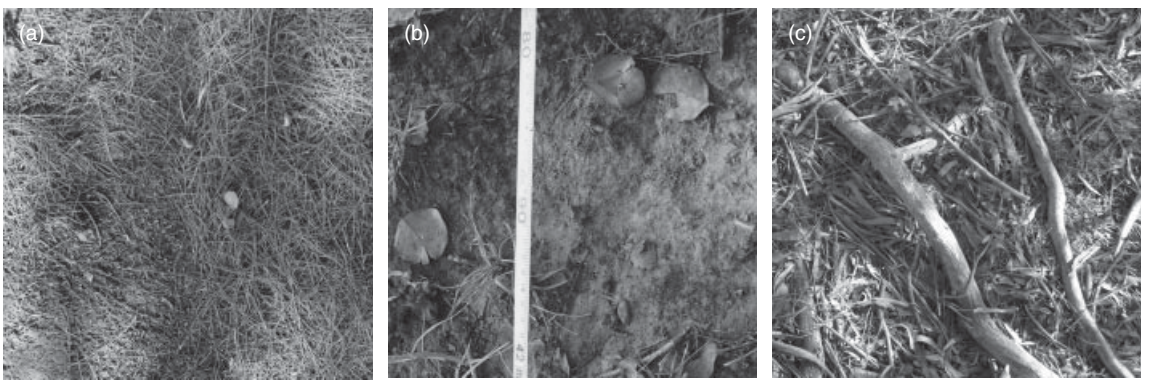


Figure 4.3 Litter on landscape surfaces after 2 years under: (a) *Casuarina* species, and (b) *Eucalyptus* species and (c) after 10 years under both species. (Photographs by David Tongway.)

In our experience, regardless of the magnitude of the project, the selected and implemented design should aim at restoring landscape processes such as improving the retention of water in eroded rangelands (Box 4.2).

4.2.5 Monitoring and evaluating restoration progress

Monitoring trends on how well landscape processes are functioning should commence as soon as the selected restoration tools and technologies have been applied, using the Landscape Function Analysis procedures described for this purpose (Figure 4.1, step 5a). Landscape Function Analysis has a number of abiotic indicators which are very informative at this stage, especially in defining the initial dysfunctional status of the land. Newly restored landscapes may be vulnerable to energetic storms early in their life; as a result, appropriate monitoring methods are needed to check that restoration trends are progressing towards goals. Early initiation of monitoring is also advantageous because repairing minor defects early on is much simpler and

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Box 4.2 Repairing landscape processes: ponding water in rangelands

Around the world, there are rangelands that have been damaged by grazing so that wind and water erosion have removed vast areas of topsoil to expose hard clay subsoils (Figure 4.4a). These landscapes are typically flat and barren, and are called scalds, hardpans, clay pans or blowouts. Such scalds have very low water infiltration rates so that during and after rainfall events most of the water runs off and is lost from the landscape. Repairing water retention processes (infiltration and run-on) in these scalded landscapes presents restorationists with significant challenges (Whisenant 1990), primarily because water runs off the land so rapidly that erosion continues to occur and very little vegetation establishes even if grazing ceases.

However, a team of restorationists in semi-arid south-eastern Australia has taken on this challenge, and has designed and implemented a restoration technology known as water ponding (Thompson 2008). Their goal was to bring scalds back to productivity. Their analysis of scalded landscapes suggested that the main problem was water retention. Using laser-levelling and machinery, they built low earthen banks along contours to form 'ponds' (Figure 4.4b). These ponds function to retain water for a much longer period after rainfall events. They found that water ponding was very effective when scalded soils had swell–shrink properties, which caused them to swell slightly when wet but then shrink as they dried out. This process forms a network of cracks, which facilitates improved water infiltration in subsequent rainfall events. The cracks also trap seeds and other organic debris. Vegetation then establishes, triggering growth pulses that improve soil properties as the concentration of organic matter in the soil increases. Water-ponding technology was less effective on scalds having soils with weak swell–shrink properties.

This team has constructed more than 50 000 water ponds on scalded areas in the Marra Creek district of New South Wales, Australia (Thompson 2008), and water-ponding technologies are now being applied, for example, to scalded rangelands in a number of African and Middle Eastern countries, and in China and the United States.

less expensive than dealing with major damage later on. For example, treating an eroded slope with small rills – that is, shallow channels (less than 0.3 m deep) carrying runoff down slope after rainfall event – is far easier and less costly than repairing deep, wide gullies (Box 4.3).

Landscape-scale restoration success can be measured by general **indicators**, such as the aesthetics of vegetation along a rehabilitated roadside, and by specific indicators, such as the absence of heavy metal pollutants leaking from a reformed mine spoil. Whether general or specific, we recommend using simple indicators that serve as surrogates for difficult to measure landscape processes. For example, directly measuring the rate and amount of water running off a landscape is technical and costly, but restorationists can quickly estimate the amount of perennial vegetation cover (Plate 4.1), which provides surface protection and obstruction to flows of water and wind turbulences. When ground cover is measured on a disturbed site (Figure 4.6a) and compared to values from a reference site (Figure 4.6b), this easily estimated cover value provides restorationists with a useful indicator of how well a restored landscape is progressing over time towards developing a cover that reduces the rate and amount of runoff, hence improving the amount of water retained and stored in the landscape.

Selecting which indicators to measure is difficult given the large number of ecosystem indicators described in scientific papers and books (e.g. Costanza *et al.* 1992; Munoz-Erickson *et al.* 2007). Given that our main interest in this chapter is on the functionality of biophysical processes in landscapes, we list 25 indicators assessed by the Landscape Function Analysis monitoring procedure that can provide restorationists with useful information about landscape processes (Table 4.1). This list is based on our experiences with restoration projects in a wide range of landscapes around the globe (e.g. Tongway & Ludwig 1997, 2002, 2007). For convenience, we group these 25 indicators into four groups: landscape organization, soil surface condition, ephemeral drainage-line stability and vegetation structure. These four groups of **indicators** are fully described in Tongway and Ludwig (2011, chs. 13–16). Landscape Function Analysis documents explaining how to assess or score indicators are available as PDF files online at http://members.iinet.net.au/~lfa_procedures/, along with spreadsheets that are

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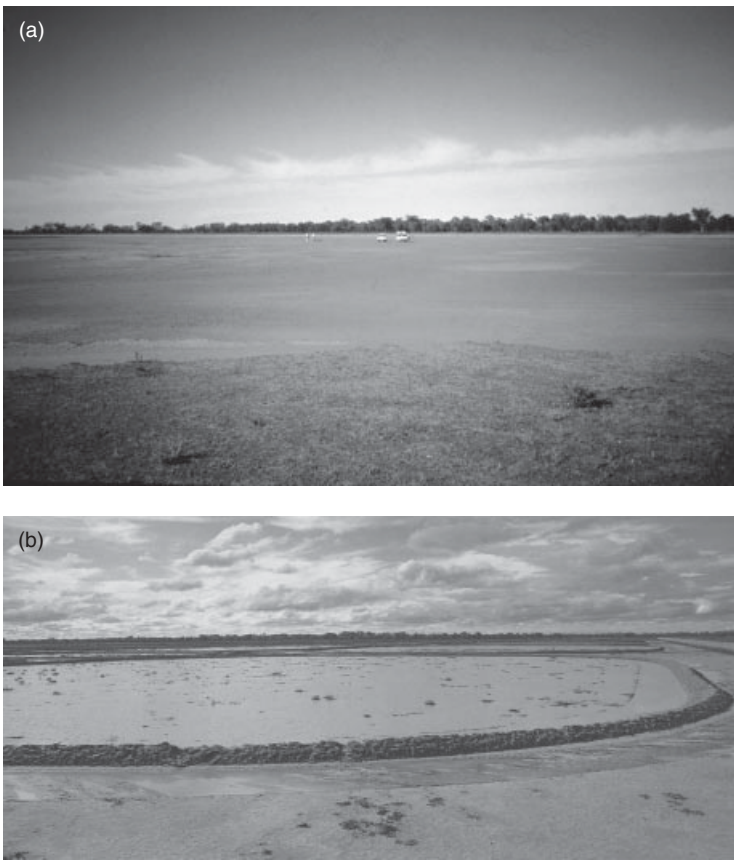


Figure 4.4 (a) A scalded landscape in semi-arid New South Wales, Australia (photograph courtesy of Anthony Ringrose-Voase), and (b) after implementing water-ponding technology (photograph courtesy of Ray Thompson.)

Box 4.3 Fixing landscape processes: mulching an eroded slope

A landscape-scale restoration technology commonly applied around the world is to cover reformed slopes, such as on rehabilitated mine sites, with coarse, rocky materials to protect these slopes from erosion, at least until vegetation establishes to provide cover. In many cases, these rocky materials fail to adequately protect slopes, which develop erosion rills (Figure 4.5).

In one such case in semi-arid New South Wales, Australia, early monitoring revealed that erosion rills were developing on a rehabilitated tailings dam wall. A project was undertaken by a student at the Australian National University to intervene and fix this problem before rills eroded into gullies (Summerfield 2006). A series of soil-slaking and dispersion tests was carried out on slope materials to determine the potential for further erosion. The soil was found to readily slake, which means that natural soil aggregates broke down into micro-aggregates when rapidly immersed in rainwater. However, dispersion (clay particles in aggregates being released into the water as a cloud) was minimal. This implied that a protective cover on the slope would counter the erosive effects of raindrops and intercept overland flows to capture sediments.

A denser cover of rocks might suffice, but a self-replacing organic mulch or plant cover would be far less expensive, and sustainable. Meadow hay, which was locally abundant in round bales, was rolled out across the slope in long lines, and subsequent monitoring found that sediment was being effectively trapped by the hay. Erosion was immediately halted and germination of seeds in the hay grew into a protective covering. Prompt monitoring of the initial landform confirmed a simple and inexpensive fix to the restoration problem.

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Figure 4.5 Erosion rills developing on a slope on a recently rehabilitated mine site. (Photograph by David Tongway.)

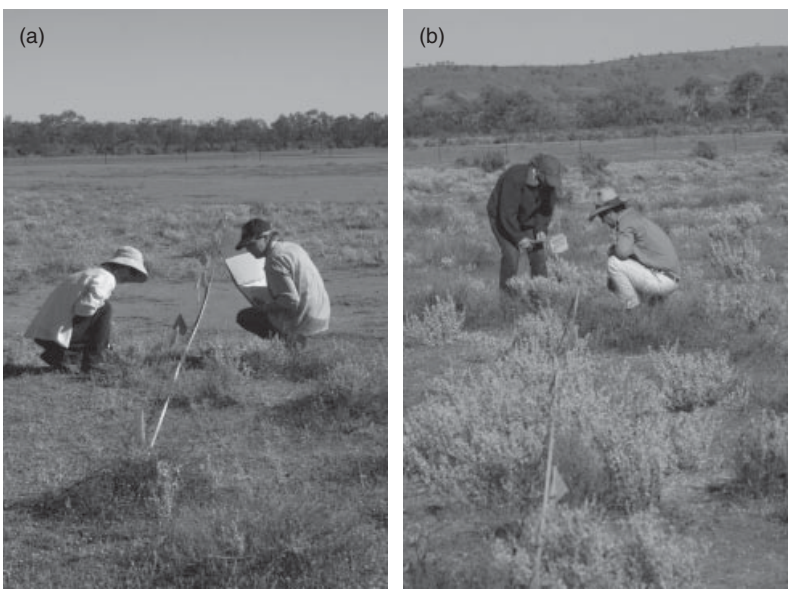


Figure 4.6 Land managers measuring perennial vegetation cover in an arid environment near Broken Hill in far western New South Wales in Australia: (a) a disturbed site with large patches of bare soil, where the restoration treatment was to simply remove domestic livestock and (b) a nearby reference site with high protective cover species. (Photographs by David Tongway.)

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Table 4.1 Landscape Function Analysis Indicators for assessing biophysical processes affecting landscape functions such as retaining vital resources (water, soil) and providing goods and services (food, materials, clean water). Numbers in brackets relate to processes numbered in Figure 4.2.

Indicator type	Indicator name/ description	Process assessed
Landscape organization	Location and size of patches that accumulate resources (litter, soil) along a gradsect*	Capacity of a landscape to capture resources such as by infiltrating water (1) and reducing runoff (2a) triggered by rainfall events
	Location and size of bare interpatches that lose resources along a gradsect	Potential for landscapes to lose resources such as water (2a) and soil (2b) during rainfall and wind storm events
Soil surface condition**	Rainsplash protection	Soil particle displacement and physical crusts formation by rain drop action, restricting water infiltration (1 and 4b)
	Perennial vegetation cover	Estimates the below-ground biomass available for decomposition (3 and 4a)
	Plant litter: amount and degree of decomposition	Soil development and nutrient cycling mediated by litter decomposition (3 and 4a)
	Cryptogam cover	Role of cryptogams in stabilizing the soil surface, preventing erosion (2a and 4a)
	Soil crust brokenness	Nature of soil physical crust affecting surface infiltration (1) and stability (2)
	Soil erosion: type and severity	Identifies the form and estimates the rate of soil loss (2b)
	Sediment deposition	Estimates the type (soil, litter) and amount of run-on material being deposited on site (1)
	Surface roughness	Degree of surface roughness to slow flows and retain mobile resources (1 and 4b)
	Soil surface dry coherence	Evaluates the resistant of the soil surface to physical disturbances (2 and 4a)
	Soil surface wet coherence (Slake test)	Estimates the cohesion (stability) of soil fragments during rain events (2 and 4a)
	Surface soil particle size distribution (Texture)	Role of surface soil texture on initial water infiltration rate (1)
Ephemeral drainage line stability***	Slope steepness	Potential for high energy overland flows to erode slopes and ephemeral drainage lines (1 and 2b)
	Slope surface protection	Amount of rock and vegetation cover regulating runoff into a drainage line (1)
	Drainage line wall vegetation	Amount of vegetation protecting drainage line walls from erosion (1 and 2b)
	Drainage line floor vegetation	Amount of vegetation protecting floors (channel beds) from erosion (2b)
	Drainage line cross-section shape (profile)	Evaluates the degree of active erosion (caving, fluting, mass wasting) on walls (2b)
	Drainage line longitudinal-section (profile)	The effect of strength of downstream flows to create linear drainage lines (1 and 2b)
	Drainage line wall erodability	The intrinsic susceptibility of exposed drainage line wall materials to erosion (2b)
	Drainage line floor erodability	The potential for drainage line floors (channel beds) to incise further (2b)

Continued

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Table 4.1 *Continued*

Indicator type	Indicator name/ description	Process assessed
Vegetation structure	Vegetation density and size	Estimates the potential role of vegetation to provide positive feedbacks (1, 4a and 4b)
	Vegetation composition	Evaluates the role of different life-forms and species on positive feedbacks (4a and 4b)
	Vegetation vertical profile	The potential for vegetation to ameliorate water and wind erosion at ground level (2b)
	Habitat complexity	Estimates the potential for the restored landscape to provide habitats for fauna (4b).

*A gradsect is a transect oriented along a gradient such as down a slope.
**The eleven indicators in this group are combined into three synthetic indices: stability (surface resistance to erosion), infiltration (capacity of surfaces to infiltrate water), and nutrient cycling (potential for soils to cycle nutrients).
***The eight indicators in this group are used to calculate an overall index of ephemeral drainage line stability or 'health' in sections or zones down the drainage line.

useful for tabulating and summarizing indicator data. These explanations give specific advice about the scale (site, patch) at which each indicator is assessed.

To further evaluate landscape-scale restoration progress (Figure 4.1, step 5b), data reflecting the initial dysfunctional state, as well as from appropriately selected reference sites, provide a useful framework for assessing the restoration trend. Reference sites do not have to be exact physical and biological replicas for the restoration sites, but ideally should have similar characteristics, such as slope and surface materials, so that surface processes are comparable (see Chapter 22). When the monitoring system is correctly deployed, data can be compared between restoration and reference sites almost immediately, so that differences between them can be compared.

To evaluate progress, restorationists can graph their monitoring data using an indicator (or a synthetic index combining indicators) selected to reflect biophysical processes of interest, for example, the potential of the developing soils on a restored site to cycle nutrients (Figure 4.7a). The *nutrient cycling index* combines a number of indicators observed in the field, but it largely reflects assessments on the amount and state of decomposition of plant litter. However, the nutrient cycling index also has broader biological implications because it implies the establishment of an effective suite of soil biota (Oades 1984, 1993; Lavelle 1997). Note that in this example (hypothetical, but based on data known to be typical of restored sites; Tongway & Ludwig 2011), the progressive trend (curve) measured over six time periods is S-shaped and this trend line is clearly towards the value expected from a reference site.

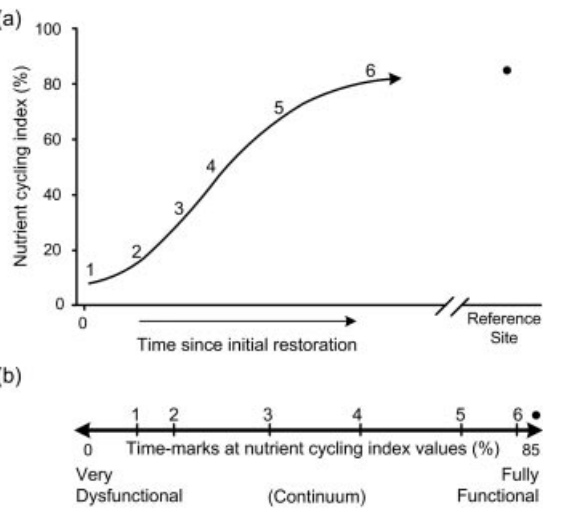


Figure 4.7 Examples of two ways to represent the ecological development of a restored site: (a) by graphing values for the nutrient cycling index over six time periods (starting at time zero) relative to the value measured on a reference site, and (b) by plotting the six values along a line representing a continuum of landscape functionality.

An alternative form of graph to emphasize restoration progress along a gradient of landscape functional-

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ity is to plot monitoring data on a line representing a continuum from a very dysfunctional to a fully functional landscape (Figure 4.7b). In this case, the fully functional end of the continuum is represented by data from a reference site, where the nutrient cycling index value was 85%.

These two graphs, referred to as 'time-traces' and 'T-mark continuums' (Bastin *et al.* 2010), provide restorationists with information they need to assess whether nutrient cycling, an important biological process, is progressing. The time scale selected should reflect the dynamics of the response, and may vary from months to years to even decades. Such graphs also provide an answer to the question: 'Trends OK?' (Figure 4.1), and help restorationists answer the bigger question: 'Goals achieved?'

In addition to restoration trends expressed by data, restorationists can also evaluate general types of monitoring information to confirm whether their goals are being achieved. For example, they can look for critical milestones such as the time at which vegetation on the restoration site begins to provide useful **goods and services** (e.g. clean water from a restored watershed). Clean water will be produced when soils on the landscape become resistant to erosion because organic matter is effectively bonding soil particles. Organisms that bind soil particles by processing finely divided organic matter also provide long-lived structures in the soil which increase its permeability to water and to gas exchange; these biological processes indicate 'soil health'. There are no simple and rapid measurements for such very fine-scaled processes, but by simply examining the nature of litter incorporation into the soil (physical burial) and its decomposition and humification (Figure 4.8), restorationists obtain a simple surrogate (indicator) for these complex biological processes.



Figure 4.8 Surface litter being decomposed, humified (dark band) and incorporated into soil on a restored site in a temperate woodland in south-eastern Australia. The Australian 50-cent coin is 3.3 cm in diameter. (Photograph by David Tongway.)

4.3 CONCLUDING REMARKS

In this chapter, we emphasized how disturbances affected landscape and ecosystem processes related to water (infiltration, runoff, run-on and erosion). We did this because of the 'primacy of water' dictum for ecosystems (Noy-Meir 1973). This dictum implies that if adequate capture of rainfall is not being achieved, landscape processes related to water retention (obstructing runoff, increasing infiltration) need to be urgently improved (e.g. a higher cover of vegetation). But, our approach extends to other limiting resources, such as building reserves of mineral nutrients and organic carbon in the topsoil. An initial landscape analysis, therefore, needs to focus on how effective all system processes are functioning and how they have been affected by disturbances.

We often find that restorationists are too ambitious in setting their initial goals. They enthusiastically specify outcomes that are not possible given the timeframe and financial resources available. For example, returning an open-cut coal mine to be like the premining landscape and used in the same way as it was previously, is usually an impossible goal because of the degree of disturbance and cost of restoration. After a thorough landscape analysis, the goals should be re-expressed in terms of where progress towards achieving them can be monitored and assessed with reliability (see discussion on sequential references in Chapters 1 and 22 in this regard). At all times we need to recall that we are dealing with complex and dynamic landscape systems, so that it may well be counterproductive to precisely define long-term goals at the outset; for example, failing to reach a specified plant density (stems per hectare) by a small margin should not mean that the restoration has failed.

The planning and implementation approach we described in this chapter provide a bridge between the hard reality of successfully restoring landscapes given limited financial resources and the critical need for landscapes to provide **goods and services** such as

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food, fibre, fuel, fresh water and timber; based on renewed and augmented stocks of what ecological economists call **natural capital** (Aronson *et al.* 2007a; Chapter 22). Successfully restoring, or reintegrating, landscapes to benefit society by building natural capital is also important in terms of the development of the dignity and self-esteem of present and future generations (Blignaut *et al.* 2007). Restoring natural capital also needs to address how costs and benefits are partitioned within society (Farley & Brown Gaddis 2007). Here we have described a simple planning procedure and a set of low-cost tools (Landscape Function Analysis indicators) that can be readily implemented in a restoration project. This is ideal for many local landscape restoration projects because it does not necessarily need big support from government or other agencies and funding organizations.

New principles in landscape and restoration ecology, such as those articulated by Turner *et al.* (2001) and Clewell and Aronson (2007), and stepwise procedures, such as those described in this chapter and by Tongway and Ludwig (2011), now permit rapid but efficient ecological analyses of important questions on how to effectively restore or rehabilitate and monitor landscape processes and functions. On reflection, we are reminded of a quotation attributed to J.W. Tukey, the great statistician: 'Far better an approximate answer to the right question, which is often vague, than the exact answer to the wrong question, which can always be made precise' (1962, 13).

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Part 2

Ecological Foundations

Restoration Ecology: The New Frontier, Second Edition. Edited by Jelte van Andel, James Aronson.
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EDITORS' INTRODUCTION

Why do we include a section on ecological foundations in a book on the eminently *applied* field of science called restoration ecology? Many readers, especially students who use this book while following a university course in restoration ecology, will already have good grounding in the basics of ecology, and may even still have their ecology textbooks available. There are, however, several reasons not just to refer to textbooks in a general way, but rather to provide our own overview. Most importantly, the editors and the authors of the four chapters in this part of the book – as scientists interested in, or actually doing, research within the context of 'live' ecological restoration projects – do not consider it fair to just leave the integration of fundamental theories and knowledge to the students. Rather, we shall actively and explicitly consider the usefulness and applicability of current ecological paradigms, hypotheses, theories, models and results from field experiments to applied ecology in general and to restoration ecology in particular.

Recall from Chapter 1 that applied ecology is ecological research that informs management practice, or in other words helps society and professionals make the right decisions on management. But, in a rapidly changing climate – in all senses of that word – the 'right decision' and the 'right thing' in ethical, legal and indeed scientific terms may change rapidly as well. In this part, therefore, the authors highlight and illustrate a selection of the fundamental topics they consider essential for students who aim at a career in ecological restoration, either as scientists or as practitioners in land, resources or natural area management. They also reflect on the applicability of theories and models to the practice of ecological restoration. For example, the theory on 'alternative stable states' of an ecosystem has been helpful to explain phenomena that earlier were not understood. Its applicability to ecological restoration is being actively explored by many, and it has triggered research on early warning indicators of sudden changes, not only in ecosystems but also in socio-ecological systems.

As this book is also meant to be useful to professionals and others already doing ecological restoration, what can those readers find of interest in this part of the book? Some may feel the scientists don't understand what really goes on 'in the field' or that what goes on in academia can ever be relevant to professional practice. Yet we argue that only if there is an active interest and mutual respect from both sides, will the interaction between 'science' and 'practice' work well. Not only is there a challenge for scientists to make theories applicable – and readily understandable to general readers – but also serious practitioners should undertake the task to explore the natural (and social) sciences for new insights and theories that might help them find solutions for, or at least strategies for addressing, practical problems. Conversely, as many scientists have noted, projects of ecological restoration may identify gaps in scientific knowledge, and theories about ecosystems may be falsified or confirmed only by results from restoration projects. Therefore, joint projects are the best sources of fruitful and interactive developments. Borrowing a phrase from Chapter 1, again, this is where 'societally contextualized science' converges with science-based management.

To line up with existing textbooks on ecology, especially the ones we like most, and thereby facilitating further background reading, we organized the chapters according to the by-now classic hierachy of organization – landscape, ecosystems, biotic communities and species populations. Later, in the various chapters of Part 3, we aim at integrating all this knowledge, across a full gamut of biomes and ecosystem types, with frequent cross-references to the chapters in this second part of the book. For example, the notion of habitat fragmentation is a field where landscape ecologists and population ecologists meet, with a common interest in the patches in the landscape that are home to metapopulations. Similarly, interactions among populations of different species in a community may have cascading effects far beyond the interaction per se, either within or outside the ecosystem under investigation. As compared to the first edition of this book, much more attention is here paid to the genetics of populations and its importance as a field of knowledge in projects of reintroductions.

Overall, our impression – and that of several other recent authors – of the state of the interface between restoration ecology and ecological restoration is that the development of scientific theory and the development of the practice of ecological restoration are far too often independent. We applaud initiatives at whatever scale to make joint efforts, involving academic researchers, teachers and students on the one hand, and people working in the 'real world' on the other. We hope, by the way, that our book may help close the gap a tiny bit. Onward now with Part 2.

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Chapter 5

LANDSCAPE ECOLOGY

Rudy van Diggelen, Richard J. Hobbs and *Ladislav Miko*

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5.1 INTRODUCTION

Not so long ago, ecological restoration was considered to be mainly a site-level activity where certain measures were taken to reverse an unwanted situation or unwanted developments. However, it is becoming increasingly clear that ecosystems do not function independently from their surroundings and that spatial relations matter a great deal (Hobbs & Harris 2001; Thompson 2011). In other words, restoration ecology and landscape ecology are growing closer together (see also Chapter 4). One example is the use of the theory of *island biogeography* (MacArthur & Wilson 1967) in reserve design and restoration planning. Another example is the use of *ecohydrological knowledge* (Succow 1982; Grootjans *et al*. 1996; Chapter 16), to assess wetland functioning in relation to landscape water flow paths. Hydrological manipulation in one particular area may cause disturbance in another, sometimes distant, area and can affect restoration perspectives significantly (van Diggelen *et al*. 1994). The same is true for the impacts and treatment of airborne pollution (Bobbink *et al*. 2010). Insights in spatial relations are therefore essential when evaluating the restoration perspectives of degraded sites.

The present chapter explores the links between landscape ecology and restoration perspectives, with a focus on flows between landscape elements, landscape alteration and *landscape-scale restoration*. It starts by defining a landscape and describing the relationships between scale, pattern and connectivity. These all have a large effect on the 'percolation' of abiotic agents and all kinds of biota through a landscape, and changes in one or more of these features affect both community composition and ecosystem functioning. Human activities have significantly altered landscape constellation, resulting in increasingly fragmented and impoverished landscapes. Restoration at the landscape scale is, therefore, essential to stop further degradation and instead improve conditions.

5.2 CONCEPTS: THE LANDSCAPE AS A SPATIAL MATRIX

As noted earlier in this book, clear definitions of basic terms are of utmost importance to facilitate communication and consensus-building, especially when interdisciplinary fields like landscape ecology and restoration ecology are merging. Such a process may bring scientists from backgrounds as diverse as ecology, soil science, geography, economy, history, the social sciences and more, in contact with non-academic professionals and practitioners who have an entirely different way of thinking. Without clear language, such encounters will produce a tower of Babel, and nothing more. In this section, we will introduce and define some of the basic concepts and terms of landscape ecology, especially those that are most relevant for restoration.

5.2.1 Landscape

The scientific concept of landscape has its roots in central Europe and was mainly developed by German scientists (Troll 1939; Schmitthüsen 1963). At that time the concept seemed clear and was exclusively viewed from a human perspective. A typical 'Landschaft' was many square kilometres in size and included several villages, farms and so on. For those researchers there was no doubt that cultural elements should be included in the concept. Later work, especially in less densely populated areas, did not automatically assume that a landscape should be viewed at the human level and much less emphasis was put on the various cultural aspects. As a consequence the concept became increasingly vague and two subsequent analyses of papers in the journal *Landscape Ecology,* by Wiens (1992) and Golley (1995), showed no clear trend in parameters such as scale of research, level of organization or subjects of study. The only elements the papers had in common were that they were all concerned with spatial relations and they were all published in *Landscape Ecology*! In the present chapter, in view of much confusion about the term 'landscape' (see also Chapter 2), we do not adopt any exisiting definition, but rather define a **landscape** very simply as 'a spatial matrix in which interactions of biotic and nonbiotic elements take place'. Intentionally, we not include any scale in this definition, and the result may seem to refer to 'habitat', rather than 'landscape'. Indeed, there is often confusion between the two terms. While geographers and spatial planners are concerned with spatial matrices and spatial relationships and talk about a 'landscape' that typically has the size of a few square kilometers, biologists and nature conservationists tend to focus on organisms and their use of a given piece of the earth. To identify that piece of the earth, they will

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use the term 'habitat' but sometimes also 'landscape'; with a variable spatial scale depending on the organisms under study. To avoid confusion, in this chapter, we use **habitat** to explicitly address the 'value' of a certain area for a (group of) species, and **landscape** to describe a spatial matrix, which we consider as something more neutral and/or general. Moreover, in section 5.4, we will differentiate between intact, variegated, fragmented and relictual landscapes as defined by the extent of habitat destruction (McIntyre & Hobbs 1999), thus combining human- and organism-oriented views on the condition or status of a given landscape.

5.2.2 Scale

Scale is a central concept in landscape ecology, mainly because temporal and spatial scales are highly correlated. Small-scale processes tend to be more dynamic and less predictable than large-scale processes and are associated with fine-scale spatial structures. Different organisms operate at different scales and may perceive entirely different environments at the same spot. For example, experimental studies by Wiens (1976) showed that fine-scale spatial structures are highly relevant for beetle movement whereas migrating geese follow large-scale structures like coastlines, canals and similar (Green *et al*. 2002). At first sight this may seem trivial, but in the context of restoration it implies that the scales at which target organisms operate and at which relevant processes occur should be identified explicitly. For example, restoring an ecosystem to benefit or rescue a marsh bird community, might be achieved by flooding 5 ha of degraded wetland, whereas it might be necessary to restructure a whole catchment and reactivate a groundwater system to restore an ecosystem with specific groundwater-fed plant communities in the same site.

5.2.3 Patches and patterns

All landscapes are heterogeneous. Parts of a given landscape that are considered to be uniform are called *patches* or *ecotopes*. As noted, the scale of a patch depends entirely on the perspective of the observer. A part of a landscape that is a patch for an elephant can be a highly diverse region for a butterfly. A group of patches constitutes a *pattern*. Topography (e.g. elevation and slope), natural disturbances (e.g. due to fire, flooding or storms) and, increasingly, human activities (e.g. farming, roads and buildings) are the principal causes of landscape pattern.

There is often a remarkable similarity in patterns, both over larger areas and over larger timescales. If only one major environmental factor determines the pattern, this may lead to the development of *zonation*, perpendicular to direction or orientation of this factor. Typical examples of factors that lead to vegetation zonation include altitudinal gradients in mountainous areas and hydrological gradients in river valleys (Figure 5.1), but also gradients in landuse intensity in the past. Even in many cases where more than one factor affects the distribution of patterns, relatively simple zonations can occur, because many factors coincide to a high degree. For instance, land use was (and in many places still is) highly correlated to natural productivity and ease of cultivation. In mountainous areas, most villages are situated in the intermontane valleys where both climate and soil fertility are most favourable for agriculture. In lowlands on the other hand, human occupation started along the edges of river valleys in close proximity to fertile floodplains, in places where the risk of flooding was considered slight. In both cases, whatever animal dung was available was used to enhance the productivity of already productive sites whereas infertile sites such as high mountain areas or dry sandy sites were not fertilized at all. Human activities thus extended pre-existing productivity gradients, thereby enabling increased niche differentiation and biodiversity.

5.2.4 Borders and corridors

Adjacent patches are separated by borders**.** On a map such borders are infinitively thin and this suggests that patches can be delineated sharply, but in practice there are always transition zones ('ecotones' or 'boundaries'; e.g. Forman 1997). These may differ in width and often contain specific species assemblages, highly deviating from communities found in the interior of a patch. Boundaries are not absolute barriers but may be relatively sharp or fuzzy, and possess higher or lower resistance to flows between landscape elements (section 5.3), thereby determining and affecting connectivity in a landscape.

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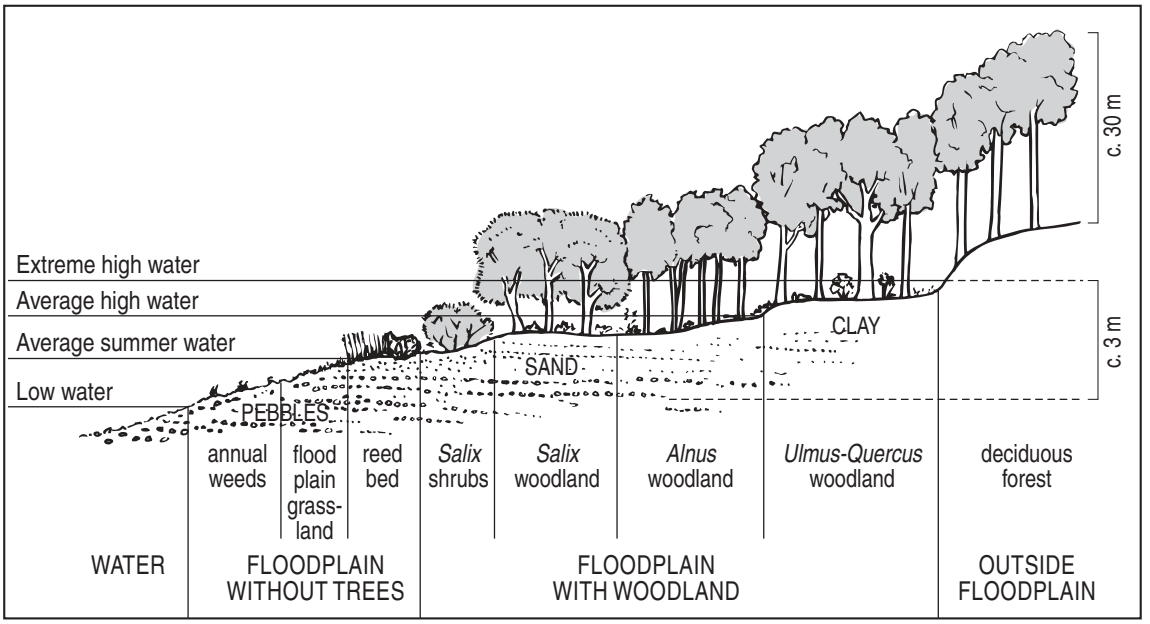


Figure 5.1 Vegetation zonation along rivers in relation to flooding frequency. (From Ellenberg 1986. Reproduced by permission of Verlag Eugen Ulmer.)

Connectivity and its effects on flows of matter and organisms have become a major research theme in landscape ecology. The relation with landscape pattern is often very complex and may range from broad-scale flows that are hardly related to any landscape features (e.g. bird migration at higher altitudes) to very localized flows that are completely determined by landscape structure (e.g. seed transport by flowing water). Model simulations show that in purely 'random' landscapes, circa 60% of the space must be covered by suitable habitat patches in order to ensure that organisms can disperse from one side of the area to the other without having to leave the habitat; that is, be part of a functioning metapopulation. In real landscapes, this percentage can be much lower, due to the presence of *corridors*, relatively narrow strips of suitable habitat that connect patches. Simulations (e.g. Gardner *et al.* 2007) show that presence or absence of corridors makes a dramatic difference for the 'percolation' of organisms within a landscape. One could say that corridors function as communication channels within the landscape. However elegant this concept may be, the recognition of corridors in reality is not easy and may differ from one species to another. Hedgerows may be corridors for beetles, but for ospreys the river that flows through a hedgerow landscape may be an appropriate corridor.

5.3 FLOWS BETWEEN LANDSCAPE ELEMENTS

Even in the second half of the twentieth century, most landscape ecologists had a rather static view of their subject. Landscapes were described and classified on the basis of certain parameters which might refer to exchange processes, but explicit incorporation of flows of matter and movement of organisms was not normally done. This changed in the last few decades of the twentieth century, when it became increasingly clear that spatial arrangement is a fundamental feature of terrestrial landscapes. Ecosystems in sites with similar abiotic conditions, but differing in spatial arrangement, may develop in entirely different ways because of differences in the inflow or outflow of resources, and/or different immigration rates of preys and competitors linked to spatial organization.

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5.3.1 Transport of matter

By wind

Large quantities of material are transported by air flows, especially along the edges of continents where winds are generally stronger than in more interior areas. Under natural conditions this is a major mechanism for the exchange of chloride between sea and inland areas. Rainwater analyses from different sites showed a decrease in Cl^- content from over 100 to less than 1 mg l^{-1} between coast and inland (Figure 5.2). In more intensively human-affected landscapes air transport of pollutants has become an important issue. Examples include the transport of sulphur dioxide and mineral nitrogen from industrial and agricultural sources, and the transport of radioactive gases. Distances covered by wind transport can be huge. Holland *et al.* (2005) estimated that part of the atmospheric N-deposition in western Europe may originate from sources in the United States, a distance of over 5000 km! Also the amount of material can be large. The deposition of air-borne nitrogen has at least been doubled or tripled in large parts of Europe from natural background values of circa 350 eq. N $ha^{-1}yr^{-1}$ and may now make up more than 25% of the available nitrogen in the system (Verhagen & van Diggelen 2006).

By water

Only a very small portion of all the water on the planet is found in the atmosphere and on the continents (Table 5.1), but it is this part that most affects landscape structure and functioning. Net exchange (precipitation minus evaporation) between atmosphere and continents amounts to $37 \times 10^9 m^3 yr^{-1}$. It is distributed very unevenly over the Earth but in most areas this water flows to seas and oceans, either through rivers and lakes as surface water or through the soil as groundwater. Eventually, also groundwater flows into the surface-water system but upwelling groundwater may in the meantime sustain **wetlands** that are outside the reach of surface water. Spring mires or groundwater-fed fen meadows high above the surface water are typical examples. The size of groundwater systems differs greatly from catchment to catchment and depends on both the topography and the permeability of geological strata, but most systems are at least several square kilometres in size. Toth (1963) developed the concept of nested systems (Figure 5.3) where small flow systems are embraced by larger systems. These systems may differ considerably, not only in flow rates but also – depending on the chemical composition of the soil strata – in water chemistry (see also Chapter 16).

Rivers transport large amounts of solutes, sediments and sometimes biomass. The latter two are deposited on floodplains during flooding periods and this causes natural fertilization in otherwise nutrient-poor landscapes. Five millennia ago, the agriculture in Egypt was based on regular flooding by the river Nile, and this could sustain a large human population in an arid environment that was otherwise very hostile.

Both surface and groundwater also transport dissolved substances such as nutrients (soluble compounds of N, P and K) and other ions. The most common ones are called major ions (Hem 1959) and they

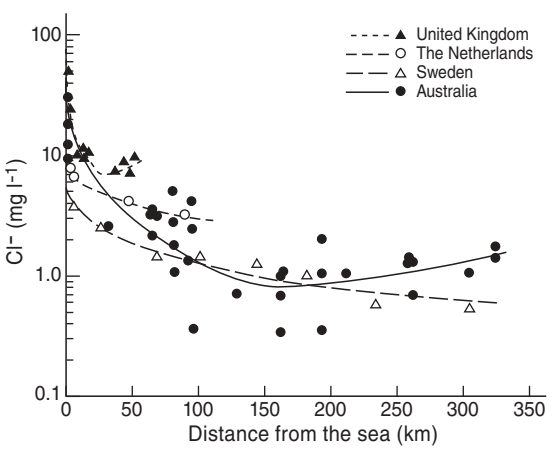


Figure 5.2 Chloride concentration in precipitation in relation to distance from the coast. (FromVoigt 1980.)

Table 5.1 Freshwater reservoirs on the land.

Reservoir	Mass (10^{15} kg)	Proportion (%)
Ice sheets	26200	80.0
Groundwater	6200	19.0
Lakes, fresh water	126	0.4
Lake Baikal	22	
Great Lakes, North America	32	
East African lakes	36	
Lakes, brackish water	105	0.4
Caspian Sea	80	
Soil, unsaturated zone	150	0.5
Rivers	2	

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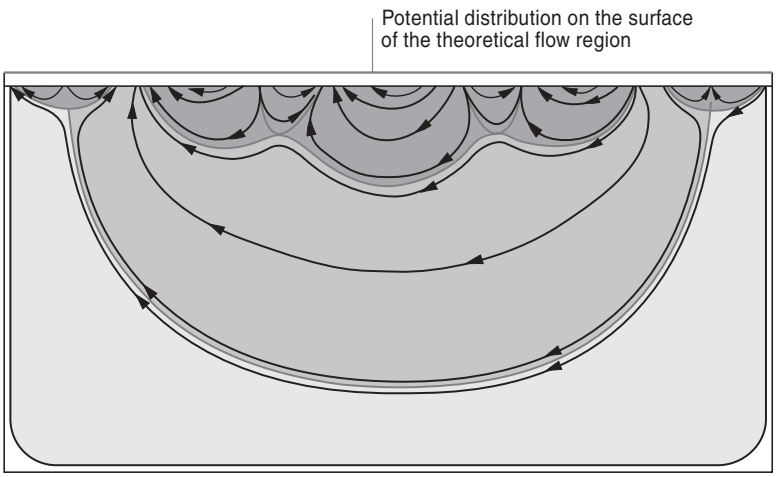


Figure 5.3 Groundwater flow systems in a homogeneous subsoil. Higher order systems lie nested within lower order systems. (From Toth 1963. Reproduced by permission of American Geophysical Union.)

constitute up to 99% of all solutes in water. The most common cations are Na^+, K^+, Mg^{2+} and Ca^{2+} whereas HCO_3^-, Cl^- and SO_4^{2-} are the most important anions. The chemical composition of ground- and surface water differs from site to site and can be used as a 'fingerprint' to trace its origin (Stuyfzand 1989; Komor 1994). Groundwater shows a very typical evolution in water composition, especially in areas with thick layers of mineral-poor sand (Figure 5.4). Both rainwater and groundwater of upper layers are generally very poor in dissolved solutes. As it penetrates deeper this water reaches layers where soluble minerals have not been washed out and these go into solution and increase the mineral load. Quantitatively the most important minerals are several Ca^{2+} compounds, especially $CaCO_3$ and $CaSO_4$, but other minerals can also be found. If groundwater flows from different systems come to the surface alongside each other (see Figure 5.3), this can result in a steep hydrochemical gradient.

By human activities

Apart from sometimes quite significant human impact on natural flows, huge amounts of matter are also intentionally transported by humans, especially in connection to agriculture. At present, in quantitative terms the most important flows are transport of water for irrigation and of fertilizer to increase crop production in less fertile areas. Water transport is practised mainly in warmer climates and consists of a redistribution of water from areas with sufficient precipitation, for example mountains, to sites with deficits. Examples can be found in the south-western United States, where water from the Colorado River is used for irrigation so intensively that the river dries up completely before it reaches the Salton Sea. In recent times there is also a development towards transporting water to areas where there are only temporal water shortages (i.e. during the dry season). For example, in the Netherlands huge canals enable the transport of water from the River Rhine to all corners of the country in order to optimize conditions for crop growth throughout the year. The impact this may have on the rearrangement of aquatic plant and animal communities is still largely unexplored (see also Chapter 17).

Not only a redistribution of water but also the use of fertilizers has enabled an enormous increase in crop production in previously marginal areas. The yearly nitrogen surplus on agricultural fields in Flanders, for instance, steadily increased from an estimated 15–30 kg $ha^{-1}yr^{-1}$ in 1900 to 329 kg $ha^{-1}yr^{-1}$ in 1990 and then decreased again to 144 kg $ha^{-1}yr^{-1}$ in 2006 (see website in the appendix at the end of this chapter). In many countries of the world a similar trend can be witnessed and this has resulted in an average productivity increase in commercial crops. For instance, for the European Union there has been a yearly growth of 1.9% $ha^{-1}yr^{-1}$ between 1950 and 1991. The effects of these developments are not restricted to agricultural areas; the yearly nitrogen load from agricultural sources into the

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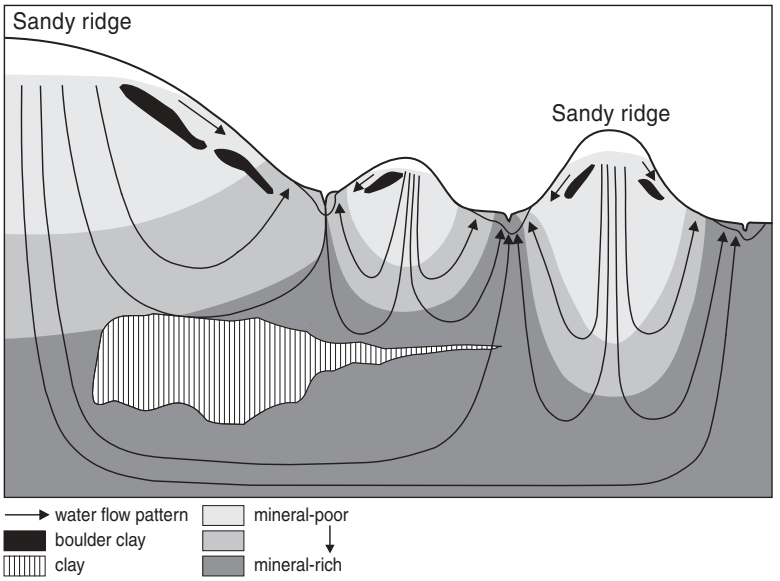


Figure 5.4 Changes in groundwater composition along its way through the subsoil. Mineral-poor rainwater infiltrates the subsoil and takes up solutes along the way. Arrows indicate direction of water flow; darkness increases with mineral content of the groundwater.

Rhine River at the German–Dutch border, for example, has increased from circa 100×10^6 kg of N in the period 1954–1957 to more than 150×10^6 kg of N in the period 1993–1995 (Behrendt 1997).

In densely populated regions, deliberate transport of matter is probably quantitatively more important than natural flows. As a result, natural differences between landscapes fade away and the boundaries between different areas of countryside become increasingly blurred. Broadly stated, organisms that are adapted to moist and eutrophic conditions are stimulated, whereas other types of organism are hampered. This trend is especially pronounced in easily cultivated – that is, generally flat – areas. Mountainous regions are much more difficult to cultivate, and **geomorphology**-based differences between landscapes are much better preserved there.

5.3.2 Dispersal of organisms

By airflows

In flat, homogeneous landscapes, wind transport of organisms is diffuse and little affected by existing corridors. Despite a general assumption that wind is an important long-range dispersal vector for plants, the available evidence suggests that long-distance dispersal by wind is uncommon in most areas, and occurs only under exceptional conditions (Nathan 2006). Examples include thermal updrafts generated by large fires (Whelan 1986) or extremely strong winds such as cyclones (Visher 1925). Under more average conditions seeds are not lifted up by the wind and the distances travelled depend on the horizontal wind speed and the characteristic speed of fall of the species (terminal velocity). Studies in wind tunnels (van Dorp *et al.* 1996; Soons & Bullock 2008), modelling approaches (Bullock & Clarke 2000) and field studies (Verkaar 1990; Coulson *et al.* 2001) found that under such conditions only a very small fraction of the seeds reached distances of more than 10–20 m from the parent plants. This fraction is larger in the case of species that produce large numbers of very light seeds and/or high above the surface of the ground, for example large marsh plants such as *Phragmites australis* and *Typha angustifolia* (Table 5.2) or trees. Species with extremely small seeds such as orchids, or those bearing spores, like mosses and ferns, have better prospects for long-distance dispersal by wind.

The importance of wind dispersal changes dramatically in more heterogeneous landscapes. Steep slopes and irregular warming of diverse surface materials enhance the importance of thermal updrafts for airflow.

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Table 5.2 Effectiveness of wind dispersal of some wetland species (R. van Diggelen, unpublished observations). Results were obtained with the simulation model of Jongejans and Schippers (1999) in a spatial context. Seed production was measured in the field, terminal velocity was measured in the laboratory under standard conditions (Askew *et al.* 1997) and height of release was taken from standard flora. The last column shows the size of the receptor area as a fraction of the source area of 576 m^2. A value of 1.00 means that the receiving area is as large as the source area.

Species	Seed production (seed m^{-2})	Terminal velocity ($m\,s^{-1}$)	Height of release	Source/area Receptor area
Agrostis stolonifera	25	1.64	57	0.2921
Anthoxanthum odoratum	2258	1.52	32	0.3357
Holcus lanatus	7383	1.68	60	2.2452
Lemna minor	—	—	—	0
Mentha aquatica	16296	2.18	55	0.5099
Phalaris arundinacea	2072	1.39	150	5.6288
Phragmites australis	18000	0.21	200	44.4788
Plantago lanceolata	1222	3.8	32	0.2032
Ranunculus acris	262	3.14	65	0.3862
Ranunculus repens	224	2.7	37	0.2599
Typha angustifolia	2600000	0.14	150	1443

Tackenberg *et al.* (2003) modelled seed dispersal of rare plant species that grew on small porphyritic hardrock outcrops in an otherwise intensively used agricultural landscape, illustrating that heat-induced air turbulence enables seed exchange between sites with distances of up to some hundreds of metres for many species despite a small size and a low number of seeds.

By water

Field studies showed that running waters contain large numbers of seeds and this suggests that they are a major dispersal vector for wetland plant species (Middleton 2000; Boedeltje *et al.* 2004; Soomers *et al.* 2011). Unlike dispersal by wind, water dispersal does not occur across whole landscapes but rather is only possible in relatively narrow corridors where it tends to be highly unidirectional (i.e. downstream). Laboratory measurements on seed buoyancy (Danvid & Nilsson 1997; van den Broek *et al.* 2005) showed that most seeds are capable of floating for many weeks, including seeds without clear morphological adaptations. Moreover, even seeds with a restricted floating capacity can travel large distances in running waters. Nilsson *et al.* (1991) calculated that only 2.5 days would be sufficient for seeds to cover a 230-km long river stretch in northern Sweden during the spring floods. Studies of riparian vegetation have indeed shown a large floristic similarity between upstream and downstream areas, which decreased slowly with distance (Tabacchi *et al.* 1990; Johansson *et al.* 1996). Tabacchi *et al.* (1990) found a sharp decrease in similarity only when the river merged with major side branches, suggesting that at such points 'propagule flows' of two or more areas with different **species pools** merge.

By animals and humans

With the exception of waterfowl (Vivian-Smith & Stiles 1994; Charalambidou & Santamarıa 2002) and fruit-eating birds (Handel 1997), animals are assumed to be of little importance for seed dispersal in most modern landscapes. This is in contrast to the past when **transhumance** was widely practised whereby livestock were moved overland from winter to summer areas, and vice versa, over distances hundreds of kilometres (Poschlod *et al.* 1996; Seifert & Fisher 2010). Also the activities of most wild animals are more restricted by roads and fences in the landscapes of today than in the past. Consequently, gene exchange of seed-bearing plants via animal vectors between (now isolated) nature reserves has decreased steeply (Mouissie 2004).

Humans have always played a role as a 'moving corridor' (Poschlod *et al.* 1996). Plants lack all morphological adaptations to dispersal by human beings, yet people have probably been the most effective long-distance dispersers since the Middle Ages (Sukopp 1972; Poschlod *et al.* 1996). Modern traffic networks facilitates rapid, long-distance dispersal, for example along motorways and railway lines (Tikka *et al.* 2001; Garnier *et al.* 2008). At the same time, the decreasing degree of agricultural

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activities in most nature reserves has probably led to less exchange with other areas (Seifert & Fisher 2010). The significance of humans for the dispersal of rare plants to such reserves is, therefore, likely to be very low except when a deliberate management scheme is set up to assure ongoing seed exchange.

5.4 LANDSCAPE ALTERATION

The concept of landscape **fragmentation** has greatly helped to clarify targets for conservation and restoration activities (see section 5.4.3), but it implies a very simplistic and not very realistic dichotomy: a landscape is either fragmented or not. McIntyre and Hobbs (1999) developed the idea somewhat by treating alterations of a landscape matrix as a continuum, ranging between 'not affected' and 'completely changed'. They distinguished four main classes of landscape alteration, based on the percentage of suitable habitat remaining: *intact*, *variegated*, *fragmented* and *relictual landscapes* (Figure 5.5). These categories differ in the amount of remaining habitat for whatever specific species may be of particular concern or interest, but there is also usually a clear correlation with other characteristics such as connectivity or degree of modification of the remaining habitat (Table 5.3). The present section will describe general trends in landscape alteration in the context of the abovementioned scheme. The advantage of using a more sophisticated framework over a simple fragmented versus unfragmented dichotomy is that it enables a more clear prioritization of conservation and restoration goals. For example, restoration is much less a priority in variegated landscapes, but maintenance of the quality of the matrix is important there to stop developments towards fragmentation. Restoring **connectivity** and improving the quality of the remaining habitat, on the other hand, should be the highest priorities in the case of relictual landscapes.

5.4.1 Intact landscapes

The actual geomorphologic structures of temperate zones of the northern hemisphere are mainly a result of erosion and sedimentation processes during the last glacial period. Glaciers and polar deserts were the

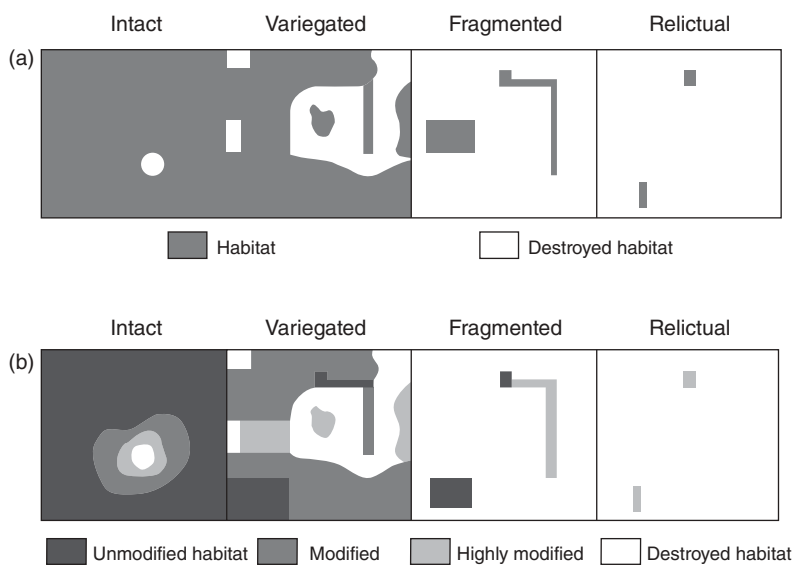


Figure 5.5 Four states of landscape alteration defined by degree of habitat destruction, as in Table 5.3, and modification of remaining habitat. (a) Four levels of habitat destruction, each characterized by a range of proportions of habitat destroyed. (b) Pattern of habitat modification overlying landscape patterns of habitat destruction depicted in (a). Although any combination of destruction and modification levels is theoretically possible, those considered to be typical of different destruction levels are illustrated. (Modified from McIntyre and Hobbs 1999.)

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Table 5.3 Four states of landscape alteration defined by degree of habitat destruction (after McIntyre & Hobbs 1999).

Level of alteration	Degree of destruction of habitat (% remaining)	Connectivity of remaining habitat	Degree of modification of remaining habitat	Pattern of modification of remaining habitat
Intact	Little or none (>90)	High	Generally low	Mosaic with gradients
Variegated	Moderate (60–90)	Generally high, but lower for species sensitive to habitat modification	Low to high	Mosaic that may have both gradients and abrupt boundaries
Fragmented	High (10–60)	Generally low, but varies with mobility of species and arrangement on landscape	Low to high	Gradients with fragments less evident
Relictual	Extreme (<10)	None	Generally highly modified	Generally uniform

dominant landforms and the climatic conditions were so harsh that hardly any organism could persist. Almost all species had to (re)colonize the released area during the following interglacial period. Delcourt and Delcourt (1983) have presented a detailed reconstruction of this process and showed that colonization rates differed significantly between species. It is assumed that this process is not yet complete, especially in the case of species with low colonization rates such as plants or low-mobility insects. The inhibition model of Connell and Slatyer (1977) predicts that under such conditions, 'priority effects' will lead to different species assemblages in otherwise similar ecosystems and such results are indeed found in the field (e.g. Urban & De Meester 2009; Klimkowska *et al.* 2010a). This implies, amongst other things, that the 'natural' or ideal **reference system** for a restoration project in a given type of landscape may differ from place to place.

Contrary to what is sometimes assumed, most intact landscapes have been subject to human impact, often for a considerable period; at least 5000–7000 years in north-western Europe and North America, 8000–13 000 years in the Mediterranean region, and at least 40 000 yr in Australia. Human densities were very low (<0.5 inhabitants per km^2) in the distant past, but in some cases human impacts still affected the landscape structure. Most prehistoric peoples lived as nomads and those who practised agriculture generally employed the slash-and-burn system whereby a certain area of woodland was burned down, used for a few years until the nutrients were depleted, and then left again in fallows for a long time. This human-initiated process led to a structured landscape of patches of different age since disturbance. Intact landscapes or landscapes structured by indigenous human communities dominated the scene in Europe until the first centuries CE and in North America and Australia until the arrival of European settlers. Nowadays they persist only in sparsely populated parts of tropical rain forests, in boreal woodlands in the cold parts of the northern hemisphere, or in hot and cold desert regions.

5.4.2 Variegated landscapes

The next, seminatural stage is associated with the development of a more sedentary form of agriculture. The settlements became fixed and human impact on landscapes increased. Uniform landscapes became more heterogeneous, and large-scale abiotic gradients were replaced by smaller gradients of human impact. This resulted in a local increase in biodiversity, through the creation of suitable patches for species that had a very limited distribution in intact landscapes (Sukopp & Trepl 1987). The landscape did become fragmented to some degree, but the connectivity between more or less affected patches was still very high. It is unlikely that these developments lead to problems for most organisms, except for large mammals. These might experience problems even at a low degree of fragmentation (Soulé & Terborgh 1999). Not surprisingly, large grazers such as auroch (*Bos primigenius*) or wisent (European bison, *Bison bonasus*) disappeared from Europe, although bison populations have recovered in some areas.

This process continued with time and human impact became ever more dominant. In certain areas humans had altered the structure of landscapes completely by

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the end of the Middle Ages (ca. 1500 CE), for example in England where most woodlands had been cut for fuel and people had to switch to peat for heating. Another example is the western part of the Netherlands and Belgium where people started to protect themselves against flooding by building dykes and creating polders from the fifteenth century onwards.

Notwithstanding the fact that the latter landscapes have very little overlap with earlier seminatural landscapes, both belong to the variegated type. In both cases, there is a large connectivity between the different types of landscape patches. Variegated landscapes were dominant in Europe until the beginning of the twentieth century but were much less common in North America or Australia. In the latter regions there was often a direct conversion from natural habitats into large-scale industrial agriculture, almost without any remnants of untouched habitat.

5.4.3 Fragmented landscapes

Developments in technology stood at the basis of the phase with industrial agriculture and led to landscape changes in rural areas at an ever-increasing speed and scale. Chemistry enabled the development of artificial fertilizer, and engineering sciences made large-scale mechanization possible. These developments became especially apparent after the Second World War, particularly in Europe where politicians feared famine and stimulated large-scale land reallotment programmes and other rationalization of agriculture. This process was accelerated further through the implementation of the Common Agricultural Policy in the European Community from the 1960s onwards.

Compared to variegated landscapes there is much less connectivity between patches, borders are much sharper and the ecological quality is much lower. Patches with a high ecological quality have become islands surrounded by a matrix of unsuitable habitat. Island theory (MacArthur & Wilson 1967) predicts that the probability of local extinction increases with a decreasing patch size and that the probability of recolonization decreases with increasing distance. Among conservation scientists today, the prevailing view is that this is also true for small patches of suitable habitat in otherwise unsuitable surroundings (Soulé & Simberloff 1986; Opdam *et al.* 2003). Though this hypothesis has never been proven, it is supported by the fact that small patches are generally poorer in species than larger ones (Rosenzweig 1995; Cook *et al.* 2002). What is clear is that exchanges of species between patches, at least in the case of organisms with little mobility, such as plants, have decreased significantly in recent decades, either because of ongoing **fragmentation** or because of the cessation of traditional management practices such as **transhumance** (Poschlod & Bonn 1998). Probably there is still some interchange between subpopulations but it is unknown whether this is sufficient to sustain a functioning **metapopulation** (Opdam 1991; Hanski 1999; see Chapter 7). Nevertheless, it is feared that present-day distribution patterns of many organisms are in fact spatially isolated relics of a former continuous population that has become fragmented. The danger is very real that many of these small populations will die out and that species will become locally extinct due to chance processes alone.

5.4.4 Relictual landscapes

When land use pressure increases further, most of the remaining patches with high ecological quality disappear and the ecological value of the landscape decreases further. The few remaining high-value patches are under high pressure. Most species are ubiquists, occurring everywhere, not only in intensively used patches but even in more natural sites. Land use in relictual landscapes is by definition not sustainable and – apart from threats to biodiversity – there are generally a range of environmental problems associated with it as well, such as groundwater pollution, salinization of the topsoil, peat subsidence and associated CO_2 emissions and soil erosion. Typical examples are found in densily populated urban areas (e.g. in north-western Europe), but also in areas that are optimal for intensive agricultural production such as the midwestern United States, parts of south-western Australia and collective farming areas in former communistic countries. Intensive land transformation in these areas leads to only small remnants of pre-existing ecosystems being retained in an otherwise completely modified matrix.

5.4.5 Effects of land use changes on abiotic conditions

Human-induced changes in landscape structure affect not only species exchange patterns but also abiotic flows. The building of dams and canals, as well as the straightening of river tracts, affect water flow rates and fluctuation patterns to a high degree. Sometimes this

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even results in a complete reversal of water flow direction. Such activities have a large impact on wetlands downstream. The straightening of the Upper Rhine along the French–German border has led to the loss of 87% of the characteristic floodplain woodland, on both the German and French sides.

Changes in groundwater flows are less obvious but can potentially also have major effects on landscapes. The most obvious effects occur when the water regime is changed. Lowered water tables during the dry season lead to increased mineralization of organic matter and hence increased nutrient availability. In low-productive wetlands, this results in a substantial increase of non-characteristic ruderal plants at the cost of typical species that are less competitive (Grootjans *et al.* 1985). Changes in water chemistry are more insidious but can have similarly large impacts. A groundwater abstraction facility does not necessarily lead to lowered water levels in a nearby groundwater-fed mire because surface water or rainwater may replace the groundwater. In the long run, however, the increased influence of nutrient-rich surface water (**eutrophication**) results in increased plant productivity, whereas a replacement with acidic rainwater leads to **acidification** of the top soil (van Diggelen *et al.* 1994). Both processes result in completely altered vegetation composition but it may take up to several decades before the effects are clearly visible or discernable. The relative importance of these processes depends to a high degree on the local situation.

5.5 LANDSCAPE-SCALE RESTORATION

Human impact on landscapes has been enormous, throughout the world, and has in most cases resulted in large biodiversity losses. To reverse further declines and especially to make ecosystems more robust against disturbances, it is unavoidable to enhance spatial relations (Grootjans *et al.* 1996; Hobbs & Norton 1996). This implies that restoration of complete landscapes gives the best chances for long-term survival of self-sustaining ecosystems.

Like any restoration programme, projects at the landscape scale consist of several phases. These are often derived from the concept of systematic conservation planning (Margules & Pressey 2000), but there are a few inherent differences as compared to 'classical' small-scale restoration projects. These differences arise from a much more explicit inclusion of **stakeholders** other than conservationists, and with scale differences, both in space and in time. In what follows, we explore these issues briefly.

5.5.1 Landscape-scale restoration as a process

Any restoration project should start with a definition of the problem and an analysis of its causes. At a landscape scale, there is hardly ever only one single problem with only one cause, but rather a multitude of problems triggered by a multitude of factors and kept going by a multitude of actors. Different stakeholders also tend to differ in their perceptions, and specifically, their choice of a reference to use as a yardstick to measure the degree of degradation and the effects of restoration activities against. Landscape actors such as farmers, tourists and conservationists may have entirely different views about what 'nature' is, or should be, ranging from production-oriented and arcadian landscapes to wilderness (Swart *et al.* 2001; see Chapter 1). Additionally, stakeholders may have conflicting commercial, political or legal interests leading to different preferences for alternative restoration options.

Another typical characteristic of landscape-scale restoration programmes is that there is much time needed to complete the actions. Larger programmes typically involve many years to even a few decades, and during that time actors may vanish or appear, public policies may change, budgets may increase or decrease and so on and as a result the final situation may deviate dramatically from the original plan. Planning and managing such processes in a changing world requires, on the one hand, clear priority setting to minimize risks of failure and disappointment, and, on the other hand, flexibility to use unexpected events and opportunities to maximize or optimize possibilities as the programme goes forward.

Numerous schemes for setting priorities have been developed, but there is not a universally agreed approach to this. Landscape-scale restoration in many cases still depends on actions taken at the individual patch scale. Deciding on priority actions depends on an initial assessment of within-patch conditions and a consideration of the landscape context. Correct diagnosis of what, if anything, is currently wrong is an essential first step. Further considerations include the degree of threat, the feasibility of the management required, the likelihood of it succeeding, and the relative value of the different patches or remnants being considered (Cramer & Hobbs 2002; Hobbs *et al.* 2003).

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Considering all these factors results in a matrix within which management categories can be recognized based on the degree of urgency and the level of intervention required. While such a scheme might seem logical, there are, in fact, endless complications involved in actually applying it. Considering more than one or a few threats at a time (e.g. excessive nitrogen input, or the presence of invasive alien species) quickly makes the assessment very complex. Assigning degrees of urgency and estimating likelihood of success are difficult, as is the assignment of value. Finally, designating some areas or actions as having higher priority than others immediately leads to there being 'winners' and 'losers'. In other words, consigning some areas to a low priority status inevitably has economic, social and political consequences, which may be unpalatable to the local community or portions thereof, and therefore untenable politically. Hence, it is essential to consider how to set priorities, but socially and politically tricky to do so effectively.

5.5.2 Perspectives

At a world scale, two opposite landscape development trends seem to be occurring simultaneously. On the one hand, all models predict a continuation of human population growth in the coming century, especially in developing countries. In combination with economic developments in the same countries, this implies increasing land use pressure there. Intact and variegated landscapes are likely to change into fragmented and relictual landscapes with associated ecological and biodiversity losses. The reverse trend seems to occur in developed countries. Here it is increasingly recognized that local conservation and restoration activities alone are not sufficient to safeguard biodiversity and that spatial connections are essential. Programmes such as the creation of the network of protected areas, Natura 2000, in the European Union (Box 5.1), or improving connectivity in south-western Australia ('Gondwana Link'; see website in the appendix) are now being

Box 5.1 Natura 2000 and National Networks in the European Union

The first official declaration by the European Commission (EC) of the need for ecological restoration is to be found in the Habitats Directive of 1992 (EC 1992a). Together with the much older Birds Directive (from 1979), the Habitats Directive establishes the legal base for the creation of the worlds largest and most ambitious network of protected areas, which is called Natura 2000 (see website in the appendix). The goal is not only to preserve certain areas for nature conservation, but also to achieve a so-called favourable conservation status of species and habitats. Natura 2000 consists in fact of two different, often broadly overlapping types of areas. 'Specially Protected Areas' (often called 'bird areas') were proposed in the Birds Directive of 2009 for the designation of 'International Bird Areas'. Areas of the second type ('Natura sites') are proposed by member states abitats Directive as so-called Sites of Conservation Interest. After inclusion in the European list they must be legally established by the relevant EU member country, and then become so-called Special Areas of Conservation. Natura sites are designated to biogeographic regions, rather than just to a particular state, and may be terrestrial, marine or both.

The terrestrial part of the Natura 2000 network was largely completed in 2010, while completion of the marine part is foreseen in 2012. The network covers 17.6% of the European Union's total land area and 100 000 km^2 of its marine environment; it consists of almost 26,000 sites and includes more than 922 000 km^2 (see website in the appendix). The new European biodiversity target, adopted in March 2010, explicitly addresses the need to restore ecosystems by 2020 where feasible. This means that further development of the Natura 2000 network will use all possible approaches – that is, full protection (non-intervention) in wilderness or near-natural sites, active management in human-induced and human-dependent ecosystems, and restoration in damaged sites or sites converted into an unfavourable conservation status. The new strategy also addresses the issues of fragmentation and connectivity, by proposing a 'green infrastructure' in the wider countryside, that is, also outside Natura 2000 sites. The strategy intentionally utilizes the concept of ecosystem services to address problems like water retention, flood prevention, erosion control, carbon sequestration and so on, and combines this with biodiversity conservation and the creation of a functional network of protected sites.

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carried out. Most likely they will develop further into even more ambitious programmes, such as the green infrastructure strategy of the European Commission (see website in the appendix), aimed at protecting and 'restoring' biodiversity also outside protected areas. Despite severe ecological losses in the recent past, if current trends continue there is hope that the tide has turned and effective landscape-scale approaches to conservation and ecosystem management issues will become the norm.

APPENDIX: REFERENCES TO WEBSITES

Gondwana link: http://www.gondwanalink.org

Green infrastructure strategy of the European Commission: http://ec.europa.eu

Natura 2000: http://natura2000.eea.europa.eu

Natura 2000 network: http://ec.europa.eu/environment/nature/natura2000/access_data/index_en.htm

Nitrogen surplus on agricultural fields in Flanders: http://www.milieurapport.be/nl/feitencijfers/MIRA-T/sectoren/landbouw/vermestende-emissie-van-de-landbouw/nutrientenbalans-van-de-landbouwbodem-internationale-vergelijking/

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Chapter 6

ECOLOGY OF ECOSYSTEMS AND BIOTIC COMMUNITIES

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6.1 INTRODUCTION

The focus of restoration ecology, and the closely allied practice of ecological restoration, is the structure, composition and functioning of ecosystems in a given landscape. Recall that an **ecosystem** encompasses the interactions between species of a **biotic community**, and between each of them and the abiotic environment in which they live. Recall also that a **landscape** is made of an assemblage of interacting systems, including ecosystems, each with its own community. In the present chapter, we start by giving a brief history of successive scientists' views on the subject of ecosystems as an ecological unit. Thereafter we present a number of examples of direct and indirect interactions between and among species within a biotic community, which in turn affect community structure and, at a higher level still, whole-ecosystem functioning. Then, we consider complexity in species interactions as a variable to be considered for those studying or attempting to carry out ecosystem restoration in a world of environmental change. At the end of each section, we indicate the impact that our exposé may or should have on the further development of the science of **restoration ecology**. We conclude by reflecting on the desired 'attributes of restored ecosystems' as given by *SER Primer on Ecological Restoration* (SER 2004), and on the interface between theory and practice in general.

6.2 ECOSYSTEMS

The views that ecologists have of ecosystems have developed and evolved enormously since the term was first introduced, 75 years ago, by A.G. Tansley (1935). Among other things, it changed as a result of the way that successive generations of ecologists, anthropologists, and archaeologists considered so-called 'natural' systems. Until recently, a 'balance of nature' paradigm prevailed, so let's begin our survey there.

6.2.1 Ecosystems in a supposedly 'balanced' world

The field of ecosystem ecology traditionally studies fluxes of energy and matter through and between ecosystems. The first studies on the functioning of ecosystems focused on the transfer of energy, and how energy fluxes determine productivity of plants, and the herbivores and predators that perch higher in the food chain. A seminal paper was that of Lindeman (1942), who studied fluxes of energy (derived from the biomass of different feeding or trophic levels) through the aquatic food web of Cedar Bog Lake in Minnesota. His example was followed by a whole generation of ecosystem ecologists, inspired by Eugene P. Odum, among others (see Golley 1996). Their work highlighted the structuring effects of energy flow in ecosystems, limiting productivity of successive *trophic levels* as progressively less energy is available when moving from primary producers (e.g. plants and algae) via herbivores to predators and, finally, the top predators. As every trophic level beyond the first one respires and discards (as urine and faeces) part of its consumption, less energy is available for higher trophic levels. As a consequence, food chains and food webs often have a pyramidal shape when biomass or energy is expressed per trophic level.

Ecosystem ecologists soon found that ecosystem productivity is determined not only by fluxes of energy, but also by nutrient flows (see e.g. DeAngelis 1992). All organisms require and take up a certain proportion of macronutrients (e.g. nitrogen and phosphorus, or silicate, in the case of diatoms), as well as numerous minor or oligo-elements. These nutrients are necessary for organisms to build new tissue and to compensate for tissue turnover. In many ecosystems, energy and carbon (a major element of carbohydrates) are not the limiting factor to the growth of organisms; rather, it is the limited availability of nutrients for part or all of the year. A key difference here is that availability of nutrients is not so much determined by input and output from the ecosystem but rather depends much more on local sources such as mineralization of nitrogen through the decomposition of dead plant material. As a consequence, the pathways followed by these nutrients moving through the ecosystem often appear to be cyclic, rather than linear, as is generally the case for energy and carbon.

At the heart of the aforementioned approaches to ecosystem ecology lies the notion that most natural ecosystems, most of the time, are 'in balance', thanks to **resistance** and **resilience** that develop as emerging attributes of ecological systems over evolutionary time. In other words, except when an ecosystem is heavily disturbed by humans or by catastrophic disruptions such as earthquakes or volcanic eruptions, the system stays in some sort of equilibrium. This implies that the inputs and outputs of an ecosystem, including

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births and deaths, and migrations and colonizations, roughly match.

Though knowledge of *feedback* relations is crucial to understanding the dynamics of ecosystems and their response to changed conditions, this notion was soon questioned by people studying real ecosystems, who found that many ecosystems are never in equilibrium (Ellis & Swift 1988). Rather, ecosystems are constantly in flux and adapting to changing conditions at various spatial and temporal scales, including changes in climate and in external inputs of nutrients (see also Chapter 21). To understand ecosystems, it is essential to know how they respond to variations in background conditions.

6.2.2 Ecosystems in a world of change

Environmental changes have always occurred, as testified by records of variation in mean global temperature over several thousand years (Intergovernmental Panel on Climate Change (IPCC) 2007b). However, our very rapidly growing human **ecological footprint**, over the last two centuries especially, is causing profound and sometimes very rapid changes in environmental conditions on our planet – due for example to industrial, agricultural, and urban greenhouse gas emissions and the artificial enrichment of aquatic ecosystems by inorganic nutrients, especially N and P, 'leaking' from intensively fertilized fields and choking out possibilities for life through **eutrophication**. This has led ecologists to ask the question 'How do ecosystems respond to these changes?'

The presence of feedback relations within ecosystems is not always an adequate safeguard against potential effects of rapid and/or profound changes in environmental conditions. In particular, some systems change significantly, even violently, in response to shocks and stress induced by profound or prolonged human influences. A striking example of this is shallow lakes, as reported by Scheffer *et al.* (1993). Many shallow lakes have experienced increased inputs of nitrogen and phosphorus as a consequence of uncontrolled seepage of field and garden fertilizers, and dumping of phosphate-based detergents. Initially, this only leads to minor effects, as long as increased densities of dead and decomposing aquatic plants locked up the nutrients in the sediment, generating a *feedback loop* that compensates, in part, for increased nutrient availability. As nutrient inputs increase further, especially of phosphorus, a shift or transition takes place, as conditions become ideal for microalgae. In the presence of unusually high nutrient levels in the water, therefore, many shallow lakes rather suddenly switch from a state with clear water and a highly diverse community of aquatic plants and invertebrates, to a murky water state, with a much less diverse community of pelagic microalgae. Submerged aquatic plants disappear, and in some cases, large populations of toxic cyanobacteria proliferate. The faunistic community in this new state is characterized by sediment-feeding fish, which exploit and remobilize the phosphorus that is stored in dead plant material in the sediment, generating a feedback loop that solidifies or 'fixes' the microalgae-dominated state in which the lakes now occur (see also Chapter 18).

The change in ecosystem state that these shallow lakes experience in response to increased eutrophication was unexpected, dramatically fast and hard to reverse. Many lakes stay in their murky state for years after anthropogenic nutrient inputs are stopped, and nutrient levels must return to levels well below those at which the initial switch to a microalgae-dominated state occurred before submerged plants are able to recover. At the basis of this lies a phenomenon whose existence was predicted by Noy-Meir (1975), who proposed that not just one but two different 'steady states' may occur in a subtropical or semi-arid region grazing system.

Indeed, we now know that many ecosystems can manifest two or more **alternative stable states**, each characterized by a distinctly different community with different feedback processes and overall functionality. Severe or ongoing human pressure on ecosystems can overwhelm the feedback processes that characterize one state, leading to a dramatic shift from one type of community to another. This new state typically has its own stabilizing feedbacks – in other words, it can become resilient and such that a quick return to the earlier steady state is effectively blocked. Only a dramatic change in conditions will allow a return to the previous state in which the previous biotic community can re-establish itself (see e.g. Suding *et al.* 2004).

Theory on the potential of such 'catastrophic changes' in ecosystems in response to (gradually) changing conditions dominated ecosystem ecology during the late 1990s and early 2000s. The resulting models on alternative stable states, that were obtained primarily from studies of shallow lakes, were subsequently applied to a range of other ecosystems in

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attempts to explain dramatic shifts in response to anthropogenic or natural environmental changes. These include semi-arid grasslands (Rietkerk & van de Koppel 1997), coral reefs (Knowlton 1992), wet dune-slacks (Adema *et al.* 2002) and rocky shores (Petraitis & Latham 1999), where large and sudden changes in ecosystem state have been observed. The success of these attempts to apply the aforementioned models of alternative stable states was limited (Bertness *et al.* 2002). Apart from a lack of experimental evidence, an important reason for this is that the theory and models developed for semi-enclosed, relatively homogeneous bodies of shallow-lake water were not sufficient to explain the dynamics of open, spatially extended and heterogeneous ecosystems such as those listed above. In ecosystems such as those, the interplay between local feedback relations between organisms and their respective environments and feedback processes occurring at large scales, generates complex dynamics that can lead them to respond in unexpected ways. Thus, a more complex theory is required to predict how these ecosystems respond to changing environmental conditions. Such a theory should explicitly take into account feedback relations and interactions that cross spatial scales, as discussed in the next section.

6.2.3 Spatial self-organization

When ecologists observe spatial patterns in ecosystems, typically they seek the cause or mechanism in environmental variations at the local or regional levels of organization. Although this is valid in many cases, a number of studies over recent decades revealed clear and consistent spatial variation in the structure of ecosystems in landscapes that exhibit no underlying variation in environmental conditions and can be explained by so-called *spatial self-organization*, a process whereby internal interaction between biotic and abiotic components of an ecosystem generates complex but recognizable and repeated spatial patterns (Rietkerk & van de Koppel 2008; see Figure 6.1). Spatial self-organization has been suggested as the mechanism in nature that leads to the creation of regular patterns, such as those found in the vegetation of some semi-arid land systems (Klausmeier 1999) or peatlands (Rietkerk *et al.* 2004a), as well as the irregular patterns found in mussel beds on wave-disturbed rocky shores (Guichard *et al.* 2003), and in some Mediterranean grasslands (Kefi *et al.* 2007).

We elaborate here on the example of banding or patchy vegetation patterns as found in arid and semi-arid lands in the African Sahel, Australia and elsewhere, which have been much studied (e.g. Valentin & d'Herbes 1999; Tongway *et al.* 2001). In this case, once again, a recurrent research question has been whether or not such patterns result from pre-existing environmental heterogeneity, from spatial self-organization or from both. Klausmeier (1999) analysed a series of spatially explicit models and showed that the patterns can be explained by spatial self-organization alone, that is they are caused by one single mechanism (cf. Thiery *et al.* 1995; Valentin *et al.* 1999). Banded or patchy vegetation promotes the infiltration of water into the soil, a process which benefits vegetation growth under arid or semi-arid conditions. In vegetated bands or patches, more water infiltrates than in bare patches. Overland flow, in particular on hill slopes, then generates a net flux of water into the vegetated patches, and decreases water availability in the bare patches. This interaction between vegetation, water infiltration, and overland flow of water fully explains the formation of spatial patterns involving so-called **runoff** and **run-on** areas, and can thus be considered as spatial self-organization.

Mathematical models indicate that spatial self-organization can have important implications for the functioning of ecosystems (Ludwig *et al.* 1999; Rietkerk *et al.* 2002), in line with indications from empirical work (Valentin & d'Herbes 1999). Indeed, for arid ecosystems, spatial patterns are predicted to compensate for reduced and unpredictable rainfall, allowing for plant growth under conditions that would not sustain plant life if spread homogeneously. This implies that spatial patterns generate *feedback mechanisms* that can compensate for changed environmental conditions, such as drought. Moreover, consistent and predictable changes occur in spatial patterning before the buffering feedbacks are overwhelmed and the system shifts to an alternative state characterized by a bare, degraded landscape (Rietkerk *et al.* 2004b). This provides a basis for the development of indicator systems that can predict sudden shifts between alternative stable states in complex dynamic systems (see below).

6.2.4 Implications for restoration ecology

Insight in the interactions between both negative and positive feedback relations is crucial to understanding

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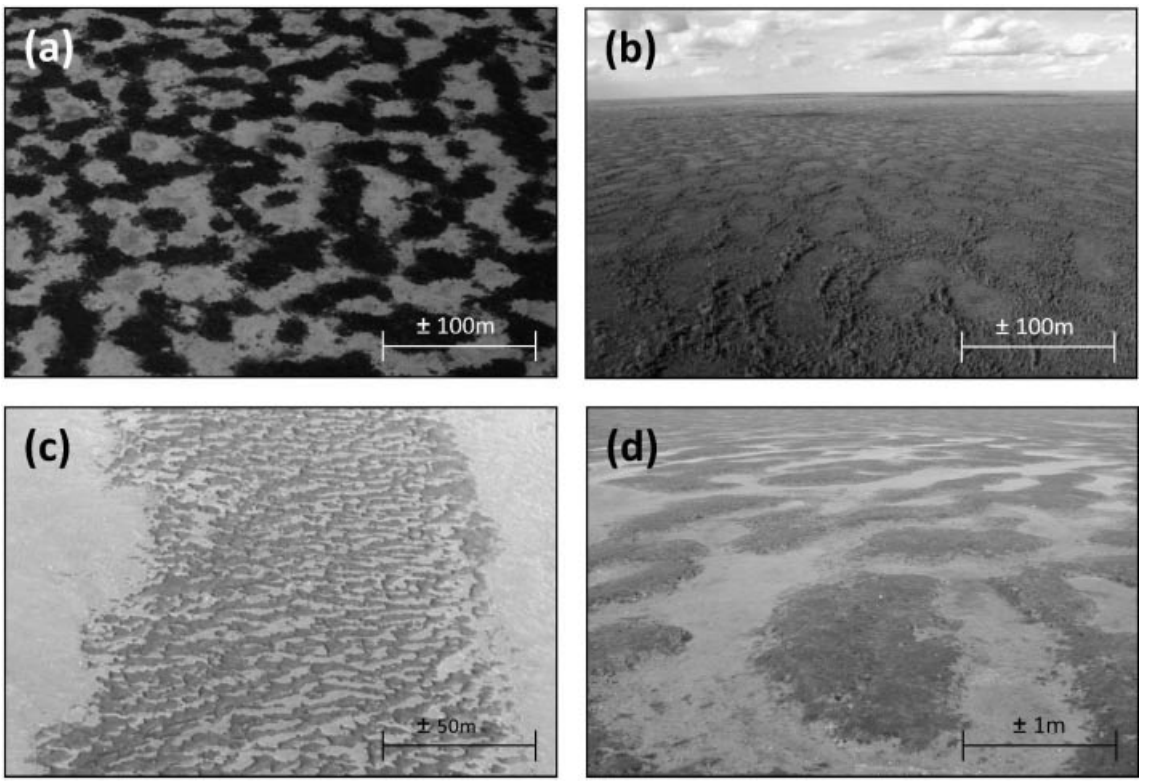


Figure 6.1 Observations of regular patterns from arid ecosystems, boreal wetlands, mussel beds and intertidal mudflats. (a) Labyrinth pattern of bushy vegetation in Niger (scale = 100 m); after Rietkerk *et al.* (2002). (b) Regular maze patterns of shrubs and trees in West Siberia (scale = 100 m); after Rietkerk *et al.* (2004b). (c) Patterned mussel bank in the Wadden Sea, the Netherlands (scale = 50 m); after van de Koppel *et al.* (2005). (d) Labyrinth pattern of marine benthic diatoms in the Netherlands (scale = 1 m); after Rietkerk and van de Koppel (2008). (Photograph (d) by Johan van de Koppel.)

the dynamics of ecosystems and their response to changed conditions. The notion of 'alternative stable states' is particularly relevant to the field of restoration ecology (Suding *et al.* 2004), as their presence is an important determinant of the success of restoration efforts. Indeed, degraded systems may also be resilient. Essential for the conservation and restoration of natural systems is the development of **indicator** systems for so-called *critical transitions* between alternate states, not only in ecological systems such as arid grazing systems (Solé 2007), but also in socio-economic systems such as the financial market (Scheffer *et al.* 2009). Research on this topic is still tentative and in a highly theoretical stage of development, outside the scope of this book, but its applicability may not be far away, for example to identify early-warning signals for future climate change based on understanding of analyses of the past.

When restoring ecosystems to their natural state, it is important to consider that the spatial structure of the original systems was, in part, self-organized, which can have large implications for the functioning and resilience of these ecosystems. Restoration efforts that do not take into account the original spatial structure will likely lead to a community or ecosystem that is more vulnerable to disturbances, supports lower population sizes, and is possibly less species-rich than the pre-disturbance ecosystem. A good example of a restoration project that explicitly took this factor into account was carried out by Tongway and Ludwig

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(1996), who performed experiments in a semi-arid region of Australia to rehabilitate degraded landscapes on bare slopes. Their study revealed that the creation of a patchy construction of 0.5 m high piles of acacia branches resulted in a 10-fold increase in water infiltration, with a huge impact on soil quality and plant production (see also Chapter 4). In other words, they improved the recovery potential of the site undergoing restoration by mimicking a natural spatial pattern, and thereby assisting the natural self-re-organization of the ecosystem.

6.3 BIOTIC COMMUNITIES

Biotic communities are not only shaped by the interactions with the abiotic environment, but also to a large extent by all sorts of interactions between different species. Organisms can affect each other by eating, by direct aggressive interference, by changing the environment, and by giving rewards for provisions such as nectar for pollination. In section 6.3.1, we start by describing a number of such direct interactions between species, such as consumption and mutualism. Then, in section 6.3.2, we consider a number of indirect effects that result from these direct physical interactions, such as competition and facilitation. We notice that in many scientific articles, direct interactions are measured by their indirect effects. We consider it essential to explicitly distinguish between the two (i.e. between mechanisms and consequences). While recognizing that the latter are more relevant in ecological restoration projects, how can we manipulate the consequences without knowing the mechanisms? Finally, in section 6.3.3, we reflect on implications of the presented information for restoration ecology.

6.3.1 Direct interactions

As mentioned, we distinguish between direct and indirect interactions between species. We briefly present basic knowledge of the following direct interactions: (1) consumption by plants and animals, with particular attention to interactions between trophic levels, (2) parasitism, a form of consumer–resource interactions, (3) ecosystem engineering of plant and animal species, and (4) mutualisms, especially plant–mycorrhiza and plant–pollinator interactions. This brief overview provides the basis for our understanding of the consequences. Our focus will be on these indirect effects, dealt with thereafter, in view of their impact on ecosystem structure and functioning, which is particularly relevant in the practice of ecological restoration.

Consumption

All organisms require resources to survive, grow and reproduce. At the level of individuals, the benefit is one-sided: a plant needs nutrients and a predator needs prey, but not the other way around. Among animal consumers, there are (monophagous) specialists that consume only one prey species, and (polyphagous) generalists that consume a wide range of prey. Consumption may result in the death of a complete organism, as is the case with many predator–prey interactions, but consumption can also be partial, as for instance when herbivores consume only part of their food plants, or plants absorb small quantities of nutrient pools. Great variations in the relevant temporal scale also occur across the range of interactions where consumption occurs in ecosystems.

The impact of consumption on community structure depends very much on the growth rate or growth potential of the prey species, and the consequences for the food chain or the food web. Imagine a spatial gradient with increasing plant productivity, be it due to increasing annual precipitation in a subtropical region or to increasing nutrient availability in the temperate zones of the Earth (see Figure 6.2). At low productivity, vegetation is too sparse to support herbivores. An increase of primary productivity, however, should

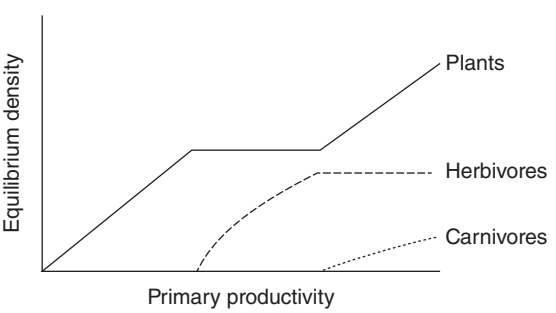


Figure 6.2 The equilibrium densities of plants, herbivores and carnivores as a function of primary productivity. The relationships are based on the model of Oksanen *et al.* (1981). (Modified from van de Koppel 1997.)

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attract more herbivores, increasing grazing pressure, maintaining a low standing crop until herbivore biomass is high enough for a population of carnivores to be sustained. From that point in the gradient onwards, the carnivores regulate the herbivore density, and as a result, standing biomass of plants can increase again. This reasoning dates back to the 1980s and is known as the *exploitation ecosystem hypothesis* (EEH), mathematically analysed by Oksanen *et al.* (1981). The model is general and ignores all kinds of variability, such as differences in competitive ability and in resource quality, but it has been a useful starting point for the further development of theories on plant–herbivore interactions. An underlying assumption is, for example, that all vegetation is equally palatable. However, tall plants, and especially the woody parts of them are generally much less attractive to herbivores than herbaceous plants or biomass because stem and wood material is much harder to digest (Fryxell 1991). This holds especially for small grazers, not for browsers. This results in a decrease in the density of grazing herbivores in areas with high plant productivity, even in the absence of carnivores (van de Koppel *et al.* 1996; see Figure 6.3 for an example).

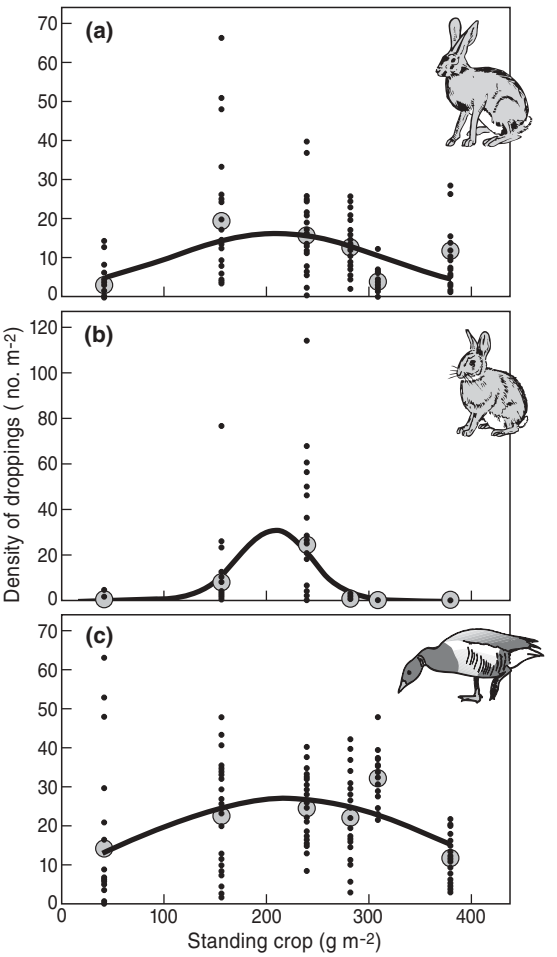


Figure 6.3 Number (means and individual observations) of annual droppings of (a) hares, (b) rabbits and (c) barnacle and brent geese in relation to vegetation standing crop on the coastal salt marsh of the Waddensea Island of Schiermonnikoog, the Netherlands. (Modified from van de Koppel *et al.* 1996.)

Parasitism

Host–parasite interactions are considered as a specific type of consumer–resource interaction, as the parasite consumes tissue of its host, just as in the case of herbivore–plant and predator–prey interactions. Similar models have, therefore, been used for these different types of direct interaction. However, the indirect effects of parasitism on the biotic community may be more dramatic, as illustrated below (section 6.3.2).

Ecosystem engineers

Every living organism changes its environment, by producing shade, by the use and consumption of resources, by excreting various products and so on. Some species create, maintain or modify their environment to such an extent that they significantly affect the growth or survival of other species in their community as well as their own. These plant or animal species, which are often considered as species with a **keystone** or a **foundation** role or position (see Chapter 2), can be called **ecosystem engineers** (*sensu* Jones *et al.* 1994). Note that this term is different from the notion of *ecological engineering*, which is used to indicate human engineering activities (Rosemond & Anderson 2003). Let us now consider two examples of direct interactions: (1) biophysical engineering, such as when beavers make dams, and (2) chemical engineering of the environment, also known as allelopathy in plant communities.

Plant and animal species that physically engineer their respective environments can have long-lasting effects, even beyond their own lifetime (Hastings *et al.* 2007). The North American beaver (*Castor canadensis*),

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just mentioned, is a frequently cited example; it creates wetlands and modifies entire landscapes through its damming and foraging activities, which are of course beneficial to themselves but harmful to other organisms. Often, however, the processes are much more subtle and nevertheless influential, such as the burrowing activities and cast constructions of earthworms that alter the mineral and organic composition of soil, accelerate nutrient cycling and facilitate drainage of soils, ultimately affecting the community composition of plants, animals and microorganisms. Direct effects of such biophysical engineering on the part of animals are usually measured by their indirect consequences, such as improving the species' own environment (self-facilitation, as in the case of beavers), or facilitation of other species (as in the case of earthworms). Examples of indirect effects of habitat modification are given in section 6.3.2.

Allelopathy – the release of organic compounds from one plant species, which reduces the germination, growth or fecundity of other plant species in the community – has long been considered as a form of unidirectional interference competition between plants. Here we prefer to consider it as a form of chemical engineering of the environment. There are many thousands of organic plant compounds released from shoot materials or exuded by roots, but only a relatively small number of them have been identified as detrimental and involved in allelopathy. What's more, even if a substance exhibits detrimental effects on plants in laboratory experiments, it might not truly hamper growth of other plant species in the field. A good example of *bona fide* allelopathy is phenolic substances occurring in forest soils (e.g. Hättenschwiler & Vitousek 2000, and references therein). They include, for example, tannins in the leaves of oak trees (*Quercus* spp.) and bracken fern (*Pteridium aquilinum*), where they function as feeding deterrent. Once released from decaying plant materials into the soil environment, phenolics influence plant growth directly by interfering with plant metabolic processes and by their effects on root symbionts. They also affect ecosystem *nutrient cycling* in various ways, and interfere with decomposition, mineralization and humification (see section 6.3.2).

Mutualism

Mutualism is a direct interaction between individuals of different species that results in an increase of fitness for both parties. Mutualistic relationships can be obligate or facultative. Two examples of mutualism that we will illustrate here, as they should be taken into account in restoration projects, are (1) plant–mycorrhiza interactions, and (2) plant–pollinator interactions.

Plant–mycorrhiza interactions can be considered as a mutualistic symbiosis. For the overwhelming majority of vascular plants, mutualistic relationships with mycorrhizal fungi are of utmost importance. Usually, the plant provides the associated fungi with carbohydrates while the mycorrhizae assist their 'host' plants with taking up water and essential nutrients, especially P, Cu and Zn, but also N, K, Mg and Ca (see Kuyper & de Goede 2005 and references therein). However, there are many different types of mycorrhizal fungi (see Ozinga *et al.* 1997 and references therein). Approximately 80% of species of temperate, subtropical and tropical plant communities are infected by *arbuscular mycorrhizal fungi*. These fungi are especially efficient in the uptake of inorganic P and several other relatively immobile ions. *Ectomycorrhizal fungi* occur mainly on woody plants and only occasionally on herbaceous plants and grasses, and they are especially efficient in N-limited ecosystems. *Ericoid mycorrhizal fungi* occur mainly in the Ericales (heathers and heaths) and are physiologically comparable with ectomycorrhizae. Several mycorrhizal fungi have enzymes that break down organic complexes such as tannin and lignin, thereby releasing N and P from organic matter found in the soil, which they then translocate as nutrients in a form that is more readily available to their host plant. This is particularly useful to plants in acid soils, where nutrient uptake by plant roots is often difficult.

Plant–pollinator interactions can be considered as a nonsymbiotic mutualism. The mutualism is opportunistic and flexible rather than fixed, neither symmetrical nor cooperative. The mutual exploitation interest may be skewed towards a consumer–resource relationship between the two parties, or even result in antagonism. In their review on 'endangered mutualisms', Kearns *et al.* (1998) pointed out that over 90% of modern angiosperm species are pollinated by animals of some kind, including insects, birds, lizards, bats and small marsupials. Specialist relationships are much more vulnerable than generalist relationships, but plant–pollinator interactions are only seldom species specific. Indeed, relatively few plant–pollinator interactions are absolutely obligate in a strict sense (Johnson & Steiner 2000). Many flowers show specialization in floral traits, yet they are often visited by diverse assemblages of animals. There is a network of relationships between

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the plant community and the pollinator community (e.g. Bosch *et al.* 2009), but the type of network differs from the network of food webs (see section 6.4.1). When pollinators visit flowers of several plant species, this may result in a reduction of seed set for each of the species. Only a few studies on visitation of pollinators include consequences for the fitness of plants in terms of seed set and reproduction (e.g. Kwak & Bekker 2006; Morales & Traveset 2009).

6.3.2 Indirect effects on community structure and succession

In many cases, it is not so much the direct interactions, but rather the indirect effects of resource consumption, parasitism, ecosystem engineering and mutualism that are most influential to community structure and succession, and ecosystem functioning. Here we illustrate a number of such consequences, in the same order as before. Thereafter, we reflect on implications for restoration ecology.

Effects of consumption: competition for resources

Theory of competition is too extensive to be treated in its entirety in this chapter. Readers should consult basic ecology textbooks, such as Krebs (2008), for further ideas and information. Here we focus on competition between plants, as this is the kind of information most relevant for restoration ecologists. Competition for shared resources, and its impact on plant communities, has received much attention from ecologists since the seminal work on the mechanisms of resource competition by Tilman (1982, 1988). Tilman developed a theory based on experiments with micro-algae competing for limiting nutrients until they reached a steady state, and applied it to plants competing for resources, such as nutrients and light. He argued that, if a plant species is able to reduce the availability of a particular resource to a lower level than that required by competing species, it may increase its chances to become the dominant species of its kind or functional group in the community. Two species could coexist if there were two limiting resources, and so on, but there could never be more species than there were limiting resources. In reality, however, many more species can coexist than there are limiting resources, for example due to environmental **heterogeneity**, transient non-equilibrium conditions or more complex food web interactions. Since the 1990s, Tilman and coworkers initiated large-scale experiments on the coexistence of competing species, particularly on the relationship between *ecosystem functioning* and *species diversity* (e.g. Kinzig *et al.* 2001; see also Chapter 2). This type of knowledge helps understanding the problematic relation between ecosystem productivity and plant species richness, also relevant in the context of ecological restoration.

Effects of parasitism

Pathogens and parasites may have a huge impact on **ecosystem structure** and **succession**. In recent times, fungal blights decimated the American chestnut (*Castanea dentata*) from the eastern deciduous forests of the United States, mountain hemlock (*Tsuga mertensiana*) from the Cascadia region of North America, various elms (*Ulmus* spp.) from much of western Europe and a whole range of *Eucalyptus* species from the forests of western Australia (Dobson & Crawley 1994). In each of these cases, the removal of a dominant, late-succession species, as a result of a fungal infestation, led to the development of forests dominated by less competitive species from earlier successional stages. Even more spectacular is the classic example in southern England of the indirect effect on vegetation change due to the viral infection of rabbits (*Oryctolagus cuniculus*), also referred to by Dobson and Crawley (1994). Myxomatosis, caused by the *Myxoma* virus, was accidentally introduced into France in 1952, from where it reached Britain in 1953. In Silwood Park, the result was a 99% reduction in the rabbit population within a few years, which resulted in the transformation of a formerly open, grassy parkland to an oak woodland dominated by pedunculate or common oak (*Quercus robur*). This change has to date proved to be irreversible, even after the recovery of the rabbit population in the 1970s. Apparently, a **threshold of irreversibility** had been crossed (see Chapter 2).

Effects of habitat modification

While the study of *competition* for shared resources and its effects on community structure has a relatively long history, the interest in the effects of habitat modification in terms of *facilitation* of other species has only recently gained momentum (e.g. Bruno *et al.* 2003;

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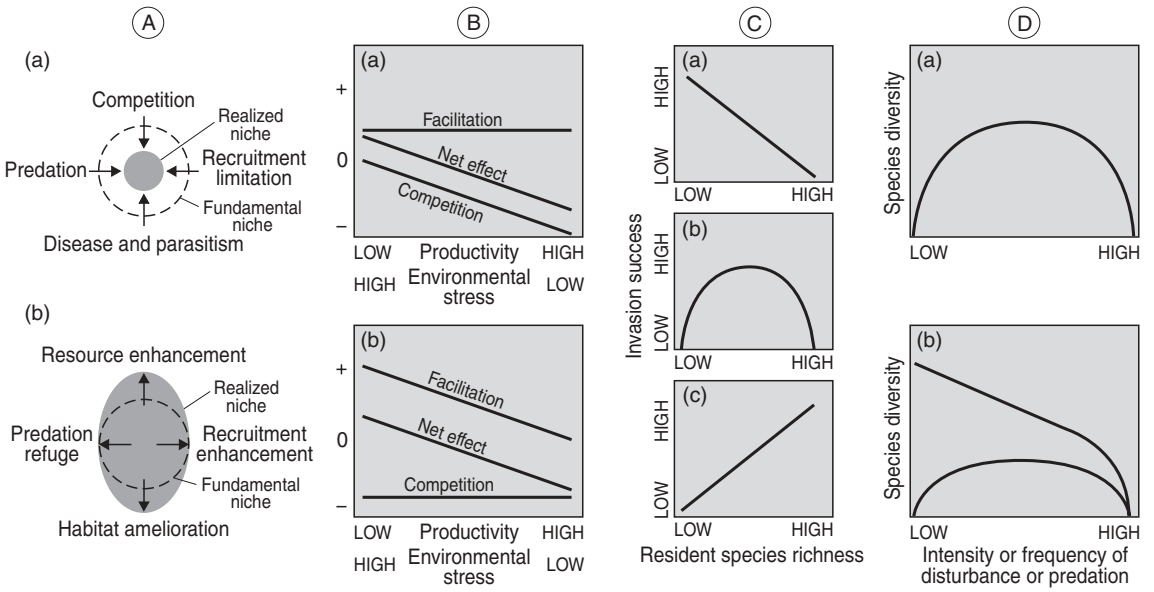


Figure 6.4 Four fundamental models of ecology, with and without facilitation, illustrating paradigm shifts if facilitation is included. (A) The realized niche can be larger than the fundamental niche due to facilitation; (Aa) without facilitation, (Ab) with facilitation. (B) Facilitation may affect the competitive abilities of species along an environmental gradient; (Ba) facilitation weak, constant, (Bb) facilitation strong, variable. (C) Facilitation may have an impact on the success of invaders; (Ca) without facilitation, (Cb or Cc) with facilitation. (D) Facilitation may change the relationship between species richness and ecosystem productivity; and (Da) without facilitation, (Db) with facilitation (lower line, primary space holders; upper line, secondary space holders). (From Bruno *et al.* 2003. Reproduced by permission of Elsevier.)

Brooker *et al.* 2008). Figure 6.4 depicts how fundamentally an ecological theory or model can change when facilitation is included along with competition. Here we focus on changes in the relative importance of competition and facilitation in plant communities as proposed in the so-called *stress-gradient hypothesis* (see Maestre *et al.* 2009). The notion of 'stress' in the latter paper is derived from the work of Grime (1979), who defined stressful environments as those in which producers are limited in their ability to convert energy to biomass. While in Grime's approach only the relative importance of competition changed along a productivity gradient, Maestre and coworkers elaborated on this idea, now also proposing a gradient in facilitation. Central to the stress-gradient hypothesis is the idea that facilitation should be especially common in communities under high physical stress or with high consumer pressure, whereas competition should be the dominant structuring force wherever the physical environment is relatively benign and consumer pressure is less severe. Indeed, overall, the relative frequency of facilitation and competition varies inversely across gradients of physical stress, also known as gradients of ecosystem productivity, whether in space or in time, but there are interesting exceptions (see also Chapter 11). Facilitation may, for instance, affect the competitive abilities of species along an environmental gradient in such a way as to keep it at a low level all along a gradient (Bruno *et al.* 2003), and – adding to the complexity – different facilitative mechanisms may function in a nested hierarchical manner (e.g. Verdú & Valiente-Banuet 2008). For example, experiments with intertidal smooth cordgrass (*Spartina alterniflora*) communities have shown that there exists an hierarchical organization of facilitation among species. The cordgrass provides shade and reduces wave action in these harsh environments, which results in a *cascade* of facilitative effects on other plant and animal species (e.g. ribbed mussels, barnacles, snails and seaweeds) (Altieri *et al.* 2007).

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There are also examples of mutually negative interactions between **ecosystem engineers**, for example in the salt marsh–tidal flat interface, where common cordgrass (*Spartina anglica*) and the lugworm (*Arenicola marina*) were found to affect each other negatively by changing their shared biophysical environment in opposite ways (van Wesenbeeck *et al.* 2007). While seedlings of *S. anglica* stabilize the sediment with their roots, preventing *A. marina* from feeding, *A. marina* strongly bioturbates the sediment, preventing *S. anglica* seedlings from establishing. All these examples show the importance of gaining knowledge about basic mechanisms in order to understand long-term cascading effects in communities. Otherwise any attempts at restoration-inspired **intervention** are likely to produce unexpected and possibly undesired results.

Allelopathic species (chemical engineers), excreting organic compounds that can reduce the germination, establishment, growth, survival and/or fecundity of other species, can also have a long-term impact on plant communities, inhibiting succession. In boreal forests, for example, the ground-layer vegetation in late post-fire successions is frequently dominated by dense clones of the dwarf shrub species *Empetrum hermaphroditum*, one of the most widespread plants in the European arctic and boreal biomes. This plant produces large quantities of phenolics and is conspicuously avoided by herbivores. Indeed, it is thought to be responsible for the strong negative effects on tree-seedling establishment and growth of Scots pine (*Pinus sylvestris*), among other plant species, and on microbial activity and plant-litter decomposition rates, thereby contributing to humus accumulation and reduced nitrogen availability (Nilsson *et al.* 1998). In general, phenolics are highly allelopathic under acidic, nutrient-poor soil conditions. In calcareous soils, by contrast, most phenolic compounds are rapidly metabolized by microbial activity and adsorption is high. There are indications that invasive **alien species** may inhibit the germination of native species by chemical interference (Ens *et al.* 2009; see also Chapter 20).

Effects of mutualism

The presence of mycorrhizae has been shown to change the outcome of plant competition in many cases, both for plants associated with arbuscular mycorrhiza and those associated with ectomycorrhiza; they are thus a determinant of plant community structure (e.g. Kiers *et al.* 2000; Stein *et al.* 2009, and references therein). Some mycorrhizal species with a compact structure increase resistance of plants against drought, pathogens, heavy metals and polyphenolic substances (Ozinga *et al.* 1997). In spite of a huge amount of knowledge about the importance of plant–mycorrhiza interactions, including in ecological restoration interventions, actual applications are still largely unexplored (Harris 2009).

Effective restoration of pollinators providing pollinator services in ecological restoration projects has also received too little attention and experimentation, even though much basic information is available (Dixon 2009). **Habitat fragmentation** and other effects of land use – such as agriculture, grazing, herbicide and pesticide use – and the introduction of non-native species have a significant impact on plant–parasite and plant–pollinator interactions (Kwak *et al.* 1998, Taki & Kevan 2007; see also Chapter 7).

6.3.3 Implications for restoration ecology

In our review thus far, we have touched upon a number of potential applications of fundamental ecological insights to ecological restoration projects, but we readily acknowledge that taking all the potential interactions, and all their indirect effects, into account is certainly impossible. Our message is twofold. First, restoration ecologists should realize that **ecosystem functioning** is complex and not easy to initiate, mimic and/or manage. They must, wherever possible, try to integrate the knowledge presented in their efforts to make ecological restoration a success, rather than ignoring the complexity and making a choice for simple solutions. Secondly, and related to this, we welcome and applaud initiatives to scientifically cope with complexity. Searching for general rules and laws, rather than presenting a huge amount of detailed information, continues to be a challenge for scientists. Though this 'coping with complexity' may seem to lead us still farther away from applicability, we consider it useful to inform the reader about promising initiatives.

6.4 COMPLEXITY IN BIOTIC COMMUNITIES

The dynamics of communities is obviously not only determined by interactions between pairs of species: recall the food webs and pollination networks we

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mentioned earlier. Indeed, nearly all organisms are embedded in networks of interactions with other organisms consisting of literally thousands of species in many cases; see Olff *et al.* (2009) for an overview of such 'ecological interaction webs'. Dealing with such complexity requires much more than merely doing inventories, or summing up detailed reductionistic sources of information, however useful that may be. Over and above such 'alpha-level' information, restoration ecologists need to be concerned with so-called emerging properties of the biotic community in the ecosystem they are concerned with.

One of the first attempts to understand the implications of ecological interactions within a network of species was launched in the late 1950s by the discussion on why the world is 'green'. Hairston, Smith and Slobodkin argued, after weighing against alternative mechanisms, that the world is green because herbivore density is generally controlled by predators (the so-called *HSS hypothesis*; Hairston *et al.* 1960). Reduction of herbivore numbers by predation would release plants from herbivore control and allow them to reach a high density, explaining why the (terrestrial) world generally has a green appearance. In spite of being fiercely criticized and discussed (Murdoch 1966), the notion that predators can indirectly affect the density of organisms that are the food of the prey they eat (e.g. two trophic levels lower in the community) has stimulated much research, and led to the development of the concept of a 'trophic cascade' (Paine 1980), which implies that consumption not only affects the prey but also affects still lower trophic levels. Trophic cascades have subsequently been suggested for various aquatic ecosystems (e.g. Carpenter *et al.* 1985; Power 1992), and terrestrial ecosystem (e.g. Jefferies 1999; Beschta & Ripple 2009). A recent book by Terborgh and Ested (2010) examines trophic cascades in many of the world's major biomes, including several that are discussed in Part 3 of this volume. Another interesting view upon the HSS hypothesis has been brought forward by Bond and Keeley (2005), who consider fires as a sort of 'selective herbivory'. Indeed, as these authors state, fire has been burning ecosystems for hundreds of millions of years, shaping global biome distributions and significantly altering plant biomass. The effects of fire on, for example, plant competition in consumer-controlled ecosystems are consistent with the predictions of the HSS hypothesis.

Contrary to what was assumed by scientists previously, the theorist Robert May pointed out in 1973 (May 1973) that more complex food webs are less stable (e.g. in terms of their ability to return to equilibrium after disturbance) than simple ones. His models of food webs moreover suggest that the *interaction strength* (in terms of its per capita effect on the prey or the predator) is of crucial importance to food web stability, and that weak interactions can, in principle, compensate for increased food web complexity. May's pivotal work strongly stimulated research into food webs in a wide range of ecosystems, and led to important insights into the processes and properties that stabilize ecological communities (Pimm 1984). First, food webs were found to be strongly compartmentalized, for example interactions within food webs are grouped in smaller subcommunities, where interactions between species within a compartment are stronger than between species of different compartments (Krause *et al.* 2003). This reduces the linking intensity within food webs, and makes the food web more stable and robust. Other studies revealed that the relative strength of interactions within food webs follows a pattern: weak bottom-up effects occur at lower trophic levels, while weak top-down effects predominate at higher trophic levels (de Ruiter *et al.* 1995; Neutel *et al.* 2007). Modelling exercises of the latter authors showed that the latter pattern strongly improves the stability of food webs, when compared to models where strong and weak interactions are randomly distributed across the web.

Up to the late twentieth century, ecological theory focused on the distribution of feeding relations within communities. Obviously, species can interact in a number of alternative ways, as described in the previous section. How does this affect our understanding of the network structure and dynamics of ecological communities? Studies on mutualistic networks between plants and animal pollinators and seed dispersers revealed that these networks have a different structure than consumptive networks (e.g. food webs); they are highly nested, where more generalist plants and animals interact with each other to form a dense core of interactions, to which the more specialist species are attached (Bascompte *et al.* 2003). In other words, mutualistic networks form a nested structure rather than a compartmented structure that is typical of food webs (Figure 6.5). How does this affect community dynamics? Nestedness was found to reduce interspecific competition and enhance the number of coexisting species. Hence, the structure promotes species persistence and structural stability, similar to the importance of compartmentation and interaction

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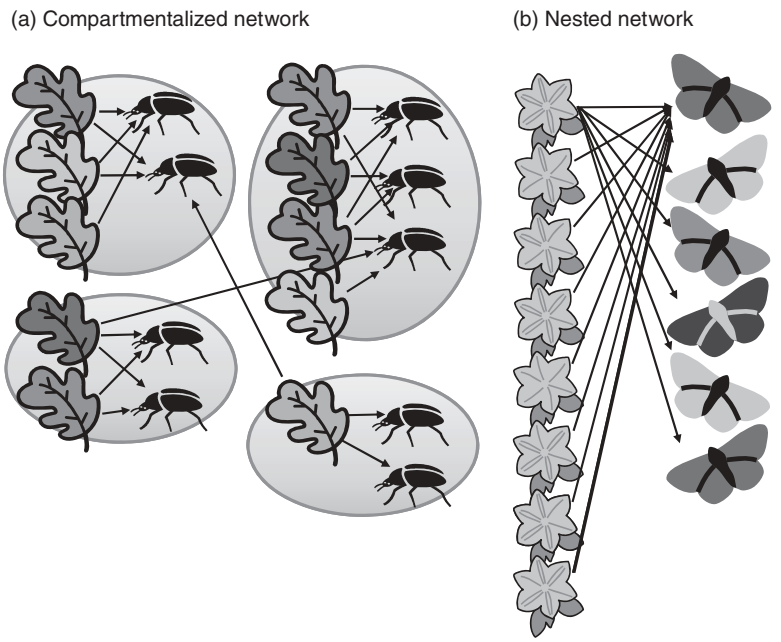


Figure 6.5 Network architecture. (a) Species form networks of interdependence such as illustrated in this figure. The nature of the interaction may be antagonistic (when one species benefits but the other loses, for instance by predation of one by the other) or mutualistic (when both species benefit from the interaction). (b) Consumptive interactions tend to be arranged in compartments, whereas mutualistic interactions tend to be nested. (Modified from Bascompte 2010.)

strength patterns in food webs. Most natural communities, however, consist of a range of possible interactions being mutualistic interactions, consumptive interactions, interference, and interactions mediated via the environment. To integrate these possible interactions into a unified understanding of the network structure remains one of the scientific challenges for the coming years.

6.5 RESTORATION OF ECOSYSTEMS: A FEW RECOMMENDATIONS

In this chapter, we have presented some of the basic concepts of the ecology of ecosystems and biotic communities, which may help those engaged in the ecological restoration and rehabilitation of degraded and impaired ecosystems based on a scientific approach to the problem. We have also alerted the reader to a number of potential implications of developing theories. So far, however, we have not referred to the criteria for the successful restoration of degraded, damaged or destroyed ecosystems that were formulated in the Primer for Ecological Restoration of SER (2004) in terms of nine attributes of restored ecosystems (see Chapter 2). What kind of recommendations can we derive from our discussion of the structure and functioning of ecosystems and biotic communities with reference to these attributes?

We recommend that ecologists and their collaborators who aim to re-establish 'a characteristic assemblages of the species that occur in the reference ecosystem' they have chosen or constructed, to explicitly consider the importance of both negative and positive interactions between and among species within the network of the community, and the very real possibility of trophic cascades, both of which can differ in restored ecosystems as compared to their respective reference systems. Note that we have hardly dealt with the effects of alien invasive species as compared to the effects of indigenous species; for this topic, please see Chapter 20.

The condition that 'all functional groups necessary for the continued development and/or stability of the

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ecosystem are represented' requires attention for the problematic relationship between ecosystem functioning and species richness (see Chapter 2). Ecosystem functions include productivity, nutrient cycling, decomposition and so on. In restoration projects that make use of functional groups, it is often assumed, or hoped, that the effects of increasing species richness on ecosystem productivity probably works through changes in functional diversity. However, there is still an unsolved dilemma that requires attention. Some experimental results favour the *redundant-species hypothesis* (i.e. only a few keystone species contribute to the productivity of the ecosystem), while others support the *rivet hypothesis*, whereby almost all or a minimum number of species essentially contribute to ecosystem productivity (for further reading, see e.g. Loreau *et al*. 2002).

We agree with the criterion that the restored ecosystem should be 'suitably integrated into a larger ecological matrix existing within the landscape, with which it interacts through abiotic and biotic flows and exchanges'. On this subject, readers should also refer back to Chapter 4, where the 'Landscape Functional Analysis' approach was introduced for monitoring and evaluating ecological restoration projects, and also study Chapter 5, which presented the basic components of modern landscape ecology. Later, readers will also find much food for thought in Chapters 16–19 on wetlands, which explicitly illustrate how ecosystems are open systems embedded within larger landscapes.

One of the most important criteria for ecosystem restoration as formulated by the *SER Primer* (SER 2004) is that restored ecosystems should be 'resilient'. The reader will recall from Chapter 2 that the notion of **resilience** is an emergent characteristic or attribute of an ecosystem expressing its ability to return to an earlier steady state after major disturbance. In principle, the more resilient an ecosystem (or restored ecosystem) is, the faster it returns to the previous steady state. Here we distinguish more explicitly between these two aspects of resilience, as they have been named and defined differently by various authors of differing backgrounds, reviewed by, for example, Gunderson (2000) and Groffman *et al*. (2006). Not recognizing the difference in the practice of ecological restoration may cause confusion. Resilience in ecological systems ('ecological resilience') is defined as the ability to return to the previous equilibrium, or as the magnitude of degradation that can be absorbed before the ecosystem redefines its structure and develops towards a new equilibrium. Once a system surpasses a threshold of irreversibility, it is disturbed and may shift to an alternative steady state, as in the above-mentioned case of shallow lakes. Resilience in engineering systems ('engineering resilience') is defined as the return time to a previous state of relative equilibrium. Only in the latter case can different 'degrees of ecosystem resilience' be distinguished.

This brings us to a final take-home message. In this chapter, we have tried to introduce the foundations of ecosystem ecology, and point out that **ecosystems** are considered the central focus of **ecological restoration**. While navigating at the interface between theory and practice, many readers may sometimes find that these two poles are incompatible. Indeed, in the restoration ecology literature there is much debate on the subject; see for example Cabin (2011).

For several reasons, we have chosen in this chapter not to confine ourselves to those parts of ecological theories about, and insights into, the structure and functioning of ecosystems that have already been proven to be applicable to ecological restoration. We are convinced that gaps between theory and practice can only be overcome once they have been explicitly recognized, for example the recognition of problems related to the applicability of theories of 'resilience' and 'complexity'. We take the view that basic, curiosity-driven science and applied science do go together, and both are needed – from all the relevant disciplines and professions – in order to tackle the highly complex problems faced in most situations where ecological restoration is necessary. In fact, this is the critical insight of **transdisciplinarity** and **sustainability science** (Chapters 2 and 22). We welcome and applaud initiatives in search of further exploring the important interface between restoration ecology and the ecological restoration of ecosystems.

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Chapter 7

POPULATIONS: ECOLOGY AND GENETICS

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7.1 INTRODUCTION

A population is defined as a group of potentially interacting organisms of the same species occupying a given space at the same time. The physical environment (the local sites) in which the populations of a species are found is termed the species' **habitat**. In restoration ecology, population processes should be approached in the context of processes taking place at the landscape scale (see Chapters 2 and 5). Therefore, in this chapter considering populations of both plants and animals, and also plant–animal interactions, we will focus in particular on the dynamics of spatially structured **metapopulations**, which are defined as assemblages of local populations connected by mutually dispersing individuals in a network of habitat patches. Within their habitat patches, species interact with a subset of the entire **biotic community** in the ecosystem. Interacting species obviously perceive the spatial scale of discontinuities in the landscape differently, depending on their trophic level, degree of habitat specialization, body size and dispersal ability, among other variable traits and factors. Habitat destruction and fragmentation, or other impacts on the spatial structure of habitats, can therefore alter the extent and outcome of interactions between populations of different species in a community.

Population ecology and the ecology of metapopulations are somewhat different, and make different contributions to restoration ecology. Population ecology focuses on understanding local abundances and can, among other things, be used to predict population persistence over time. Metapopulation studies (see section 7.3, below) explicitly link population ecology to biogeography, link the regional occurrence of species and specifically contribute to restoration ecology in terms of optimizing among-population processes that are critical for species persistence; specific interventions may include determining the best ways of adding, reinforcing, reintroducing and connecting populations. Both fields require detailed biological knowledge of a species and long-term data sets providing not only mean values but also spatio-temporal variances in demographic parameters (vital rates) at different life stages of populations under a range of relevant environmental conditions.

The fate of populations is not only determined by demographic and environmental parameters, but also by genetic factors. Populations that have become small and isolated due to habitat destruction and fragmentation generally suffer increased extinction risk for several reasons, including demographic, environmental and genetic factors and their interactions, and often it is not easy to identify the primary cause. Population viability analyses (Menges 2000) and estimates of *minimum viable population* (MVP) size (Traill *et al.* 2007) – concepts that are being applied to conservation and restoration – depend on whether genetic variation is included or not. Yet, the role of genetic factors in the persistence or extinction of threatened species has been long debated. This debate has been inspired by the fact that in some species, populations that have gone through a bottleneck of even a single pair, resulting in high levels of inbreeding and low genetic variation, nonetheless are able to persist (Groombridge *et al.* 2000). Frankham (2005) considers it risky to use such examples to argue that genetic factors do not play a role in determining the fate of small isolated populations, as they in fact may represent exceptions: a much larger fraction of genetically impoverished populations might have gone extinct compared to similar-sized populations with higher levels of variation or lower levels of inbreeding, as indeed shown in experimental studies (Reed & Frankham 2003). For instance, genetic variation as measured by heterozygosity appears to be on average 35% lower in threatened (IUCN red list) plant and animal taxa than in related, nonthreatened, taxa (Spielman *et al.* 2004a). Low genetic variation also reduces opportunities for populations to tolerate changing or fluctuating environmental regimes or the ability to evolve and adapt to them (Bijlsma & Loeschcke 2005; Bakker *et al.* 2010). Without considering genetic factors, extinction risks tend to be underestimated and restoration strategies may be inappropriate.

In this chapter we will first deal with local population ecological and genetic processes that are relevant for **restoration ecology** and show how knowledge of these processes can help in planning and managing succesful **ecological restoration** (section 7.2). We will then elaborate on these processes in the spatial context of metapopulations and discuss the challenges of restoration from a metapopulation perspective (section 7.3). Next, we will discuss the implications of changes in the spatial structure of the habitat for trophic interactions between populations that respond at different spatial scales and its relevance for restoration ecology (section 7.4). Finally, in section 7.5, we reflect on new challenges implied by restoration as compared to conservation of populations. In Box 7.1 we present commonly used measures of genetic varia-

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Box 7.1 Estimating genetic diversity and its use in conservation and restoration

Measuring genetic diversity. A good quantification of genetic variation allows assessment of variables that are important for decision making in conservation and restoration, including within- and between-population divergence, local adaptation, inbreeding and gene flow. At the population level, genetic diversity is often measured as (1) P = proportion of loci that is polymorphic (the fraction of all loci for which two or more different alleles have been observed), (2) H = average heterozygosity (the proportion of loci at which individuals on average are heterozygous, i.e. have two different alleles) and (3) A = allelic diversity (the average number of alleles observed per locus). All of these parameters are generally positively related to fitness (Reed & Frankham 2003; Leimu *et al*. 2006).

Use of near-neutral genetic markers. Different types of genetic markers can be used as a basis for such estimates, from DNA or protein to phenotypic variants. DNA-based markers offer the advantage that they generally yield a large number of polymorphic loci. Some of these, like Amplified Fragment Length Polymorphism (AFLP), are relatively easy to develop, but lack the ability to discriminate between homozygotes and heterozygotes due to dominant inheritance. Others, like microsatellites (Simple Sequence Repeats, SSR), do not bear this disadvantage (co-dominant inheritance) but do take a bit more time to develop. With the rapidly declining cost of sequencing, sequence-based markers like Single Nucleotide Polymorhisms (SNP) are becoming more widely available, offering opportunities of genotyping vast numbers of polymorphic loci with co-dominant inheritance.

Estimating population genetic parameters. From the distribution of the observed neutral genetic variation between and within populations and individuals, a number of basic population genetic parameters can be assessed. Estimates are based on deviations of observed heterozygosity from expected heterozygosity. Any nonrandom mating amongst individuals included in the sampling results in a deviation (deficit) of heterozygotes compared to those expected in infinitely large, outbreeding, perfectly random mating populations without mutation, migration or selection (Hardy–Weinberg equilibrium). Deviations of subpopulations relative to the total population (F_{ST}) indicate population differentiation, while deviations of individuals relative to their subpopulation (F_{IS}) indicate inbreeding within populations. The degree of population differentiation (F_{ST}, or G_{ST}, the equivalent for multiple loci) is inversely related to effective population size N_e and the number of migrants (m) and hence can be used to infer gene flow, while F_{IS} can be used to infer the degree of inbreeding within populations.

Use of neutral versus quantitative genetic markers. Genetic diversity based on DNA markers predominantly assesses neutral molecular variation. Unfortunately, neutral molecular variation generally has poor predictive power for phenotypic and quantitative genetic variation on which natural selection acts, and that is important in local adaptation to the environment (Reed & Frankham 2001; McKay & Latta 2002, and references therein). Therefore, a combination of studies with neutral and quantitative markers is often advised in conservation and restoration (Kramer & Havens 2009). Neutral genetic studies are well suited for assessing gene flow to identify historical and current movement and mixing of populations, inbreeding and divergence within and between populations. Quantitative genetic trait studies such as common garden, reciprocal transplant and quantitative trait loci studies are better suited to estimate fitness costs associated with inbreeding, adaptive genetic diversity and adaptive population differentiation. Combining neutral genetic and quantitative genetic studies are especially useful to dissect adaptive versus random population genetic divergence. For instance, the ratio of Q_{ST} to F_{ST} (or G_{ST}) – where Q_{ST} is the equivalent of F_{ST} for quantitative trait loci – has been used to identify traits involved in adaptive differentiation, that is, traits that show larger population divergence (Q_{ST}) than that observed for neutral loci (F_{ST}).

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tion and indicate the value of their use in conservation and restoration science.

7.2 LOCAL POPULATIONS

Destruction and fragmentation of habitat lead to a reduction in the population sizes of resident species, as well as increased isolation among populations, resulting in reduced migration and *gene flow*, that is, the movement of alleles between populations by migration, or transport of pollen and seeds. Reductions in population size are often the start of a self-reinforced negative spiral towards extinction that is known as the *extinction vortex* (Figure 7.1). Small, fragmented and isolated populations become inbred because of the higher proportion of matings that occur between relatives, often leading to lower ofspring fitness (*inbreeding depression*). Such populations are also more prone to a loss of genetic diversity because rare alleles are more easily lost from small than from large populations as a result of *random genetic drift*, as explained in section 7.2.3. The increased inbreeding and loss of genetic diversity lead to reduced fitness and potential for adaptation, further reducing population size and the susceptibility of populations to effects of demographic stochasticity, environmental variation and catastrophies, until extinction occurs (Frankham *et al.* 2005).

As far as the species level is concerned, ecological restoration programmes aim at restoring habitat conditions and/or **reintroducing** or **reinforcing** populations, thereby enhancing population size and promoting greater connectivity among populations (Montalvo *et al.* 1997; McKay *et al.* 2005). In this section we consider population ecological and genetic processes that are relevant in the context of ecological restoration. Restricted gene flow affects the performance of populations in various ways. On the one hand, it facilitates the process of local adaptation (section 7.2.1). On the other hand, it results in increased inbreeding and associated inbreeding depression within populations (section 7.2.2) and restricts the opportunities to restore genetic variation that is becoming depleted by random genetic drift (section 7.2.3); the strength and impact of these genetic processes stongly depend on population size. Finally we will

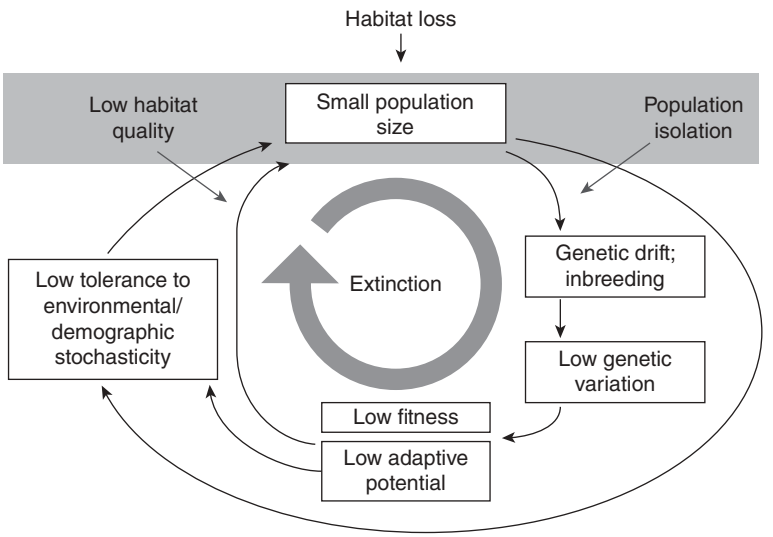


Figure 7.1 The extinction vortex. Habitat destruction leads to low quality of remaining habitat, isolation between remaining populations and small population size (grey bar). Reduction of population size leads to a progressive increase in inbreeding and genetic drift, loss of genetic variation and reduced fitness, further decreasing population size until extinction. Reduced population size also increases susceptibility to effects of environmental and demographic stochasticity and catastrophies, further enhancing extinction risk. Other effects of habitat destruction (increased isolation and low quality of remaining habitat) enhance the spiral to extinction through their negative effects on genetic variation and fitness. Ecological restoration aims to counteract these effects. (Modified from Frankham *et al.* 2005.)

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discuss the consequences of inbreeding and genetic drift for population fitness and viability and the prospects of 'genetic restoration' (section 7.2.4) in order to counteract the negative effects of inbreeding and genetic drift.

7.2.1 Local adaptation

Local populations have two basic ways in which to adapt to their environment and changes therein. *Phenotypic plasticity* is the ability of an individual to produce different phenotypes or behaviours from the same genotype under different environmental conditions, a mechanism that is important for sessile organisms in particular. Although this might suggest that phenotypic plasticity is a nongenetic mechanism, the extent to which plants are able to show phenotypic plasticity in traits ususally has a strong genetic basis and is, itself, subject to natural selection. The second mechanism is by *adaptive genetic differentiation* in response to selection pressures in the local environment. If the variation in the traits under selection has a genetic basis, selection may increase the frequency of alleles in a population that enhance local fitness. The latter process will result in **local adaptation**, the 'home advantage' of genotypes in their local environment, provided that gene flow between populations is restricted, so that the differentiation that evolves is not continuously swamped by import of alleles that have experienced different selection pressures (Kawecki & Ebert 2004). Local adaptation, being an adaptive response of populations, is of concern in reintroduction programmes, as translocation implies the risk of introducing individuals that are maladapted to the conditions in the restoration area (examples are given in Chapter 8).

There is ample evidence for local adaptation of plant populations to their respective environments (Hufford & Mazer 2003), but it may in fact be less prevalent than was previously thought. A meta-analysis of plant transplantation studies (Leimu & Fischer 2008) shows that in more than 70% of the studied cases local genotypes outperform foreign genotypes at their site of origin. However, when these analyses are restricted to reciprocal transplant studies only, it appears that in half of the studies in fact one of the two local populations performed best at both sites (outperforming the other population both at its local and nonlocal site). Only in 45% of the cases studied did both local populations perform best at their own home site, thus exhibiting local adaptation in the strict sense (Kawecki & Ebert 2004). Also, local adaptation of plants to the biotic component of their environment is much less evident than local adaptation to the abiotic environment. In fact, host–parasite studies, including those of plant–pathogen and plant–herbivore interactions, generally show parasite local adaptation (Greischar & Koskella 2007), indicating that host plants suffer more from their local than from nonlocal biotic threats. This is especially true for parasites that have higher migration rates and shorter generation times than their hosts (Gandon & Michalakis 2002). The relative importance of abiotic and beneficial or detrimental biotic factors as determinants of fitness may thus affect the extent of local adaptation (Cremieux *et al.* 2008).

Nonetheless, local adaptation of populations is, and should be, an important consideration in the choice of **provenances** used in reinforcement or reintroduction. For instance, local adaptation may be one of the main factors explaining why the establishment success of reintroduced populations of rare or extinct wetland plant species in Switzerland is best explained by ecological similarity between source and introduction sites (Noël *et al.* 2011; Figure 7.2). Consequently, the choice of provenances in plant reintroduction programmes is commonly based on considerations of minimizing geographical distance to the restoration site or, more

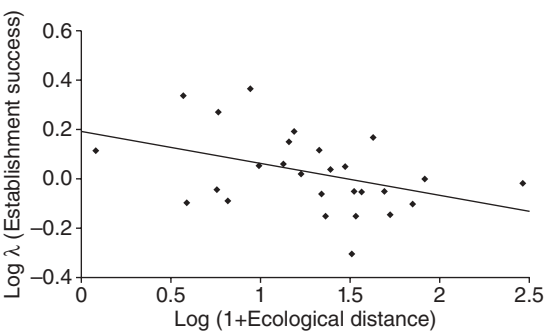


Figure 7.2 The relationship between establishment success of populations of 14 reintroduced wetland plant species in Switzerland (log λ, change in log population size per year) and the ecological distance between source and introduced site (based on PCA scores capturing differences in humidity, pH, nutrients, light, temperature and continentality). Life history traits and propagule pressure could not predict establishment success. (From Noël *et al.* 2011.)

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importantly, matching habitat conditions (Vander Mijnsbrugge *et al.* 2010) in combination with genetic considerations explained in section 7.2.4.

7.2.2 Inbreeding

As a result of restricted gene flow between populations, individuals within a population become related over successive generations and mating will occur between individuals that are related by ancestry, a process called *inbreeding.* Inbreeding results in a redistribution of genetic variation. The fraction of individuals carrying two copies of the same allele at any particular locus (homozygotes) increases at the expense of individuals carrying two different alleles at a locus (heterozygotes). In other words, inbreeding leads to a loss of heterozygosity. The latter is generally accompanied by *inbreeding depression*, the lower reproductive fitness of progeny resulting from matings between relatives than of progeny resulting from mating between unrelated parents, for two reasons. First, populations accumulate recessive mutations that have slightly deleterious effects on fitness. In heterozygotes, their negative effects are masked by the presence of a dominant functional allele; loss of heterozygosity leads to increased expression of the recessive deleterious alleles in a homozygous state. Second, many beneficial traits show a *heterozygote advantage* (heterozygotes have trait values higher than either of the homozygotes, *overdominance*); loss of heterozygosity abolishes this advantage.

Inbreeding depression is common. Crnokrak and Roff (1999) show that inbreeding depression occurs in 90% of 157 examined data sets from natural populations, including many plants. Inbreeding depression is not only associated with reduced offspring fitness but also with increased population extinction rate, as for example shown for the annual evening primrose relative, *Clarkia pulchella* (Newman & Pilson 1997), and for the shore campion, *Silene littorea* (Vilas *et al.* 2006) (Figure 7.3). These studies corroborate results from stochastic computer simulations showing that inclusion of realistic levels of inbreeding depression significantly increases extinction risk (O'Grady *et al.* 2006). Inbreeding depression is especially a problem in small populations as the extent of inbreeding is inversely related to N_e, the *effective population size*, defined as the number of breeding individuals that would result in the same rate of inbreeding as observed in the census population if that population had been 'ideal' (a population with random mating, constant population sizes etc.). N_e is often roughly an order of magnitude smaller than the actual census population size, for instance due to fluctuations in population size. This is because the years with small population sizes disproportionally contribute to an increase in the extent of inbreeding in a population.

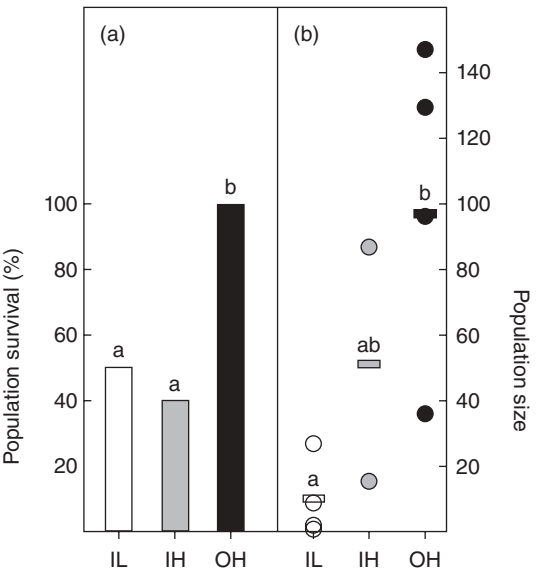


Figure 7.3 Effects of inbreeding and genetic variation on population extinction risk and population size of surviving populations in a reintroduction experiment of shore campion (*Silene littorea*) in Spain. (a) Experimental populations initiated with inbred plants and low genetic diversity (IL, white bars) or inbred plants with enhanced genetic diversity (IH, grey bars) had lower survival probability than populations initiated from outcrossed plants (OH, black bars). (b) Surviving populations initiated from inbred plants with low genetic diversity (white dots) also had lower population sizes in their second year than populations initiated from outbred plants (black dots). Symbols indicate different populations; vertical bars indicate population means and different letters indicate significant population type differences. (Adapted from Vilas *et al.* 2006.)

7.2.3 Genetic drift

Transmission of alleles from parents to their offspring is essentially a random sampling process. Allele frequencies will therefore fluctuate from one generation

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to the next, a process called *genetic drift*. In small populations, the consequences of such random sampling are much more pronounced than in large populations. First, in small populations rare alleles are more easily lost and common alleles are more easily fixed by chance than in larger populations, resulting in a loss of genetic variation. Second, in small populations, random changes in allele frequences due to genetic drift easily override changes in allele frequences due to natural selection, making the process of natural selection less effective. Third, when a large population becomes fragmented into smaller populations, different alleles may get lost or fixed in different population fragments, resulting in random genetic differentiation between habitat fragments. This contrasts with adaptive genetic differentiation as a result of a response to natural selection imposed by local selection pressures that underlies local adaptation (section 7.2.1). This may be one of the reasons that local adaptation is much more commonly observed in large than in small populations (Leimu & Fischer 2008), suggesting a lower ability to respond to environmental variation and change through adaptive genetic differentiation in small than in large populations.

Loss of heterozygosity and genetic diversity due to inbreeding and genetic drift in small populations generally results in a reduction of average fitness in the population (Reed & Frankham 2003). For instance, in the rare marsh gentian (*Gentiana pneumonanthe)*, size and reproduction of plants strongly increases with the number of loci at which they are heterozygous (Oostermeijer *et al*. 1995). A meta-analysis of plant studies by Leimu *et al*. (2006) shows that genetic variation – measured as expected heterozygosity, number of alleles or proportion of polymorphic loci (see Box 7.1) – increases with population size and is significantly and positively related to fitness. Since molecular variation at neutral loci will generally not be strongly related to the quantitative variation that is important for adaptation and the ability to evolve (Reed & Frankham 2001), one might expect that measures of genetic variation based on near-neutral DNA markers are less strongly related to fitness than measures based on protein or phenotypic markers. This is not born out by data; according to the meta-analysis by Leimu and coworkers the associations are at least as strong for DNA as for allozyme data. Of course, associations between population size and fitness not only are mediated by genetic factors, but also may in part be due to nongenetic causes such as reduced quality of small habitat fragments, and these factors may interact in their effects on population fitness.

7.2.4 Genetic rescue and genetic restoration

Due to inbreeding and genetic drift, alleles with slightly detrimental effects accumulate in small populations (called the 'genetic load' of a population), causing low mean population fitness. **Genetic rescue** is the intended introduction of (unrelated) individuals from other populations to reduce the genetic load, that has been advocated as a new management strategy to help avoid extinctions of such low-fitness populations (Tallmon *et al*. 2004; Edmands 2007). Even if one had wished to do so, restoration programmes that involve reinforcement or reintroduction of populations often cannot use source material from the exact local populations. Hence it introduces 'foreign' material, resulting in outcrossing with plants from different, genetically diverged populations, a process called *admixture*. Genetic rescue can be viewed as finding a balance between the positive effects of admixture (heterosis and increased genetic variation) and its negative effects (outbreeding depression).

Heterosis (or hybrid vigour) is the increased reproductive fitness of offspring resulting from admixture. In section 7.2.2 we have seen that this can be based either on dominance or overdominance of favourable alleles. Most of the experimental studies in plants indeed show increased fitness of interpopulation crosses, indicating potential for genetic rescue, including the rare yellow pitcher plant (*Sarracenia flava*) (Sheridan & Karowe 2000), the field mustard (*Brassica campestris*) (Newman & Tallmon 2001) and the rare Bavarian scurvy-grass (*Cochlearia bavarica*) (Paschke *et al*. 2002). The second potential advantage of admixture is increased genetic variation and the production of novel genotypes, increasing the adaptive potential of populations and their ability to cope with future environmental change. Conversely, there are risks of admixture if populations are locally adapted. The first risk is that it will dilute the locally adapted gene pool (i.e. reduce the pool of local alleles whose additive effects increase fitness); this process is called *extrinsic outbreeding depression*. The second risk is that admixture may lead to the breakdown of co-adapted gene complexes (positive interactions between alleles at different loci) that may have evolved in the local population;

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this is called *intrinsic outbreeding depression*. For instance, in crosses between individuals from different North American populations of partridge pea (*Chamaecrista fasciculata*) which have differentiated via co-adapted gene complexes, the positive effects of heterosis are progressively counteracted by the negative effects of intrinsic outbreeding (Fenster & Galloway 2000). In contrast, in many species such as the rare whorlded sunflower (*Helianthus verticillatus*), the positive effects of heterosis continue in subsequent generations without any sign of outbreeding depression. The importance of outbreeding depression is still much debated and is currently on the top priority list for conservation genetics research (Frankham 2010).

Genetic rescue has been extremely successful in a number of animals (Hedrick & Frederickson 2010), including adders (*Vipera berus*), greater prairie chickens (*Tympanuchus cupido pinnatus*), Mexican wolf (*Canis lupus baileyi*) and Florida panther (*Puma concolor coryi*), as well as in plants (Tallmon *et al.* 2004). Hedrick (2005) emphasizes, however, that genetic restoration involves more than just genetic rescue. Genetic rescue focuses on removing detrimental variants that increase in frequency in small isolated populations due to genetic drift, whereas the more comprehensive process of *genetic restoration* should not only focus on removing detrimental variation, but also consider how increased gene flow affects the other two types of variation: neutral variation and adaptive variation. Firstly, migrants may quickly spread in the population, increasing their representation in the gene pool and reducing the amount of neutral genetic variation that might be adaptive in future environments. Secondly, a few successful migrants may overwhelm selection that would otherwise maintain adaptive variants, reducing their frequency, a process called *genetic swamping*. For instance, in experimental populations of the field mustard (*Brassica campestris*), one immigrant per population increased fitness compared to no-immigrant controls (Newman & Tallmon 2001). Higher levels of immigration also increased fitness but led to less phenotypic divergence than with one migrant per generation, suggesting that lower immigration is sufficient to increase fitness without impeding the facilitation of local adaptation. An example of genetic restoration in animals is that of the Florida panther (Hedrick & Fredrickson 2010), the last surviving puma subspecies in eastern North America, that had in recent times nearly gone extinct in the state of Florida. Genetic restoration guidelines were to introduce eight pumas from a population in Texas that formerly had been connected to the Florida population by gene flow, to achieve an initial circa 20% ancestry from introduced Texas panthers, followed by one migrant per subsequent generation to eliminate detrimental variants while preventing the elimination of adaptive variants and increase the levels of neutral variation. Even though eventually no subsequent migrants were introduced, the admixture resulted in increased fitness, a doubling of heterozygosity, a decline in inbreeding correlates and a threefold increase in population size (Johnson *et al.* 2010).

7.2.5 Corollaries and consequences

The success of genetic restoration programmes in the past two decades has shifted our view regarding the risk of introducing foreign genetic material for restoration. Although outbreeding depression is a real phenomenon, its negative effects often do not outweigh the positive effects of heterosis, not only in first-generation hybrids, but also far beyond that. This has sparked renewed attention for the positive effects of low levels of gene flow for fitness and adaptive evolution and has provided faith in genetic restoration as a management tool if properly applied. Hedrick and Fredrickson (2010) recently devised 10 guidelines for successful implementation of genetic restoration, four of which specifically aim at minimizing the risks associated with admixture by continued management schemes that adjust the extent and number of repeated introductions. It is also worth taking a step back and asking whether the risk that intentional admixture will reduce population fitness is always the most relevant question to consider in an ecological restoration programme. After all, preserving or reintroducing populations with suboptimal fitness may in many cases be preferred over the final absence of populations that would result if no restoration at all is undertaken (cf. van Andel 1998; Kiehl 2010).

7.3 METAPOPULATIONS

Population processes take place in landscapes consisting of networks of habitat patches and, therefore, disciplines that explicitly link local abundance to regional occurrence are necessary to understand species abundance patterns at larger scales and how to restore them. Metapopulation ecology and genetics

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approaches have been developed to deal specifically with consequences in sets of local populations whose dynamics are characterized by frequent extinction and recolonization. We start this section by presenting the scientific approach of metapopulation ecology and genetics (section 7.3.1), and then illustrate how they contribute to restoration ecology, focusing on the 'rescue' of metapopulations (section 7.3.2), in analogy to the rescue of populations.

7.3.1 Metapopulation ecology and genetics

Metapopulation approaches are useful in the context of restoration as they can provide guidance as to how to optimize not only within-population, but also among-population, processes that are critical for species persistence across their respective ranges, including patch connectivity and migration rates. Theoretical models can be classified according to the type of spatial organization of suitable habitat patches in the landscape matrix that they assume. Two extremes are (1) the mainland–island models derived from island biogeography (MacArthur & Wilson 1967) and (2) Levins's models (Levins 1969) described below. Most mainland–island models assume that there is one large source patch (mainland) and numerous smaller habitat patches (islands) that can go extinct and be recolonized from the mainland patch. In contrast, Levins's model assumes more evenly sized patches, any one of which can go extinct and then be recolonized from nearby patches. The spatial organization of most natural metapopulations will share characteristics of both and can be classified in more detail. Not all sets of populations are characterized by frequent extinctions and recolonizations, a key feature of metapopulation dynamics in the strict sense (Hanski 1999). Also, large patches do not necessarily act as sources. If their intrinsic growth rates are low, for instance due to low patch quality, they can act as sinks rather than sources within the metapopulation. In that case, restoration efforts that focus on large patches may in fact endanger the metapopulation as immigrant sources are neglected. Such knowledge is thus of vital importance when deciding which patches are important to focus on in restoration projects and programmes.

Migration rates play an important role in metapopulation persistence. On the one hand, migration rates should be large enough to ensure that recolonization rates exceed extinction rates, key to metapopulation persistence. On the other hand, migration rates should be small enough to allow demographics of patches within the metapopulation to proceed independently. Spatiotemporal variation in demographics among patches in a metapopulation is essential for species persistence as it ensures the presence of source patches at all times.

The structure of metapopulations may suggest that they should be well buffered against loss of genetic variation, better than single local populations. Indeed, compared to an unfragmented population of the same total size, structures with several small fragments that are ill connected (low levels of gene flow) initially retain higher genetic variation (Frankham *et al*. 2005). This is because different alleleles will be fixed and lost in different fragments; the chance that they are lost from all fragments is therefore smaller than in a single large population. However, due to the low effective population sizes of the constituent fragments, all metapopulation structures are likely to suffer higher levels of inbreeding than a single large population. Due to the larger extinction probability of smaller fragments, any subdivided population structure will therefore eventually have lower total genetic diversity than a single large population. The role of genetic rescue in restoration of metapopulations could therefore be at least as important as in restoration of unfragmented populations.

7.3.2 Rescue of metapopulations

Similar to what we have seen for single populations (section 7.2.4), metapopulation persistence is enhanced by ecological and genetic rescue. The metapopulation rescue effect refers to the positive effect of the number of immigrants on occupancy of suitable patches, reducing extinction risk. Practices that enhance dispersal (reinforcement, stepping stones and corridors) therefore generally contribute to metapopulation rescue, as they increase the proportion of suitable habitat that is occupied and the successful colonization rate (establishment effect). Even a very limited amount of migration can have a profound effect upon the recipient population. We illustrate this with some examples given by Stacey *et al*. (1997). White-footed mice (*Peromyscus leucopus*) have persisted in a remnant network of woodlot patches in North America, connected by migration routes. Populations linked by these high levels of migration have higher growth rates than populations linked by lower levels of migration and

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there is clear evidence for a similar rescue effect in several other small mammal species. Pool frogs (*Rana lessonae*) that occur in natural metapopulations along the Baltic coast of Sweden reproduce only in distinct water bodies. Over a 6-year period, populations isolated by greater than 1 km became extinct, whereas less isolated populations tended to persist.

In the aforementioned examples of metapopulation ecology, genetic aspects have not been considered. We now refer to a number of studies on the genetic rescue of metapopulations. Populations of blacktail prairie dog (*Cynomis ludovicianus*), which appeared to consist of several family groups called 'coteries', remain spatially distinct from each other because of a rigid social structure. Regular influx of male immigrants reduces inbreeding within local populations and elevates levels of heterozygosity, potentially 'rescuing' populations from inbreeding depression and possible extinction (Stacey *et al*. 1997). Also, for small mammals such as pikas (*Ochotona princeps*) migration among habitat fragments appears to be important in maintaining genetic variation within the metapopulation and preventing the loss of heterozygosity in component populations. In metapopulations of the checkerspot butterfly *Melitaea cinxia*, many local populations are small and inbred. Inbreeding depression is strong, especially under less favourable environmental conditions, and inbred populations suffer increased extinction risk (Nieminen *et al*. 2001). Since most populations within the metapopulation are small, the total number of migrants and thus the potential number of recolonizers within the metapopulation is low, increasing metapopulation extinction risk and calling for enhanced migration and metapopulations rescue. Similar observations have been made for plants. For example, in metapopulations of the white campion (*Silene latifolia*) effects of inbreeding are mitigated by higher gene flow into patches with genetically related than into patches with genetically unrelated individuals (Richards 2000). The effect is probably due to the higher success of outcross pollen in patches with genetically interrelated individuals than in patches consisting of unrelated individuals, pointing at a role of connectivity through pollen-mediated gene flow on persistence of isolated patches. In 27 populations of the marsh grass *Parnassia palustris*, distributed over three metapopulations, between-metapopulation crossings result in higher seed production than within-metapopulation crossings, especially for smaller populations. This *genetic rescue* is probably due to alleviation of the low pollen compatibility within metapopulations due to low genetic diversity (Bossuyt 2007).

7.3.3 Corollaries and consequences

Several generalities arise from metapopulation theory (cf. Maschinski 2006). Persistence is enhanced by higher numbers of suitable patches, larger average patch size, larger fraction of large patches at the interior, higher within-patch reproductive rates, enhanced patch connectivity, higher immigration rates and lower emigration rates. Metapopulation models help to predict the fate of a metapopulation as a whole, to assess the value of individual patches for species' persistence, and to manage migration by stepping stones, corridors and repeated introductions. They can also serve to estimate minimum viable metapopulation sizes (MVM), which is the minimum number of interacting local populations necessary for long-term persistence of a metapopulation. The MVM is thought to be governed by an equilibrium between the rates of extinction and of recolonization of suitable habitat patches. Metapopulations that are not at extinction–recolonization equilibrium are heading for extinction.

Even though most relevant models suggest that the largest patch in the metapopulation is the most important determinant of overall persistence, in any particular restoration programme it is often difficult to judge the relative benefits of enhancing size per patch (decreasing local extinction probability of subpopulations) versus constructing more patches (increasing metapopulation viability). Nicol and Possingham (2010) point out that the optimal metapopulation structure strongly depends on the specific metapopulation parameters and suggest stochastic dynamic programming as a tool to design optimal restoration strategies.

7.4 SPECIES INTERACTIONS AFFECTED BY HABITAT FRAGMENTATION

Habitat fragmentation of plant populations not only affects individual plant species themselves, but also their interactions with potential mutualists such as mycorrhizae and pollinators, as well as antagonists such as herbivores and pathogens (see also Chapter 6). This is because the spatial scale of population processes

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and species–area relationships depend on trophic rank (Holt *et al.* 1999). Reductions in size and increased isolation among habitat fragments of different species can therefore disrupt trophic interactions. We distinguish between ecological and evolutionary genetic consequences of fragmentation for such interactions. The former reflects alterations in distribution, abundance and dynamics of potentially interacting species, affecting their encounter rate or interaction frequency. The latter, amongst other factors, reflects alterations in the genetic constitution of the potentially interacting species that affects the outcome of their interactions. Moreover, ecological and genetic consequences interact, that is, changes in encounter rate can drive life history evolution of organisms involved. In this section, we discuss some of the ecological consequences (section 7.4.1), and then, in section 7.4.2, some of the genetic and evolutionary consequences of habitat fragmentation for species interactions.

7.4.1 Ecological consequences

The spatial scale at which population processes operate differs among species, depending on their trophic rank, degree of habitat specialization, body size and dispersal ability, among other things. Consequences of alterations in spatial habitat structure such as fragmentation therefore differ between species, and consequently change or disrupt interactions such as pollination, parasitism or predation, and interspecific competition. Habitat fragmentation is most strongly felt by species if they have larger body size, lower dispersal capacity, are habitat specialists and are positioned at higher trophic levels (Tscharntke & Brandl 2004). The presumed increase in sensitivity to fragmentation with trophic rank indicates that fragmentation has important consequences for the outcome of multitrophic interactions. An example is the work of Elzinga *et al.* (2005, 2007). They performed a three-year study in a series of fragmented populations of the white campion (*Silene latifolia*) along the river Waal (Netherlands), to assess the effects of plant population size and isolation on trophic interactions between the plant, one of its specialist herbivores, the fruit-predating moth *Hadena bicruris*, and a range of hymenopteran insects that parasitize the herbivore (Figure 7.4). These studies have shown that the herbivore is present in virtually all plant patches, even the smallest and most isolated ones. However, the incidence of the most common parasitoid, *Microplitis tristis*, strongly declines with plant population size (Figure 7.4a). The same is true for the parasitoid *Eurylabus tristis*, especially in isolated patches; in order to have a 50% probability of occurrence, a plant population size of 10 appears to be required for closely connected patches but a population size of more than 700 is required if the nearest neighbouring patch is two kilometers away (Figure 7.4b). Accordingly, parasitism rates of the herbivore are lower in smaller and more isolated plant patches (Figure 7.4c). Presence of the herbivore is thus not affected at the current scale of fragmentation of the plant's habitat, but that of the parasitoids is, corroborating the idea that higher trophic levels are more sensitive to fragmentation. Release of herbivores from parasitism in small isolated patches could result in increased herbivory. Indeed, the proportion of predated fruits on plants is much higher in small than in large populations (Figure 7.4d), but this may also be due to behavioural responses of the herbivore to host density.

Fragmentation not only alters interactions of plants with their herbivores and associated parasitoids, but also with diseases. Most airborne diseases have a threshold host population size below which they cannot persist; this threshold is higher for pathogens with low transmission efficiency. Both small host-population size and low connectivity may thus decrease the probability of host populations to be infected, as shown in several natural systems (Antonovics *et al.* 1997, and references therein). One of the ecological consequences of corridors designed to increase **connectivity** of target species is that they may also, inadvertedly, facilitate the spread of herbivores and diseases (Hess 1996). Thus, whereas fragmentation may be detrimental for pollination service, it may reduce the contact rate with diseases. Since diseases can severely impact natural populations (McCallum & Dobson 2002), it should be ascertained whether the benefits of *corridors* outweigh their risks.

7.4.2 Evolutionary genetic consequences

As mentioned, **habitat fragmentation** results in loss of genetic variation, and increased levels of genetic drift and inbreeding. The genetic consequences of fragmentation for species interactions can be profound. A classic example of the effect of low levels of genetic variation and heterozygosity on resistance is the African cheetah, *Acinonyx jubatus* (O'Brien & Evermann 1988).

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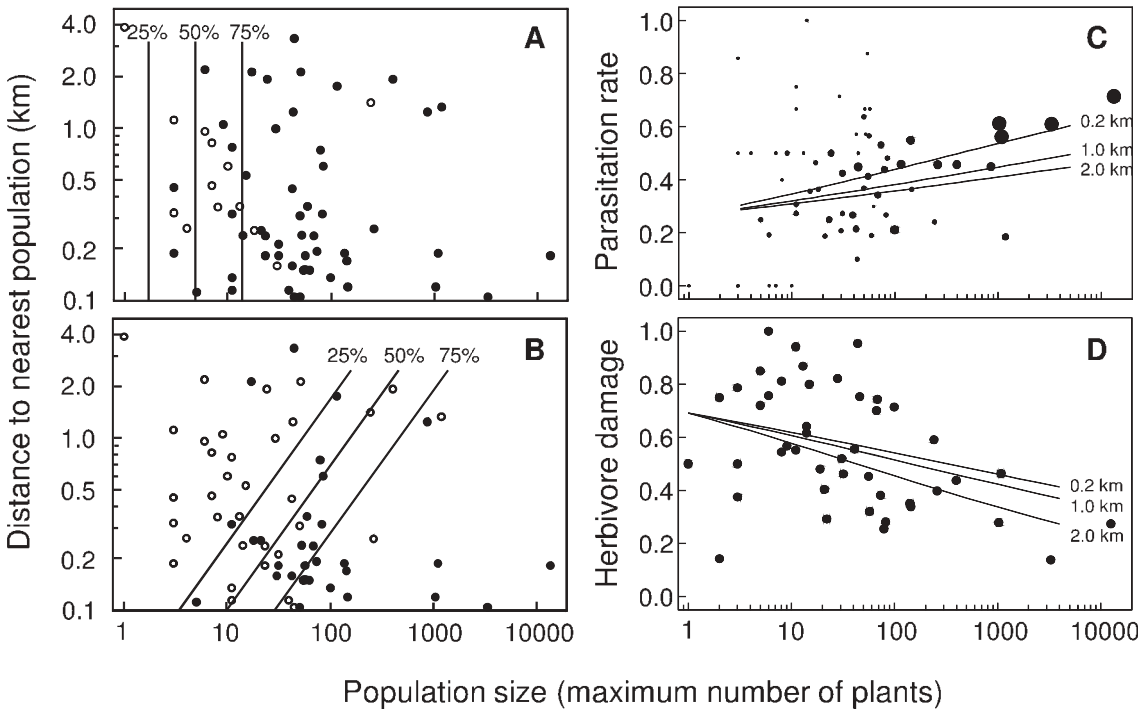


Figure 7.4 Mismatches between the effects of decreased population size of white campion (*Silene latifolia*) on its fruit herbivore *Hadena bicruris* and on the hebivore's parasitoids *Microplitis tristis* and *Eurylabus tristis*. (a) Presence (closed dots) and absence (open dots) of *M. tristis* as a function of plant population size and connectivity. Lines indicate population sizes required for 25%, 50% and 75% presence. (b) Same for *E. tristis*. (c) Effect of plant population size on the proportion of herbivores that is parasitized. (d) Effect of plant population size on the proportion of fruits predated by the herbivore. Lines indicate estimates for three levels of connectivity (distance to nearest population 0.2–2.0 km). (Modified from Elzinga *et al.* 2005, 2007.)

Populations with low levels of genetic variation at both neutral markers and functional genes of the immune system show high incidence of the parasite-induced disease 'feline peritonitis', although causal relationships have yet to be proven. Another way in which inbreeding affects the outcome of species interactions is through effects on the extent of adaptive plasticity. The fresh-water tadpole snail (*Physa acuta*) shows adaptive morphological and behavioural responses in the presence of predatory fish that contribute to predator avoidance. Inbreeding reduces the extent of these responses by half (Auld & Relyea 2010) thereby impeding its induced defense responses. But not only animals experience genetic consequences of fragmentation that impact their interactions with pests and predators. Also in plant populations, low levels of genetic variation and inbreeding (resulting in loss of heterozygozity) can decrease their resistance to herbivores and pathogens (Spielman *et al.* 2004b). For instance, inbred plants of monkey flower (*Mimulus guttatus*) show increased suceptibility to spittlebugs (*Philaenus spumarius*) (Carr & Eubanks 2002). However, the magnitude and even the direction of the effect of inbreeding on resistance commonly vary among and even within populations. An illustrative example is the study of effects of experimental inbreeding in white campion, *Silene latifolia* (Ouborg *et al.* 2000), using a large number of inbred lines created by brother–sister matings for four generations, resulting in a range of inbreeding levels within each line. Contrary to expectation, experimental inbreeding on average slightly increases resistance of *S. latifolia* to one of its common pathogens, the anther smut fungus *Microbotryum violaceum*. But most strikingly, the effect of inbreeding is inconsistent among

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lines, with some showing a strong increase while in others a strong decrease in resistance with inbreeding coefficient is observed. The inbreeding lines of *S. latifolia* also show varying levels of inbreeding depression in traits involved in the attraction of vectors of the disease, that is transmitted by pollinating insects, such as flower size and nectar production. Inbreeding depression in resistance and attraction traits even appear to be uncorrelated (Ouborg & Biere 2003), further hampering predictions of the overall effect of inbreeding on the probability of becoming diseased.

7.4.3 Corollaries and consequences

Habitat fragmentation has ecological consequences (changes in encounter rates among species) and genetic consequences (changes in the outcome of interactions) for species interactions that cannot be viewed in separation. Dynamics of host and pathogen population sizes feed back on the dynamics of frequencies of resistance and avirulence alleles and vice versa. For instance, changes in encounter rates with mutualists or antagonists can induce changes in selection pressures on resistance, avoidance and life-history traits (Hochberg & Moller 2001). Moreover, rapid evolution can take place if species interactions are changed, as in climate change-induced shifts and species invasions (Chapters 20 and 21). For instance, habitat fragmentation can select for traits related to dispersal (Olivieri *et al.* 1995). Likewise, loss of interactions with pollinators may select for traits related to reproductive assurance. These examples make it clear that to be effective, restoration efforts must incorporate considerations of the likely, multiple effects of interventions, manipulations and management on species interactions. This suggests the need to preserve or enhance pollinator interactions, genetic variation for defense-related traits, and minimize risks of connectivity on disease transmission, as many restoration programmes indeed already do.

7.5 FROM CONSERVATION TO RESTORATION: PERSPECTIVES

Conservation science and restoration ecology are complementary disciplines. Restoration may become essential if conservation efforts have failed to preserve local populations. Genetic aspects of restoration are challenging because in the case of both population reinforcement and species reintroductions the question has to be answered: from which external sources will provenances be taken? The knowledge that plant populations are often adapted to local site conditions implies that external seed sources may not match the conditions of the target site (McKay *et al.* 2005). Indeed, research-based 'seed transfer zones' have to be delineated, defined as the geographical regions within which individuals (seeds, seedlings, or adults) of native species can be transferred with no detrimental effects on population mean fitness (Hufford & Mazer 2003). Ecological similarity (matching habitat conditions) between source and introduction site may be at least as important as small geographic distance (Vander Mijnsbrugge *et al.* 2010; Noël *et al.* 2011).

Another important challenge for restoration ecologists is that conservation efforts may no longer be sufficient to ensure that populations can stand impending future unfavourable change due to the rapidly increasing habitat degradation and fragmentation, globalization of pests and diseases and climate change. Indeed, understanding the response of populations and communities to climate change, and their genetic consequences, is one of the most pressing research questions for the near future (Kramer & Havens 2009). As climate change is far beyond the control of organizations in charge of nature management, this is a most challenging argument to move from conservation to restoration, indeed (see also Chapter 21). Seed sourcing for restoration may therefore shift from a purely local provenancing strategy to a strategy based on careful admixture with seeds from more distant sources to maximize evolutionary potential (Broadhurst *et al.* 2008) or even from sources that better match the future local climate predicted by climate models (Crowe & Parker 2008). There is an increasing body of literature about mismatches between interacting populations of different species as a result of changing temperature regimes. For example, reduced spatial variability in plant phenology as a result of experimental and observed warming in the growing season resulted in a decline in the offspring production by female caribou, *Rangifer tarandus*, in Greenland (Post *et al.* 2008). Similarly, Visser *et al.* (2006) show from their analysis of a 20-year data set in a Natural Park in the Netherlands that the synchrony between offspring needs of the insectivorous great tit (*Parus major*), and the caterpillar biomass of this bird's main food species, have been disrupted

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during the recent, unusually warm, decades and are not likely to be repaired in the decades to come.

These examples show that the recognition of interactions between populations of species that meet in a community is crucial in any restoration programme. Therefore, we conclude this chapter by referring to 'community genetics', a new field of science focused on the evolutionary genetic processes that occur among interacting populations in biotic communities. Heritable genetic variation within species, especially dominant or **keystone species**, can have effects beyond the population level, a phenomenon referred to as the *extended phenotype effect* (Whitham *et al.* 2003). For example, distinct genotypes of narrowleaf cottonwood (*Populus angustifolia*) support unique arthropod communities that remain consistent over many years. This is an example of so-called *community heritability* (Keith *et al.* 2010). There is increasing evidence that the extended phenotype effect can affect ecosystem processes ranging from nitrogen mineralization and litter decomposition to community structure of the insect species associated with a particular species of plant. For instance, differences in resistance among Pinyon pines to a keystone herbivore have community-level consequences for bird, mammal and rhizosphere microbe communities (Whitham *et al.* 2003). Genotypic diversity in a dominant old-field plant species, late goldenrod (*Solidago altissima*), affects arthropod diversity and community structure as well as net annual primary productivity. The magnitude of this effect can be as large as the effects generally observed for between-species diversity (Crutsinger *et al.* 2006).

One of the consequences of the extended phenotype effect of genes is that we have to reconsider how we should estimate minimum viable population (MVP) size. Whitham *et al.* (2003) defined MVIP as the minimum viable interacting population size, the size of a population needed to maintain genetic diversity at levels required for other interacting species in the community as well. No empirical estimates have been made to date, but clearly these will be larger than MVP. These observations emphasize the cascading effects of the impact of human activities on the evolution of species and communities.

In Chapter 21, the authors address how restoration ecologists and practitioners can apply theories on evolutionary and community dynamics to anticipate and incorporate future – and largely uncertain – environmental changes. In the present chapter, we have explored the foundations of the mechanisms of selection and evolution, knowledge that is indispensable for estimating whether the current *evolutionary potential* of species is a sufficiently sound ecological basis to 'restore to the future'. A bit more than 40 years after the pivotal work of Heslop-Harrison (1964), entitled 'Forty years of genecology', we can now state that the interface between population ecology and populations genetics has come of age.

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Chapter 8

REINTRODUCTIONS: LEARNING FROM SUCCESSES AND FAILURES

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8.1 REINTRODUCTION OF SPECIES AND RESTORATION ECOLOGY

The very first *attribute of restored ecosystems* mentioned in the *SER Primer on Ecological Restoration* (SER 2004) is that 'the restored ecosystem contains a characteristic assemblage of the species that occur in the reference ecosystem and that provide appropriate community structure'. In this context, intended introductions of species are an important tool, because dispersal is very often a major constraint, especially in highly fragmented habitats and landscapes. Thus, even if the SER Primer speaks in terms of whole ecosystems for the most part, restoring species diversity (*sensu* Falk *et al.* 1996) is a crucial part of ecological restoration. More specifically, this phrase refers to the reintroduction of species or subspecies that have been lost or whose populations have been seriously reduced and weakened for various reasons.

In response to the increasing occurrence of **reintroduction** projects worldwide and to help ensure that they achieve their intended conservation benefit, the Reintroduction Specialist Group of the International Union for the Conservation of Nature (IUCN) Species Survival Commission has developed guidelines (IUCN 1998) in the context of the IUCN's broader policies pertaining to biodiversity conservation and sustainable management of natural resources. According to the IUCN, the principal aim of any reintroduction should be to establish a viable, free-ranging population in the wild, of a species, subspecies or race, where it has become globally or locally extinct, or extirpated. The population should be reintroduced within the species' former natural **habitat** and range, where it should ideally persist with minimal or no need for long-term management. The objectives of a reintroduction may include the enhancement of the long-term survival of a species, the re-establishment of a keystone species in an ecosystem (or an emblematic species from a cultural point of view), or the maintenance and/or repair of **biodiversity** in (semi)natural landscapes. In the literature, both the terms **reintroduction** and **translocation** are being used. Strictly speaking, these terms do not mean exactly the same thing. Reintroduction is to establish a species within its historical range through the release of wild or captive-bred individuals following exterpation in the wild (IUCN 1998). Re-establishment is often used as a synonym, but implies that the reintroduction has been successful. A translocation is a deliberate and mediated movement of wild individuals or populations from one part of their range to another.

Community, ecosystem and landscape changes and transformations carried out in the past may have major consequences for the success of reintroduction attempts because the ecosystem or habitat at issue may have become permanently unsuitable for the species of concern, for example due to **climate change** (see below, section 8.8). However, even when habitat suitability is ensured, many reintroductions fail. There are, indeed, many other factors involved in reintroduction becoming either a success or a failure. **Keystone species**, for example, play a critical role in communities, and their effects are generally much larger than would be predicted from their relative abundance (see also Chapter 2). If keystone species become threatened or go extinct in their habitat it can be expected that the system changes dramatically and that, next to trying to reintroduce the keystone species into its habitat, the changes may have become so extensive that reintroduction becomes very difficult. It has been shown through modelling work that even random removal of species can lead to cascading extinctions far beyond the target one (Borvall *et al.* 2000; Lundberg *et al.* 2000), and that cascading extinctions are positively related to species abundance and **connectivity** (Law 1999). If ordinary (i.e. nonkeystone) species can have such effects, what can we expect if keystone species become extinct? No clear field data are available at present, but this question stresses the need for the conservation of keystone species while they are still present in their original habitat.

In this chapter, I will highlight some of the important aspects of the art and science of reintroducing plant and animal species that largely determine the outcome – either success or failure.

8.2 SOURCE POPULATIONS

Individuals targeted for reintroduction can come from various sources, and as a first step a careful assessment should always be made of the taxonomic status of the candidate sources or **provenances**. Even though the species concept as a basic taxon unit is controversial, individuals should ideally be of the same subspecies as those that were locally extirpated. Genetic studies should be carried out, if possible, to determine the relative degree of taxonomic and genetic similarity between possible substitutes and the pre-existing population.

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Genetic analyses may also permit prediction of the likelihood of hybridization taking place with other taxa in the target or release area or region. For this reason, it is preferable that source animals for reintroductions be taken from wild populations and not from captive ones. Captivity can affect adaptive behavioural traits. For plants, it is important that seeds or **propagules** of locally adapted **provenances** be used because many local populations show a home-site advantage and nonlocal genotypes may be maladapted (see Chapter 7). For plants and animals, the source population should ideally be closely related genetically to the original native stock and also show ecological characteristics (morphology, physiology, behaviour, habitat preference etc.) similar to the original population or subpopulation.

If a subspecies has become extinct in the wild and in captivity, a substitute form may be chosen for possible release or reintroduction. Such substitutions can actually be seen as a form of benign introduction. Selection of a suitable substitute should focus on extant subspecies and consider genetic relatedness, phenotype, ecological compatibility and the conservation value of potential candidates. For example, a local population of ibex (*Capra ibex*) that became extinct in former Czechoslovakia was replaced by reintroductions of Austrian *C. ibex* and Turkish *C. hircus aegagrus* and *C. ibex nubiana* from the Sinai desert (reviewed in Stanley-Price 1989). The inevitable hybrid forms dropped their kids in the middle of the winter, 3 months earlier than pure *C. ibex*, resulting in the death of all offspring. This case illustrates the need to assess both hybridization risks and ecological compatibility (Seddon & Soorae 1999). In general, there is a need for information on whether the introduction can literally be considered a **reintroduction** or whether it entails a risk of effects like those related to unintended **invasions** by aliens.

Additional considerations concern the pool or source from which organisms are removed. Removal of individuals for reintroduction should not endanger the wild source population, and individuals should be removed from a wild population only after the effects of translocation on the donor population have been assessed and evaluated. This is especially so when the source population is threatened. Sometimes this can go well, especially with territorial species where empty territories can be taken quickly by 'superfluous' animals which did not have a territory (Bain & French 2009), but a species may become so threatened in the wild that it is taken into captivity, and the loss of wild animals may leave only captive populations. Examples include the Arabian oryx (*Oryx leucoryx*), the Przewalski horse (*Equus przewalskii*) and the sorocco dove (*Zenaida graysoni*; Stanley-Price 1989). In such cases, there is still the potential to breed species in captivity although the results of genetic and phenotypic changes such as genetic drift, inbreeding, domestication, increased tameness and the loss of behavioural traits will tend to preclude the chances for successful reintroduction and subsequent *in situ* conservation. Attempts of the reintroduction of captive-bred animals into suitable habitats include programmes for the black-footed ferret (*Mustela nigripes*), the golden lion tamarin (*Leontopithecus rosalia*) and the red wolf (*Canis rufus*). Unfortunately, the success rate of reintroduced captive-bred individuals is highly variable and often very low (James *et al*. 1983). The process of translocation (including catching, captivity and transport) may lead to altered corticosterone levels and chronic stress and this can have serious effects on the performance of translocated animals as has been found in widely different species like the chukar partridge *Alectoris chucar* (Teixera *et al*. 2007) and elephants (Pinter-Wollman *et al*. 2009).

A special hazard related to the reintroduction of animals is the risk of unintentional introduction of disease or pathogens. The guidelines of IUCN (1998) prescribe that prospective release stock should be subjected to a thorough veterinary screening process before transport from the original source. There are many examples of devastating effects of diseases introduced unintentionally. The parasitic round worm *Pneumostrongylus tenuis* was the likely cause of the failure of elk (*Cervus canadensis*) to survive in the Adirondacks (Severinghaus & Darrow 1976); following successful release in the region in the early nineteenth century, presence of the species has not been reported in the region since 1953. Another example concerns amphibians, which are declining at alarmingly fast rates worldwide. Four hundred and thirty-five species have shown rapid declines, and nine species have become extinct since 1980, while 113 more are possibly extinct (Skerrat *et al*. 2007). At present amphibians are threatened by the disease chytridiomycosis caused by the fungus *Batrachochytrium dendrobatidis* (Walker *et al*. 2008). This highly lethal pathogen has been shown to be introduced in novel habitats (e.g. the island of Majorca) with relocated individuals that were, alas, already infected with the fungus. A recent survey revealed that many breeding facilities for amphibians in different parts of the world are infected with

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the parasite. Care has to be taken to thouroughly check relocation candidates for deseases and other parasites.

8.3 FOUNDING NUMBERS, DIVERSITY AND POPULATION STRUCTURE

In general, the number of individuals that are released in reintroduction attempts is small. This means that founding groups are susceptible to the same dangers of increased extinction risks as small, natural populations: environmental fluctuations, demographic stochasticity and inbreeding. Therefore, to achieve the highest possible success, a primary goal of reintroduction should be to maximize the initial rate of population increase in order to shorten the period during which the introduced population is exposed to these risks. This can be brought about by releasing a high number of individuals in a high-quality habitat. Komers and Curman (2000) investigated how the rate of increase of more than 30 newly reintroduced populations was affected by various population characteristics such as population size, sex and age structure in Artiodactyla (even-toed ungulates). Their results were in line with the general notion that reintroduction success increases with the number of animals released (Figure 8.1). The function became asymptotic at about 20 animals. When fewer than 20 animals were released, the variance in growth rate increased substantially and, of a number of factors, only age structure explained a significant portion of this variance. The population growth increased with the proportion of mature animals in the population (Figure 8.2). This finding could be explained by a higher fecundity of mature females.

Loss of genetic variability, due to genetic drift and/or inbreeding, is especially likely when an effectively small number of individuals is used in founder populations. Because of its importance, many conservation plans call for the maintenance of genetic variability in translocated populations. Stockwell *et al.* (1996) examined 10 translocations in mosquito fish (*Gambusia affinis* and *G. holbrooki*). These populations had significantly lower levels of heterozygosity than their respective parental source populations. The reduction in the diversity of relatively rare alleles varied from 24 to 40%, while the initial translocations involved hundreds of mosquito fish, which have various reproductive traits that appear to minimize the effects of

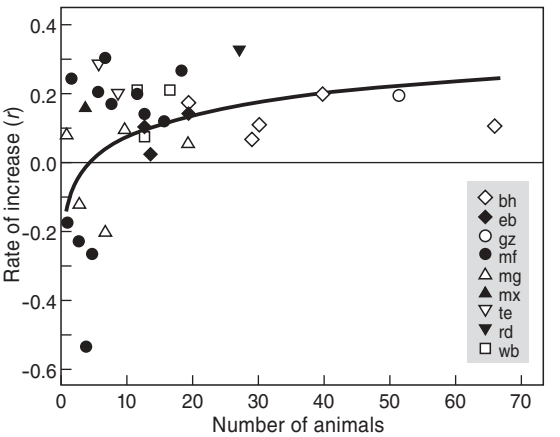


Figure 8.1 The rate of population increase in relation to the number of animals in reintroduced ungulate populations. Source species are shown in the key: mf, mouflon; mx, muskox; te, tule elk; rd, red deer; mg, mountain goat; eb, European bison, wb, wood bison; bh, bighorn sheep; and gz, mountain gazelle. (Modified from Komers and Curman 2000. Reproduced by permission of Elsevier.)

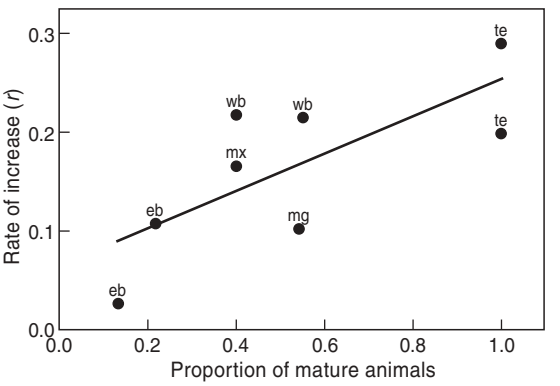


Figure 8.2 The rate of population increase in reintroduced ungulate populations in relation to the proportion of socially mature animals in populations of fewer than 20 animals. Source species: mx, muskox; te, tule elk; mg, mountain goat; eb, European bison; wb, wood bison. (Modified from Komers and Curman 2000. Reproduced by permission of Elsevier.)

bottlenecks on genetic diversity. Similar effects have been found in other introduced populations (e.g. seabream, trout, salmon, Anolis lizards, house sparrow, common myna, reindeer and ibex), as reviewed by Stockwell *et al.* (1996). Reductions in allelic diversity

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are often due to loss of rare alleles, which typically have little effect on overall heterozygosity. It is clear that reintroduction programmes should attempt to create populations with high levels of genetic diversity. Starting with the highest possible number and ensuring a high initial population growth rate will help to maintain high genetic diversity, but the effects of genetic diversity on the success rate of reintroductions is still to be further explored (see also Chapter 7).

Sometimes, insights in **metapopulation** theory may be used to understand the success rate of reintroductions. Singer *et al.* (2000) related the fate of a number of bighorn sheep (*Ovis canadensis*) reintroductions to this species naturally occurring in metapopulations. At present, most extant populations of bighorn sheep consist of fewer than 100 individuals occurring in a **fragmented** distribution pattern whereas the species formerly occupied a more continuous and wider range. Singer *et al.* (2000) investigated the correlates for the rate of colonization of 79 suitable, but unoccupied, patches by 31 translocated populations of bighorn sheep released into nearby patches of habitat. Dispersal rates were 100% higher in rams than in ewes. Successful colonizations of unoccupied patches (24 out of 79 patches were colonized) were associated with rapid growth rates of the released population (Figure 8.3), years since release (Figure 8.4), larger area of suitable habitat in the release patch, larger population sizes and a seasonal migration tendency in the released population (Figure 8.5). In this study area, colonization rates were much higher than other studies have reported (Singer *et al.* 2000), and this could be attributed to the presence of larger regions of unoccupied suitable habitat with a greater probability for

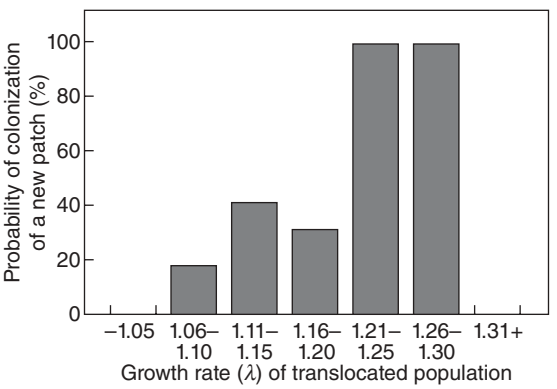


Figure 8.3 Probability of successful colonizations of new patches is correlated with population growth rates (λ) of 31 translocated populations of bighorn sheep in the western United States in 1946–1997. (Modified from Singer *et al.* 2000. Reproduced by permission of Wiley-Blackwell Publishers.)

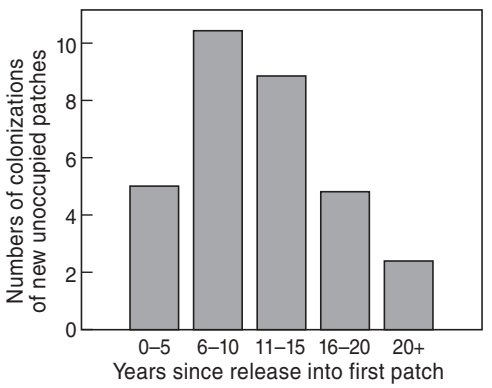


Figure 8.4 Probability of successful colonizations in relation to the number of years since release in the first patch for 31 translocated populations of bighorn sheep released 1947–1991. (Modified from Singer *et al.* 2000. Reproduced by permission of Wiley-Blackwell Publishers.)

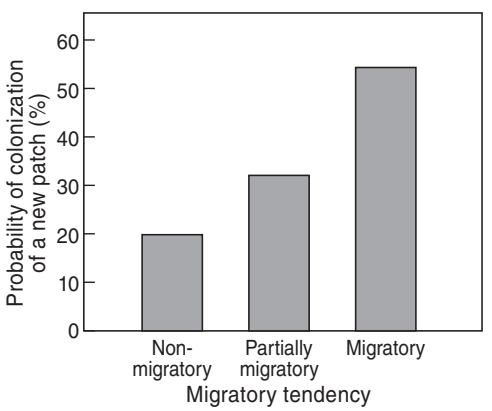


Figure 8.5 Probability of successful colonizations in relation to migratory tendency in the release patch for 31 translocated populations of bighorn sheep. Migratory, >75% of the population uses distinct seasonal changes; partially migratory, part of the population migrates; nonmigratory, year-round use of the same ranges. (Modified from Singer *et al.* 2000. Reproduced by permission of Wiley-Blackwell Publishers.)

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detection than the other studies. It is possible that bighorn sheep existed mostly in metapopulations but that human disturbance has accelerated extinction rates, and that extant bighorn sheep (meta)populations now occur in a non-equilibrium state. The results of this study also indicate that many restoration projects in the past probably suffered from poor procedures. Many prior translocations consisted of small founder groups (typically fewer than 25 animals) released into small, isolated patches of habitat, probably representing a near-perfect prescription for failure.

8.4 THE REINTRODUCTION SITE

Reintroduction in the core of the historic range of a species has sometimes been indicated to be better than reintroducing along the periphery (Griffith *et al.* 1989; Wolf *et al.* 1996). However, Lomolino and Channell (1998) found that 23 out of 31 species of endangered mammals persisted on the periphery, rather than in the core or central portion of their historic range. In addition, persistence was greater for insular than for continental populations. According to Lomolino and Channell, the peripheral part of the range encompasses a much more diverse collection of habitats and environmental conditions than the core sites, at the centre of the species' range. They referred to the California condor (*Gymnogyps californianus*) which was also succesfully released to a site in northern Arizona, well outside the condor's present range, but also providing protection from anthropogenic threats. From their review of reintroductions of marsupials in Australia, Short *et al.* (1992) came to the conclusion that the success rate of island introductions (60%) was far greater than for those in mainland Australia (11%), even though the successful island introductions were all to islands with no historic record of the occurrence of the reintroduced species. Success of introduction of these macropods appeared to depend critically on control or exclusion of exotic terrestrial predators such as foxes and cats.

A crucial aspect of any reintroduction plan is an assessment of the availability and quality of the reintroduction site. Reintroductions have a chance of success only if the habitat and landscape requirements of the species are satisfied over the long term. The area should have sufficient carrying capacity to sustain growth of the reintroduced population and support a viable self-sustaining population over time. Identification and elimination, or reduction to a sufficient level, of previous causes of population decline and/or habitat transformation should take top priority. In a habitat suitability study for an otter reintroduction project in Utah, United States, it was found that 94% of the studied streams were unacceptable for reintroductions. Escape cover was the most limiting habitat attribute, whereas food for the otters appeared to be available in adequate quantities (Bich 1988). This study, therefore, led to the recommendation that no otter reintroductions should be made until riparian zones were rehabilitated and protected, since re-establishment of stream-bank vegetation was deemed essential to provide escape cover for the reintroduced animals. Similarly, Howells and Edwards-Jones (1997) studied the feasibility of reintroducing wild boar (*Sus scrofa*) to Scotland through an assessment of suitable woodland habitats that could support a minimum viable population of the target animal. This species had already been the focus of earlier attempts to restore the extinct species and to reintroduce it into Britain (Howells & Edwards-Jones 1997). Based on a review of wild boar ecology, the authors identified woodland habitats suitable for supporting the species. Only long-established woodlands containing some stands of seminatural origin and larger than 500 ha in size were considered. None of the woodlands were deemed optimum habitat for wild boar and none was large enough to support a minimum viable population of 300 animals. The study concluded that the goal of re-establishing a self-sustaining population of wild boar in Scotland was unrealistic in the short term and reintroduction did not take place. Habitat destruction and modification can also be caused by invasive organisms. Such invasions often result in dramatic changes in **ecosystem structure** or **function** (Gordon 1998; Hobbs & Mooney 1998). **Invasive species** may not only lead to changes in ecosystem properties but can also hamper reintroductions through predation. Attempts to recover razorback suckers (*Xyrauchen texanus*), an endangered piscivorous fish species, by reintroducing them into their native range of the Colorado River have not been successful because of predation on the young suckers by non-native fishes (Johnson *et al.* 1993).

In another study, Bergerud and Mercer (1989) reviewed 33 reintroductions of caribou (*Rangifer tarandus*) that took place in eastern North America between 1924 and 1985. Twenty introductions resulted in sustained populations and 13 failed, of

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which the majority were lost to predation by wolves. The fate of these 33 introductions is consistent with the view that predation (natural and hunting) is a major factor in the decline of caribou in eastern North America following European settlement. In Europe, meanwhile, attempts to reintroduce black grouse (*Lyrurus tetrix*) and capercaillie (*Tetrao urogallus*) have been hampered, in part by predation by goshawk (*Accipiter gentilis*) and pine marten (*Martes martes*; Kalchreuter & Wagner 1982). Predation may have particularly severe impacts on very small populations, especially if a more common primary prey species is present ('prey switching'), while at the same time the number of reintroduced individuals is almost always small or very small. If predation is a serious risk, a single reintroduction of a given size class is preferable to multiple reintroductions of the same total number of individuals.

8.5 REINTRODUCTION TECHNIQUES

In the majority of cases of reintroductions or translocations of animals, the focus is on populations of a single species, and choices have to be made concerning which stages in the life cycle of species are most suitable for translocation activities. Should it be eggs, subadults, or adults? For plants, reintroductions can also aim at re-establishing a viable population of a single species, but the focus tends to be on communities, either sown or transplanted.

If no targets have been set, as is frequently the case, success can not be measured. But more often, there is an array of possible targets, that cannot always be met simultaneously. For example, if the aim is to re-establish a plant community similar to the **reference** community, does this imply that species richness, species composition or relative abundance of various species should be favoured? Are rare species more important than 'common' species? These and similar questions can be asked in case of re-establishment of populations of a single species as well: does a viable population imply the number of individuals, or also a minimum of genetic variability (see Chapter 7)? Pavlik (1996) clarified the discussion by distinguishing between project success (according to goals and objectives) and biological success (dealing with the performance of a population or a community). A few commonly applied techniques will be discussed below, for plants and a number of vertebrate groups.

8.5.1 Plants

Strategies for the reintroduction of **endangered** plants, that is, at the level of species populations, have been extensively dealt with in the volume edited by Falk *et al.* (1996), and several examples will be shown in Chapters 9, 14 and 15. Here we focus on the re-establishment of plant communities. If seeds of target species (characteristic of a reference plant community) are no longer available in the soil seed bank, they have to immigrate from elsewhere, or be deliberately reintroduced. In a recent review, Kiehl *et al.* (2010) evaluates a number of techniques for the establishment of **semi-natural grasslands** that have been applied in restoration projects in central and northwestern Europe. The techniques include, among others, (1) seeding of commercially produced site-specific seed mixtures, (2) transfer of fresh seed-containing hay and (3) transfer of turves and seed-containing soil. The establishment of species-rich grasslands with habitat-specific species composition appeared to be most successful when seeds, seed-containing plant material or soil are spread on bare soil of ex-arable fields after tilling or topsoil removal, or on raw soils such as in mined areas, provided that an appropriate follow-up management (e.g. hydrological measures, grazing and cutting) can be assured in the long run. The final establishment rates were lower than 40% when restoration sites were dominated by grasslands with dense swards. One of the classic examples of *in situ* restoration of a degraded meadow by hay transfer from a reference site is presented in Box 8.1, showing that hay transfer is a useful starting point but only partly results in a community similar to the reference site. Transfer of blocks of turf – including vegetation and soil – of, for example, $0.5\,m \times 0.5\,m$ with a minimum depth of 0.3–0.5 m, has been successfully applied as a method of environmental mitigation (reviewed by Bullock 1998).

There are many parallels between the causes for success and failure of plant and animal reintroduction attempts. Godefroid *et al.* (2011) examined 249 plant species reintroductions. They found that survival, flowering and fruiting rates were generally low. Even more problematic was that the data showed a downward trend over time After 4 years, flowering percentage was only 6% on average. A statistical treatment of the data revealed a number of variables associated with success. Reintroduction success is increased when using material originating from multiple populations. There was also a clear positive relationship between the number

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Box 8.1 *In situ* restoration of a degraded meadow: Somerford Mead

A particularly well-studied example of restoration of a plant community is the case of Somerford Mead, an old flood-meadow along the River Thames near Oxford, United Kingdom (e.g. McDonald *et al*. 1996; McDonald 2001). In the 1950s, it harboured an *Alopecurus pratensis/Sanguisorba officinalis* plant community. From 1960 to 1982, however, it was used as grassland for haymaking or silage cutting and received artificial fertilizers. From 1982 to 1985, it was ploughed and used for barley. In 1985, it was agreed to take Somerford Mead out of this high productivity scenario and set in motion regimes to re-create an *Alopecurus/Sanguisorba* flood-meadow plant community. In July 1986, a seed mixture was harvested from the reference site Oxey Mead, an ancient flood meadow, 2 km downstream. Its exploitation had not changed since at least the thirteenth century. As a result, it featured a notably low-fertility grassland community, the *A. pratensis/S. officinalis* association (MG4, according to Rodwell 1992). The seed mixture was broadcast over prepared soil on Somerford Mead the following October. In 1989, a management experiment began in Somerford Mead consisting of an annual hay cut at the end of June followed by 4 weeks of grazing in October – by sheep or cattle – in comparison to a control, nongrazed treatment. Both the cattle- and sheep-grazed plots became more similar to the community in the reference site, but were still far from the species composition of Oxey Mead, even 15 years after the reintroduction of target species. So, while the project has been considered successful, the reference ecosystem was used more as a source of inspiration than as a living system to be copied or emulated.

of introduced individuals and their survival. Success was also much higher when seedlings were used instead of seeds. The problem with seeds is that they only rarely will germinate and grow into new plants in the wild, and that the seedling stage is the most vulnerable part of a plant's life cycle. The source population also proved to to be important. The survival of propagules from stable source populations was twice as high as that from declining populations. A possible reason for this could be that declining populations already have a lower genetic diversity (and may have lost some rare alleles). Finally, proper management of the out-planting site increased reintroduction success.

8.5.2 Fish and herpetofauna

For successful reintroduction of fish and amphibians, the restoration of historical spawning areas, or the provision of new, suitable spawning habitats, are important. Both translocation from the wild and the release of captive-bred individuals are commonly applied techniques. Stocking appropriate life stages of target species is clearly important for successful introductions or reintroductions. For fish, using older/larger individuals has been more successful than using spawn (Noakes & Curry 1995), whereas the reverse seems to have been the case for amphibians. Cooke and Oldham (1995) monitored the establishment of large populations of the European common frog (*Rana temporaria*) and common toad (*Bufo bufo*) for 6 years in a newly created reserve following stocking with spawn of both species and with toads rescued from a site to be destroyed. Transfer of spawn proved to be more effective as a means of establishing a new population of toads than transfer of adults.

Most reintroduction projects involving amphibians and reptiles have not been very successful (Dodd & Seigel 1991), but efforts undertaken for the natterjack toad (*Bufo calamita*) represent an interesting exception. The species is endangered in Britain and has been legally protected since 1975. This amphibian suffered a major decline during the first half of the twentieth century, due partly to **habitat** destruction but mostly to **successional changes** in its specialized biotopes and anthropogenic **acidification** of breeding sites. Extensive autecological research over the past 25 years has provided the foundations for an intensive, 3-year species-recovery programme funded by statutory nature–conservation organizations (Denton *et al*. 1997). Management of heath and dune habitats focused on restoration and maintenance of early stages of serial succession, initially through physical clearance of invasive scrub and woodland vegetation, followed by applying grazing regimes similar to those prevalent in earlier centuries. In some cases, extra

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breeding pools were constructed to either increase or stabilize natterjack toad populations that had become reliant on one or very few pools at small sites, or to promote range expansion within large habitat areas. At least six out of 20 experimental reintroductions have resulted in the foundation of expanding new populations, and an additional eight have shown initial signs of success (Denton *et al.* 1997).

Translocations of fish seem to be more succesful than those of amphibians with the natterjack toad as an exception.

8.5.3 Birds

In birds, making use of captive-produced eggs that are being hatched by common species like chickens is a common and viable reintroduction technique (Derrickson & Carpenter 1983). Sometimes eggs are collected from wild populations. Fostering has proved to be a much better technique than the release of hand-reared individuals as they are much more prone to all sorts of danger (e.g. predation). This has been found, among others, in whooping crane (*Grus americana*), hand-reared capercaillie (*Tetrao urogallus*), white storks (*Ciconia ciconia*) and common raven (*Corvus corax*). Releasing individuals straight into the wild – known as *hard-release* – is not recommended by Bright and Morris (1994). Most species of birds (and mammals) rely heavily on individual experience and learning as juveniles for their survival. They should be given the opportunity to acquire the necessary information to enable survival in the wild. Therefore, *soft-release* techniques have been developed whereby the animals are kept in pens or other holding devices and slowly are made acquainted with their new environment.

A commonly used 'soft-release' technique for the introduction of birds of prey is called *hacking*, that is, the release of free-flying young birds at a site where food is provided until independence. Hacking was used in the reintroduction of Montagu's harrier (*Circus pygargus*; Pomarol 1994). It took place in an enclosure measuring 3–4 m × 2 m × 1 m high. The reintroduced harriers were between 20 and 30 days of age. After 5–8 days the enclosure was opened. The young birds became independent on average 34 days after their first flight (at 70 days of age). Over a 5-year period, 87 birds were reintroduced with a success rate of 83%. Only three birds had been seen returning to the area in subsequent years. Hacking has also been applied very successfully in the many reintroduction projects of the peregrine falcon (*Falco peregrinus*). Over the past 25 years, more than 1000 birds have been reintroduced in this way in many parts of the United States.

Many attempts have been made to establish several hundred avian species worldwide. Among them are many raptors. At least six species of owls and 15 species of diurnal raptors have been established successfully. Examples of raptors that have been reintroduced or newly introduced are the little owl (*Athene noctua*) in Britain, eagle owl (*Bubo bubo*) in Sweden and Germany, goshawk (*Accipiter gentilis*) in Britain, white-tailed sea eagle (*Haliaeetus albicilla*) in Scotland and other parts of Europe, bald eagle (*Haliaeetus leucocephalus*) in New York and California, Seychelles kestrel (*Falco araea*) on Praslin (Seychelles), and peregrine falcon (*F. peregrinus*) in the United States, Canada and Germany. A raptor that almost became extinct is the Mauritius kestrel (*Falco punctatus*). As a result of habitat loss and pesticide contamination, by 1974 only four birds were known to exist in the wild, including one breeding pair. Then, in 1973, a conservation project was begun, using techniques such as captive breeding, supplemental feeding of wild birds, provision of nestboxes, hand rearing and release of captive-bred and captive-reared birds by hacking, fostering and predator control (Jones *et al.* 1995). A total of 331 kestrels were released in the 10 years up to the end of the 1993–1994 breeding season; one-third of these were captive bred and the rest were derived from eggs harvested from the wild. By the 1993–1994 season, an estimated 56–68 pairs had established territories in the wild with a postbreeding population, including floating birds and independent young, of 222–286. Since the pesticides responsible for their decline are no longer used, the number of Mauritius kestrels should continue to rise through natural recruitment. The distribution of suitable habitat suggests that an eventual population of 500–600 kestrels on Mauritius is possible. Due to its outstanding success, the release programme for the Mauritius kestrel ended after the 1993–1994 breeding season (Jones *et al.* 1995).

8.5.4 Mammals

As with birds, mammals can be taken from wild source populations or from captive breeding stock. Catching animals from the wild can be a costly and time-consuming operation, and is not without risk.

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Mammals should also be given the opportunity to acquire the necessary information to enable survival in the wild, and soft releases are therefore recommended. Mammals propagated in an enclosure tend to develop an affinity for their immediate surroundings and therefore, upon release, exhibit a slow dispersal rate. This behaviour generally enhances survival. An example of a successful soft release is the case of the scimitar-horned oryx (*Oryx dammah*) in Tunisia, which had disappeared from that country in 1902 due to desertification, competition with domestic livestock, habitat disturbance and, of course, hunting. In December 1985, five males and five females were reintroduced from a zoo in Britain into the Bou-Hedma National Park, which is a 2400-ha fenced area that has been protected from domestic livestock since 1977. They were acclimatized in a 600-m^2 pen for 4.5 months and then released into a 10-ha pre-release enclosure. Social organization was established peacefully, and the oryx adjusted to the new climate and natural foods. In July 1987, the oryx were released from the enclosure into the park (Bertram 1988). In 2005 there were 130 animals in the park while, sadly, the species has gone globally extinct in the wild.

Sometimes spectacular or what might be called 'heroic' techniques are indeed the only solution to achieve a reintroduction. In a translocation project for the North American beaver (*Castor canadensis*) in Idaho, for example, the mountains, heavy forests and lack of roads made transplanting a labour-intensive, expensive and time-consuming task (Heter 1950). In addition, it resulted in high beaver mortality. The use of planes and parachutes with animal-holding boxes proved to be a much more efficient and less expensive method of transportation (Heter 1950). In 1948, 76 live beavers were dropped with only one casualty. Observations made in 1949 showed that the beavers that had participated in the airborne transplantation had settled and were well on their way to producing colonies (Heter 1950). At present beavers range widely and in great numbers in the state of Idaho.

There have been quite a few attempts to reintroduce large carnivorous mammals in areas from which they were **extirpated**, or disappeared, among them wolf, bear, wild dog and lynx. Reintroduction of large carnivores is always very difficult. They require extensive, high-quality areas, with substantial prey for which they may compete with humans. In addition, as discussed in section 8.7, they are associated with depredation of livestock in many people's minds (Stahl *et al*. 2001), and some people may also feel uncomfortable when large predators are reintroduced into their neighbourhoods (see Hayward & Somers 2009). Nevertheless reintroductions can be successful and, as an example, an overview of the reintroduction attempts of the European lynx (*Lynx lynx*) is given in Table 8.1. To summarize, in the past 37 years, lynx reintroductions have been carried out at 15 different sites in eight countries. Of these, five were successful, four are of uncertain status and six clearly failed. In an analysis of these reintroductions, Linnell *et al*. (2009) concluded that, in most cases, basic rules had been violated: bad planning, widespread use of captive-born lynx, no attention being paid to genetic origin, very little pre-release site evaluation carried out and very small numbers (in one case, only two males) reintroduced. Despite these *ad hoc* attempts, the reintroduction of the lynx in Europe has become a success and, together with natural expansion of the species, the distribution of the lynx in central and eastern Europe has enormously increased.

There have been quite a number of succesful mammal reintroductions. Part of this success can be attributed to opportunistic dispersal characteristics and a high reproduction rate.

8.6 ECOSYSTEM EFFECTS OF REINTRODUCTION ATTEMPTS

The Great Lakes ecosystem in the midwestern United States has changed dramatically over the past 50 years. A review of historical changes reveals complex interactions of overfishing, invasion by non-indigenous species, eutrophication, extensive habitat modification and toxic contamination. Native fish species that required tributary or near-shore habitat for spawning and nursery areas have declined markedly. Among surviving **native species**, such as walleye (*Stizostedion vitreum*), stock diversity declined with the loss of tributary-spawning stocks and lake-spawning stocks became dominant. With the rarefaction of native species, the abundance of formerly subdominant species increased. Species such as smelt (*Osmerus mordax*), gizzard shad (*Dorosoma cepedianum*) and white perch (*Morone americana*) depend less on critical tributary and near-shore habitat (Koonce *et al*. 1996). It seems that a complete restoration of the Great Lakes is unlikely, due to naturalization of exotic species, habitat degradation and destruction, urbanization of many of

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Table 8.1 Overview of lynx reintroductions in Europe, 1970–2007 (from Linnell *et al.* 2009).

Country	Release location	Years	Male	Female	Total	Source	Status	Fate	Size
Australia	Turrach, Styria	1977–1979	6	3	9	Wild	O	F	—
Czech Republic	Bohemian Forest	1982–1989	11	7	18	Wild	O	S	75
Czech Republic	Podyi NP	1993–1994	2	2	4–6	Captive	U	F	—
France	Vosges	1983–1989	12	9	21	Wild and captive	O	S	30
Germany	Bavarian Forest	1970–1974			5–10	Wild and unknown	U	F	—
Germany	Harz	2000–2006	9	15	28	Captive	O (24) and U (4)	U	?
Italy	Gran Paradiso NP	1975	2	0	2	Wild	O	F	—
Poland	Kampinos	1992–1999	14	17	31	Captive	O	U	>10
Poland	Pisz Forest	2003–2006		2	4	Captive	O	U	?
Slovenia	Dinaric Mountains	1973	3	3	6	Wild	O	S	130
Switzerland	Western Alps	1971–1976	7	5	12	Wild	O (6) and U (6)	S	100
Switzerland	Engadin	1972–1980	2	2	4	Wild	U	F	—
Switzerland	Jura	1972–1975	5	5	10	Wild	O (4) and U (6)	S	80
Switzerland	Jorat Plateau	1989			3	Unknown	U	F	—
Switzerland	Eastern Alps	2001–2007	5	6	11	Wild	O	U	?

Status: O, officially sanctioned reintroduction; U, unofficial or clandestine reintroduction.
Fate: F, failed; S, success; U, uncertain; ?, unknown population size at present.

the lake's shorelines, heavy fishing mortality, lack of native gene pools and complicated political jurisdictions that rarely help environmentalists to work towards a common goal (Meffe 1995; see also section 8.7). **Invasive species** pose a special problem. The Great Lakes ecosystem is now home to at least 139 non-indigenous species of fauna and flora that have become established following invasions or intentional introductions. About 10% of the exotic species have caused economic or ecological damage. Despite activities to reduce the causes of decline of the indigenous species, most problems have not yet been solved adequately. Nevertheless, several reintroduction attempts have been made with various species. Much attention for example has been given to the reintroduction of the lake trout or charr (*Salvelinus namaycush*).

Large carnivore reintroduction not only is important to enrich systems from a species-richness point of view but also may be vital in restoring key **ecosystem processes** such as predator-prey interactions. In Yellowstone National Park (United States), the grey wolf, *Canis lupus*, had been deliberately extirpated, as part of the management plan, from 1926 to 1995. In 1995, a reintroduction programme was begun after which wolf numbers steadily increased. In the riparian areas of the park, the systems-level results were spectacular. Since the wolves had disappeared, these areas had suffered from heavy browsing by the native elk (or wapiti) (*Cervus canadensis*), inhibiting recruitment of woody plants like aspen and willows browzed by the elk, which in turn led to cascading effects on other parts of the riparian ecosystem. These included loss of

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Figure 8.6 Willow along Soda Butte Creek in summer 1997 (left) and summer 2001 (right). Following a 70-year period of wolf extirpation, heavy browsing of willows is evident in the 1997 photograph. In 2001, after 6 years of wolf recovery, willows show evidence of release from browsing pressure (increases in density and height). (Photographs: left, Yellowstone National Park; right, William J. Ripple.)

wetlands, loss of riparian beaver and loss of food web support for aquatic and avian fauna (Ripple & Beschta 2004). When the wolves returned, these effects were reversed: pressure by elk declined, the browse plants came back and, with them, the beaver and many other lost taxa (Figure 8.6). As shown by Ripple and Beschta (2004), the reason was a change in perceived risk by the elk in these landscapes associated with various terrain features (and their fear-related factors). This example demonstrates the large effect that predation can have on the spatial distribution of prey, with various ripple effects on ecosystem structure, content and development. At present, several other studies are being carried out in areas where large predators or raptors have returned or increased, and in these studies as well large impacts have been found on prey behaviour and even migration patterns (Jonker *et al.* 2010).

Both the Great Lakes and the Yellowstone wolf examples described above demonstrate that humans play a crucial role in determining the success or failure of reintroduction programmes. In the Great Lakes area, human activities have made complete restoration of the system unlikely, while in Yellowstone National Park, after long and intense debate, reintroductions of the top predator have paved the way for a highly successful ecosystem restoration programme.

8.7 SOCIETAL ASPECTS AND CONCERNS

Reintroductions are generally long-term projects that require the commitment of long-term financial and political support. It is important that socio-economic studies be made to assess the impacts, costs and benefits of the reintroduction programme on, for and to local people. According to the above-cited IUCN (1998) guidelines, a thorough assessment of attitudes of local people to any proposed reintroduction project is necessary to ensure long-term protection of the reintroduced population, especially if the cause of a species' decline was anthropogenic (e.g. over-hunting, over-collection or loss or alteration of habitat due to human activities). The relevance of these guidelines should not be underrated because there are many examples of

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failures due to not paying sufficient attention to the attitudes of local communities. From an extensive literature review on exclosures, afforestation, reforestation, rehabilitation and other regeneration or environmental repair operations, over several million hectares in Mediterranean bioclimatic areas, extending from the Atlantic Ocean to the Aral Sea, combined with 50 years of personal field experience, Le Houérou (2000) concluded that, while the main constraint for success was the restoration of those habitat elements that had caused degradation, the most difficult constraints to overcome usually are of a socio-economic and/or sociocultural nature. Poaching can also be a problem, for example in the 1978 relocation of 22 tule elk (*Cervus elaphus nannodes*) from the Tupman Tule Elk Reserve near Buttonwillow, California, to nearby Fort Hunter Liggett reserve. Factors conducive to the high poaching rate were tameness of the relocated elk, location of release site, lack of monitoring and resentment by locals to changing policies at Fort Hunter Liggett (Hanson & Willison 1983).

Resentment can especially be strong among local people against predators. Thus, when nine European lynx (*Lynx lynx*) were released in central Austria in 1975 – 100 years after the last native lynx had been killed – there was strong local opposition from hunters, especially in Carynthia, in the southernmost part of the country. This Austrian state has few federal forest estates, but many large private forest estates pursuing trophy hunting by tourists as a source of income (Gossow & Honsig-Erlenburg 1986). Similar problems are encountered with wolves. In response to popular resistance, the red wolf (*Canis rufus*), reintroduced to the Alligator River National Wildlife Refuge in North Carolina, was classified as a 'non-essential experimental population' and did not have the full protection of the Endangered Species Act when released. Proposed reintroduction of grey wolves (*Canis lupus*) to Yellowstone National Park met similar opposition from livestock managers and owners and hunters, and from various state agencies as well (Wilcove 1987).

Some animal species have a much more positive popular image than wolves and lynx. Thus, the release of high-profile and popular 'flagship' species may raise public awareness of conservation issues and generate funding for wider programmes. In Saudi Arabia, for example, the first national wildlife conservation project targeted the houbara bustard (*Chlamydotis macqueenii*), which is threatened as a resident. Programmes directed towards the reintroduction of this large, charismatic bird have attracted wide public attention owing to the emblematic status of the bird throughout the Middle East as the premier quarry for falconers, and thus these programmes have helped generate support for other, lower profile species in need of protection (Le Cuziat *et al*. 2005). The aesthetic value or economic benefits of an animal may also be tied to the generation of public support and the means to raise public awareness of conservation issues. In Latvia, the reintroduction of the European beaver (*Castor fiber*) resulted in the creation and conservation of wetlands; their value in water purification has been estimated at up to £1.3 billion sterling (ca. 2 billion euros), and beavers reintroduced into rivers in France and Sweden have become tourist attractions (Seddon & Soorae 1999).

8.8 PERSPECTIVES

In conclusion, it seems clear that the idea of reintroducing species within their former territory or habitats has gained acceptance within the context of the restoration paradigm. An important incentive is that, in most cases, species are not able to colonize these areas by themselves and need a little help. Nevertheless, as has been amply demonstrated, much can go wrong and indeed has gone wrong in more than 700 documented reintroduction attempts carried out to date (Seddon *et al*. 2007). The ones that were successful, however, teach us that it can be done and that success should not be attributed to sheer luck alone. If reintroduction programmes take into account that the habitat is suitable (or can be made suitable again), the founding population is sufficiently large, the population structure is right, a high level of genetic diversity is ensured, the proper techniques are applied, careful planning has been applied and the public has been consulted properly, and their approval obtained, then the chances for a successful reintroduction are enhanced. But even then we have to realize that we live in a dynamic world with occasional periods of rapid ecosystem change, either naturally or human induced.

Recently, and with good reason, much attention has been paid to the possible consequences for ecosystems of human-induced **climate change** (see several chapters in Part 3 of this book). It is expected that some regions of the Earth will experience high levels of warming (>4°C), as well as altered precipitation (Intergovernmental Panel on Climate Change (IPCC)

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2007a). A wide range of effects is expected, some of which already can be clearly noticed: (1) shifts in species distributions, (2) often along elevation gradients, (3) changes in timing of life history effects, (4) loss of habitats (range contraction), (5) increase of diseases, parasites and zoonoses (e.g. Lyme borrelioses and plague) and (6) extinctions (Mawdsley *et al.* 2009). As all these effects work out differently for different species, it can also be expected that local communities might change fundamentally and that differential movement of species can potentially lead to novel combinations with consequences for predator–prey and competitive interactions (Stralberg *et al.* 2009). As the world gets warmer, there will be a general tendency for species to move or migrate towards the poles and to higher altitudes. Conservation efforts may make use of this by increasing the extent of protected areas or by establishing protected area networks and corridors along elevational gradients to facilitate movements. For some species, however, this will simply not be possible (polar bear), while others will face physical barriers difficult to overcome. In this situation, translocation can be considered as is being done for two extinct British butterflies for which models predict that conditions have sufficiently improved that they can be reintroduced to Britain (Carroll *et al.* 2009). But as current practices may not be enough to avoid species loss, it has also been contemplated to move species to sites where they do not occur or have not been known to occur in recent history, a process that is known as assisted colonization or assisted migration (Hoegh-Guldberg *et al.* 2008). Sympathetic as it may sound, this idea has met with much criticism and strong arguments have been put forward that it is not a good idea (Rubenstein *et al.* 2006). So is there an *uncertainty* how species will respond, especially species that are understudied, while also in the receiving community fundamental processes may have been altered (e.g. competition with existing species), leading to profound changes in the functioning of ecosystems. Needless to say, it is also vital to increase the effectiveness of existing conservation measures and to do everything possible to **mitigate** the human-induced stressors.

Ecosystem dynamics with rapid shifting species assemblages (see Chapter 21) makes reintroduction an even more tricky endeavour than it already is. The very high frequency of attempts, however, make clear that people, somehow, also feel an urge to repair some of the damage they have inflicted on 'wild' nature, which is a reason for hope.

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Part 3

Experiences and Lessons, Biome by Biome

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EDITORS' INTRODUCTION

In the 'walk around the world' we now begin, the intrepid reader of Part 3 will be visiting ongoing restoration programmes across an array of ecosystem types stretching from the Arctic to the Amazon. A near complete cross-section of biomes is included, with the one major exception we have noted before, the Earth's overexploited, polluted and – to speak plainly – imperilled oceans. Each chapter's authors will describe and analyse the effects of past and current disturbance factors, as well as which restoration measures and interventions have been, are being or should be tried. An ecological evaluation of failures and successes across 11 ecosystem types, set in a huge array of sociocultural and political settings, will help pave the way towards the practical recommendations and research horizons we will discuss later, in Part 4.

In Chapter 2 of this book, we introduced a trio of perspectives of ecological restoration, focused on landscape 'integrity', ecosystem 'health' and 'biodiversity', i.e. 'keeping all the parts', in the sense of Aldo Leopold, and all conservationists since him. Then, in Part 2 we presented the 'ecological foundations' upon which we are building, according to that trio of distinct angles of approach. Here in Part 3, we have asked the authors to bear these three approaches in mind, and we invite you, the reader, to do the same, as you read this series of biome-specific reviews and case studies. Here, the question is not so much which ecological foundations are applicable to ecological restoration, but rather what does the practice of ecological restoration entail in the 'real world', in a specifc place and setting? What can we learn from the evaluation of future perspectives of ecosystem development in a large array of biomes, as presented here?

You will recall that throughout the book we endorse the view advocated by SER (2004) that, ultimately, whole ecosystems are the appropriate level of attention, and intervention, for projects and programmes of ecological restoration. Indeed, whether the overarching level of interest is the reintegration of a disturbed and dysfunctional landscape, the restoration of an impaired or destroyed ecosystem, or the maintenance of biodiversity (e.g. the reinforcement or reintroduction of threatened species in a given set of biotic communities and ecosystems), knowledge of ecosystem patterns and processes is essential. But when it comes to resolution, in the sense of how we perceive 'nature', and also to interaction and consensus building with stakeholders, landscapes and biodiversity – not to mention ecosystem services (see Part 4) – are all crucial to effectively moving 'the ball' forward.

We have arranged the next 11 chapters in an order that corresponds with current textbooks on climatology, global ecology and biogeography, and also to provide a convenient way to consider our world as a whole. Imagine that you drop out of the sky and land in the equatorial region of Africa, and then start walking north. After leaving the tropical forests, you pass into the subtropical semi-arid and arid semidesert and desert regions of the Sahel and Sahara, before arriving, somewhat thirsty, in the Mediterranean Basin. Further north, you find the temperate forests, temperate dry grasslands and heathlands of Europe, and then finally reach the Arctic, or the Alpine regions, depending on whether you continue north or climb up a mountain. These biomes are in fact treated, more or less worldwide, in Chapters 9–15. Thereafter, we leave the terrestrial ecosystems altogether, and move to the wetlands. Chapters 16–19 treat four different aquatic ecosystem types, namely, mires, rivers and floodplains, freshwater lakes and finally salt marshes.

As compared to the first edition of this book, we are pleased to note that – in addition to the eight updated chapters – three of the guided visits we will make in this 'walk around the world' are brand new. We are indebted to Karen Holl for contributing a chapter on restoration of tropical forests (Chapter 9), to David Bainbridge for his chapter on restoration of arid and semi-arid lands (Chapter 10) and to Dean Apostol and Ayn Shlisky for presenting their views on the restoration of temperate forests in western North America (Chapter 13), where human impact is of a more recent date as compared to the situation in Europe (see Chapter 12).

All the chapters in this part follow a similar approach. They start by a description of ecosystem characteristics in an historical perspective, in search for the identification of 'reference ecosystems', and an analysis of the effects of disturbance factors. A relatively large part of each chapter is devoted to understanding past and current ecosystem structures and processes, a condition for any ecological evaluation of various ecological restoration approaches. Each chapter uses the same terminology, distinguishing between natural recovery, near-natural restoration, ecological restoration, rehabilitation and reclamation (see the glossary at the end of the book). Each chapter finishes off with a discussion called 'Perspectives'. So, now it is time to start our walk. Onward.

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Chapter 9

RESTORATION OF TROPICAL FORESTS

Karen D. Holl

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9.1 INTRODUCTION

Tropical forests are the most diverse ecosystems on Earth. These forests are found within 23.5° N or S of the equator in Asia, Oceania, Africa and Central and South America, in areas with a mean monthly minimum temperature of >18°C and a difference of <5°C between the warmest and coldest months. There are many tropical forest types that range along both moisture and elevation gradients (Holdridge *et al.* 1971). Rain forests are typically categorized as areas receiving >1500 mm of rain with >100 mm of rain in each month, whereas seasonal tropical forests generally have 3- to 6-month dry seasons when rainfall is <50 mm per month, and dry forests receive <1500 mm rainfall annually (Whitmore 1998). Tropical forests are found from sea level to beyond 3000 m elevation, and are categorized as lowland (<800–1000 m), premontane (~1000–−1500 m) and montane (>1500–3000 m), although the transitions between these altitudinal belts vary regionally. Tropical forests are found on well-drained soils, as well as on seasonally or permanently flooded soils (riparian forest or freshwater swamps) and along coasts (mangroves). This chapter focuses on nonwetland tropical forests.

Over half the tropical moist forest biome has been cleared over the last several decades (Asner *et al.* 2009), and much of the remaining forest is affected by fragmentation, selective logging and hunting. While the rate of tropical deforestation has slowed in some countries, it continues at a rapid pace in others (Asner *et al.* 2009). The causes of deforestation are complex and interrelated, and their relative importance varies by region (Geist & Lambin 2002). In Latin America, much of the forest has been cleared for pasture land and commercial agriculture, such as soybeans, sugar cane and coffee. In Africa, forest land is often cleared or degraded to supply firewood and/or arable land for subsistence agriculture; recently there has been increasing concern about the extensive bushmeat hunting and how the paucity of large mammals within some forests will alter plant–animal interactions, such as herbivory and seed dispersal, and in turn forest dynamics (Wright 2003). In Asia, much of the forest has been cleared for timber and/or agriculture with the land area in industrial-scale agriculture increasing in recent years. Smaller areas of tropical forests have been highly impacted by mining and oil drilling. As the majority of forest clearing has been carried out for a mix of logging and different types of agricultural uses, this chapter focuses on the restoration of such lands.

Despite ongoing pressures to clear tropical forests, there is substantial interest in restoring these forests, and tropical forest cover is increasing in certain regions (Asner *et al.* 2009). The motivation for restoring tropical forests comes from an interest in enhancing or restoring the delivery of **ecosystem services** (e.g. sequestering carbon, minimizing erosion and improving water quality, maintaining hydrological cycling and harbouring biodiversity) and maintenance of **natural capital** (Aronson *et al.* 2007a). In particular, there is increasing awareness that tropical forest clearing is the cause of approximately 15% of carbon emissions globally (van der Werf *et al.* 2009), so any effort to reduce carbon emissions must slow deforestation and forest degradation, and increase carbon stocks in degraded and cleared forests, a set of measures known collectively as *REDD+*. Moreover, there is a pressing need to restore forests to reduce erosion into nearby waterways and to conserve the high diversity of tropical forest organisms. In certain areas of the tropics, agricultural land is being abandoned and undergoing secondary succession due to changes in commodity prices and rural–urban migration (Marín-Spiotta *et al.* 2008; Letcher & Chazdon 2009). Together these changes offer opportunities to restore tropical forests, which necessarily must be balanced with the need to sustain human **livelihoods** in these regions.

Given the limited funds available for restoring tropical forest, it is critical to assess what type of **intervention** is needed in order to select the most effective forest restoration strategy (Lamb *et al.* 2005; Holl & Aide 2011). In this chapter, I first discuss factors limiting tropical forest *recovery*. I then briefly outline an approach for selecting an appropriate methodology from the different strategies used to facilitate tropical forest recovery and describe these methodologies in detail. This framework is broadly applicable to a range of tropical forest types, and I draw on examples from many of them. I conclude the chapter with thoughts about how to pay for tropical forest restoration and important considerations for tropical forest restoration in the future.

A common assumption of many restoration efforts is that if the full complement of plant species is restored this will result in the colonization of other groups of species (e.g. fauna and microbes), as well as the recovery of desired ecosystem functions (e.g. nutrient cycling and erosion control). Given that our knowledge

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on these topics for tropical forests undergoing restoration is limited, in this chapter I focus on summarizing results to date on restoring tropical forest plant communities, note when relevant information is available on other organisms and ecosystem functions and highlight the need for research on specific topics.

9.2 FACTORS AFFECTING THE RATE OF NATURAL RECOVERY

The rate of autogenic tropical forest recovery from human disturbance is notoriously variable. In some cases, tropical forest biomass and species composition may recover within a couple of decades (Marín-Spiotta *et al*. 2008; Letcher & Chazdon 2009), whereas in other cases the areas may remain in a state of arrested succession due to highly degraded soils or competition with aggressive ruderal species (Chazdon 2003; Lamb *et al*. 2005). In order to most effectively design tropical forest restoration strategies, it is critical to understand factors influencing the rate of natural tropical forest recovery generally, and to identify which factors are most important in the specific system being restored.

9.2.1 Ecological processes affecting tropical forest regeneration

Tropical forest plants commonly colonize degraded lands from seeds primarily dispersed from sources outside the site. Alternatively, plants may establish from three sources within the site – the *in situ* seed bank, seedlings already present and established at the time of land abandonment and/or resprouts from stumps, roots or stems – if these modes of regeneration remain after human disturbance. Many studies demonstrate that *dispersal* of animal-dispersed seeds – the primary form of dispersal in tropical rain forests – is often extremely low in former agricultural lands (reviewed in Holl 2002; Meli 2003). Moreover, most seeds falling in abandoned agricultural land are from species already present in the site or from a few small-seeded pioneer species, and seed rain is usually concentrated under remnant trees. Therefore, tropical forest recovery is commonly limited by a lack of **propagules** of forest species. In some sites, particularly those that were logged or used for short-term or low-intensity agriculture, there may be regeneration from resprouting and seed banks within the site; but, the extent of these forms of regeneration is highly variable (discussed below).

If forest plants either arrive at or are present in the site, then several factors may limit their establishment, survival and growth. These include competition from aggressive ruderal vegetation, stressful microclimatic conditions, limited soil nutrients, high seed predation/seedling herbivory and plant pathogens (Holl 2002; Meli 2003), and their relative importance varies from site to site.

A factor that has been shown to limit survival and growth of forest species in many sites, particularly in agricultural land, is aggressive existing vegetation that was either planted or rapidly colonized after the land was abandoned. **Exotic** pasture grasses (e.g. *Imperata cyclindrica*, *Melinus minutiflora, Pennisetum* spp. and *Saccharum spontaneum*) often form a monoculture in previously grazed areas (e.g. Hooper *et al*. 2002; Kettle 2010). In other cases, dense ferns (e.g. *Dicranopteris* spp. and *Pteridium* spp.) or other ruderal vegetation compete with forest seedlings (Cohen *et al*. 1995; Zimmerman *et al*. 2007). This residual vegetation may slow recovery by providing shelter for seed and seedling predators; competing for soil moisture, nutrients and light; increasing the probability of fire; reducing seed germination and emitting allelopathic chemicals which limit seedling growth (reviewed in Holl 2002).

Stressful microclimatic conditions may also limit seed germination, and seedling survival and growth, particularly in seasonally dry forests (Vieira & Scariot 2006). Light levels and air and soil temperatures are commonly much higher, and humidity and soil moisture levels are much lower in agricultural lands compared to forests. These microclimatic conditions may reduce survival and growth, particularly of later successional seedlings which are adapted to regenerate in the forest understorey and light gaps. Moreover, drier conditions in pastures, along with high grass biomass, make them particularly susceptible to the spread of fire, which kills the seeds and seedlings of most forest species (Janzen 2002; Nepstad *et al*. 2008). In contrast, pasture grasses are generally well adapted to resprout after fire, so repeated fires can lead to a transition to savanna vegetation (i.e. grasslands with trees spaced at a sufficient distance that the canopy does not close) in drier areas.

Next, in some sites, seedling growth is limited by soil conditions. Much of the tropics are covered by oxisols and ultisols, which have low nutrient levels and high acidity, whereas some areas have more fertile, volcanic

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soils, such as andisols and inceptisols. After human use, soils may be highly compacted, which impedes root growth and water holding capacity. Many tropical soils are phosphorus deficient (Vitousek & Sanford 1986), but nitrogen and other nutrients may also be limiting in some sites. Moreover, in certain types of soil, aluminium or iron may be present in sufficiently high levels as to be toxic to plants and therefore to slow or inhibit tree growth (Davies 1997). Finally, many tropical trees form mycorrhizal associations, which facilitate phosphorus uptake, but agricultural land uses may substantially alter microbial communities (Carpenter *et al.* 2001; M.F. Allen *et al.* 2005), which in turn affects *nutrient cycling*.

Seed predation and seedling herbivory can also be major obstacles to recovering agricultural lands. Common seed predators in the tropics include small mammals, bruchid beetles and leaf-cutter ants, which can consume more than 80% of seeds of some species within a few weeks (Nepstad *et al.* 1990; Jones *et al.* 2003). Likewise, herbivores – primarily insects but also mammals – can cause extensive damage to certain plants (Nepstad *et al.* 1990; Holl & Quiros-Nietzen 1999).

Finally, in some cases, plant pathogens cause extensive mortality of certain trees planted in restoration projects. For example, M.F. Allen *et al.* (2005) recorded >50% mortality of one tree species (*Cochlospermum vitifolium*) planted to restore tropical dry forest in Mexico, apparently caused by *Fusarium* sp., a widespread pathogenic fungus. Seed predation, seedling herbivory and plant pathogens are notoriously variable among species and over time, and thus can have a strong impact in some cases, but are less commonly the crucial factors limiting forest recovery.

9.2.2 Overarching factors affecting the rate of colonization and establishment of forest plants

The relative importance of the above-mentioned processes in influencing dispersal and establishment limitation, as well as the rate of natural recovery within specific sites, is influenced by the adaption of specific systems to local abiotic conditions, the past land use type and intensity and the surrounding landscape matrix (Holl 2007; Figure 9.1). In the tropics, the rate of natural forest *recovery* is largely related to the abiotic conditions with which these systems have evolved, including rainfall, temperature and soil type (Holl 2007). Natural **resilience** is often higher in drier than wetter tropical forest, in part because dry tropical forests have a much greater percentage of trees, shrubs and vines with wind-dispersed seeds (Vieira & Scariot 2006), which more readily disperse into open areas. Moreover, resprouting is more common in tropical dry forests (Vieira & Scariot 2006). Recovery also tends to be faster in relatively warmer and lower elevation areas, which generally favour more rapid growth (Zarin *et al.* 2001). Finally, differences in soil fertility across sites can strongly influence plant growth rates and forest recovery (Moran *et al.* 2000; Zarin *et al.* 2001).

The relative importance of different factors limiting forest recovery is also influenced by past land use

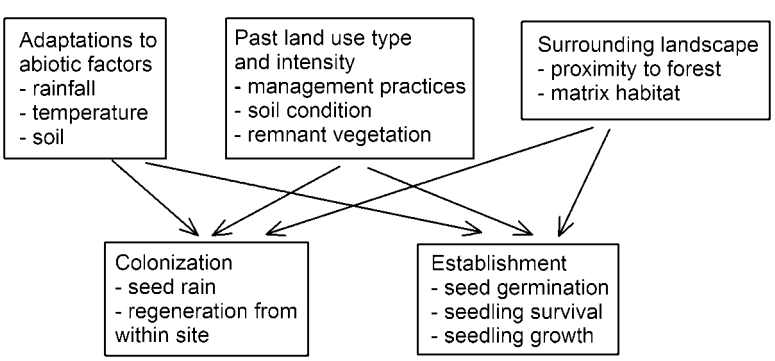


Figure 9.1 Factors affecting colonization and establishment of forest plants in cleared lands in the tropics. (Modified from Holl 2007.)

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Figure 9.2 Former site of shifting agriculture in semi-evergreen seasonal forest (annual rainfall 1000–1200 mm) on the Yucatan Peninsula in Mexico. The site was used for 2 years for subsistence agriculture and had been abandoned for only 2 years when this photograph was taken. Substantial regeneration is taking place due in part to extensive resprouting. (Photograph by Karen D. Holl.)

history (Figure 9.1). The intensity of past land uses, which can range from selective logging to grazing to small-scale or industrial agriculture, affects many site-specific factors (reviewed in Chazdon 2003; Holl 2007). For example, both the intensity and duration of past land use affect the availability of propagules within a site (i.e. seed bank, resprouts and existing seedlings); lands used for selective logging or shifting agriculture are more likely to retain a seed bank of forest species than those used for extended grazing or monoculture crop production (Meli 2003; Holl 2007), which results in more rapid forest recovery (Figure 9.2). Past land use practices also influence the remnant vegetation in a particular site, which in turn may affect the rate of recovery. Aggressive pasture grasses are generally present in former pasture lands, but are much less likely to be an obstacle to recovery in lands that have been logged for timber or used for other agricultural crops. In contrast, if remnant trees are intentionally retained within agricultural lands, such as shade trees for coffee, cacao, tea or grazing animals in pastures, these trees can play an important role in facilitating natural recovery by attracting seed-dispersing animals, ameliorating stressful microclimate conditions and increasing soil nutrients (Loik & Holl 1999; Harvey *et al.* 2004). Even within a given land use type, the frequency and intensity of disturbance can vary; for example, the biomass accumulation rate in land used for shifting agriculture decreases with the number of times that land has been cleared following a fallow period (Lawrence *et al.* 2010). A host of management practices, including fire, herbicides and the use of heavy machinery, strongly affect the rate of recovery.

In addition to the natural resilience of the system, as expressed by rates of natural reseeding and reprouting, and the type and intensity of past land use, the composition of the surrounding landscape matrix also affects tropical forest recovery (Figure 9.1). Many studies have demonstrated the importance of proximity to intact tropical forest as a source of forest seeds and seed dispersers (Rodrigues *et al.* 2009). In areas used for large-scale industrial agriculture, such as sugar cane in Brazil, and elsewhere, nearby seed sources are often lacking (reviewed in Holl 2002), which can greatly limit the potential for natural recovery. The surrounding landscape matrix also affects recovery in other ways. Small patches of forest, riparian vegetation, living fences and remnant trees within the agricultural land use matrix that serve as sources of seeds, enhance the

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mobility of seed-dispersing fauna (Harvey *et al*. 2004; Chazdon *et al*. 2009a), and in turn facilitate the recovery process. In contrast, surrounding land uses can impede survival and growth of forest species within adjacent regenerating forest through the spread of agricultural chemicals, invasive species, or fire. Given the importance of the surrounding landscape matrix in tropical forest recovery, promoting surrounding agricultural practices that facilitate faunal movement and minimize negative impacts on recovering areas should certainly be part of efforts to facilitate forest recovery, although the remainder of this chapter focuses on restoration strategies within specific restoration sites.

9.3 SELECTING A RESTORATION STRATEGY

As a first stage in any restoration project, one needs to clearly identify the goals (Figure 9.3). These goals and specific objectives will necessarily need to be developed along with a consideration of the resources (e.g. financial, labour, sources of seeds or seedlings) available to achieve these goals and the natural **resilience** of the target ecosystem (Holl & Aide 2011). A goal of most tropical forest restoration projects will be to restore the species composition and processes of the pre-disturbance forest. However, given the competing needs of providing for human livelihoods and maximizing certain ecosystem services, there will be trade-offs concerning which goals will be prioritized (Holl & Aide 2011). For example, is it more important to restore the full suite of plant species or to maximize erosion control or sequester carbon? Large areas of cleared tropical lands are planted with trees that will be used for wood and fibre products, or that serve to diversify agricultural cropping systems. Such reforestation efforts do not aim to 'restore' the full complement of forest species and functions, but rather serve to increase tree cover and provide some ecosystem services. In addition, they may be critical for meeting the needs of people living in the region.

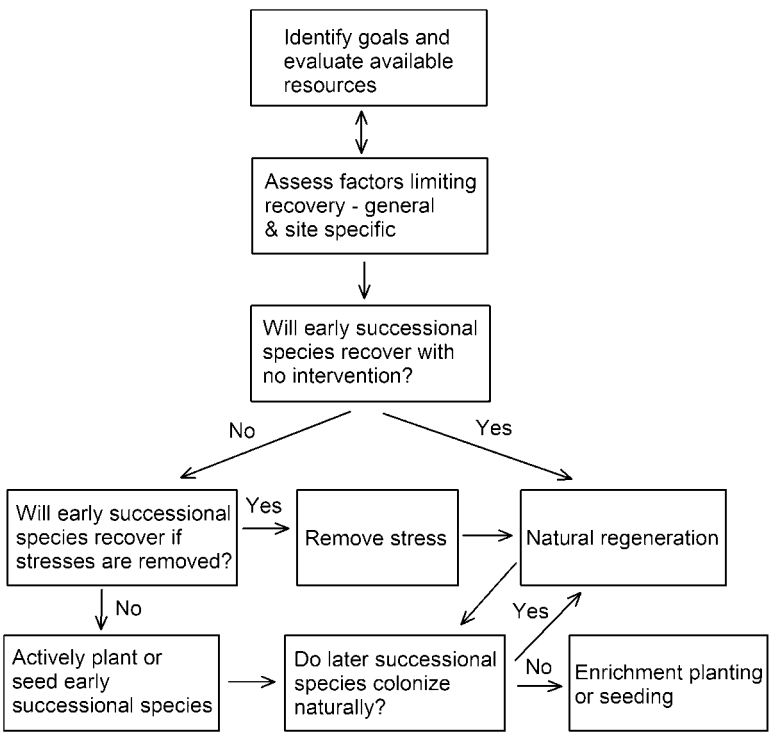


Figure 9.3 Process for selecting a tropical forest restoration strategy.

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Next, it is important to assess which of the factors discussed in the previous section are likely to slow the initial phase of recovery and document the rate of natural recovery, in order to most efficiently use the limited resources available for the large expanses of degraded tropical lands that should be restored. The likely rate of natural recovery rate can be assessed by understanding the ecology of the system, observing natural recovery in the area to be restored and neighbouring sites, and reviewing similar cases from elsewhere, as reported in the literature.

A first question to ask is whether woody species, in particular those typical of early succession in the target area, will either resprout in or colonize the site naturally. There are a growing number of examples of tropical secondary forests that have recovered similar biomass, and in some cases similar species composition – as compared to nearby **primary forests** – within a few decades (e.g. Dent & Wright 2009; Letcher & Chazdon 2009). For example, in Puerto Rico, forest cover has increased from <10% in the 1930s to >40% by the year 2000, and forest biomass and species richness in these regenerating forests are similar to those of mature forests (Aide *et al.* 2000). If regeneration is likely to be high, then lands should be left to recover naturally. Not only is this approach less resource intensive, but also, in cases where there is extensive natural regeneration, planting trees can either slow recovery (Sampaio *et al.* 2007) or strongly influence the **successional trajectory** (Murcia 1997; Celentano *et al.* 2011).

If recovery is slow, the next question to ask is whether there is a residual factor affecting seedling establishment that, if removed, would accelerate the rate of natural recovery (Figure 9.3). If there is sufficient colonization through seed dispersal and from sources within the site, then it may not be necessary to actively introduce seeds or seedlings, which is usually time consuming and expensive. For example, large-scale tropical dry forest restoration efforts in north-western Costa Rica have focused on controlling fire during the dry season, which has been largely successful in allowing for natural recovery (Janzen 2002). This approach of removing barriers to establishment is sometimes referred to as an **assisted natural regeneration** (Dugan *et al.* 2003; Shono *et al.* 2007). Shono *et al.* (2007) discuss an approach for restoring *Imperata cylindrica*–dominated grasslands in Asia, where they mark all woody regeneration and then clear surrounding grasses to reduce competition and fire risk. They also clear fire breaks around the sites and do follow-up with enrichment planting of specific target species. These efforts to remove obstacles to natural regeneration without actively planting or seeding are usually much cheaper and leave less of a human imprint on the long-term species composition than planting and maintaining tree seedlings from the outset (Lamb *et al.* 2005), which can strongly affect the successional trajectory.

If colonization of woody species is limited by lack of **propagules**, due to low seed dispersal and sparse regeneration within the site, then it is necessary to intervene to introduce woody species (Figure 9.3). This is done most commonly by planting tree species and, in some cases, by direct seeding or creating more favourable habitat for seed-dispersing animals. Different approaches for introducing forest plant species are discussed in more detail in the following section.

As the naturally regenerating or actively restored forest matures, one must consider whether the full complement of later successional plant species recolonize over time (Figure 9.3). Many studies show that tropical **secondary forests** ranging in age from 30 to 60 years tend to lack large-seeded, mature forest species (Martínez-Garza & Howe 2003; Zimmerman *et al.* 2007); this is likely due to dispersal limitation, which is exacerbated in locations where large seed dispersers have been overhunted (Wright 2003). Therefore, numerous authors have suggested that for former agricultural lands where pioneer species rapidly colonize, the most effective restoration strategy is to plant selected mature forest species that do not readily recolonize (Martínez-Garza & Howe 2003; Lamb *et al.* 2005). In some cases, even if forest species are introduced in the early stages of restoration, it may be necessary to plant later successional species once site conditions are more favourable (discussed in more detail below; Lamb *et al.* 2005; Kettle 2010). Some later successional species have shown high survival in recently abandoned pasture (Loik & Holl 1999; Hooper *et al.* 2002), but more research is needed on when in the successional process these species should be introduced to maximize survival and growth.

9.4 STRATEGIES FOR ACTIVELY REINTRODUCING PLANT SPECIES

As noted earlier, if some or all native forest species do not colonize the site within a time frame that is

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suitable for the project, then it will be necessary to take actions to actively increase colonization. In this section, I discuss considerations for choosing methods to introduce and manage these species.

9.4.1 Tree planting

The most commonly used strategy is to **reintroduce** woody species, as seedlings, cuttings or seeds, which can help to overcome several of the obstacles to recovery. Specifically, trees provide the canopy architecture to encourage seed dispersal by birds, shade out light-demanding pasture grasses, ameliorate stressful microclimate conditions, and often improve soil structure and soil nutrient availability (Holl 2002; Cusack & Montagnini 2004; Figure 9.4); these effects in turn serve to enhance seedling establishment of forest species. There are several choices to be made when designing a planting strategy, including species selection, planting density, propagation method and seedling maintenance protocol.

Native species should be used preferentially for tropical forest restoration. Over the past two decades, there has been considerable research to increase knowledge of the natural history and nursery requirements of many tropical tree species (e.g. timing of fruiting, germination requirements and light and soil requirements), and to screen which of these species establish and grow rapidly in plantations (e.g. Rodrigues *et al.* 2009; Kettle 2010). Some studies have shown that planting fast-growing **exotic species** is a cost-effective approach to accelerating recovery, as these species may facilitate establishment of native species in the understorey (Ashton *et al.* 1998; Janzen 2002). These exotic trees can be logged after roughly a decade, allowing the native species to grow while also providing a source of income to landowners if there are nearby markets. Concerns, however, have been raised about potential long-term negative effects of these species on soil chemistry (Boley *et al.* 2009; Wei *et al.* 2009).

A few different native species–planting approaches are used (Lamb *et al.* 2005). Most commonly, a small subset of rapidly growing species are planted in hopes that they will create a closed canopy within 1–3 years and thereby facilitate forest recovery by attracting dispersers and creating microhabitat conditions favourable for forest seedling establishment (Lamb *et al.* 2005). The specific species selected, particularly when only a few are used, can strongly influence the composition of species that recruit in the understorey (Cusack &



Figure 9.4 Former pasture lands in Costa Rica 3 years after abandonment. The two sites looked identical at the start of the study. Control treatment (left) and plantation of four tree species to shade out grasses and facilitate seedling establishment (right). (Photographs by Karen D. Holl.)

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Montagnini 2004; Wydhayagarn *et al.* 2009). Others have planted a mix of 20–30 slow- and fast-growing species to facilitate recovery, which provides more initial diversity (Tucker & Murphy 1997). A less common approach is to plant a large number (>50) of species with different growth rates and of different successional stages and growth forms at the outset (Lamb *et al.* 2005; Rodrigues *et al.* 2009); this requires more resources and knowledge for seed collection and propagation, and later successional species often have lower survival rates when planted into recently abandoned agricultural lands (Florentine & Westbrooke 2004). A final strategy is to plant larger seeded species that do not colonize naturally after an initial canopy has become established, either by planting fast-growing species or by natural establishment (enrichment planting; Lamb *et al.* 2005).

Tree seedlings and cuttings

The most common propagation method is to collect seed and then grow seedlings in nurseries for 2 months to a year prior to planting. This minimizes losses due to failed seed germination, seed predation and mortality of very young seedlings, which can be considerable (Holl 2002). Moreover, since tropical forest trees fruit throughout the year, seeds can be collected and germinated in the nursery at different times, and then the seedlings planted out simultaneously. Many tropical species have survival rates greater than 80% and grow 1–2 m per year, but survival and growth rates are notoriously site specific (Butterfield 1995; Holl *et al.* 2011).

Tree seedlings are usually planted in rows separated by 2–4 m, depending on the resources available and the desired rate of canopy closure; clearly, denser plantings require more seedlings but are more likely to close canopy sooner. Another approach is to plant patches of one or several tree species, which mimics the natural colonization process whereby shrubs and trees establish patchily (Zahawi & Augspurger 2006). This patch-planting approach is less resource intensive, given the smaller number of seedlings to grow, plant and maintain (Holl *et al.* 2011). It may, however, be more difficult from a practical standpoint, due to the irregular planting design, and will likely result in slower canopy closure (Holl *et al.* 2011), which in turn exposes young trees to more competition from aggressive grasses and the risk of fire during the dry seasons.

Some species of tropical trees are commonly propagated from cuttings of branches (often called 'stakes') to provide shade in cropping systems and serve as living fence posts. These stakes (typically 1–2 m tall) provide another alternative for reforestation and may develop more rapidly, in terms of above- and below-ground biomass, than those grown from seed (Zahawi & Holl 2009; Kettle 2010). Stakes do not require nursery facilities for propagation and are less costly to propagate, plant and maintain than seedlings. However, only certain species can be propagated vegetatively, large stakes can be difficult to transport, and stakes may result in lower genetic diversity when planted out than new stands produced from seedlings.

Direct seeding

Several past studies have demonstrated highly variable success with direct seeding, even amongst different species at the same site (Nepstad *et al.* 1990; Hooper *et al.* 2002). This variability is likely due to differences in seed germination rates, as well as losses due to seed predation, seedling herbivory, competition with pasture grasses and desiccation during seasonal dry spells. Direct seeding seems to be most effective for larger seeded species that have more resources stored within the seeds than smaller ones, and when seeds are introduced as part of enrichment planting after the canopy has closed (Nepstad *et al.* 1990; Hooper *et al.* 2002; Cole *et al.* 2011). Direct seeding is far less costly than planting seedlings or stakes (Lamb *et al.* 2005; Cole *et al.* 2011).

Regardless of whether seeds are directly introduced in the field or germinated under greenhouse conditions, collecting tropical seed from a wide variety of species can be difficult, as many tropical forest trees do not set seed every year. Moreover, many tropical forest tree seeds rapidly lose viability when dried, making storage impossible. In most cases, introducing a mixture of seedlings, cuttings and seeds will be most effective, depending on the biology of the individual species.

Seedling maintenance

After forest species are introduced, it is often necessary to maintain them for one to a few years following introduction. In areas where there are dense pasture grasses or other ruderal vegetation, this vegetation is commonly cleared with a machete, or less commonly a grass-specific herbicide (e.g. poast and fusilade), every few months, for a year or two (Craven *et al.* 2009; Holl *et al.* 2011). If soil nutrients are particularly low,

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then fertilizing seedlings may increase growth rates, although the effect of fertilizer on seedling growth is mixed (Carpenter *et al.* 2004; Zanini & Ganade 2005). If herbivory is high, then it may be necessary to take actions, such as fencing, to protect seedlings from mammalian herbivory (Holl & Quiros-Nietzen 1999) or use fungicides on leaf cutter ant colonies to control ant herbivory (Nepstad *et al.* 1990). Such maintenance efforts necessarily increase costs and can also have negative side effects, so they should be carefully tailored to site conditions. For example, widespread use of fertilizers may inhibit succession by encouraging the establishment and growth of weedy species (Harcombe 1977), and herbicides can reduce natural regeneration by forest species (Griscom *et al.* 2009).

9.4.2 Encouraging seed dispersal

Given that tropical forest recovery is often dispersal limited, another potential means for facilitating recovery, particularly in pastures lacking remnant trees, is the use of artificial structures, such as perches for birds, to enhance seed dispersal by frugivores. If such structures are successful in attracting animals into abandoned agricultural lands, then this approach would seem promising. Not surprisingly, however, such efforts have met with mixed results, since tropical forest trees can be both dispersal and establishment limited, and perches only serve to overcome dispersal limitation.

Several studies have investigated the use of bird-perching structures, which generally consist of branches or posts 2–5 m tall with a perching structure on the top (Holl 1998; Shiels & Walker 2003). In all these studies, a variety of fruit-eating birds were observed on perches, and seed rain under perches was higher than in areas without perches, but well below the number in forest and under remnant trees. Most seeds falling below perches were from ruderal species that are widespread in active agricultural land or pioneer species. The few studies that have measured seedling establishment below perches, however, have only found higher establishment of seedlings where pasture grasses were cleared or competition with other vegetation was minimal (Miriti 1998; Shiels & Walker 2003), suggesting that perching structures will only serve to facilitate recovery if barriers to establishment are low. Kelm *et al.* (2008) have suggested that bat boxes may serve as a strategy to increase seed dispersal by bats, but their efficacy in increasing seed dispersal in open pastures and their effect on seedling establishment have yet to be demonstrated.

A number of studies have also demonstrated that piles of branches and logs serve as perching structures and shelter for a number of bird species, while reducing light levels and temperatures at the soil surface, and providing safe sites for woody seedling establishment (Peterson & Haines 2000). In one study in Venezuela, artificially created piles of logs resulted in higher woody seedling establishment during the first year following pasture abandonment (Uhl *et al.* 1982). This promising technique for facilitating recovery should be tested more widely.

9.5 PAYING FOR TROPICAL RESTORATION

Given the large areas of land that have been deforested in the tropics and the competing need to provide for human livelihoods, a major question is how to pay for restoring tropical forests, particularly given that most are located in countries with relatively low per capita income. In addition to the costs of active restoration strategies, removing lands from agriculture or other uses for tropical forest restoration necessarily means a loss of income to people in these regions, particularly in areas that are particularly good for farming or have high value for resource extraction. Therefore, for forest conservation and restoration to succeed over the long term, they must be balanced with production systems carried out in other areas (e.g. for agriculture and timber). Additionally, landowners and other relevant **stakeholders** must be compensated for foregone income on lands where direct use is restricted. Fortunately, there are some promising approaches for paying for these costs.

First, given the increasing recognition of the need to restore **natural capital** to improve the flows of **ecosystem goods and services** that forests provide, both locally and globally (Aronson *et al.* 2007a), there are increasing numbers of programmes worldwide, and specifically in tropical forests, that financially compensate land owners for maintaining and restoring watersheds that provide these services (Wunder 2007). The efficacy of these programmes has been variable and, particularly with respect to tropical forest restoration, has generally not been well evaluated to date (Wunder

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2007). However, there is some evidence that payments to small farmers and indigenous groups in Costa Rica have helped to cover the initial costs of tree planting and increase the number and diversity of trees planted (Cole 2010).

Secondly, as discussed previously, as part of regional, national, and global effort to reduce carbon and other greenhouse gas emissions, there has been an enormous amount of discussion about programmes to pay landowners in the tropics to reduce net carbon emissions from tropical deforestation, and enhancing long-term carbon storage in degraded lands. Certainly, such efforts must focus first on preserving intact forests. Moreover, there are complicated issues related to respecting indigenous peoples' rights, establishing baseline rates of deforestation and ensuring that payments are effective in reducing the drivers of deforestation (Blom *et al.* 2010; Brown 2010). Nonetheless, funding from such programmes may soon dramatically increase the amount of funding available for tropical forest restoration. Regenerating forests have the potential to sequester a considerable amount of carbon, particularly over the first few decades (Marín-Spiotta *et al.* 2008). However, there are certain to be trade-offs to consider between maximizing **carbon sequestration** or other ecosystem services, on the one hand, and maximizing **biodiversity** conservation in restored tropical forests, on the other (Lamb *et al.* 2005).

Finally, agro-successional restoration (i.e. incorporating a range of agroecology and agroforestry techniques as a transitional phase early in forest restoration) could be used as a means to defray restoration costs and provide for human livelihoods (Lamb *et al.* 2005; Vieira *et al.* 2009). Many of the management techniques used by farmers for decades to reduce weed competition and enhance soil fertility when cultivating tropical crops and trees are similar to those used for restoration. For example, interplanting some forest tree species with shade-tolerant agricultural crops, such as cacao or coffee, may help to reduce the initial costs of planting and maintaining tree seedlings. Others have suggested managing cows to both disperse seeds of some hard-seeded tree species (Miceli-Méndez *et al.* 2008), as well as to reduce grass biomass in areas where forest tree seedlings have been established. However, using grazing animals as a restoration tool requires careful management to minimize damage to forest seedlings.

9.6 PERSPECTIVES

Tropical forest restoration is critical to both conserve biodiversity and maintain ecosystem services. It is not, however, a substitute for preventing deforestation of existing forests. It is heartening that some tropical forests are able to quickly recover the structure and species composition of intact forests (Chazdon *et al.* 2009b). But rates of recovery are extremely variable depending on factors illustrated in Figure 9.3, and there are many other cases where it appears that less common and mature forests species have not recovered after a number of decades.

There is a strong mismatch between the temporal scale of human decision making and that of ecosystem recovery. In other words, humans want to see change quickly, or even immediately, but most ecosystems take years to decades to recover from disturbance without active interventions aimed at restoration. In most cases, a bit more patience to allow systems to follow the natural recovery process is needed. By waiting for at least a few years, it is possible to assess whether intervention is necessary and, if so, how to best allocate efforts. This caution is necessary not only because of the lack of resources available for restoration, but also because extensive human intervention can actually redirect recovery to a state quite different from the previous forest.

This chapter has focused on restoring plant communities, but certainly it is also necessary to consider whether faunal species colonize and utilize sites targeting for restoration (Bowen *et al.* 2007, Lindell 2008). This will depend on both nearby source populations and habitat quality. Two recent reviews of faunal utilization of naturally regenerated secondary tropical forests (Bowen *et al.* 2007; Chazdon *et al.* 2009b) reported that the number of faunal species generally increases with time from abandonment, but that the degree to which the number and composition of faunal communities recover is highly variable and that, not surprisingly, it is influenced by past land use and the surrounding landscape. There have been fewer studies of fauna in actively restored sites, and additional research is needed. Studies suggest that restoration efforts that succeed in enhancing vegetation structural complexity increase the number of both insects and birds (Grimbacher & Catterall 2007; Morrison *et al.* 2010), and that proximity to intact forest is important (Anderson 1993; Grimbacher & Catterall 2007).

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Although ecosystem services are a motivation for restoring tropical forests, there has been relatively little study of the effect of forest restoration efforts on the recovery of ecosystem processes, besides carbon accumulation. Some studies provide promising results for the prospect of restoring nutrient cycling in restored forests (Macedo *et al.* 2008; Celentano *et al.* 2011) but long-term studies are important to determine how successful restoration efforts are in promoting the recovery not only of tropical forest structure, but also of the processes and functions that translate into ecosystem services to society.

Finally, throughout this chapter I have discussed tropical forest restoration efforts to date, which generally aim towards a species composition similar to that present prior to disturbance. Tropical forests, like all ecosystems globally, will be strongly impacted by climate change (J. Wright *et al.* 2009). Increasing carbon dioxide levels will not only directly affect plants, but also result in increases in temperature, decreases in cloud cover at high elevations, and changes in the timing and amount of precipitation. This means that in the tropics, as elsewhere, restorationists will have to make difficult decisions about selecting sources of seeds locally versus from more extreme conditions. They will also need to consider both the physiological tolerances of plants and animals to a changing climate and how these tolerances, along with limited capacity for dispersal, will affect ecosystem processes and biotic interactions.

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Chapter 10

RESTORATION OF ARID AND SEMI-ARID LANDS

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10.1 INTRODUCTION

Arid and semi-arid lands occur in areas where climatic conditions create water limitations and the water lost through evaporation exceeds the water gained from precipitation (Bailey 1996). Truly arid regions are called deserts, and they may be cold, temperate or hot, but all are relatively very dry. Definitions vary, but areas with annual precipitation of 25 cm or less are often considered as deserts. Semi-arid regions, often called steppes, typically surround or occur adjacent to deserts, but may also occur in isolation. The severe water limitations and climatic extremes that prevail in these regions render arid and semi-arid regions vulnerable to disturbance and very slow to recover (United Nations Environment Programme (UNEP) 1992; Aronson *et al.* 2002; Bainbridge 2007a). In other words, they have less **resilience** and **resistance** than most other **biomes**.

Arid and semi-arid lands make up approximately 40% of the Earth's continental surface and are home to more than 2 billion people (Adeel *et al.* 2005). Many of these are city dwellers, but ecosystem deterioration in the rural drylands – a common shorthand term for arid and semi-arid lands – is widespread and getting worse. Approximately 250 million people at present are affected by the loss of productivity from **degradation** of ecological resources or **desertification**, while as many as 1.2 billion people will be affected in the next few decades (Randriamiarina 2009). This will lead to increased suffering, growing numbers of environmental refugees and regional and international migrations that will no doubt cause civil unrest and turmoil (Sachs 2007). Half of the dryland dwellers earn very little money and as they live with very limited resources they are very vulnerable to unforeseeable events and slow-moving processes (Dobie 2001).

The semi-arid regions of the planet are more commonly occupied and more intensively managed than the arid areas, but all are vulnerable to ecosystem deterioration or desertification. A review of desertification risk in 2001 suggested the vulnerability classes and estimates of area involved and population at risk as given in Table 10.1.

Many of the more extreme desert areas are rarely used, although indigenous people in the past survived in some of them (Figure 10.1). It is important to remember these past uses by people because they often shaped the ecosystems we see today (Nabhan *et al.* 1982). Often, areas in the transition zones between arid and semi-arid regions are used by people only during wet periods (Felger & Moser 1985). Some of the most severely damaged areas are **abandoned** after their usefulness declines through over-exploitation (see Chapter 2). The lands at risk of desertification should be further categorized by current and historic use, current condition and tenure (ownership or use rights), but this has not been done in a systematic manner. Despite many similarities, the challenge of desertification can be very different from one region to the next, and perhaps even from one valley to the next.

In this chapter, I attempt a comprehensive approach to restoration that explicitly examines the socio-economic drivers that create unsustainable pressures on arid lands in addition to nonhuman drivers. In addition, I develop a *holistic approach* to restoration considering the people that are most affected by desertification. The goal is to integrate the best practices from past societies and cultures around the world that have addressed similar problems, with the latest findings from research and development on more sustainable ecological, technical and political or economic solutions (Bainbridge 2007a). A key aspect of this effort is to understand these problems well enough to

Table 10.1 Estimates of land area considered vulnerable and corresponding numbers of impacted human populations. Note: The global population density map is limited to latitudes 72°N to 57°S. Not all vulnerable lands are arid and semi-arid lands. After Eswaran *et al.* (2001).

Vulnerability class	Area subject to desertification		Population affected	
	Million km²	% global land area	Millions	% global population
Low	14.60	11.2	1085	18.9
Moderate	13.61	10.5	915	15.9
High	7.12	5.5	393	6.8
Very high	7.91	6.1	255	4.4
Total	44.24	34.0	2648	44.0

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Figure 10.1 Agave roasting pit. This seasonal Kumeyaay village site was occupied for thousands of years. It is located in the extreme desert with annual rainfall <7.5 cm. Much can be learned from careful analysis of resource utilization by these successful cultures. Restoration efforts can include species like agave (*Agave deserti*) that provide food for wildlife and insects as well as people. (Photograph by David Bainbridge.)

address the root causes, and not just the symptoms (Mitroff & Silvers 2009).

10.2 CAUSES OF DESERTIFICATION

The causes of desertification are complex and often interlinked in ways that are not readily apparent (Hallsworth 1987; Bainbridge 2007a). Mismanagement often leads to ecological decline and desertification. The causes commonly include socio-economic, administrative and ecological factors.

10.2.1 Socio-economic factors

The most critical socio-economic pressure on people who live in drylands is often simply basic survival (i.e. obtaining enough food to eat, or the small amount of cash needed for critical purchases). Population growth can compound the challenge. This often leads to overstocking of domestic livestock or, more generally, overuse of resources. The quest for respect, power or a sufficient dowry or resources for marriage (based on animal ownership) can also be a factor. Ignorance or greed may lead to management practices that are ill-advised, in the long term, and unsustainable.

The socio-economic factors that lead to desertification must be explored at the scale of the local area or region (see e.g. van Dresser 1976; Termorshuizen & Opdam 2009). The goal should be a long-term perspective, not just 1 year, 5 years or 10 years, but rather 50 or 100 years, or 1000. Even in regions where the transition from the agrarian to the industrial regime is still underway, or has hardly begun, a centuries-long perspective is often possible thanks to colonial archives (Wardell *et al.* 2003) and oral histories of indigenous people. Improving understanding of the drivers of desertification as well as the local ecosystem response can encourage more sustainable practices and restoration in use by land managers.

10.2.2 Administrative factors

Tenure (ownership or use rights) plays an important role in management decision making in drylands (Bainbridge 2007a). While in some areas tenure rights may be very clear, with known boundaries and legal documents supported by courts and law or cultural

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precedent, many of the arid and semi-arid lands are without clearly defined owners or explicitly owned by the government, but lacking clear management and supervision. Both situations lead to over-exploitation and discourage investment of time, energy and financial capital in long-term projects of conservation and restoration. The result is overuse, soil loss and eventually decline to bare rock and abandonment. Restoration efforts can be facilitated if tenure can be clarified by agreement or legislation. Satellite photos and mapping can make tenure allocation easier (Williamson 2000).

10.2.3 Ecological factors

In arid and semi-arid lands, water is the major limiting factor for plant establishment and growth. In degraded or desertified areas, this deficit becomes even more critical. Even if viable seeds are still present in the soil **seed bank**, they cannot germinate or grow without water; and changes in surface soils, microclimate and removal of vegetation and litter increase **runoff**, limit water retention and slow water movement into the soil (infiltration). As soil water is restricted by these changes, the decline in biomass intensifies grazing pressure on the few remaining plants in a downward spiral that may end with barren rock.

10.3 THE RESTORATION RESEARCH CHALLENGE

Restoring degraded ecosystems in arid and semi-arid lands requires a clear understanding of the complex interplay of environmental and social factors and the increasing impact of **climate change** (Reynolds *et al.* 2007). Basic research is also needed to better understand less disturbed **reference ecosystems** and to identify effects from climate change. The unpredictability of climate in most desert and semi-arid regions, and the extreme conditions at the soil surface make restoration challenging even when adequate financial resources are available. Restoration research is needed to help clarify the best strategies for each site and situation.

Renewed funding for fieldwork and applied research is urgently needed. Training for both participating in and managing **transdisciplinary** field studies is extremely important, yet rarely offered. Problem-oriented group studies like those proposed here are among the best method for developing these skills. These types of applied transdisciplinary studies do not fit in comfortably with the current academic environment (Bainbridge 1985, 2007b; Janssen & Goldsworthy 1996).

10.3.1 Improving understanding of the socio-economic and ecological setting

The primary challenge of restoration is to reverse the process of desertification, to capture and retain more water and to begin re-establishing plant communities and **ecosystem health** and complexity. Many techniques can be used to improve water capture, storage and infiltration, depending on soil conditions, budget and equipment availability. These include decompacting or scarifying the surface to break up crusts and increase water capture, laying out rock lines (Figure 10.2) or grids to slow surface flow and increase absorption, spreading brush or vegetation and creating swales, microcatchments or berms to capture rain (Tongway & Ludwig 1996; Lancaster 2008; Chapter 4). Soil amendments, planting and restoration of soil microorganisms can also increase water capture and infiltration. Establishment and succession can be very slow on undisturbed arid and semi-arid lands, and any additional damage due to mismanagement makes plant establishment even more difficult (Bainbridge 2007a). Techniques to capture and store water are essential, but just a start.

In the drylands, more than anywhere else, restoration planning must be based on understanding, intervention must be timely and restoration workers must be persistent. The planning effort should include consideration of ecosystem structure, function and use. Traditionally planning has focused on **ecosystem structure**, 'How many plants should be planted per acre or hectare? What canopy cover should be sought?' but repairing **ecosystem function**, 'How does water flow through the site? What is the soil health?' is often more important (Aronson *et al.* 2002; Bainbridge 2007a). Restoring function can speed *recovery* and make long-term success more likely (Allen 1988; Whisenant 1999). Attempting to return a plot of land to the historic plant community by seeding or container planting without restoring the soil and water functions that supported that community has led to many costly failures. Restoration of protected areas

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Figure 10.2 Rock lines (Burkina Faso), brush piles, soil berms or terraces can be used to stabilize soil and retain water to allow for infiltration during rainstorms. These low-cost interventions work well in some arid and semi-arid lands to initiate recovery and aid restoration. (Photograph by William Critchley, VU University, Amsterdam.)

can be straightforward because use pressure can often be eliminated. Developing restoration efforts for land used for production is much more difficult and requires careful ecological and socio-economic analysis of management activities (Scherr & McNeely 2007).

Desertification gained worldwide attention with the Sahel drought in the 1970s, although in retrospect it was perhaps more cyclic drought than human-induced deterioration. In any case, the publicity led to the creation of a number of initiatives to reduce or control desertification, including the United Nations Convention to Combat Desertification (UNCCD), adopted in 1994, and a number of new research institutes, programmes and proposals around the world, resulting in much talk, but little action. However, the recognition of the need for more comprehensive projects led the United Nations to launch the *Integrated Drylands Development Programme*, in 2002. This recognition that deterioration would not halt and restoration would be unlikely to occur without integrated action was a critical step in understanding. The growing realization in recent years that climate change is likely to make the challenges of desertification worse has led to renewed efforts to undertake research that will provide better approaches for understanding, managing and restoring arid and semi-arid lands.

10.3.2 Identifying the causes of desertification

Improving our understanding of the social and ecological settings is critical because arid and semi-arid ecosystem restoration is challenging, costly and slow (Figures 10.3 and 10.4). Minimal research funding has limited the understanding of **desertification** and restoration **trajectories** needed to disentangle symptoms and causes (Bainbridge 2007b). Research on the ecological symptoms of desertification has been much more common than analysis of the causes of desertification. The technical solutions developed to treat these symptoms often fail because the causes have not been addressed. The causal chain (Figure 10.5) must be followed from the field to the government policies and international trade agreements that shape local economies.

When the causes of desertification are not well understood suggested solutions can lead to new,

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Figure 10.3 Restoration work in progress, mesquite (*Prosopis glandulosa*) mounds (1995). Re-establishing trees or shrubs can provide critical habitat and initiate recovery of many species. Multipurpose tree crops like the nitrogen-fixing mesquite tree can also provide food and resources for people and livestock. (Photograph by David Bainbridge.)



Figure 10.4 Mesquite mound after 13 years (2008). The fine-leaved mesquite captures blowing sand to create nebkas or mounds. Capturing blowing sand and soil symbionts under the canopy creates a mound with a moist, resource-rich environment for plant, insect and animal species. (Photograph by David Bainbridge.)

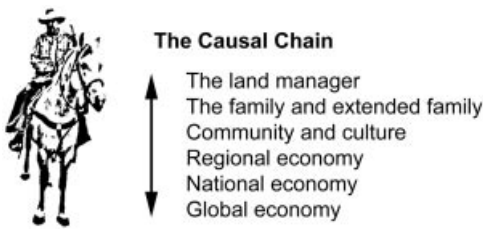


Figure 10.5 The causal chain of desertification or restoration. To understand what we see in the field, we need to understand the policies that guide behaviour. Improved management and restoration may require changes in financial and political policies that create incentives for conservation instead of exploitation.

more serious problems. The specialized narrowly focused research rewarded in academia and by funders can lead to misunderstandings of complex **socio-ecological systems**. Desertification often involves cumulative (over decades) and synergistic effects that can make isolating causes and symptoms difficult. Research on desertification has focused on a small range of factors, most commonly a subset of ecological symptoms while the more sensitive issues of political and economic causes are ignored or neglected. To be successful, restoration must include ecological and cultural factors.

Understanding is also limited by the lack of historical baseline information for both ecological and cultural factors. To develop an effective restoration plan,

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we need to know how the **degradation** came about. What went wrong? This type of information can be provided by historical ecology and, going forward, with consistent monitoring. Drylands monitoring programmes currently in operation must provide a broader spectrum of information to improve our understanding of ecological and cultural sustainability and restoration opportunities (Scherr & McNeely 2007). In developed countries, information from census bureaus, health and education departments and economic analysis may make it possible to apply integrated measures like the *Genuine Progress Indicator* (Costanza *et al*. 2004), but in many areas there will be little or no information available and field work will be needed. Failure to address the social causes of desertification can lead to ecosystem collapse and political and cultural unrest as environmental refugees migrate from the arid and semi-arid lands.

10.3.3 Rediscovering traditional solutions

Restoration begins with understanding, and it is essential to understand how arid and semi-arid ecosystems have been managed by people for hundreds, or even thousands, of years if we want to restore them. Ecological assessments should always include a review of traditional management practices and their impact on the environment. Valuable lessons may be learned by studying traditional solutions for managing these fragile lands (Nabhan 1979; Evenari *et al*. 1982; Wilken 1987; Agarwal & Narain 1997; Rivera 1998). Rediscovering and applying the traditional wisdom developed over centuries of experimentation and innovation can improve yields and sustainability in arid and semi-arid lands, offering the potential for restoration in use by pastoralists, ranchers, farmers or agroforesters and speed restoration of lands freed from management by abandonment or inclusion in protected areas.

Students and faculty can also help improve the application of traditional knowledge to restoration. We can learn much from studying the water-efficient waffle gardens of the Zuni (Figure 10.6), the terraces of Yemen, clay pot irrigation in ancient China and the graceful water wheels of Hama, Syria. It is essential to rediscover the best practices of the past, not only for each region but from around the world. The Society for Ecological Restoration now includes an *Indigenous Peoples' Restoration Network* in their activities (Martinez 2010). This project deserves personal, foundation and government support. Further study and education on best practices from the past and present are important everywhere, but are even more critical for areas where



Figure 10.6 The annual maintenance of the *acequias* or irrigation ditches is a community-building activity as well as a method of maintaining critical water infrastructure. This water can improve production on farms and ranches and reduce pressure on adjacent drylands to allow restoration to begin. Social activities that promote cohesion should be included in restoration projects. (Photograph by Rick Romancito.)

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migrants and refugees may have arrived with practices and beliefs that do not fit their new environment.

Recent work has highlighted the importance of **traditional ecological knowledge** as a key to success in arid land management and restoration (Committee on Science and Technology 2005; Youlin 2005). The UN Convention of Parties to Combat Desertification (UNCCD) first established an ad hoc committee on traditional knowledge in 1999 (UNCCD 1999, 2005). This represented a major turning point as the value of knowledge acquired over generations of experimentation was recognized. Understanding traditional practices should be the first step in any large-scale restoration or management programme for the drylands.

10.3.4 Transdisciplinary integrated restoration research with stakeholder engagement

Although I was trained as an ecologist and spent much of my career working on ecotechnical solutions to resource management and restoration problems and basic research, it became increasingly clear to me that the social factors that drive behaviour are more important than the ecological factors (Bainbridge 2007a, 2009). Including local people in research and demonstration adds strength but complexity. The residents of the arid and semi-arid lands, often portrayed as victims, typically have excellent coping capacities, are innovative and are extremely responsive to economic signals and opportunities (Dobie 2001; Critchley 2010). They often do a remarkable job with what they have, as Thomas Sheridan (1996) showed in his ecological and cultural analysis of a small town in Sonora, Mexico. The farmers, ranchers and pastoralists causing damage are often well aware of the environmental problems they are creating but are typically caught in a system with drivers and incentives that discourage sustainable management. Arid and semi-arid lands restoration may depend more on government economic policy (including reduction or removal of farm subsidies in developed countries), international trade agreements and World Trade Organization policy than on ecological research. More emphasis in restoration must be placed on policy change at this level.

Stakeholder engagement is essential to understand and address the complex problems of desertification and dryland restoration. The boundaries of the problem analysis must be large enough to capture the system, to reach across disciplines from employment to ecosystem resilience. Even when environmental and economic models of management activities are developed, they are rarely integrated. But to develop solutions that will work, they must be integrated and include feedback and interactions that more accurately represent the complexity of real-life systems (Reynolds *et al.* 2007). A **transdisciplinary** systems approach is essential for unravelling these types of complex problems (Meadows 2008; Chapters 2 and 22). NGOs with long-term experience in an area may be able to provide very useful insight and information about restoration and management opportunities and challenges. This will require new types of funding and support within government, academia and nongovernmental organizations (NGOs).

The elements needed for success include involving all affected stakeholders, conducting research to improve understanding of social and biophysical processes and developing long-term programmes to suggest, demonstrate, test and refine solutions. These are described in the following section on management.

10.4 THE MANAGEMENT CHALLENGE

The need for integrated approaches to arid and semi-arid lands research and management has been increasingly recognized by research groups, NGOs and advocates (Haberl *et al.* 2006; Reynolds *et al.* 2007). Since the 1990s, a number of initiatives have been started to encourage more interdisciplinary, multidisciplinary and transdisciplinary research, but the results overall have been disappointing (Glenn *et al.* 1998). In part this is the result of limited funding, but even the money that has been spent has yielded less than expected, often because local communities have not been engaged, encouraged and empowered (Chambers *et al.* 1991). Stakeholder outreach is critical (Partridge *et al.* 2005; Prell *et al.* 2007). When stakeholder engagement is managed well, I have also seen it ease conflicts between competing groups.

10.4.1 Setting sustainability goals

The importance of setting sustainability goals for a community or region cannot be underestimated (van Dresser 1976). Putting people first can help promote

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cooperation with the local community (Chambers 1995; Gómez-Pompa & Bainbridge 1995). Interrelating social and ecological factors provides the critical insight needed to understand the problems and suggest solutions. The challenges in determining what makes a particular community sustainable need to be understood, including questions of health, education, employment, innovation, community involvement, crime and corruption, culture and opportunities for improvement. Often the goals may be as simple as safe and comfortable housing, adequate food, clean water and economic opportunity. It is important to compare the relations between these over time by ethnicity, caste and income class as well. The Genuine Progress Indicator or the *Index of Sustainable Economic Welfare* can help us understand the sustainability of social systems (Costanza *et al*. 2004). Developing **ecological footprint** and sustainable area budgets for the area or region may also be instructive (Rees 2006; Levine *et al*. 2010). These can help establish budgets for energy, water, food or other resources that would be sustainable over the long term. If the community and culture are not sustainable, successful environmental restoration will not be possible.

Evaluating the **sustainability** of socio-economic systems involves measures of both structure and function much like the ecosystem factors. The flow of money is very important, but many social system interactions do not involve cash flow, and labour contributions or gifts and exchanges have not been recorded, studied or counted by conventional economics. Ecological impacts are even less likely to be costed and incorporated in accounting (Bainbridge 2006). All countries also have shadow economies (illegal activities or economic enterprises with no records and no taxes). These shadow flows may be very important, particularly in marginal arid lands. Understanding these economic factors can be critical in analysing the resource management practices leading to desertification or restoration.

Reducing or eliminating economic incentives that promote poor management can lead to changes in resource utilization that lead to restoration in use. Destructive incentives can be corrected by the activities of association, cooperation and lobbying, but those who benefit from current inequities and subsidies are very reluctant to see policies and programmes change. The problem is rarely at the farm or ranch level, but further up the economic system with the banks, companies and organizations involved in resource management and finance. In the 1980s, for example, we found that dryland farmers in Sonora, Mexico, were being forced to abandon their sustainable locally adapted traditional corn varieties. To obtain credit, they had to agree to use high-response corn and buy chemical fertilizer. This increased risk and debt, with inevitable failures driving people off the land, leading to land consolidation, further involvement in illegal activities and emigration. Challenging and changing long-standing subsidies and incentives are never easy. In developed countries, protesting land managers may be snubbed, ridiculed or shunned; but in developing countries, the risks are much higher (Sinha 1991). Engaging stakeholders in efforts to reshape socio-economic drivers to be more sustainable is critical to improve management, to facilitate restoration in use and to encourage the conservation and restoration of important ecosystems in reserves or protected areas.

10.4.2 Developing and demonstrating solutions

More than half of the people living in drylands still depend on farming, grazing, fuelwood harvesting, hunting, poaching or wild gathering for a significant part of their living. All will have to add restoration to their existing management activities if they intend to move toward more sustainable **socio-ecological systems**. Restoration activities can improve the quality of life and the economic viability of small farm, forestry or ranch enterprises (Tiedeman 2005). Restoration may be undertaken on individually owned or controlled land, or else on lands and resources held in common, leased from or held by the government.

Land managers are most likely to adopt new practices if they have seen, visited and participated in a working demonstration, yet demonstrations are rarely included in restoration programmes. Degraded and damaged lands are almost worthless and are not costly to purchase or lease for restoration research and demonstration. Cooperative on farm or ranch demonstrations are very useful and can be encouraged by protecting land owners with a funding guarantee of no loss of income or yield while they experiment with new crops or management practices. This strategy proved useful for the Carter Foundation (set up by former US President Jimmy Carter) in efforts to improve agriculture in Africa. Small landholders are conservative and often work to minimize risk rather than

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Figure 10.7 The waffle gardens of the Zuni were remarkably effective in capturing rainwater, and protecting plants from winds and animals. Lessons from traditional societies can be applied to restoration efforts. These waffle gardens would be well suited for nurseries growing native plants for restoration work. (Photograph by Jesse Nussbaum, 1911. Courtesy Denver Public Library, Western History Collection.)

maximize output. A no-loss guarantee, provided by a participating NGO or government programme, can encourage participation and experimentation with restoration activities.

I would suggest a new approach to the development and implementation of solutions that includes local, long-term research and validation. This approach would engage local communities in transdisciplinary systems analysis, research, demonstration and extension needed for successful restoration. The most important groups involved in solving the problems of dryland desertification are the local communities. Yet they are often a weak link, hampered by poverty, lack of respect by outsiders for their wisdom and internal power relationships that limit their ability to voice their concerns. Encouraging local farmers and ranchers to participate can help offset the narrow goals of special interest groups and their economic and political dominance.

While much has been learned about the functioning of some dryland ecosystems in the last 80 years, much remains unknown. Long-term transdisciplinary research is needed to better understand the challenges we face and the opportunities for improving management practices and restoring arid lands. Diverse stakeholders need to be collectively engaged in designing and delivering strategies that simultaneously address the challenges of meeting goals for rural **livelihoods**, food security and environmental **sustainability** (Scherr & Rhodes 2006). Restoration research and implementation teams can provide insight about the ecosystem and the current and historic national and international economic incentives and cultural pressures that determine land management practices (Figure 10.7). A system-oriented approach to restoration that incorporates socio-economic goals as well as environmental goals is much more likely to succeed than a more traditional eco-technical solution. It is also more likely to get local community buy-in and support. This type of project cannot be fast or short-lived because it takes time to build trust and to research, test and demonstrate solutions. Costs may be much lower than those of many traditional aid programmes, but long-term commitment for the communities and the researchers is essential.

Developing effective restoration programmes will require demonstrating solutions at the field, farm and watershed levels before promoting their widespread use (Leigh 2005). Demonstration is the ultimate test of practice and understanding and is the best way to encourage land managers, volunteers, companies and organizations to become actively involved. Land managers can be very skeptical, and only after they see,

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touch and apply these methods personally will they believe that they work. Studies in California showed that it took nine interactions with extension and demonstration to initiate change in adding one best management practice (Lubell & Fulton 2007). Demonstration can be done at the farm, ranch, park, watershed or regional level (Naveh 1989; Campbell & Siepen 1994). Dryland managers are justifiably risk averse and cautious, but will readily adapt new approaches that work. These new methods will spread far beyond the demonstration project site with little or no additional spending.

Demonstration projects are well suited for undergraduate and graduate students in both applied and theoretical research programmes. Working with local families can provide critical feedback and reality checks for proposed solutions while improving the sophistication and technical capabilities of small landholders. Field restoration projects also provide students and faculty with transdisciplinary project experience, stakeholder engagement skills and the opportunity to test and refine equipment and plant materials, as well as their understanding of how ecological and social systems behave (Aronson *et al.* 2007a; Bainbridge 2007a). The Natural Environmental Research Council and the Economic and Social Research Council in the United Kingdom currently offer 20 interdisciplinary study awards each year in recognition of the importance of this work (http://www.nerc.ac.uk), but these are for individuals, not teams.

Study teams in these **transdisciplinary** fields of study, **intervention** and ameliorative development must include a wide range of **stakeholders** from the local communities and/or encourage their participation in regular reviews because they are most familiar with the problems and will often be able to rapidly eliminate many of the proposed options. A systems approach working with local communities has rarely been used in analysing arid and semi-arid lands management and restoration. The work done by P. S. Ramakrishnan and his colleagues and students in north-eastern India was a good prototype for the work that is needed (Ramakrishnan 1992). Students lived in and studied traditional land management systems, analysing a wide range of cultural, ecological and economic factors. Box 10.1 presents the outline for a

Box 10.1 A restoration and demonstration project chronology

Year 1. An experienced restorationist/geographer/agroecologist/anthropologist, preferably with considerable experience in the region, revisits the area, reviews the literature, history and current political economy, talks with the local people, and meets with key stakeholders. This research begins to establish the framework for restoration work and potential demonstration projects. A catalogue of native plant communities and rare and endangered species, local cultivars of vegetables, grains, fruits and livestock, their pests and diseases, and economics is begun. Communities suitable for a long-term study/demonstration are evaluated and discussions with community groups, NGOs and governmental organizations will help select a study site.

Year 2. The project team leases (or buys) a representative land holding, farm or ranch for ten years with an option to renew. An experienced restorationist or field research project manager, preferably married with children, is hired to live on site. The presence of a spouse and children facilitates integration with the local community, improves understanding, and reduces the risk of romantic complications. One of their first tasks in the field will be to select and hire a local field staff person from the community. The research programme also recruits and begins training the first team of undergraduate and graduate students. This might include an environmental historian/geographer/anthropologist (a good PhD project), restoration ecologist, agricultural engineer, organic gardener (or animal scientist for range), soil scientist, agroecologist, hydrologist or microclimatologist, and public health/nutritionist/emergency medical technician. Prospective students should ideally be conversant if not fluent in the local language and include some from farm or ranch backgrounds and experience living in primitive conditions. Both men and women would where possible, live with local families. When this would be culturally difficult or inappropriate, they could live on the site property. Applications from married couples and families should be encouraged. The restoration team would be equipped with a container full of restoration tools and supplies, construction and vehicle repair tools, and equipment for restoration work and farm operation.

Continued

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Box 10.1 *Continued*

They would also have a used but serviceable ¾ ton 4×4 flatbed truck and four-wheel-drive tractor, 30–50 hp, with plow, spader, box scraper, backhoe, and bucket loader.

The goal for this year would be adding to the understanding of the local culture, ecosystems, microclimates, soils and economy – adding to the regional research from year 1. The goal would be to begin developing a history of the political ecology and environmental changes at the project site for the last 50 years or more. This would begin with library research and continue with interviews of the village elders and observation. The restoration ecologist would begin developing a local and regional overview of ecosystem function and structure and identify a plant restoration palette and start a seed banking programme. Seed collection would be a priority. If appropriate, a nursery for native plants and economic cultivars of interest would be started with community involvement.

The facility would be built or retrofitted as an example of sustainable design with assistance from the student team, staff and local workers. Renewable energy and local resource capture would be demonstrated with a solar photovoltaic array, solar hot water system, passive solar heating and cooling, rainwater harvesting system, improved water and irrigation systems, and proper treatment of water supply and wastes. If needed, seismic safety issues would be addressed with an onsite retrofit. A demonstration organic garden and agroforestry options and composting system would also be designed and started, with the goal of developing value-added products. The garden would help feed the team and would test varieties suited to local site conditions.

The soils science and hydrology/microclimatology students would establish a sampling framework and complete initial surveys of the area. Both would work with local teachers and students if possible to engage the community in the research. The public health/nutrition student would help keep the team healthy and would also work to better understand health problems and nutritional limitations in the local community.

The students and staff, truck, and tractor would be made available to help with community projects as appropriate. Funding would be provided to hire students from the local school or community to help with restoration research and implementation and gardening/facility operations.

Year 3. Work would begin on restoration projects and, as appropriate, economic development. The primary goal would be working with local stakeholders to develop two or three demonstration projects for restoration. Land tenure issues might be addressed as well. Restoration activities might include fencing springs and riparian areas to improve water quality and stabilize riparian ecosystems. It might also include water and soil conservation demonstrations using gabion dams, rock lines, terraces or swales. Business opportunities that could benefit the local community might also be explored, such as developing an organic certification for a local crop such as nopales (*Opuntia* (prickly pear) cactus pads) and developing value-added products such as cactus fruit syrup, goat cheese or organic mesquite flour and corn baking mixes. The project students and staff might also help start a garden at the local school.

The first annual open house and welcome to the community would be a fiesta, with food, music, and dancing. This type of annual cultural event has proved to be a critical factor in improving the interactions between the Mapami Biosphere Reserve and neighbours in the Chihuahuan desert.

Year 4-onward. Additional restoration projects (and economic development demonstrations) would be developed in partnership with the local community. Existing programmes that link business students with local vendors/producers in Chile and Mexico can provide valuable insights (see for example the *Proyección Social* 'Community Outreach' programme at the Universidad del Pacifico, Lima, Peru).

Restoration, demonstration efforts, and supporting facilities would be analysed using a standardized sustainability dashboard or scorecard (http://esl.jrc.it/envind/dashbrds.htm). Projects that have succeeded or appear likely to succeed would be replicated and promoted. Those that had failed to meet expectations would be revamped or dropped.

Note: the challenges caused by political instability and drug violence would need careful consideration in many areas. Even in the 1980s concerns about the *narco-trafficantes* (drug dealers) were common in much of northern Mexico and today it is much worse (Grant 2008).

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long-term transdisciplinary restoration research and demonstration project in northern Mexico.

10.4.3 Funding

By my estimate, funding a study like this in the arid lands of a developed country like the United States might cost $5 million over 10 years. In Mexico and other developing countries, the cost would be considerably less. Secure funding for the long term, perhaps 10–20 years or more, is essential. The Long-Term Ecological Research sites of the National Science Foundation and a few development and conservation projects around the world have shown that long-term integrated research is invaluable. Inadequate funding, too little, too short, has hampered much of the research on ecological restoration and integrated development. Long-term funding is needed to ensure that students can complete projects and find continuing support for career advancement. Projects like this can provide meaningful change not only in the community where it is implemented, but throughout the region and for similar climate/cultural areas in other areas of the world. The benefits will also include new faculty and managers trained in systems analysis and arid and semi-arid lands restoration.

The World Bank and other international institutions are increasingly cognizant of the importance of economic incentives for improving land management, but this growing recognition has led to little improvement on the ground. The legacy of past economic colonialism through abusive loans and development programmes has also left a series of tragic consequences. The need for external funding support for the developing countries that will feel the most severe impacts of desertification and climate change is recognized in both the Climate and Desertification Conventions. The United Nations Framework Convention on Climate Change (UNFCCC) places particular emphasis on the responsibility of developed country parties for funding climate change mitigation and adaptation due to their disproportionate contribution to the problem of climate change (Lorimer *et al.* 2009). If we adopt a funding goal of just $5 per resident affected, we would have $1.25 billion to work with, enough for 5000 local, integrated, multidisciplinary, long-term management for restoration efforts.

Efforts to address the causes of desertification also require funding (Glenn *et al.* 1998). These would not be costly, but are politically challenging. While there have been many examples of worthwhile projects that have made technical improvements to agriculture in the drylands, there are few examples of the drylands being systematically considered in economic and trade policies, either nationally or regionally (Dobie 2001). Restoration of arid and semi-arid lands on a large scale will demand reform of these economic policy drivers. James F. Reynolds and coworkers have outlined the *Drylands Development Paradigm* for research that interlinks coupled *human–ecological systems* (H–E systems; Reynolds *et al.* 2007). This paradigm consists of five principles of particular significance in drylands and focuses on inter- and intrarelationships in dryland systems:

1. H–E systems are coupled, dynamic and co-adapting, so that their structure, function and interrelatioships change over time. Understanding dryland desertification and development issues requires the simultaneous consideration of both human and ecological drivers.

2. A limited suite of 'slow' variables are critical determinants of H–E system dynamics. Identifying and monitoring key 'slow' variables are particularly important in drylands where highly fluctuating 'fast' variables often mask fundamental change related to slow variables.

3. Thresholds in key slow variables define different states of the H–E systems. The costs of intervention rise nonlinearly with increase in land degradation or the degree of socio-economic dysfunction. Managers should adopt the precautionary principle.

4. Coupled H–E systems are hierarchical, nested and networked across multiple scales. Drylands are often distant from economic and policy centers and have difficulty influencing policy drivers.

5. The maintenance of a body of up-to-date local environmental knowledge (LEK) is key to functional co-adaptation and restoration of H–E systems. The Drylands Development Paradigm also addresses the needs of research, management, and policy communities.

10.5 PERSPECTIVES

The world's drylands are beset by problems of overuse and mismanagement, and most are experiencing declines in ecosystem health and productivity. Growing human populations and changing economic structures can add further pressure to fragile lands (Depner 2011). Desertification is causing increasingly severe

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Figure 10.8 Project manager Dr Laura Jackson at the restoration research farm near Eloy, Arizona, explored options for restoring abandoned farmland. Simple techniques of water harvesting hastened recovery, but the project also illustrated the challenge of working on long-term problems with short-term funding. (Photograph by David Bainbridge.)

problems for local communities and families and despair with the suicide of more than 200 000 farmers in India in a little over 10 years (Sainath 2009). It leads to unnecessary suffering, migration and displacement, and unrest. Water is perhaps the most critical concern, but desertification also involves equally pressing concerns about food, economics, justice and biodiversity. These problems are all expected to become worse as climate change disrupts rainfall and stream flow in arid and semi-arid lands (Ribot *et al.* 1996; Lorimer *et al.* 2009). Solving these problems demands an understanding of ecological and cultural histories because they develop over time and almost always involve subtle or not so subtle signals and incentives that encourage people to do the wrong thing. Historical insights can help us plan policies or developments that restore ecosystem structure and function, protect and restore endangered species and ecosystems, and improve the quality of life today and for future generations.

Restoration research has improved our understanding of the ecological issues involved in restoration, but this has done little to improve management. Successful restoration in protected areas has been possible, but the key challenge today is improving management of areas in use by addressing the ecological and socio-economic causes of desertification. This effort will benefit from setting sustainability goals, better understanding less disturbed reference ecosystems, developing and demonstrating restoration approaches, ensuring funding for long-term research and addressing the potentially critical impacts of climate change (Figure 10.8).

We must address the complex problem of desertification and restoration of arid and semi-arid lands with intelligence, commitment and compassion (Bainbridge 2007a). Solutions are likely to be very different from one area to the next, reflecting the cultural, administrative and political differences present even when ecological factors are similar. Restoration is both possible and essential and can help protect vulnerable ecosystems and communities from increasing risks from global climate change while contributing to the development of viable eco-economies (Brown 2001, 2005; Critchley 2010).

The costs of ecological restoration are not insignificant, but the cost of not acting will be higher in terms of human suffering and ecosystem damage. Combining restoration and improved management can provide

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multiple benefits. As Scherr and Rhodes (2006) note, 'Synergies can be delivered by enhancing coordination and complementarity between existing conservation and production strategies. Diverse stakeholders need to be collectively engaged in designing and delivering strategies that simultaneously address the challenges of meeting goals for rural livelihoods, food security and environmental sustainability' (p. 23). Well-funded restoration efforts in protected areas can be undertaken with optimism and expectation for success. Restoration projects for lands actively being used or exploited or abandoned lands have been less common and demand much more attention. If a range of options that previous research has suggested are 'best bets' are tested and evaluated on each project arid and semi-arid lands, restoration projects can avoid repetitive failures and improve restoration practices more rapidly.

Solutions that halt and reverse desertification can be found, but they won't reveal themselves without much improved, long-term, transdisciplinary research and demonstration at field, community, and regional levels. Restoration can improve the outlook for people and the environment and reduce the risks of ecosystem collapse and extensive migration. This is made even more important by the added stress of climate change with rising temperatures, less rainfall, reduced streamflow and more extreme weather events. Healthier and more productive ecosystems from improved management are more resilient and reduce the risk of ecosystem collapse.

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Chapter 11

RESTORATION OF MEDITERRANEAN-TYPE WOODLANDS AND SHRUBLANDS

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11.1 INTRODUCTION

There are only five Mediterranean-climate regions (MCRs) on Earth – the Mediterranean Basin, most of California, central Chile, southern South Africa and south-central and south-western Australia. They all have cool, or cold and relatively wet winters alternating with long, hot and dry summers. Spring and autumn seasons are ephemeral in comparison, and highly variable. During much of the year, droughts lasting weeks or even months are frequent, with grave consequences on all biota, since water is the key limiting factor for growth and well-being of all organisms, including humans. Yet, biodiversity is unusually high in all five MCRs. Well-adapted woodlands and shrublands, which are the subject of this chapter, are numerous and noteworthy, in ecological, cultural and socio-economic terms.

Climate, geology and evolutionary biogeography of MCRs have all contributed to alpha, beta and gamma biodiversity of these regions. In the Mediterranean Basin, California and Chile, the predominantly young, orogenic systems produce intense geomorphologic dynamics with poorly developed, shallow soils (Bradbury 1981). The uneven relief with steep slopes in large parts of the territory and spreading of unconsolidated and soft substrata increase the risk of soil degradation. In sharp contrast, MCR landscapes in South Africa and Australia are ancient and stable; as a result, they have highly weathered and leached soils that are very poor in nutrients (Rundel 1998). Human land use histories have also contributed to ecological diversity in all five regions, and must be taken into account when contemplating or undertaking ecological restoration.

Natural *wildfires* are common in most of the five MCRs, owing to the high accumulation of fuels leading to enhanced flammability in summer, the frequency of lightning storms and, in some areas, periodic but intense, hot and dry winds such as the Santa Ana in California and the Mistral in southern France. An exception is central Chile where the Andean Cordillera protects the MCR area from summer storms and lightning (Rundel 1998). As a result, central Chilean sclerophyllous vegetation is ill adapted to frequent fires, never having had selective pressure from this form of disturbance over evolutionary time. Nonetheless, in recent decades anthropogenic fires have become much more common, and this is causing profound changes in the characteristic features of central Chilean landscapes (Armesto *et al.* 2009).

In spite of the similarities in climate, many striking differences can be found among MCRs, in addition to fire regime. As mentioned, historical differences in *land use* practices, including the time span of degradation processes, socio-economic dependence on local resources and cultural perceptions of the relationship between humans and nature, all have great impact on biota and ecosystem dynamics. The Mediterranean Basin is the only MCR in the so-called Old World, where humans have practised agriculture for as long as 13 millennia in some areas (Purugganan & Fuller 2009). The process, initiated in the Near East, is thought to have spread to the entire Mediterranean region over the course of about three millennia (Zeder 2008). In the process, people consumed resources and transformed, or 'resculpted' natural **landscapes** and **ecosystems** to their own ends (Blondel *et al.* 2010). Therefore, environmental **degradation** in the region is ancient (Thirgood 1981). However, the intentional fires, herbivory by domestic livestock, agroforestry practices and constant trade of wild and domestic species of plants and animals first developed in the Mediterranean Basin itself, are now common practices there, and indeed in most of the MCRs (Armesto *et al.* 2007). They cannot be described simply as environmental destruction. Instead, in more neutral terms, we may refer to the profound transformation of the 'original' or pre-Holocene landscapes (Blondel *et al.* 2010). Certainly, the combination of the great diversity of physical conditions (geology, topography and soils) and of land use histories, and finally the large number of possible pathways and stages of succession occurring after various disturbances all give to Mediterranean landscapes a particular patchwork pattern and kaleidoscopic quality that Blondel and Aronson (1999) called a 'moving mosaic'. Both the interpretation of these landscapes, and the procedures for carrying out ecological restoration there, are highly complex.

In the four MCRs other than the Mediterranean Basin, intentional anthropogenic transformation of landscapes was less intense and extensive until very recently. However, the indigenous cultures of each four of those regions also have a long history of landscape modification, mostly through the intentional use of fire. Natural fire regimes were often altered, affecting ecosystems dynamics, landscape structure and biodiversity in the process (Pausas & Keeley 2009).

Of course, urbanization, industrialization and 'metropolization', and the globalization of commodity and service markets, are driving current land uses and

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cultures to higher convergence in all five MCRs, just as elsewhere, but still the 'fingerprint' of land use history is strong enough to influence current restoration approaches, of which there are a large number indeed in the various MCRs. As elsewhere, the first step towards restoration is to identify and halt degradation processes. Such processes affecting MCRs today are land degradation produced by long-term overuse of natural resources, and further degradation produced in case of land abandonment in semi-arid areas, anthropogenic forest fires and the spread of invasive species. Once one or more ecological **thresholds** have been crossed, however, certain degradation processes may not be reversed spontaneously, but only through human **intervention** in the form of restoration actions and manipulations. In particular, in recent decades, anthropogenic fires have increased in frequency and intensity, not only in Chile (see above) but also in the other MCRs. This represents a serious threat to ecosystems, wild biota and, of course, the built environment. To cope with fire-induced damages to ecosystems and to humans, *post-fire rehabilitation* started in California in the 1930s and is now being applied in the other MCRs as well. Later in this chapter (section 11.2.5), we will dwell on the topic of fire regime intervention and restoration in some detail.

Since the mid-nineteenth century, several countries in the Mediterranean Basin have carried out **afforestation** programmes to protect watershed headwaters areas, regulate streamflow, reduce flash floods, control soil erosion and provide forest products. Programmes in Spain (Martínez García *et al.* 1996) and France (Vallauri *et al.* 2002) were particularly extensive. In contrast, afforestation in central Chile only began in the mid-twentieth century, and there top priority was given to timber production, and most often the use of exotic trees was favoured over native forest restoration (Becerra & Bustamante 2009). In south-western Australia and South Africa, afforestation and restoration practices have also begun in the recent past, but generally speaking the strongest emphasis of restorationists in those two MCRs has been put on the control of invasive alien species (e.g. Richardson & van Wilgen 2004), as is now the case in California as well (E.B. Allen *et al.* 2005; D'Antonio & Chambers 2006).

The rapid increase of global trade and travel in recent decades has facilitated the spread of invasive organisms of all kinds. In the case of the MCRs, the predominant direction of invasion has been from the Mediterranean Basin to the other four regions, and there have also been major invasions of alien plants from Australia into South Africa (see also Chapter 20). Negative effects of **invasive species** on Mediterranean ecosystems include reduced biodiversity changes in soil properties that make the site unsuitable for native species (Yelenik *et al.* 2004), and more frequent fire following annual grass invasions (Minnich 2008). However, biological invasions of both plants and animals are now clearly on the rise in the Mediterranean region as well, and much more attention is being accorded with this problem, by ecologists, horticulturists and conservation authorities (Quézel *et al.* 1990; Filippi & Aronson 2011a,b).

11.2 RESTORATION OF MEDITERRANEAN-TYPE WOODLANDS AND SHRUBLANDS

In this section, after discussing restoration priorities (section 11.2.1), we review some of the most prominent tools used in ecological restoration programmes in the range of ecosystems covered in this chapter. These include (1) post-fire emergency rehabilitation techniques such as sowing of herbaceous cover crops and mulching (section 11.2.2), and techniques to ameliorate reintroduction of key native tree species such as microsite preparation, tree shelters and bird perches (section 11.2.3), (2) invasive plant species control (section 11.2.4) and (3) the restoration of natural or moderate, cultural fire regimes (section 11.2.5). Approaches and techniques vary from region to region. We shall only explicitly consider **rehabilitation** activities as part of early post-fire measures, although they have short-term objectives not always related to the *recovery* of reference or pre-disturbance ecosystems. Furthermore, we will concentrate on the Mediterranean Basin, Chile and California. For more information on current restoration activities in Australian and South African MCR woodlands and shrublands, see Chapters 4 and 20, respectively.

11.2.1 Restoration priorities

The specific objectives of restoration differ widely among the different Mediterranean-type **woodland** and **shrubland** ecosystems, and are determined by the degree of degradation, and by climatic, biotic and socio-economic constraints (Table 11.1). As elsewhere

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Table 11.1 Framework for the restoration of Mediterranean ecosystems. Drivers for restoration are identified, as well as actions that can be undertaken to attenuate them, and available techniques to implement these actions. Each driver must be offset to ensure successful restoration.

Driver	Action	Technique
Persistent anthropogenic disturbances, unwanted species	Release disturbance	Limited access to people, herbivores, etc. Fire prevention, windbreaks Species control (fire, herbicides, clearing)
Low propagule availability	Artificial introduction Promote dispersion	Seeding, planting Bird-mediated restoration, frugivory-mediated restoration (artificial perches, catches and habitat amelioration)
Adverse environmental conditions	Reduce soil losses Ameliorate soil properties Improve microclimate	Emergency seeding, mulching, sediment traps Amendments, nutrient immobilization, mulching, drainage, soil preparation Shelters, mulching, microsite selection

in the Old World, the great and continuous density of historical layers in the Mediterranean Basin renders difficult the selection and use of a precise historical **reference system**, such as is frequently sought in New World settings (Egan & Howell 2001). References for ecological restoration are usually taken from pre-disturbance ecosystem information, in the case of recently disturbed ecosystems (e.g. due to fires), and from historical information or from reference ecosystems supposed to be natural, remaining in well-preserved sites. Sustainable seminatural ecosystems of socio-economic and cultural interest may well be taken as references for restoration projects, especially in areas like the Mediterranean region and highly transformed parts of the other four MCRs. In this case, as always, goals must be clearly defined in relation to site-specific constraints and opportunities. A good example is the *dehesa* or *montado* woodlands in Spain, Portugal and the rest of western Mediterranean Basin, which are artificially opened and managed savanna-like landscapes designed and maintained for silvopastoral or agrosilvopastoral uses (Aronson *et al*. 2009). In other MCRs, landscapes and disturbance regimes existing before the European settlements in the sixteenth–nineteenth centuries very often guide restoration actions.

Despite the wide range of MCR restoration objectives, some features are common to all MCRs:

1. Soil and water conservation is generally the main priority, for reducing and preventing soil losses and for regulating water and nutrient fluxes (Cortina & Vallejo 1999).

2. Increasing ecosystem resilience to disturbances, and ensuring the sustainability of restored lands by promoting the re-assemblage of plant, animal and microbial communities resilient to current and future disturbance regimes.

3. Improving landscape quality, from a local, cultural perspective, and the provision of ecosystem services (Figure 11.1).

4. Promoting biodiversity, fostering the reintroduction of key native species, while eradicating alien invasive species, and battling their re-establishment.

11.2.2 Early post-fire rehabilitation

In some cases, quick action is urgently needed before a degradation process reaches or exceeds a certain threshold beyond which restoration becomes prohibitively expensive or impossible. This may be the case in some fire-sensitive systems, where wildfire removes vegetation cover, leaving an unprotected soil. In eastern Spain, for example, many plant communities dominated by obligate seeders (species unable to resprout after fire), growing preferentially on soft bedrocks and, especially, on equator-facing slopes, commonly show slow post-fire *recovery* (Pausas *et al*. 1999) and thus high **erosion** and **runoff** risk. Early post-fire restoration can either be integrated in an ecological restoration programme, or just concentrate in short-term non-ecological objectives (e.g. plantations for timber production). Emergency action after wildfires has been practised in California for nearly a century, primarily to mitigate flooding and erosion. Federally mandated and financed post-fire activities in California, and throughout the United States, was formalized in 1974 through the Burned Area Emergency Rehabilitation

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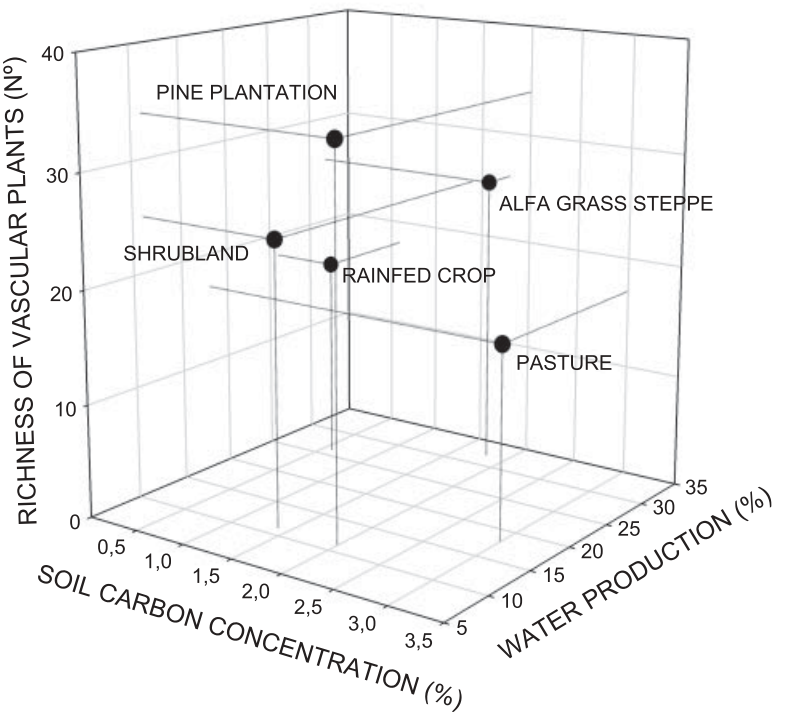


Figure 11.1 Indicators for ecosystem services provided by alternative land uses: soil carbon concentration for carbon sequestration, richness of vascular plants for biodiversity and water production for water regulation. This information may help evaluating restoration options. Average level of soil organic carbon (0–20 cm depth), richness of vascular plants (from floristic inventories) and water production (precipitation minus evapotranspiration and interception) in landscape units from a semi-arid area in south-eastern Spain (Derak 2010). Alfa grass: *Stipa tenacissima*.

programmes, now called Burn Area Emergency Response. In the Mediterranean Basin, there is no specific, nation-wide regulation for early post-fire rehabilitation; instead decisions are taken at the management project level.

To provide rapid soil protection, two main (non-exclusive) techniques are used: (1) *seeding* with herbaceous species, often including fast-growing, non-native species, and (2) *mulching*, that is, protection of soil surface with various kinds of organic materials. Seeding and mulching can be applied on large scales and in remote areas by using aerial means. Both seeding and mulching may reduce soil losses, surface crusting and water evaporation, and enhance water infiltration (Bautista *et al.* 2009).

There are also many examples recorded of the low efficiency of post-fire seeding on soil protection as a result of poor germination. Further, regrowth of native plants is often inhibited when introduced species have much higher germination rates (Beyers 2009). In the framework of ecological restoration, seeding would be only justified on degraded ecosystems with high post-fire degradation risk, showing low short-term regeneration capacity, and when using native species that combine both highly enough regeneration rate and low competition with late-successional species (Bautista *et al.* 2009).

11.2.3 Reintroduction of woody species

In many degraded lands affected by fires and/or other disturbances, it is necessary to **reintroduce** key **native woody species** to foster and accelerate succes-

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sion (Vallejo *et al.* 2009). To ensure successful establishment, selection of woody species for restoration should be based, as much as possible, on the natural flora and vegetation of the area, and on the specific biophysical characteristics of the site. Traditionally, pine trees were planted in many areas in the Mediterranean Basin for catchment protection and sand dune stabilization. Pines commonly have high survival rates, allowing a relatively quick **revegetation** success. However, extensive pine plantations also provide an excellent fuel bed for large, devastating fires. Pine woodlands also have low **resistance** and **resilience** in the face of recurrent fires, and Mediterranean pines do not resprout after fire. On the contrary, most native hardwoods and, in general, woody sclerophyllous trees and shrubs resprout (Paula *et al.* 2009). Therefore, combining pines and hardwoods would take advantage of the complementary features of both groups of species, for example the high survival and fast growth of pines and the high fire resilience – that is, efficient resprouting capacity – of oaks (Pausas *et al.* 2004). Early attempts to introduce broad-leaved resprouting species in the Mediterranean Basin (e.g. *Quercus* spp.) failed because of high seedling mortality and, even until the late twentieth century, techniques for introducing these species in Mediterranean conditions were poorly developed. Since the last few decades, the introduction of hardwoods is becoming common in afforestation programmes, although the degree of success is still variable. Recently, **afforestation** objectives are widening their scope, so the diversity of introduced species is increasing in MCRs. New programmes even consider shrubland restoration, such as the restoration and rehabilitation of mixed *espinales* in a central Chile programme led by Carlos Ovalle of the Instituto Nacional de Investigaciones Agropecuarias. That long-standing programme is developing management and intervention techniques useful in restoring the structure and former levels of diversity and productivity of the mixed, anthropogenic *Acacia caven* formation (Ovalle *et al.* 1999). Therefore, new species, never tested before, including shrubs, are becoming of interest for restoration.

The reintroduction of hardwoods and other native woody species in degraded lands would require improved restoration techniques, in order to increase their degree of success. Drought is the critical factor hindering seedling survival under Mediterranean conditions. However, irrigation is seldom used in restoration projects of southern European countries or indeed any of the MCRs. In central Chile, for example, where summer drought is particularly long and severe, all available water is reserved for other uses, mostly agriculture and tourism. In general, in the MCRs, as in all semi-arid and arid regions, the implementation costs of watering restoration sites in rugged and remote areas are prohibitively high. Therefore, as irrigation is not feasible, in most cases, improving rainfall capture and *water-use efficiency* become key factors for plant survival and growth. Two common practices in this regard are seedling manipulation and site preparation practices (Table 11.2). As elsewhere, species assemblages and nursery and field techniques must be tailored to different landscapes and landscape units, and restoration strategies should make use of available resources and functional processes remaining in the degraded site.

Table 11.2 Mediterranean restoration techniques concerned with water.

Objective	Technique
Increase water-use efficiency	Selection of drought-tolerant species and ecotypes
	Seedling preconditioning
	Improve below-ground performance
	Improve nutritional status
Increase water supply	Soil preparation and amendment
	Irrigation
	Microsite selection
Reduce water losses	Tree shelters
	Mulching
	Microsite selection
	Control of competing species

As most woody late-successional species do not form a permanent seed bank (Huston & Smith 1987), seeding woody species is an attractive technique to reintroduce target species owing to its low cost, the low impact of field operations and the improved possibilities for treating remote areas through aerial seeding. However, high predation risk and uncertain seed germination and seedling establishment under dry conditions are serious managerial constraints for the direct use of seeding (Vallejo *et al.* 2009). From several pine-seeding experiments carried out in Spain, right after major fires, only one produced acceptable seed germination rate and seedling survival, despite very favourable weather conditions (Pausas *et al.* 2004).

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Seedling quality

How to characterize seedling quality is subject of much debate. Seedlings should be able to withstand unfavourable growing conditions (transplant shock, seasonal water stress and drought cycles), and take advantage of short favourable climatic periods to achieve sustained growth. Seedling quality has been substantially improved over the past decade (Cortina *et al*. 2006). Most approaches are based on nursery manipulations simultaneously affecting several plant morpho-functional traits. Seedling size together with other, mostly visually assessed, characteristics are used to define acceptable stocks. However, above-ground size may not be a good indicator of seedling quality under dryland conditions. Indeed, the relationship between seedling morpho-functional traits and establishment success is not clear, as seedling fate may be ultimately driven by the complex set of interactions allowing fast and deep rooting. The few long-term studies undertaken to date suggest that the positive effects of enhanced seedling quality may endure for a decade after planting (Cortina *et al*. 2006). Fortunately, many sophisticated *nursery* practices are now available to manipulate seedling traits, although there is still much scope for improvement in this area, particularly through the use of alternative, biodegradable and recycled materials as containers, as well as substitutes for standard soil mixes. Already, however, seedling quality is probably no longer a major limiting factor for the establishment of common species in the Mediterranean and in the other MCRs, provided that current knowledge is applied.

Microsite selection and nurse plants

The recognition of the importance of microhabitat heterogeneity – particularly the role of positive plant–plant interactions and the role of 'safe sites' – has contributed to the elaboration of a new paradigm for ecological restoration in MCRs. Facilitative interactions are especially important under semi-arid conditions, where isolated vegetation patches act as 'resource islands', mainly in terms of shade and soil fertility (Maestre & Cortina 2004). *Facilitation* may show a unimodal response to *stress*, with a maximum at intermediate levels and declining both at the lowest and highest levels of stress (Maestre & Cortina 2004), but the relationship between facilitation and stress is not simple. The patterned landscape of semi-arid tussock steppes (*Stipa tenacissima*), common in southern Spain and throughout northern Africa, is a clear example of this, as tussock microsites have higher organic matter, higher water availability, lower temperatures and lower soil penetration resistance than intertussock patches. These environmental modifications facilitate the development of bryo-lichenic communities, and introduced woody plants (Maestre *et al*. 2003a). In other systems, the nurse plant can be a spiny shrub, as it protects planted seedlings from grazing (Gómez *et al*. 2001). In the Sierra Nevada, southern Spain, 4 years after planting, seedlings of *Quercus*, *Pinus* and *Acer* spp. planted under shrubs had, on average, rates of survival three times higher than those planted in open microsites (Castro *et al*. 2002). In contrast, under semi-arid conditions, *Pinus halepensis* may not be capable of facilitating the establishment of woody shrubs (Maestre *et al*. 2003b). The outcome of plant–plant interactions depends on the level of stress and on the morpho-functional attributes of benefactor and beneficiary species. Uncertainty in the results of plant–plant interactions represents a major challenge for the use of facilitative interactions in restoration programmes.

Heterogeneity in biotic and abiotic conditions in dry areas may be relevant to restoration success. Large-scale changes in slope aspect and bedrock can substantially affect the outcome of restoration. Further, subtle small-scale changes in soil properties and microtopography can also be important. Patchiness of plant population survival and persistence in apparently homogeneous areas are frequently associated with small differences in soil moisture, soil depth, stoniness, texture or nutrient availability (Figure 11.2). As plant responses to these factors tend to be nonlinear, it is very important to identify thresholds that may explain such differences in plant performance. A wide array of ecotechnological tools and techniques, which in many cases mimic abiotic conditions and biotic interactions, is currently available (see below). But it is important to note that the effect of local biotic and abiotic conditions on plant performance is commonly much greater than the effects of the various ecotechnological tools employed by restorationists (Cortina *et al*. 2011).

Soil preparation and amendment

Various soil preparation techniques have been developed to improve water supply to planted seedlings and ameliorate soil physico-chemical properties in degraded

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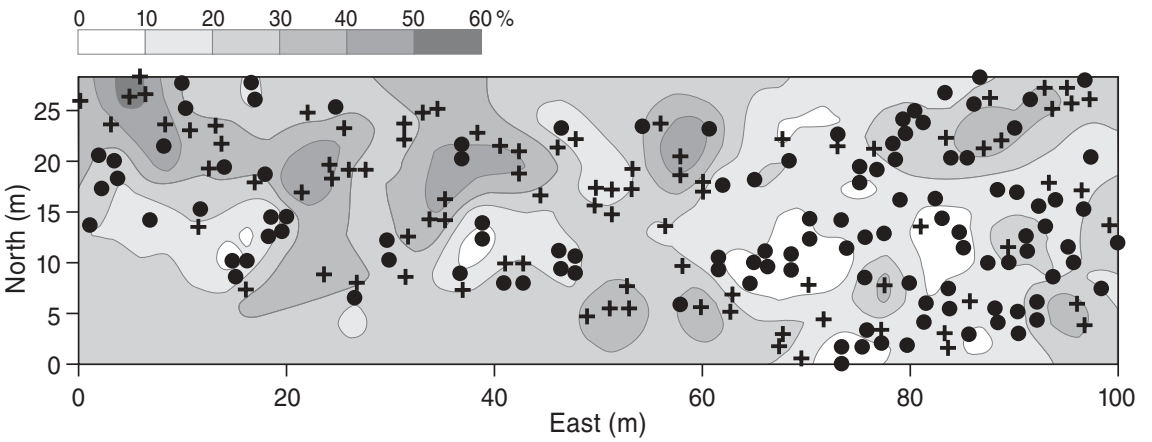


Figure 11.2 Small-scale spatial distribution of the amount of bare soil covering planting holes (as shown by the grey scale, in %; darker areas had more bare soil), and of seedling survival 1 year after planting. Crosses (+) and circles (•) are dead and live seedlings, respectively. There is a significant negative relationship between the amount of bare soil and survival (logistic regression; $P < 0.001$). (Elaborated from Maestre *et al.* 2003a.)

soils. The array of available techniques is very large. **Runoff** harvesting aims to intercept runoff and redirect water to the planted seedling. Successful results have been obtained in arid areas (Bainbridge 2007a; Figure 11.3), where low-infiltration surfaces allow runoff concentration in vegetated patches and increase the productivity of the whole system. In the example of Figure 11.3 (Fuentes *et al.* 2004), water harvesting increased seedling survival for the most drought-sensitive species assayed (i.e. *Quercus ilex*) and growth rate for the most tolerant (i.e. *Pinus halepensis*), although significant differences between species, in both variables, still remained. Therefore, the impact of additional water inputs provided by water harvesting would affect seedling survival right after outplanting under the most extreme dry conditions and for the most sensitive species. This is critical for the potential success of the plantation project, as seedling survival is not granted for many species and drought conditions (see Figure 11.5). Soil depth is very often a major limiting factor for seedling survival as shallow soils have low water holding capacity. Indeed, increasing planting hole depth from 40 to 60 cm increases seedling performance by 15% in eastern Spain, and the survival rate of planted woody species is very low for soils shallower than 40 cm in this region (Alloza 2003).

Mediterranean soils are frequently poor in soil organic matter and low in phosphorus availability (Vallejo *et al.* 1999). To what extent soil nutrient impoverishment is hampering restoration is a matter of discussion. Soil organic matter intervenes in many soil processes affecting plant growth, but especially in soil structure (i.e. stability versus soil crusting and erosion, and water-holding capacity) and soil fertility.

Positive response to the addition of resources (e.g. water, nutrients, or both) is considered an **indicator** that something was limiting. Planted seedlings commonly respond well to inorganic and organic fertilizers, and negative and null responses are associated with metal toxicity, salinity and increased above- and below-ground competition (Valdecantos *et al.* 2002). There is a wide range of organic residues available for improving soil fertility.

Artificial tree shelters

Artificial tree shelters are used to modify the physical environment of planted tree seedlings, acting effectively as mini-greenhouses. If properly designed, they can help reduce seedling transpiration and improve overall performance (Bellot *et al.* 2002), as well as provide protection against herbivory. The use of tree shelters has gradually increased, being readily adopted by land owners and other practitioners. Ventilated tree shelters help avoid excessive warming, while improving seedling survival and growth, and increase

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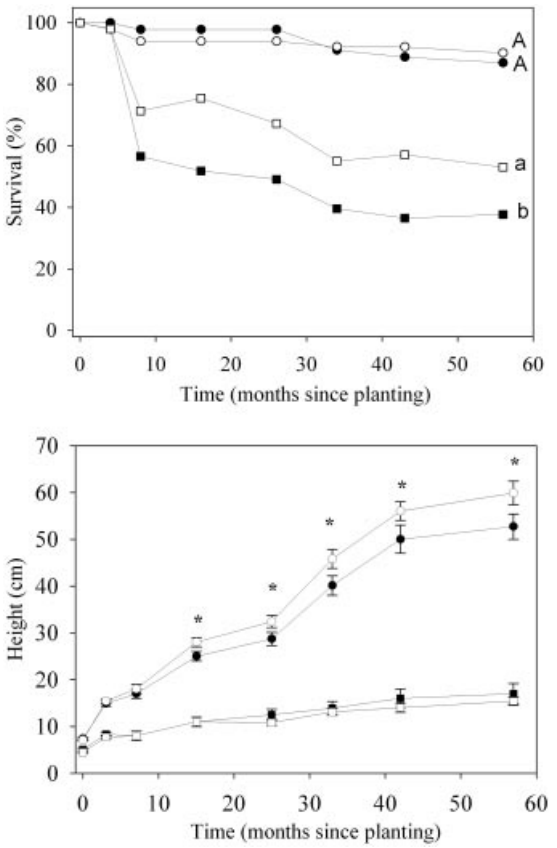


Figure 11.3 Survival and growth of Aleppo pine (*Pinus halepensis*, circle) and holm oak (*Quercus ilex*, square) seedlings in planting holes with (white) and without (black) water-harvesting microcatchments during the first year after outplanting. Field experimental data on degraded forests in the Region of Valencia (Spain). Different uppercase or lowercase letters within each species mean significant differences in survival between treatments ($P < 0.05$). For height growth, differences are indicated with *. (Modified from Fuentes *et al.* 2004.)

average stem size (Bellot *et al.* 2002; Figure 11.4). Nevertheless, the use of this technique alone does not guarantee plantation success. The root–shoot ratio of protected seedlings is often lower inside tree shelters than in unprotected seedlings, and this reduces the capacity of seedlings to withstand prolonged drought. Tree shelters significantly increase seedling growth in height with, however, the risk of producing elongated, 'leggy' stems. However, thanks to their slow growth rates, most Mediterranean tree seedlings growing inside tree shelters gradually acclimatize to adverse climatic conditions outside the shelter and improve shoot growth. When this does not happen, unbalanced growth in stem height may occur, and the plant becomes highly susceptible to wind damage.

Costs and benefits of ecotechnological investments

Between 1992 and 2010, CEAM Foundation and University of Alicante (Spain) established 217 experimental plantations on degraded semi-arid and dry subhumid areas. Initially, plantations used prevailing technology at that time, that is, using a few species (mostly pines and a small number of holm oaks), and simple nursery cultivation techniques and basic soil preparation. Over the past decade, plantations have incorporated innovations in species selection, nursery production, soil preparation and tending (e.g. mulches, tree shelters, organic amendments etc.), according to the discussion in previous sections. Seedling survival after the first summer in the field (a major indicator of plantation success) was strongly dependent on the number of consecutive days with no significant rainfall (precipitation events <5 mm) in both old and new plantations (Figure 11.5). But the slope of the relationship between survival and drought length decreased as advanced technologies were implemented. Under severe drought, survival rate would double, and the risk of total failure would decrease significantly by using advanced ecotechnology. One obvious interpretation of these results is that plantations carried out on harsh sites would require higher technological inputs and investments to achieve a given target than those on less harsh sites.

Bird-mediated restoration

The role of plant–animal mutualisms has been suggested for cost-efficient restoration plans (Handel 1997). Bird-mediated restoration is based on the observation of succession of abandoned woody crops, such as olive groves, carob groves, almond groves and vineyards. In these contexts, natural succession is significantly faster than in nonwoody crop fields thanks to the role of the trees as perch sites for frugivorous birds. These birds discharge seeds of late-successional species that germinate around the perching tree forming a nucleus of intermediate or advanced succession

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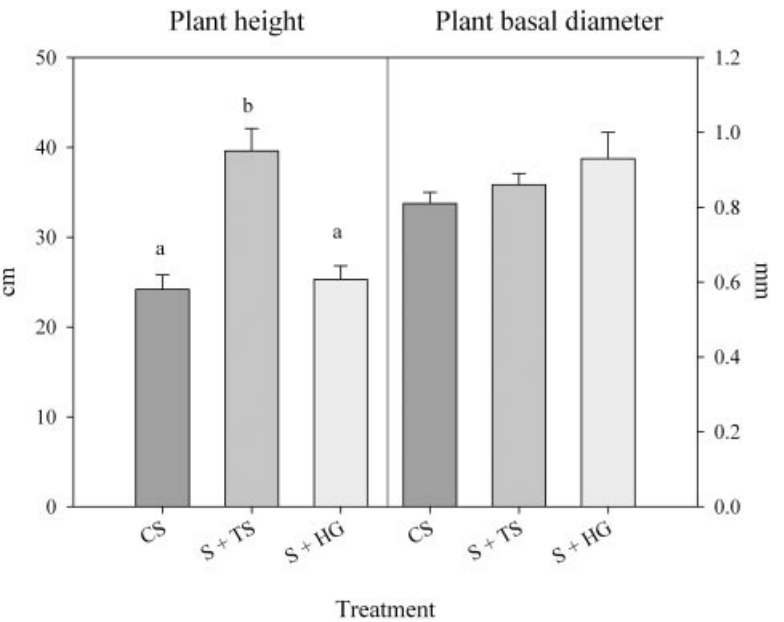


Figure 11.4 Seedling height and diameter (mean and standard error) of holm oak (*Quercus ilex*) seedlings nine years after planting. CS: control seedling, S + TS: seedling with tree shelter, S + HG: seedling with hydrogel. The plantation was conducted in burned degraded forests in the Region of Valencia (Spain). Different letter means significant differences among treatments at the $P < 0.05$ level. Notice the low stem growth rate of holm oak in these degraded lands, on equator-facing slopes and under dry climate (average annual precipitation for the monitoring period: 360 mm). (Modified from Chirino *et al.* 2009.)

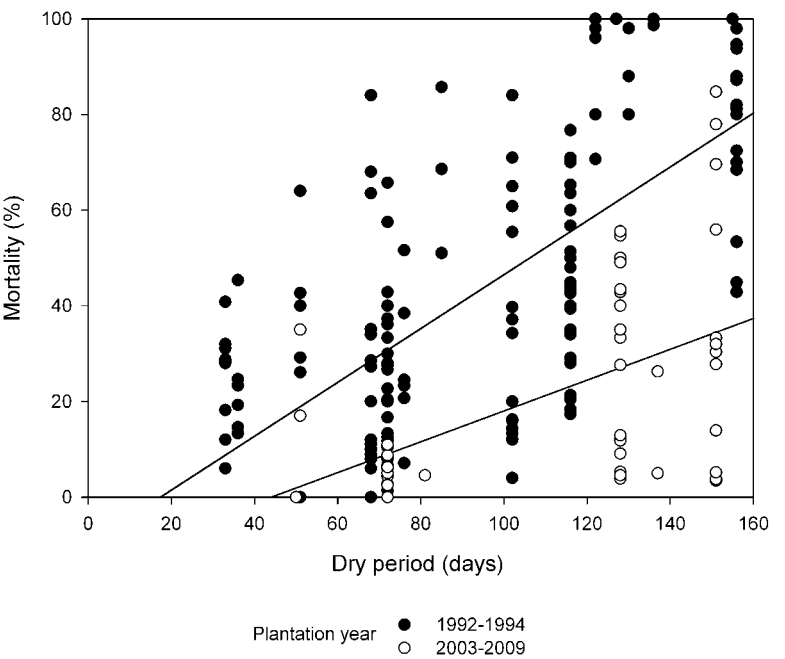


Figure 11.5 Percentage of plants surviving in relation to the length of the dry period during the first post-plantation year, for several native species planted in eastern Spain. The first set of plots (1992–1994) includes plantations using conventional techniques at those times. The second set (2003–2009) includes plantations using recent technical innovations. Regression lines for each plantation period are significantly different (ANCOVA significant interaction between plantation year and dry period, $P < 0.0001$). 'Dry period' refers to the maximum number of consecutive days with precipitation less than 5 mm. See the text for more details. (Elaborated from the CEAM-University of Alicante database. J.A. Alloza unpublished data.)

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taxa (Pausas *et al*. 2006). In fact, these birds act as **ecosystem engineers**, *sensu* Jones *et al*. (1994). Furthermore, the perch tree may also create a favourable microsite for germination and survival. Dead trees may also be used by birds as caches (e.g. for acorns). These bird-mediated facilitation processes inspired a restoration technique based on providing bird perches (dead trees and artificial woody structures) in old-field sites to accelerate colonization rates and ecosystem restoration. Although being an attractive and inexpensive technique to help succession, it has seldom been applied to Mediterranean ecosystems and most examples come from tropical forest ecosystem restoration projects (see Chapter 9). In many areas of extensive old-fields, where there is generally a very low seed availability of late-successional species, this technique could be especially appropriate.

11.2.4 Principles of control for invasive alien plants in MCRs

The principal goal of restoration after invasive species control is to create a stable stand of native vegetation that is resistant to further invasion (D'Antonio & Chambers 2006; see Chapter 20). The degree of success of this undertaking depends upon the extent and density of the invasion, the extent to which soil and ecosystem characteristics have been altered, life histories of **invasive** and **native plant species** and interactions among these characteristics (Table 11.3). Invasive plant species include all life forms from herbs to shrubs and trees, and the range of techniques to control them includes mechanical removal (cutting, mowing, fire and solarization), chemical control with herbicides, and biological control by insects or other herbivores. Some techniques that have been effective in MCRs are reviewed here.

Often, the extent of invasion is too large for mechanical and chemical control to be effective across large and complex landscapes. In these cases, efforts have focused on isolated populations or preserves that are particularly threatened by alien invasives, as in the case of the riparian tree and shrub invader *Tamarix ramosissima* in California. This tenacious species has been **eradicated** by hand control and herbicide in defined stands, but introduced *Tamarix* still dominates the riparian zone of thousands of kilometers of rivers in the western United States. Following careful testing, a host-specific biocontrol beetle, *Diorhabda elongata*, from Eurasia, has recently been released, and is now beginning to show good results in efforts to control *Tamarix* across large areas (Ehleringer *et al*. 2009). Where normal riparian hydrologic regimes still exist, native riparian trees are recolonizing and the abundance of the invasive *Tamarix* is declining.

Invasive species can be more readily controlled if they have not invaded at high density. In the Azores, that have woodlands of Mediterranean origin but an oceanic climate, low-density invasive trees were removed with cutting and herbicide from a laurel forest, followed by successful establishment of planted native trees (Heleno *et al*. 2010). The moist climate likely promoted establishment, as seedlings in a summer-dry Mediterranean climate may suffer higher mortality. Alien trees also re-established from seed in this experiment, but in a real restoration situation would need to be controlled by future treatment. Native

Table 11.3 Probability of restoration success after the invasion of alien species based on invasive species characteristics.

Invasive species characteristic	Probability of restoration success	
	Higher	**Lower**
Extent of invasion	Small	Large
Control technique	Biological control	Mechanical or chemical
Plant size	Large (woody)	Small (herbaceous)
Density of invasion	Sparse	Dense
Recolonization ability	Low	High
Seed bank longevity	Short-lived	Long-lived
Seed bank density	Sparse	Dense
Soil and ecosystem feedback	Minor	Major

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insects and birds increased in abundance after control of invasive trees, an important finding given the conservation value of these remnant native forests (Heleno *et al*. 2010). The Asian invasive Tree of Heaven, *Ailanthus altissima*, was successfully controlled with tree cutting plus herbicide application in Spanish woodlands, but the authors did not report vegetation recovery (Constán-Nava *et al*. 2010). They recommended afforestation to avoid future recolonization of *A. altissima*. If invasive plants are controlled while their populations are sparse or their areas are small, any subsequent escapes, spreading or reinvasion can be controlled with relatively small efforts (D'Antonio & Chambers 2006).

Recolonization or re-establishment ability by **native species** is a critical prerequisite to restoration following invasive species control. In the study by Heleno *et al*. (2010), native seeds became the most important component of the seed rain just one year after clearing invasive trees, and the authors suggested this showed a renewed **successional trajectory** leading toward a native-dominated community. By contrast, Mediterranean annual grasses were the most abundant species to recolonize in California coastal sage scrub after mowing and grass-specific herbicide that reduced the alien grasses (E.B. Allen *et al*. 2005). Native shrubs had limited establishment under the constant impact of colonizing invasive species, and removal of invasive species was recommended every 5 years to maintain native dominance (E.B. Allen *et al*. 2005). Similarly, the Mediterranean grass barbed oats (*Avena barbata*) may compete with establishing native shrubs in abandoned farmland in Australia, and must also be periodically controlled (Standish *et al*. 2008). The Australian site had low soil nutrients (Standish *et al*. 2008), while the California site had high soil nutrients (E.B. Allen, *et al*. 2005), indicating that Mediterranean annual grasses have a broad ecological amplitude for invasion, especially barbed oats, which occurred in both study sites.

Seed bank density and longevity are also critical factors in the invasion process. The seed bank density of alien grasses was two orders of magnitude greater than that of native forbs and shrubs in California coastal sage scrub (Cox & Allen 2008). Fortunately, the seeds of many alien grasses – especially the dominant *Bromus madritensis* and *B. diandrus*, both from the Mediterranean region – are short lived, so that carefully timed spring fire (before the seeds have dispersed) has been a useful tool in restoring perennial grassland (Gillespie & Allen 2004). However, given the ability of these annual grasses to recolonize or re-establish, fires must be set every 5–7 years. This high frequency of fire is a good tool for restoring perennial, fire-adapted grasslands, but is incompatible with native shrub or tree recovery, as frequent fires will not allow woody plants to establish or grow to maturity. Other means of alien annual-grass control are needed for shrub and woodland restoration, such as timed grazing in spring to reduce annual seed production. Seed bank longevity is also a factor in the successful control of *Tamarix*, which has a short-lived seed bank; the few seedlings that establish after mechanical or chemical control can be readily eliminated with follow-up treatment.

The degree of soil or ecosystem alteration following invasion will also determine the feasibility of restoring invaded systems in MCRs. Invasive *Acacia saligna*, from Australia, has caused elevated soil nitrogen of South African fynbos, which impedes restoration efforts because the native shrubland is adapted to low levels of soil nutrients (Yelenik *et al*. 2004). Hand clearing of the invasive shrub promoted colonization by *Ehrharta calycina*, a nitrophilous native perennial grass. As a result, it was recommended that fire or mulch be used to control high soil N and promote re-establishment of native shrubs. Bark mulch was effective in immobilizing N and allowing establishment of native shrubland that was invaded by alien Mediterranean annual grasses in California (Zink & Allen 1998).

As mentioned earlier, Mediterranean Basin woodlands and shrublands are apparently more resistant to biological invasions than those of other MCRs, and thus are – in theory – more amenable to restoration. Indeed, invasive plants from the Mediterranean Basin often come to dominate in other MCRs because they are more aggressive than the native species, or because environmental conditions (e.g. fire, grazing and soil nutrients) have changed so that the native species are no longer able to thrive. Some of the environmental drivers may be controlled (e.g. reducing fuel for fire or reducing grazing intensity), while others are less easily manipulated, such as reducing soil N on a large scale. Another approach to restoration is to select native species with physiological traits that inhibit invading species, and establish vegetation that is resistant to invasion (Funk *et al*. 2008). This approach will succeed if ecosystem disturbance rather than species traits have allowed invasion. However, if the environmental drivers have been controlled and the invasion is still ongoing, as has been observed in California coastal

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sage scrub, then periodic mechanical or chemical control may be required (E.B. Allen *et al.* 2005), and invaded systems will require long-term management to achieve and then maintain desired conservation values.

11.2.5 Restoration of fire regimes

One of the challenges in landscape management of Mediterranean ecosystems is to restore, or reinstate, natural (historic) fire regimes. For this purpose, both fire suppression and prescribed fires may be appropriate tools to test. However, prescribed fires have also been used to reduce fuel loads and fire intensity without examining the natural fire regime. Indeed, restoring fire regimes is never a simple task because of the impact on and implications for native biodiversity. The main difficulties are as follows:

- Natural fire regimes vary spatially with climate and vegetation structure, and different ecosystems have species adapted to different fire regimes. Moreover, the natural or historic fire regimes are not always known. In ecosystems with surface fire regimes, fire scars from old trees can be used to infer past fire regimes; however, in crown-fire ecosystems (e.g. the chaparral- or matorral-like communities of all MCRs), this is not an option as most trees are fully burned and the main stem dies after the fire. In ecosystems intensively and perhaps over-used for millennia, including many in the Mediterranean Basin, old trees are very rare and can hardly be used for fire regime estimation; in such situations we lack an historical reference. Aerial photography and remote sensing have been used to reconstruct fire regimes to the earliest available imagery.
- Most fires in natural fire regimes occur in summer, when vegetation is most flammable, while for safety reasons most prescribed fires are set in the wet winter season. However, plants and animals exhibit different physiological and phenological conditions in different seasons, and as a result prescribed fires may not have the same effects and impacts as natural fires. For instance, birds nesting in spring are more susceptible to prescribed than to natural fire, and there is much evidence of varying plant regeneration responses to prescribed fires in differing seasons (e.g. Keeley 2006).
- Mediterranean climate and landscapes are very attractive to humans, and are among the most populated ecosystems on Earth, and the most visited by tourists. In most MCRs, people colonize landscapes in houses interspersed with vegetation, generating a large wildland–urban interface. In such conditions, natural fire regimes are difficult to restore without affecting human activities and infrastructures. There is still a lack of cultural, political and socio-economic understanding of living in flammable ecosystems (Pausas & Vallejo 2008).
- As mentioned above, invasive alien species are one of the major problems in MCRs and, with the exception of the Mediterranean Basin (where post-fire aliens are relatively uncommon), and frequent fires often increase the opportunities for invasion by alien plants (Keeley *et al.* 2005). Given the current high (unprecedented) propagule pressure of alien species, restoring natural fire regimes may imply the increase of invasive alien plants (Keeley 2006). This often leads to a challenge for managers who must choose between restoring natural fire regimes and altering those fire regimes to favour communities of native species, while altering the natural community structure.

In addition to these difficulties to restore the historic fire regime, climate is changing very fast in many or all of the MCRs, and due to the strong link between climate and fire, restoration of fire regimes should also be conducted with full consideration of projected climatic scenarios of coming decades. Moreover, climatic change also has consequences on other factors that may modify forest structure and flammability, such as drought and pests. According to some researchers (e.g. Fulé 2008), such considerations make local historical references of limited value while references from drier sites become more appropriate. Needless to say this is a fertile topic for debate, and long-term research and adaptive management will be necessary on a site-specific basis.

11.3 PERSPECTIVES

Major challenges for woodland and shrubland restoration in Mediterranean climate regions must be confronted in the coming decades. Some of these relate to previously identified, but still poorly implemented, needs that have emerged in the course of maturing restoration theory and practice, such as project evaluation and social involvement. Other research and development horizons relate to new and, above all, rapidly changing climate scenarios in the non-analogue **Anthropocene Era** we are now entering. For example, restoring sustainable fire regimes, while

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also reducing wildfire threats to humans and built environments in fire-prone areas, is certainly of the most challenging issues in the land management and restoration of MCR woodlands and shrublands.

11.3.1 Evaluation and social involvement

Ecological restoration has a strong socio-economic component, particularly in highly populated areas such as the MCRs, where human societies have co-evolved with landscapes for centuries or millennia. Thus, social actors should participate in defining the objectives of restoration actions and through the evaluation process. The ecosystem service approach (Millennium Ecosystem Assessment (MA) 2005) provides an excellent opportunity to involve people and encourage participative management. There are many examples of such initiatives, and on the use of decision-making tools, such as multicriteria decision models, to support the identification of restoration targets in MCRs (Díaz-Balteiro & Romero 2008).

In order to improve our understanding of the success or failure of restoration actions, there is a need for long-term monitoring and evaluation of restoration actions. Evaluating ecological restoration success on the ecosystem and landscape scales can be performed using carefully selected suites of indicators (e.g. Aronson & Le Floc'h 1996; Vallauri *et al.* 2005). Although widely accepted standard protocols are not yet available, recent initiatives integrate biophysical and socio-economic aspects of restoration projects (e.g. Bautista & Alloza 2009, for Mediterranean Basin woodlands and shrublands).

11.3.2 Restoration and climate change

Woody vegetation that evolved in the Mediterranean Basin during the Pliocene shares common features such as sclerophylly, evergreeness and the ability to resprout after fire of many species (Blondel & Aronson 1999). However, these life-history traits are associated to Tertiary lineages that arose from tropical and temperate ancestors prior to the appearance of Mediterranean climate conditions in the last 3–5 million years (Herrera 1992; Blondel *et al.* 2010), and the Quaternary taxa evolved under Mediterranean climate in the various MCRs in the world do not show such convergent traits (e.g. they are not sclerephyllous, and many of them do not resprout after fire) (Verdú *et al.* 2003). Therefore, MCRs show a long-standing common background of characteristic woody taxa that have survived drastic climate change, both slow and fast. An open question is whether these species will endure projected climate change in their respective MCRs, in a human-altered and much more fragmented habitat.

Climate change must be taken into account when restoring ecosystems at the present time, considering that they should be functional by the middle of the twenty-first century under changed climate. It has become increasingly clear that knowledge of the past is not necessarily a good – or even sufficient – guide for understanding or planning for the future (Pahl-Wostl 2007). This is particularly so when considering the adaptability and acclimation capability of various species or functional types to a projected new climate, and the associated fire regime conditions. For example, no one knows how ecotypes and genotypes of Mediterranean plant species will respond to the projected intensification of drought and new, more severe fire regimes. Taking a precautionary principle, it is probably wise to fully explore the adaptation and acclimation potential of native species beyond local seed sources (Crowe & Parker 2008) before assisting the migration of currently alien species or subspecies from drier areas. To cope with the *uncertainty* induced by climate change, restoration and management must be **adaptive**, trying to improve ecosystem resistance and/or resilience, and managing landscapes to facilitate species migration (Stephens *et al.* 2010).

Increased knowledge of the pattern of climate variability may be used to plan restoration activities. In many Mediterranean semi-arid and arid regions, interannual variability in precipitation is strongly associated to El Niño Southern Oscillation (ENSO). Increased rainfall during ENSO events is crucial for plant recruitment and productivity in these systems and may cause long-lasting effects on vegetation depending on the prevalent herbivore pressure (Holmgren & Scheffer 2001). Indeed, field studies in arid zones of North America have indicated that successful recruitment of woody vegetation takes place during rainy ENSO events, especially when herbivores were excluded (Bowers 1997).

Holmgren and Scheffer (2001) proposed that increased tree and shrub establishment during rainy ENSO events could be improved by controlling main herbivores, thereby facilitating a switch of degraded

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semi-arid ecosystems towards a more productive state. Because of positive feedbacks, a more productive state would tend to be maintained despite the relatively short duration of the rainy pulse that triggered the increase in primary productivity. This is an attractive proposal with major implications for future restoration programmes of original Mediterranean semi-arid and arid shrublands and woodlands, since ENSO events are potentially predictable several months in advance, they are connected to climate in distant MCRs, and model forecasts are steadily improving (Goddart *et al*. 2001). ENSO events have become more frequent in the last few decades, and their frequency might increase further as a result of global climate warming (Timmermann *et al*. 1999). We could therefore take advantage of these changes by coupling reforestation programmes and herbivory control to forecasted high rainfall ENSO events to enhance the probabilities of plant establishment at probably lower costs than those involved with traditional restoration programmes. Hopefully, increasing knowledge of projected future climate systems will allow optimizing restoration timing by forecasting, and taking advantage of, recruitment cycles.

MCR ecosystems have been subjected to long-term human pressure that has deeply modified their characteristics and spatial distribution, often resulting in degradation deserving restoration actions. Nowadays, new disturbances emerging since the post-industrial era interact with old disturbances, and on top of them global change is introducing further stress and complex changes in the disturbance regime. Biophysical approaches and technologies to address ecological restoration in MCRs have developed quickly during the last two decades, although mostly considering static references and targets. Under the scientifically acknowledged rapid dynamics of global change, the current challenge is to adapt ecological restoration theory and practice to these accelerated dynamics, including the socio-economic perspective. MCRs, with their extreme complexity, both biophysical and social, would be excellent pilot regions for testing new ecological restoration approaches in the face of global change.

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Chapter 12

RESTORATION OF TEMPERATE FORESTS: AN EUROPEAN APPROACH

Anton Fischer and *Holger Fischer*

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12.1 INTRODUCTION

Temperate forests occur mainly in western and central Europe, eastern Asia and northeastern North America, but also in small areas of the southern hemisphere (e.g. in New Zealand, Tasmania and southern South America). The climate in these regions is characterized by (1) 4 to 8 months with average temperature of 10°C or above, (2) precipitation of 500 to 800 mm, but also, in some places, up to 2000 mm per year, and (3) 0°C mean temperature for the coldest month (temperate oceanic forests) or at least one month with average temperature below zero, during which temperatures sometimes drop to below −10°C (Food and Agricultural Organization (FAO) 2001a). While the world's forests cover about 3.87 billion ha (29.6% of the world's total land area), temperate forests make up only 11% of the total (FAO 2001b,c). Most of the land within this zone nowadays has been converted either into agricultural land (59.5%) or urban areas/villages and infrastructure. In this chapter we focus on the forests of central Europe with a long history of overexploitation and degradation, followed by approximately three centuries of forest management. We also refer to temperate forests in central China (see Boxes 12.1 and 12.2) with a similar human impact sequence but on different time scales. Another approach, developed in a different context in North America, is outlined in Chapter 13.

Forest restoration means: bringing a section of the landscape back closer to a 'more natural' situation. What is 'natural'? Bradshaw (2002) calls it 'original ecosystem' and focuses on the two major attributes, **ecosystem structure** and **ecosystem function**, with typically high values for both. Degradation reduces values for both; natural *recovery* as well as ecological restoration mark the way back to the original stage. Remaining fragments of the formerly widespread ecosystems could be used as a certain template, but bear in mind that with changing environmental conditions even 'pristine' or 'original' ecosystems will change. Such templates can be called **reference forests** (Dudley 2005), defined as 'carefully preserved natural or near-natural forests that can provide information about natural species' mix and ecology, that can be used in planning and measuring the success of restoration'. In the temperate zone such references may be used (e.g. in North America; see Chapter 13). In other parts of the world, like in central Europe and temperate Asia, such remains of the former 'natural' vegetation are extremely rare, by far not enough to be used as a template for restoration. Therefore the concept of **potential natural vegetation** (PNV; Tüxen 1956) can be used. It refers to the vegetation that would occur under recent site conditions but without the impact of humans, expressed in terms of recent vegetation types. It therefore offers restorationists a valuable tool, allowing them to identify and map sets of site conditions suitable for plant growth in terms of vegetation types, especially in areas where the natural vegetation has disappeared more or less completely. In other words, the concept can be used as a system of reference. Most important: because the PNV is a reflection of the site conditions, with changing site conditions it changes simultaneously. The *Map of the Natural Vegetation of Europe* (Anonymous 2003, scale 1:2.5 million) is the most comprehensive PNV map for Europe. Land with site conditions favourable for temperate forests, mentioned there as 'mesophytic deciduous broad-leaved and mixed coniferous/broad-leaved forests' (unit 'F') represents an area of 24.6% of the whole of Europe from the Atlantic Ocean to the Ural Mountains. In the central part of Europe, however, it corresponds to more than 80% of the area.

Not only have large parts of the former forest area been converted into farmland and urban land in recent centuries, but also, compared with the PNV, the tree species composition of about two thirds of the remaining forest stands has been radically modified (see also section 12.2). For example, in large parts of central Europe, European beech (*Fagus sylvatica*) has to a large extent been replaced by conifers, mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). According to the tree species composition, only less than one quarter of the recent forest stands can be interpreted as near-natural, but they are indeed managed. Only very few, small and remote forest stands can be interpreted as 'primeval' like the Urwald Rothwald in the Austrian Calcareous Alps, and even these are influenced by indirect human impact such as climate change. Nevertheless, (1) native tree species, (2) dead wood providing habitat for numerous insects, fungi and animal species and (3) a wide range of tree ages are prerequisites for maintaining high natural **biodiversity**, and can also be present in forests under management aimed at achieving near-natural forest stands.

This chapter addresses the way 'back' from different levels of converted ecosystems to temperate forests. We start with forests that are only slightly affected by

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direct human impact (i.e. close to PNV), and step by step consider systems increasingly distant from this state. We conclude at the extreme of sterile substrate exposed to plant life, that is very far from PNV (see Figure 12.1).

The terminology used in forestry dealing with this topic is commonly different from that used in **restoration ecology**. Figure 12.1 therefore compares the two terminologies and explains the meaning of the terms used in the forestry context. To clarify when and how the wide spectrum of distances between existing vegetation on one hand and the potential natural vegetation on the other emerged, the chapter starts with a short introduction to the history of temperate forests and forestry (section 12.2).

12.2 A BRIEF HISTORY: TEMPERATE FORESTS AND HUMAN IMPACT

During the time of maximum glaciation in the last ice age, about 15 000 years ago, global climate was relatively cold (mean world temperature about 4 K, in Europe about 8 K lower than today) and dry (continental). Those parts of central Europe not covered by ice were occupied by tundra–steppe. Many tree taxa

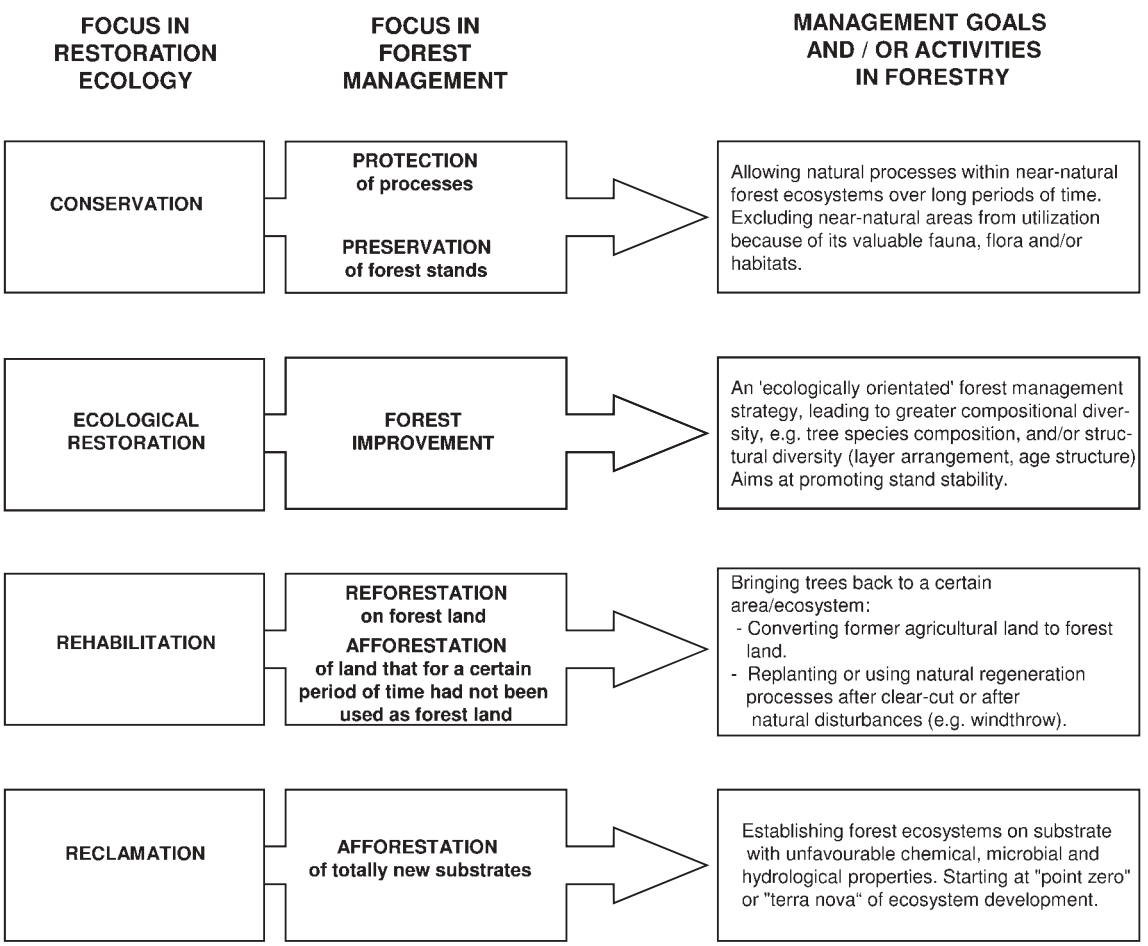


Figure 12.1 Terminology used in forestry as compared to restoration ecology.

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survived the ice age by migrating to southern Europe, such as oak (*Quercus* species) and European beech (*Fagus sylvatica*), while a few species of conifers survived in the eastern Alps, such as larch (*Larix decidua*).

At the end of the last ice age, ambient temperature increased rapidly (Ganopolski & Rahmstorf 2001), and large areas of Europe again became suitable for tree growth. Hundreds of pollen diagrams (Lang 1994) reveal that in central Europe pine (*Pinus*) and birch (*Betula*) were the first to colonize the land, followed by oak (*Quercus*) and hazlenut (*Corylus*) migrating to the north (Huntley 1988). Finally beech (*Fagus sylvatica*) came to occupy large areas of Europe. Figure 12.2 presents the relatively late but ultimately triumphant post-glacial procession of beech across Europe. According to site conditions (PNV; see section 12.1), tree species other than beech as well as forest types other than beech-dominated forests are restricted to very limited and rather extreme parts of the extant range of habitats in central Europe.

Unlike temperate forests in other continents, this patchy mosaic of European forests never had a chance to spread and establish itself without human disturbance, mainly because after the last ice age humans conquered the entire European continent. Throughout central Europe, people started to build permanent settlements during the Neolithic. For this purpose, they cut down the oak forests that were dominant at that time, to make way for agriculture and livestock husbandry (Küster 1997, *inter alia*). While forests generally were pushed back more and more, man-made small-scale disturbances gave new sites for pioneer tree species like birch and pine. When beech started to colonize the area, many places had already been occupied by humans.

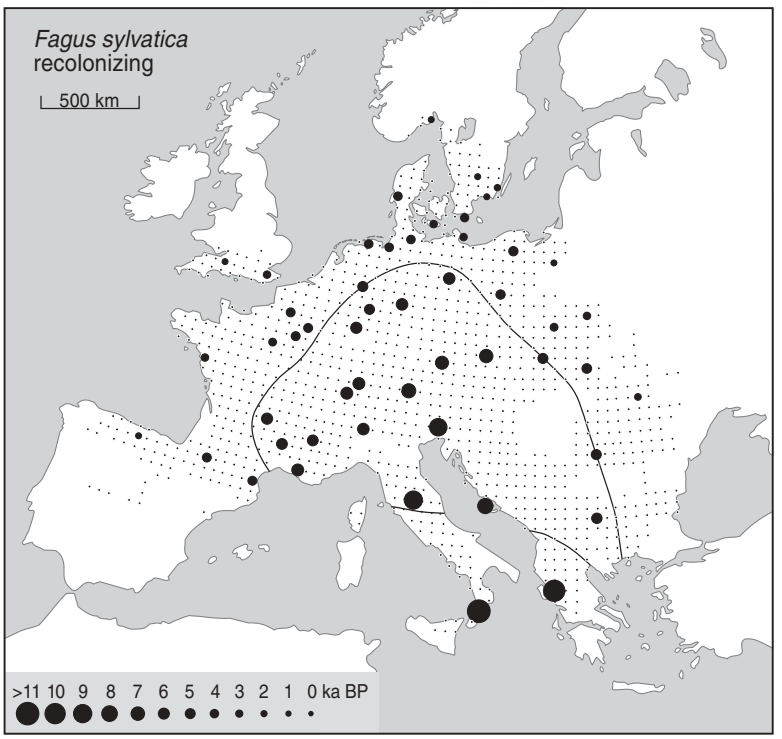


Figure 12.2 European beech (*Fagus sylvatica*) recolonizing Europe after the end of the ice age. Dot size characterizes the time period since the first record; figures are in kiloyears before present (ka BP). Spotted area: recent distribution. Lines: northern border of distribution in 10 000 BCE (lower line) and 5000 BCE (upper line). Modified from Lang (1994), with the permission of the author.

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As was once true worldwide – and is still the case today in many developing countries of Africa, Latin America and Asia – throughout Europe up to the nineteenth century wood, charcoal and timber were essential resources for the survival of humans and for economic development (establishing coppice forests). Timber and wood were used for the construction of houses, bridges and ships, and as energy supplies for domestic heating and cooking, the fabrication of furniture, instruments, utensils and fences, and various early industrial purposes. Additionally, forest land was used as grazing ground for cattle, goats and sheep, and as a source of nutrients for arable fields (e.g. litter raking). Consequently, human pressure on forests was extremely high and more or less anarchic. Forest area decreased rapidly to the point where, in central Europe for example, less than 20% remained by the Middle Ages (Bork *et al*. 1998), and the remaining forest stands became more and more devastated and transformed.

The first recorded attempts to restore and improve devastated forests worldwide were carried out in the fourteenth century: the oldest managed forest of the world is the *Nürnberger Reichswald* in southern Germany (Sperber 1968). Nevertheless, for the next several centuries, forest utilization usually meant forest plundering. It was only in the early eighteenth century that Hans Carl von Carlowitz (1645–1714), member of the administration of the mining industry in Freiberg–Saxony and responsible for timber production, realized that only with well-planned forest management could timber production be maintained sustainably. In his book *Sylvicultura oeconomica*, the first textbook on silviculture, von Carlowitz (1713) wrote, 'We have to make every effort in science and forest practice to find methods for protection and production of timber so that permanent sustainable utilization can be realized' (translated from German). Apparently, this was the first time that the approach was presented in a textbook and the term 'sustainable' explicitly used.

Since the middle of the eighteenth century, regulated forest management has been introduced into many parts of Europe. Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) produce huge quantities of seeds that are easy to harvest, transport and handle in tree nurseries. They are easy to regenerate, grow quite well even on poor or devasted soils and produce high wood volume with many uses. Today these two tree species make up about three quarters of the temperate forests in central Europe, whereas the natural potential of the deciduous trees would be three quarters European beech and other deciduous tree species, with only one quarter conifers (Figure 12.3).

Many characteristics of today's managed forests, such as canopy closure, stand structure, and microclimate, are closer to those of the natural forest stands of the past than what prevailed during recent centuries

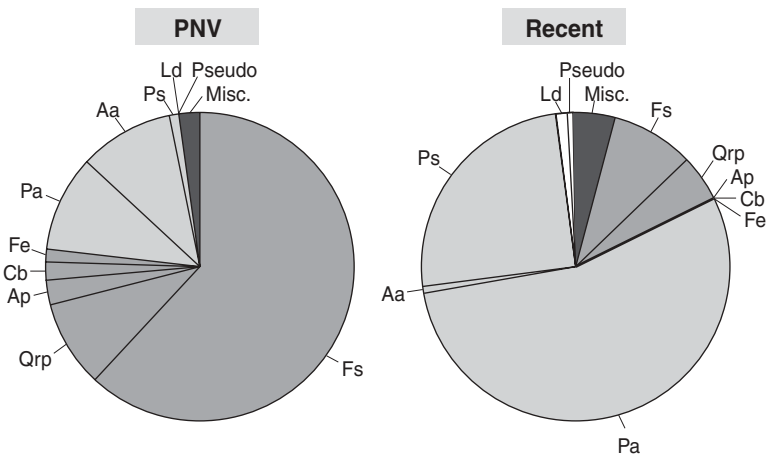


Figure 12.3 Tree species composition according to PNV (left-hand diagram) and recent vegetation (right-hand diagram) for Bavaria/Germany. Diagrams are based on data from Walentowski and Gulder (2001). Deciduous trees: Fs, *Fagus sylvatica*; Qrp, *Quercus robur* and *Quercus petraea*; Ap, *Acer pseudoplatanus*; Cb, *Carpinus betulus*; Fe, *Fraxinus excelsior*. Coniferous trees: Pa, *Picea abies*; Aa, *Abies alba*; Ps, *Pinus sylvestris*; Ld, *Larix decidua*; Pseudo, *Pseudotsuga menziesii*. Misc., miscellaneous.

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prior to reforestation. Nevertheless, soil quality may change under the influence of decomposing needle material that usually promotes soil acidification and thereby reduces biological activity especially under poor soil conditions. Additionally heavy windstorms in February 1990 and the following years brought down mainly spruce and pine trees (e.g. CONFOREST 2007), showing that a shift in favoured tree species from conifers to broadleaves like European beech is essential in terms of not only ecology but also economy.

Similar to central Europe, the temperate forests in central China have been under strong human impact for several millenia. Box 12.1 provides a brief history of their development with focus on the Loess Plateau

Box 12.1 History of forests and forest utilization in the Loess Plateau in central China

The Loess Plateau in central China covers an area of more than 500 000 km^2 and comprises the world's largest continuous deposits of loess in layers up to 200 m deep. Loess is composed of tiny wind-blown dust particles, glued together by secondary carbonization. It has a rock-like structure, but is prone to erosion under the influence of surface water runoff during heavy rain events. In the south-eastern part of the Plateau, annual precipitation ranges between 470 and 650 mm with a maximum in summer. The mean annual temperature is 8–12 °C, and mean temperature of the coldest month (January) is 0 °C. Both soil and climate here generally provide excellent conditions for temperate deciduous forests to grow: The annual drought



Figure 12.4 Erosion gully and deforested land in the Loess Plateau near Luochuan, China. What looks like a forest patch on the plateau is a village with some planted trees. (Photograph by A. Fischer 1999.)

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period in spring favours species that develop their leaves relatively late in the year, thus *Quercus liaotungensis* is the dominant tree species of the potential natural vegetation (PNV; see section 12.1), accompanied by *Prunus* and *Pyrus* as well as deciduous shrubs of the genera *Prunus, Lonicera, Euonymus, Rosa, Crataegus, Forsythia, Syringa, Caragana*, and *Sophora*. On dry south-facing slopes *Pinus tabulaeformis* and *Platycladus orientalis* (Chen *et al*. 2007).

The Loess Plateau is also the birthplace of Chinese civilization and culture. In the heart of the region resides the tomb of the legendary 'yellow emperor', said to have reigned some 5000 years ago. Since that time, the region has been intensively and continuously used. In 221 BCE, Qin Shi Huang Di founded the Chinese Empire and the capital city grew into the modern city now known as Xi'an, located at the southern edge of the Plateau. For the next 1100 years, this was the epicentre of the Chinese Empire, resulting in exceptionally high land use and resource pressure and, therefore, in large-scale deforestation and devastation of the formerly vast forests. Today, surviving forest fragments are exceedingly rare, and the loess soil surface is exposed and vulnerable. Approximately 50% of the region is badly affected by water and/or wind erosion (Li & Fischer 2006). The sediment load of the Yellow River, which passes through the Loess Plateau, is on average 37.4 kg per cubic meter of water, and may reach 500 or 600 kg per cubic meter during flood periods (Zhu 1981). In the late 1990s, repeated strong summer droughts and disastrous floodings convinced the Chinese government in 1998, to implement a *National Forest Protection Program*, wherein the native forests of 17 provinces – covering ca. 30 million hectares in the Upper Yangtze and Yellow River basins – were put under a complete logging ban. Together with the *Sloping Land Conversion Program*, an integrated water and soil conservation programme for agricultural restructuring ('Return Farmland to Forest'), implemented in 2001, two legal instruments to fight against forest degradation and soil erosion are now in place. Both are designed to protect remaining forest stands and to encourage new plantings of trees and shrubs.

The restoration efforts have led to the following questions: Which tree and shrub species should be planted and where should they be planted? Can other services than erosion prevention be included in these watershed conservation and afforestation measures? (See Box 12.2.)

in Central China. It is the basis for understanding the needs and options of forest restoration there.

Over the last few decades, not only changing forest management practices but also soil **acidification**, **eutrophication** and global **climate change** have influenced species composition. All of these factors are therefore relevant to the search for adequate and effective forest restoration measures. We now discuss them in turn:

• Acidification and eutrophication: The chemical composition of the planet's atmosphere has significantly changed over the last century, primarily due to industrialization: increased H^+ concentration ('acid rain') as well as increased mineral–nitrogen concentrations in the precipitation over much of the northern hemisphere. The acidification and eutrophication of the soil resulted in change in floristic composition, which has been detected by repeated recording of the species composition on permanent plots or by comparing sets of phytosociological relevées from the same region and the same vegetation type over a significant period of time (A. Fischer 1999, and references therein). Although soil analyses showed decreasing pH, an increase of plant indicators for acidic soil could in fact only be found in a few areas with very strong, local emission of industrial origin. As the most important trend in forests, the representation of nitrophilous species is steadily increasing (Figure 12.5). Also tree increment has generally been increasing (Röhle 1995).

• Global climate change: According to current knowledge, most of the global warming observed over the last 50 years is caused by human activities (Intergovernmental Panel on Climate Change (IPCC) 2007b). Anthropogenic increase of CO_2 content of the atmosphere from 280 ppm in 1750 to 379 ppm in 2005 is well documented, and the processes forcing temperature increase – in the twenty-first century, the mean global surface temperature may increase between 1.1 and 6.4 K as extremes – seem to be rather well understood. The growing season has lengthened from northern Scandinavia to Spain and Greece by about 11 days since the early 1960s (Menzel & Fabian 1999). First migrations of shrub and tree species can be seen meanwhile: *Ilex aquifolia* in Scandinavia is spreading further north, following the northward shift of the 0°C January isotherm (Berger & Walther 2007); oaks in the Catalonian Montseny mountains in the eastern Pyrenées, northeastern Spain, are invading the beech forests of

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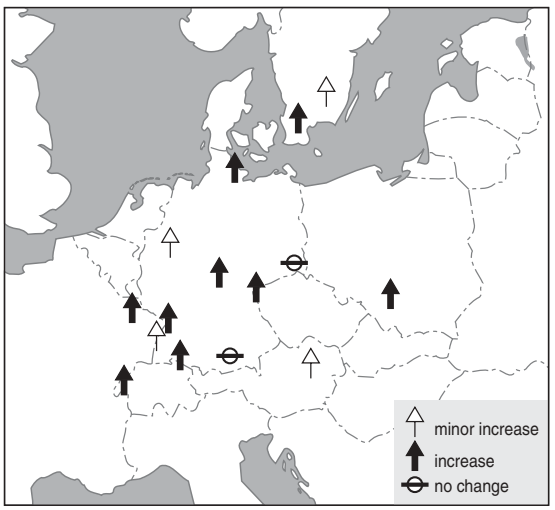


Figure 12.5 Change in the representation of nitrogen-indicating plant species in central European forests between the 1950s and 1990s. (Modified from A. Fischer 1999.)

the upper montane belt, and are starting to replace beech there (Peñuelas & Boada 2003). Non-native species from adjacent areas may also invade and gradually become new elements of the local communities, as on the southern edges of the Alps, for example, evergreen broad-leaved tree species such as *Trachycarpus fortunei*, *Cinnamomum glanduliferum* and *Prunus laurocerasus*, originally cultivated in gardens, are becoming naturalized and leading to 'laurophyllization', to use the evocative term of Klötzli and Walther (1999). Nevertheless, although there is a close correlation with climatic parameters, other causes such as changes in land-use practices may also play an important role in this change in species composition.

In China, protection of the remaining forests as well as reforestation are seen as important tools to adapt to new climate conditions (Natural Forest Protection Program; Ting 2001). The causes of this type of changes can be influenced neither by changing forest management practice nor by restoration measures; change is possible only by reducing emissions. Nevertheless, the consequences of increasing temperature for forests are not interpreted as being entirely negative: for temperate forests generally, timber productivity is expected to increase by 5–6% over the next few decades. In China, afforestation campaigns and ecological restoration measures are now considered high-priority tasks for the future.

12.3 STEPS TOWARDS FOREST RESTORATION: BETWEEN PRIMEVAL FOREST AND STERILE SUBSTRATE

The way from a recent situation of a certain part of the landscape to a near-natural forest situation can be short, if the recent vegetation stand is close to the site potential (PNV). It may, however, be long, if the recent situation is more or less far from the PNV stage. We will start with the near-natural situation and finish with considering bare areas waiting to be restored (use Figure 12.1 as a guideline).

12.3.1 Conservation: near-natural forest management

Seen from a global point of view, forest utilization in the temperate zone is a must if sustainability is set as an overall goal in land use management. Growing conditions for forests providing high-quality timber are excellent here. The paradigm is that a long-term preservation of forest ecosystems can be combined with multifunctionality and utilization: timber production and other socio-economic benefits such as biodiversity protection, production of high-quality drinking water, CO_2 storage, recreational purposes and the creation of attractive landscapes. The goal is to change species composition, forest structure and regeneration processes of remaining near-natural forests as less as possible while using the goods and services (Mansourian *et al.* 2005). For this purpose, a management approach has been developed called 'Continuous Cover Forestry' or, in recent terms, 'near-natural forestry' or 'close-to-nature forestry' ('Naturgemässe' or 'Naturnahe Waldwirtschaft') (Pommerening & Murphy 2004). It is based on the following principles: (1) continuous and uninterrupted maintenance of forest cover, (2) timber harvesting by extraction of single trees or small groups of trees, (3) mixed age classes, (4) promotion of native tree species, including broadleaves, (5) mixed-species composition instead of monocultures, (6) natural tree regeneration instead of seeding or planting trees and (7) conserving old trees and dead wood, habitat for fungi, insects and vertebrates, as an important means of maintaining species diversity.

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The populations of several ungulates in the temperate zone are often larger than expected without human impact. They play a certain role in forest ecosystems, for example wild boars (*Sus scrofa*) activate seeds buried in the soil ('soil seed bank') by digging activity. However, grazing by wild deer species may be problematic due to their selective damage on tree regeneration (e.g. *Abies alba* in central Europe, and *Tsuga canadensis* and *Thuja occidentalis* in North America). A balance has to be found between game animal density and the requirements of native tree species regeneration.

The ecological roles of large grazers such as aurochs (*Bos primigenius*) and tarpan (*Equus przewalskii gmelini*), which were hunted to extinction centuries ago, are not well known. Although there are many contemporary examples of open woodland resulting from several thousands of years of domestic cattle grazing in forests (Olff *et al.* 1999), it is hard to extrapolate the results to forest ecosystems of former times because important ecosystem elements are now missing (e.g. large predators such as wolf, lynx and brown bear).

Although major human impact on temperate forests in southern South America (e.g. *Nothofagus pumilio*) is relatively recent compared to the situation in Europe and Asia, the problems are similar to what prevailed in Europe circa 200 years ago: conversion to pastureland and farmland, and overutilization. Improved management methods in Chile and Argentina are needed (Gea-Izquierdo *et al.* 2004; Newton & Featherstone 2005), and much research is now taking place.

The main goal of Continuous Cover Forestry is to work 'as close to nature as possible'. It is possible to keep the ecological quality of forest stands high even while they continue to be exploited for timber and non-timber products (Conservation in Figure 12.1) and before they need any restoration measures.

12.3.2 Ecological restoration: conversion and transition of forest stands

Today most forests of the temperate zones of Europe and Asia are managed and exploited, mainly for timber production. As a result, they differ dramatically from natural forests: on large areas there occur only one or few tree species, and most trees are relatively young and of similar age. Many such stands show increased susceptibility to damage by windstorm, snow, ice, drought, insects, fungi and possibly soil degeneration as compared to forests composed of site-adapted species. This is due to low overall **resilience** and a lack of ecological self-regulation. For example, the amount of dead wood, which serves as an important resource and habitat for many functionally important groups of organisms (see section 12.3.1), is quite low: between 3 and 12 $m^3 ha^{-1}$ in many European countries, with the maximum of circa 20 $m^3 ha^{-1}$ in Austria (Parviainen 2009). This has many impacts on **ecosystem functioning** and **biodiversity**.

In many European countries there is a growing trend to bring such artificial forests back to a more near-natural situation, which means increasing or improving tree species biodiversity, tree layer structure, age structure, content of dead wood and soil quality. Changing demands of society, an enhanced level of ecological understanding and the expected risks related to climate change have forced the development of strategies to improve secondary coniferous stands (Hansen & Spiecker 2005). Two basic **ecological restoration** strategies for temperate forests can be distinguished (Figure 12.6):

- Conversion**:** changing tree species composition of secondary coniferous stands into mixed broad-leaved forests, usually by artificial regeneration in terms of 'advance planting' in middle-aged stands.
- Transition**:** changing monolayered forest stands into two- or multilayered stands, for example by moving from an even-aged to an un-even-aged forest stand via changes in the timber rotation period employed, or even striving for management that allows a continuous canopy cover through selective harvesting on small areas, respectively avoiding extensive harvesting on large scale (in particular clear-cutting).

There are some indications that mixed stands can be more productive than monospecific stands (Bartelink 1999), thanks to complementarity in crown morphology, shade tolerance, tree height and diameter dynamics, rooting depth and/or phenology, on the one hand, and/or to facilitation, which refers to positive interactions and feedbacks among species, including synergism and symbiosis, on the other hand. However, even for the best-investigated mixture in central Europe, namely Norway spruce and European beech, this question is not as yet well understood (Pretzsch & Schütze 2009). According to Knoke *et al.* (2008) the trend towards mixed forests seems due mainly to ecological drivers, while sound economic analysis of mixed forests is still rare. Mixed-species stands would be better able to respond to disturbance factors than monocultures (resilience). Moreover, there is substantial evidence

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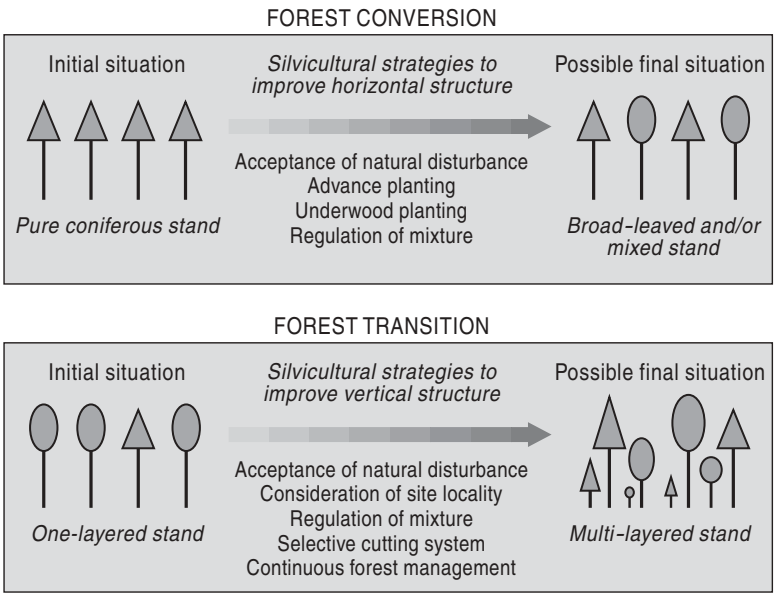


Figure 12.6 Silvicultural strategies to improve forest stands that are poor in structure.

that mixed-species stands are also more resistant to both biotic and abiotic disturbance factors. In North America, this topic is addressed as 'biocomplexity' (Carey 2003) and is identified as a leading goal in restoration of for example temperate coniferous forests. Forests with such enhanced biocomplexity also show better economic performance because of risk buffering (Knoke *et al.* 2005) in a changing world.

The morphological and chemical properties of soil organic matter and humus can be used as a sensitive **indicator** for the conversion capability of forest ecosystems (Puhe & Ulrich 2000). While in pure Scots pine or Norway spruce stands, the decomposition of litter material is limited as a result of low mineralization or bioturbation intensity, with increasing proportion of deciduous tree species the thickness of this layer decreases. Simultaneously a change of *humus forms* which are ecologically inactive (such as moder-like humus) towards comparably active humus forms (such as mull-like humus) took place (H. Fischer *et al.* 2002). Furthermore, in the initial phase of forest conversion, the total humus stock increases whereas in later stages soil organic reserves continuously decrease (Figure 12.7). The easier the prevailing litter can be decomposed the faster humus integration occurs.

In conclusion, forest transition and conversion as two steps of forest restoration and improvement represent a way back to higher naturalness, which also may lead to improving soil quality, reducing the danger of specific pests (insects, fungi) and of wildfires (deciduous trees instead of conifers) and anticipating expected global climate change.

12.3.3 Rehabilitation: forest stand regeneration after wind throw

Rehabilitation in forestry includes two aspects (Figure 12.1): (1) **reforestation** with native species after clear-cutting or after disturbing events like windfall, and (2) **afforestation** of land that had been used for other purposes earlier, usually as agricultural fields or pastures, transferred back into forest land for, for example, soil erosion prevention, timber production or CO_2 storage. First we discuss the tree recruitment after wind throw (this section), then the afforestation of former agricultural land (section 12.3.4).

From the point of view of economically oriented forestry, large-scale disturbances due to storms, fires and tree diseases are catastrophes: they disrupt long-term

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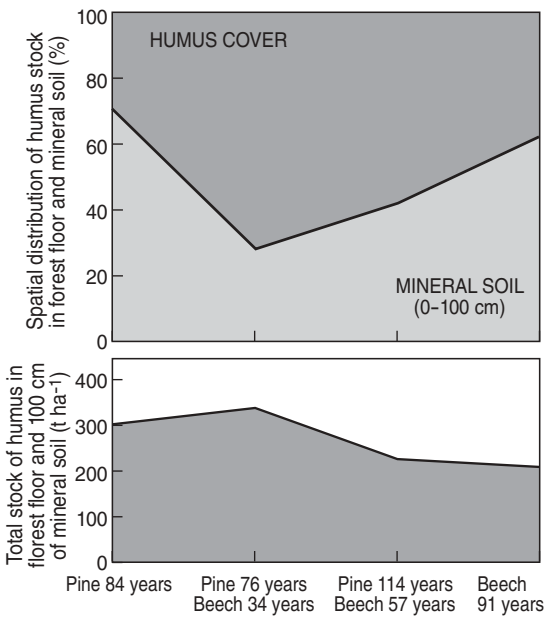


Figure 12.7 Accumulated humus stock and relative distribution of soil organic matter in forest floor and mineral topsoil (to 100 cm) in a chronosequence of four study sites in northeastern Germany. These parameters are used as indicators of forest conversion. (From H. Fischer *et al.* 2002.)

management plans, reduce timber value and thus affect wood markets. However, they can also be considered as opportunities to improve the degree of naturalness in managed forests in the near term.

Whereas in the boreal zone wildfire is the most important large-scale cause of disturbance in forest ecosystems, windstorm is more important in the temperate zone. In central Europe, the 1990s were a period with several strong winter storms (e.g. 28 February to 1 March 1990), producing 100–120 million cubic meters of dead wood. The memorable storm that hit western Europe on 26 December 1999, produced about 115 million m^3 dead wood in western France alone (data summarized in A. Fischer *et al.* 2002). These storms caused a strong impact on forestry and also stimulated new scientific studies on forest dynamics following disturbance (A. Fischer 1998; Schönenberger *et al.* 2002). Should foresters wait for natural tree regeneration or should they plant trees? Three main management options for **reforestation** were analysed: (1) management-free stand development, (2) clearing the wind-throw area, followed by free stand development and (3) clearing and then establishing a new tree layer, usually by planting. Species composition (plants, animals and fungi) as well as the successional trends are different depending on the intensity of mechanical impacts, the pre-storm stand history and, as a result, the specific species pool of the affected forest stands (Brang *et al.* 2004). Plant species with a persistent seed bank are promoted by the clearing procedure: after soil disturbance, buried seeds are stimulated to germinate. Without clearing, soil seed-bank species are concentrated to the pit and mound systems around the bases of fallen trees. Many young trees will be destroyed by cutting and clearing. Therefore natural regeneration of late-successional tree species may work much better in uncleared areas (Fischer & Fischer 2009). These species may quickly dominate under natural tree regeneration, if saplings are present in the area or mature trees occur in the close vicinity. Mycorrhizal fungi need living trees to survive; in uncleared areas young trees are present, and they are carriers of the suitable fungi. Survival rates of fungi are therefore rather high (see in A. Fischer 1998).

Summarizing, wind throw not only causes problems for forestry but also offers options to improve the ecological quality of the forests:

- Windfall in artificial spruce or pine stands may induce a change back to a higher proportion of deciduous trees (see section 12.3.2), either via natural regeneration or via planting native, site-adapted tree species.
- Free stand development (without clearing) in a number of forest stands is an option to create a small-scale patch mosaic, leading to a variety of ecological niches (biocomplexity; see section 12.3.2) and therefore to increase biodiversity in managed forests.
- Using the natural regeneration potential may reduce costs (for seeding and planting) and prevent root deformations (causing bad tree growth). Nevertheless, pest outbreaks in managed forests have to be prevented.

Altogether it is an ecologically valuable possibility to include natural regeneration processes into reforestation strategies, while at the same time saving money.

12.3.4 Rehabilitation: afforestation of former agricultural land

Afforestation of abandoned pastures or arable fields plays an important role in landscape planning, since abandonment in the 1980s and 1990s was common in

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many parts of Europe. The EEC regulation 2080/92 from 1992 (European Commission (EC) 1992b) aimed at reducing the area of arable fields to reduce subsidies for surplus of agricultural products, to contribute towards an improvement in forest resources as well as of countryside management and environmental balance, and to absorb CO_2. In landscapes with high agricultural intensity, afforestation diminishes the pollution of seepage water with nitrate, which often is a problem in terms of purification of drinking water. Natural retention areas can be an important contribution to flood regulation. Up to 1999 about 1 million ha were afforested in Europe, mostly in Spain and Portugal (about 650 000 ha; Institut pour le Développement Forestier (IDF) 2001), and still the calculated afforestation potential is enormous: in Denmark the political afforestation aim is 500 000 ha (1995–2050), in Ireland it is 600 000 ha within 20 years and in Germany the scenario is 1.2 million ha or more (no time period indicated; Weber 1998). While there is still a strong forest decrease worldwide, in Europe the forest area increases slightly and in China strongly (FAO 2010).

Afforestation of former agricultural land starts with a soil that contains enormous numbers of microorganisms and insects. Many native plant species may also be present in the soilborne seed bank or as established individuals, and the site may often be suitable for tree growth immediately. Two long-term permanent plot studies have been established for analysing the vegetation processes after abandonment of former agricultural areas, including analysis of the influence of different treatments: (1) an abandonment experiment in Baden-Württemberg (Schreiber 1997), and (2) a succession experiment in the New Botanical Garden of Göttingen (Figure 12.8; Schmidt 1993; Dölle *et al.* 2008). Although the aims of these two studies, as well as the analysed vegetation types, the geographical situation and to some degree the methods of recording, differ in detail, the general trend and message are obvious: trees will establish and build up forest stands within a few years to decades, whereas the successional pathways back to forest may be quite different. The species composition and the period involved in the changes depend on the local **species pool** as well as the vegetation structure at the beginning of the developmental process.

As a consequence, there are two main options for afforestation measures on abandoned land:

1. If there is enough time available and no fixed species composition planned for the future forest stand, then 'doing nothing but waiting' is an option. Depending on (a) the presence or absence of mature trees in the close vicinity and (b) the presence or absence of small or young individuals of shrubs and trees in the recent vegetation stand, a patch mosaic will establish including a large variety of species and structural types, thus leading to a relatively high degree of natural biodiversity. The final stage of management-free development will be a relatively closed forest canopy anyway.

2. Usually, however, the highly valued functions of forests, as mentioned above, require afforestation work to start as soon as possible, to adapt both species composition and future forest structure to the functions being focused on. Therefore, usually a 'guided development' or 'directing ecological succession' (Luken 1990) of such forest stands is preferred. Native tree species (see PNV, section 12.1), in temperate Europe especially deciduous trees (e.g. *Fagus sylvatica*, *Quercus robur and Q. petraea*), are aimed at and should be preferred in growing-stock objectives. Some tree species such as ash (*Fraxinus excelsior*), sycamore maple (*Acer pseudoplatanus*), cherry tree (*Prunus avium*) and mountain elm (*Ulmus glabra*) may benefit from the generally favourable soil conditions of the abandoned fields and meadows, but this high nutrient status associated with

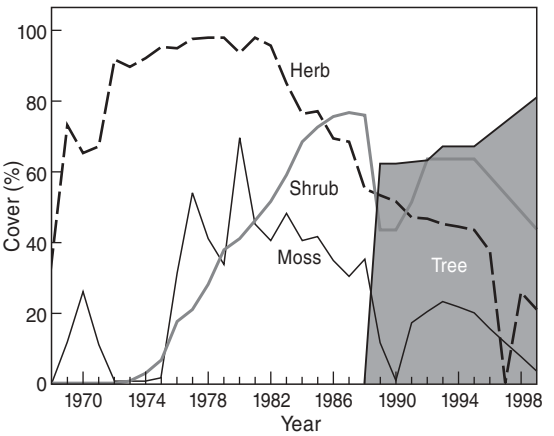


Figure 12.8 Succession experiment in the New Botanical Garden of Göttingen, Germany. Relative cover (%) of moss, herb, shrub and tree layers 1968–1999 (free development). The steep increase of tree cover (shaded area) at the end of the 1980s occurs when shrubs (<5 m tall) start gowing above the 5 m height level. Values for 1994 and 1996–1998 are interpolated. (Based on Schmidt 1993, with new values for 1993–1999 added; Schmidt, unpublished observations.)

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Box 12.2 Afforestation in the Loess Plateau in central China

Afforestation in the Loess Plateau (Schmitt *et al*. 2002; Fischer *et al*. 2006, 2007) is essential to reduce soil erosion and bring this area back to a path of ecosystem health and resiliency. Aspects to be considered include:

- Loess has excellent water storage capacity, but precipitation in the region is limited. Native species are adapted to these conditions thanks to their relatively low levels of water consumption as compared, for example, to black locust (*Robinia pseudacacia*), introduced in China from North America via Europe. This latter species has been intensively used in the Loess Plateau for afforestation in recent decades, with mixed results. For young trees there is enough stored water available in the soil for establishment, but older trees quickly use up underground water supplies, leading to a 'dried soil layer' (Wang *et al*. 2006), reaching down 5 m and more. As a result, many well-planted *Robinia* stands are now dead or dying.
- The regional pool of native woody plants of the Loess Plateau includes over 500 species (e.g. species from the genera mentioned in Box 12.1). Here as elsewhere, indigenous species are better adapted to the local ecological conditions than introduced species, and this advantage can and should be used in afforestation and restoration efforts.
- Remaining secondary forests in remote areas include only a relatively small number of forest types (forest communities). The most important site factor determining the distribution of these forest communities is water availability, which in turn is strongly affected by slope exposition and inclination (e.g. steep and very dry south-facing slopes as opposed to gentle north-facing ones). Because of the omnipresent loess cover, the differentiation of site conditions regarding substrate and soil is minor, and the limiting factors relevant for afforestation and restoration are easy to detect in the field. Thus, detailed site-specific planning can be developed according to the patch mosaic of local siteconditions.
- For native species such as *Quercus liaotungensis*, *Acer truncatum*, *Prunus sibirica*, *Pinus tabulaeformis* and *Platycladus orientalis*, experimental plantings to scientifically test establishment and early growth have shown good rates of establishment (A. Fischer *et al*. 2007).

Afforestation and restoration, however, face several problems:

- Only very few native species have to date been used for restoration purposes. For most species, nursery material is not available. There is also little quality control for production of plant material, to date, or for genetic provenances of seed material used.
- Forest restoration preferentially is done, and is most needed, on steep slopes. Such steep slopes, however, have long been used for grazing in the past. Consequently, as soon as grazing is halted, so as to open the way for afforestation, a more or less thick cover of grasses and herbs reappears, thereby reducing the chances for establishment of planted trees and shrubs, not only due to competition, but also because this natural vegetation provides excellent habitat for small wild mammals such as mice and rabbits, which feed on the planted seeds and young trees.

Tree and shrub plantings not only help slow and ultimately prevent soil erosion, there also are a range of economic products of direct use value that result. Timber takes several decades until it can be harvested. Other valuable products such as fruits, leaves, oils and ingredients, however, can be harvested within a few years after planting. The social and cultural benefits of these plantings is also important: growing human population and rising living standards lead to increasing demand for recreational areas and facilities. Enjoying forest lands, learning about forests (eco-tourism) and other nature-based leisure activities is in increasingly important activity in a country with only limited forest land.

The results of restoration measures during the last two decades in China are impressive: the annual loess load of the Yellow River in the period 1998–2007 was approximately one quarter of the loess load in the period 1955 to 1969 (unpublished Chinese Survey Reports 2007).

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full radiation also induces intensive competition by grasses and herbs (H. Fischer 1998, 1999). Additionally, fencing may be a need for a certain period in those cases where large populations of wild ungulates, mainly roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), are present.

For afforestation measures in the temperate zone of central China, the reduction of soil erosion is most important (Box 12.2). The options as well as the limitations of afforestation there are briefly outlined. Although climate, soils, species pools and vegetation history are rather different compared to central Europe, the main lesson learned in central China is the same as in central Europe: preference for native, site-adapted species for reforestion measures.

12.3.5 Reclamation of post-mining landscapes: starting at point zero

The concept of **reclamation** in restoration ecology refers to projects addressing the conversion of land which is perceived as being unutilizable to – or back to – a productive condition. In forest management it includes **afforestation** of completely new land, for example rough sand or stone material (Figure 12.1) with little or no recent organic material accumulation and only a few or no soil-dwelling microbes, animals or **propagules** of plants (e.g. seeds or rhizomes). In such an extreme case, both vegetation development and forest management start on sterile material at 'point zero' of ecosystem development (Gerwin *et al.* 2009).

Reclamation of open-cast mining land following mine closure is another example. Mining of course is an important field of economic activity in many countries. In Germany alone, mining areas account for 0.5% of the total land area (Pflug 1998). Devastated areas, particularly following open-cast mining activities, among which the states with brown coal conveyor technology are the most important in Europe, are in need of rebuilding land and ecosystems (Bradshaw 1983; Hüttl & Weber 2001). Existing ecosystems were destroyed completely, and the removal of the overburden covering the mineral or coal resource changes the topography and hydrology on a large scale. Afforestation is a common practice to improve the ecological situation and the ability to use such lands (Figure 12.9). Fast-growing tree species and alley-cropping plantations conceived as 'energy forests' have become widely used in recent years (Bungart *et al.* 2001).

After the newly created landscape structure is mechanically modelled, often soil amelioration is needed (Heinsdorf 1996). On substrates with low pH,



Figure 12.9 Post-mining landscape in Germany. Afforestation with *Pinus sylvestris*. (Photograph by H. Fischer.)

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large amounts of CaO are used to raise soil pH; a cultivable soil layer of at least 100 cm thickness may require 40 000–50 000 kg CaO ha^{-1} . Lack of nitrogen in the initial soils is also an important limiting factor. Traditionally, inorganic fertilizers were used, whereas in recent years there has been a trend towards the use of organic waste materials and special humus material (Katzur *et al.* 2001). The first afforestation experiments on bare post-mining soils in Europe were carried out and published in Germany by Heuson (1929) and Copien (1942). Even then they promoted mixed stands, and to date there are long-term experiments with many species: pine, oak, lime and larch as well as pioneer tree species such as alder, poplar, birch, red oak and black locust. For pine-dominated ecosystems on former lignite mine sites, for example, internal cycling processes consisting of litter fall, decomposition of litter and nutrient uptake by plants play an important role in nutrient supply, as is also known for pine stands on naturally developed soils (Rumpel *et al.* 1999; Fettweis *et al.* 2005). In pine stands of about 30 years of age, roots were found below the amelioration horizon. Chronosequence studies show that shortly after afforestation a forest biocoenosis develops spontaneously, including soil fauna and symbiotic microorganisms such as mycorrhizal fungi and nitrogen-fixing bacteria (Wöllecke *et al.* 2007).

In the case of afforestation of former arable land, spontaneous succession may also be an option on post-mining sites. According to the high diversity of microsites a high diversity of species, structures, ecological niches and ecosystems will establish, and in the course of some decades or at least few centuries, these ecosystems will change permanently into forest.

12.4 PERSPECTIVES

In many parts of the temperate climate zones, both climate and soil conditions are excellent not only for tree growth, and therefore timber production, but also for food production. As a result, arable fields expanded over recent centuries, and timber was over-exploited, resulting in a decrease and fragmentation of the former forest areas. Both in Europe (see section 12.2) and in temperate Asia (see Box 12.1), this process started several thousand years ago. The need for forest restoration in these two regions is different: in Europe the focus is on afforestation of abandoned agricultural land and improving existing forests, while in central China, the focus is on afforestation of devastated land as a means of erosion prevention.

In a time of intense global forest loss, and growing attempts to mitigate anthropogenic climate change due to greenhouse gas emissions, reforestation and afforestation are important aspects of landscape management. As the recent 'Global Forest Resources Assessment' (FAO 2010) shows, the decline in global forest area over the last decade was significantly lower than it was in the previous decade, mainly because of reforestation and afforestation activities in Europe and central Asia, especially China. To date, only a few fast-growing species, often introduced from other parts of the world, have been used for large-scale afforestation projects. The pool of native woody species, however, in all parts of the temperate zones is impressively large (see Box 12.2 for the Loess Plateau). These species can be used for the site conditions to which they are best adapted (according to the PNV). Remaining forest patches, even if they are small, are centres of local biodiversity and therefore should be integrated into afforestation measures.

Within the implementation phase of the EU directive on afforestation of agricultural land, conflicts may arise, since planned afforestation sites on marginal soils often harbour the last remnants of historical cultural landscapes valued by many people. These considerations have to be taken into account to achieve consensus on the objectives and implementations of forest rehabilitation and reclamation projects.

The global environment today is changing fundamentally (see section 12.2), including the climate, the chemical composition of the atmosphere and, as a consequence, soils. Soil erosion in many parts of the world, including temperate zones, is strong and ongoing. The predicted environmental changes ('global climate change') will also affect established forest ecosystems and may exceed the capacity of forest tree populations to adjust physiologically and developmentally. Uncertainty in predicting the most likely scenario necessitates special silvicultural responses (H. Fischer & Wagner 2009): to safeguard a variety of tree species with different ecological demands and mixed stands with tree species resilient against environmental changes and disaster occurrence, not only on forest stand level but as a general strategy. Altogether it seems evident that species composition in European forests will change within the twenty-first century as a consequence of global climate change, beech nevertheless seems likely to continue to be the dominant tree

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species in many forest communities and forest stands there (A. Fischer 1997).

Restoration measures have to be permanently adapted to ongoing environmental changes. The new establishing and regenerating forest ecosystems will not be exactly the same as those that occurred before the onset of intensive human impact. More woody species than these, forming tree species mixtures in late-successional phases such as certain pioneer tree species, therefore have to be used in reforestation projects, and all can be found in the native regional species pool. Introduced species quite often cause problems which may become obvious only many years after planting (e.g. see *Robinia pseudacacia* in Box 12.2). Despite the ongoing changes in site conditions, the general species composition of the main units of temperate forest vegetation are expected to persist in the decades to come; therefore, they can be used to construct ecosystems of references for forest restoration. The most important aspects of forest restoration in a broad sense throughout the temperate zone remain the use of native woody species, the use of site-adapted species, inclusion of natural processes (e.g. using natural regeneration instead of planting) in management plans, and inclusion of remnants of former larger forest stands in restored forest landscapes.

In this chapter, we have focused on the structure and species composition of restored or rehabilitated forests, inspired by the ideal of restoring forest ecosystems to a state that resembles the 'potential natural vegetation' as closely as possible. We fully recognize that, in addition to this general approach, several other aspects may be important at the local scale, for example urban forests for recreation, or short-rotation coppices for the production of renewable energy. Sometimes, but not always, ecological and socio-economic functions can be combined. For further reading, we refer to the book edited by Mansourian *et al.* (2005), which is based on WWF's extensive global efforts. It is a source of information for both researchers and practitioners on how forest functions can be integrated into landscape-scale conservation and restoration plans.

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Chapter 13

RESTORING TEMPERATE FORESTS: A NORTH AMERICAN PERSPECTIVE

Dean Apostol and *Ayn Shlisky*

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13.1 INTRODUCTION

In this chapter we present an overview of ecological restoration within temperate forests of western North America, including Canada and the United States, but not Mexico. We discuss historic changes to these forests and conservation and restoration policies that influence restoration. A case study is included that provides a restoration perspective on ponderosa pine forests in Colorado state, which presents issues typical across the Intermountain West.

We believe there are four major conclusions about restoration of western North American forests illustrated in this chapter:

- Forest restoration needs vary across western North America as a function of forest type and related geography.
- The biggest restoration challenge in forests of the Pacific Northwest, United States, is stitching older, structurally complex forests together using restoration silviculture and road removal.
- The biggest restoration challenge in the intermountain area is thinning out forests to improve fire **resistance** and **resilience**.
- The problem is huge, restoration is only part of the answer to forest conservation, and managers are learning as they go.

Western North America – generally lands west of the continental divide – includes highly varied temperate forests adapted to a wide range of climate, elevation and aspect. For the purposes of this chapter, these forests can be divided into four subregions (see Figure 13.1); they are bounded on the north by boreal forests of Canada and Alaska, and, to the south, by the temperate and subtropical forests and woodlands of Mexico. While still largely 'natural' in comparison to temperate forests elsewhere, these North American forests have been altered and degraded as a consequence of logging, road building, fragmentation and changes to fire frequency and intensity. It is these changes that necessitate restorative work.

Forests across the region are mostly of natural origin, with a majority of them in public ownership. About two thirds of the forests of the United States within 'Cascadia', also known in the United States as the Pacific Northwest, are in public ownership, and 75% of the forests of the Intermountain West are public. In western Canada (British Columbia and Alberta) well over 90% of the forests are owned by the public, managed by provincial governments. Starting from the northwestern part of this region and heading east and south-east, conifer-dominated rainforests extend from south-eastern Alaska, south through British Columbia, Washington, Oregon and northern California. These rainforests generally extend only about 150–300 kilometres inland, to the mountain spine that includes the Coast and Cascade ranges in the Northwest, and the Northern Sierra Range in California. Islands of rainforest extend further east, with outliers in Glacier National Park in western Montana, some 800 km east of the Pacific coast (Smith *et al.* 2007). As one travels south and east, the climate becomes more continental and drier, and rainforests give way to fir or oak–pine woodlands in southern Oregon and northern California, and from there to pine–fir forests and woodlands east of the mountain spine. The Intermountain West of the continent (the area generally between the Cascade–Sierra and Rocky mountains) is a series of high, mostly north–south-oriented mountain ranges separated by deep and wide valleys. The US Forest Service reports that the intermountain western United States has forest cover on more than 20% of the total land area. Hardwood forests in the form of aspen stands (*Populus tremuloides*) and riparian cottonwoods (*Populus* spp.) make up about 7% of all the forests in the west (Smith *et al.* 2007).

Annual precipitation varies greatly with elevation, with effects on plant assemblages all across the region. The Pacific rainforest region is dominated by sitka spruce (*Picea sitchensis*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*) and, in the south, the famous coast redwood (*Sequoia sempervirens,*) which is among the tallest trees on Earth. Deciduous trees play a minor role, usually limited to early-successional stages following disturbance, though bigleaf maple (*Acer macrophyllum*) is fairly long lived, is somewhat shade-tolerant, and can persist for hundreds of years. Conifers, particularly Douglas fir, redwood, spruce and cedar, can live well over 1000 years (Franklin & Dyrness 1988). The southern part of the northwest region has a wide variety of oaks and oak relatives, including Oregon white oak (*Quercus garryana*), California black oak (*Quercus kelloggii*), canyon live oak (*Quercus chrysolepis*), brewers oak (*Quercus brewerii*), tanoak (*Lithocarpus densiflorus*) and chinkapin (*Castanopsis chrysophylla*), a relative of the chestnut. Pine trees also become more dominant as one moves south, including ponderosa (*Pinus ponderosa*) and sugar pine (*Pinus lambertiana*). In

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Figure 13.1 Distribution of four subregions of temperate forests of the western United States and Canada. (From Commission for Environmental Cooperation Working Group 2006.)

interior montane areas, Englemann spruce (*Picea englemanii*), grand fir (*Abies grandis*), white fir (*Abies concolor*), noble fir (*Abies procera*), white pine (*Pinus monticola*) and western larch (*Larix occidentalis*) are found. Just below and at the timberline are mountain hemlock (*Tsuga mertensiana*), whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*) and other species that can tolerate long winters with cold, snowy conditions predominating (Franklin & Dyrness 1988).

Plant communities across eastern Oregon and Washington, and the Intermountain West, are determined primarily by available moisture. Lower elevations are mostly treeless, with transitional savanna areas that have scattered junipers (*Juniperus* spp.) and pinyon pine (*Pinus edulis*). Ponderosa pine savannas and woodlands occupy sites with about 35 cm or more of annual moisture (Burns & Honkala 1990). Tree density and diversity increase as one moves upslope, particularly on the windward side of mountain ranges, which catch Pacific moisture. Higher elevations in the interior West include spruce (*Picea* spp.), lodgepole pine (*Pinus contorta*) and subalpine fir, and middle

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elevations are dominated by the Rocky Mountain subtype of Douglas fir, lodgepole pine, western red cedar, western hemlock and aspen. Sagebrush (*Artemisia* spp.) and juniper border the lower elevation limits of intermontane forests. Ponderosa pine occupies the zones between the shrublands and fir forests, and extends across all western states.

As one moves south and east, forests become more isolated, and are known as 'sky islands' in Arizona and New Mexico due to their occupying only the higher mountain tops (Warshall 1995). Conifers are dominant in nearly all upland forest settings.

Woodlands dominated by deciduous, coniferous or mixed-gallery forest trees occur along the major rivers and streams of the western United States (Obedzinski 2001). They are highly productive, and provide critical **ecosystem services** within the riparian corridor and adjacent uplands. Cottonwood is the dominant genus, as mentioned already, along with alders (*Alnus* spp.) and a wide variety of willows (*Salix* spp.). Forested riparian areas are frequently dominated by conifer trees in surrounding uplands. Maples, alder and Oregon ash (*Fraxinus latifolia*) are common in riparian areas of the Pacific Northwest (NatureServe 2010).

13.2 INFLUENCES OF HUMAN SETTLEMENT

Western North America was settled by Indian people thousands of years before the arrival of Europeans. In the south-western United States, Indian people were agriculturists who grew beans, squash and corn (maize) in irrigated plots on alluvial soils. The Anasazi people lived in stone villages built along defensible cliffs in the Four Corners region, where they exploited nearby forests for food, firewood and building materials. There is evidence that the decline of the Anasazi, which predated the arrival of Europeans by nearly 200 years, was at least in part due to over-exploitation of forest resources, particularly pinyon pine and juniper trees. These trees were gradually cleared from ever wider areas around main settlements for building material and fuel. The loss of forest was exacerbated by prolonged drought that eventually led to severe food shortages and **abandonment** of the area (Kohler & Matthews 1988; Diamond 2005).

Further northwest in Cascadia, Indian people had one of the highest population densities in North America despite not having agriculture. But they did have abundant aquatic resources, particularly salmon, which migrated in great numbers far upstream into continental areas. Coastal people lived in rainforests along navigable rivers and bays. The major rivers were trading routes, particularly the Columbia and Fraser. Indian people in Cascadia were skilled wood workers, and forest trees were used for many purposes, including building materials, tools, weapons, clothing and even baby diapers (Stewart 1984). Western red cedar in particular was known as the 'tree of life', and it was used for many purposes, from canoes to houses to clothing.

Drier forests, particularly pine and oak woodlands, were managed through use of prescribed fire (Bonnicksen *et al*. 1999). Burning was done primarily to promote food sources, including game, bulbs, acorns, hazelnuts (*Corylus cornuta*) and certain seed-forming grasses. In mountain areas, huckleberry (*Vaccinium* spp.) patches, an important staple, were maintained through periodic burning (Boyd 1999).

The climate of much of western North America is characterized by wet winters and dry summers, which in turn provides seasonal windows for safe burning. However, there is much debate over the extent to which Indian people 'created' the landscapes of western North America as opposed to merely influencing it. It is safe to say that they worked with it and helped give it shape, probably to the extent of altering plant communities and extending some of their ranges (Bonnicksen *et al*. 1999).

In the nineteenth century, European settlers spread over the region in waves, bringing many changes to forests, some deliberate and some accidental. They arrived relatively late, that is 250–300 years after European settlement of the eastern part of North America. However, their impact preceded their migration. Traders and explorers arriving by ship along the Pacific coast in the late eighteenth century probably introduced diseases to which the native people had no immunity, such as measles and small pox. These were devastating, and may have reduced Indian populations to a fraction of what they had been. It is likely that this also led to a reduction of seasonal fires, which by the time the settlers arrived could have meant forests were denser and had thicker understories than had been the case for centuries (Pyne 1982).

European settlers brought steel tools and a cash-based economy with them. Forests of Cascadia, especially those near major streams and bays, were levelled within a few decades. The timber was used to build

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growing cities up and down the coast. Settlers used fire to clear away unwanted forests in interior valleys to establish farms. They introduced cattle and a large number of weedy grasses and forbs. The absence of Indian-set fires allowed brush to overtake some formerly open savannas and woodlands. Others were kept open, but plant composition was altered from heavy grazing. Millions of sheep were herded across open, unclaimed land to distant markets, and nearly every high meadow was grazed, sometimes down to bare earth. This led to substantial soil **erosion** in some areas.

13.3 CONSERVATION AND RESTORATION POLICIES

Due to rugged terrain or aridity, much of the forest land of the region was not attractive to settlers. Both the US and Canadian governments made a series of decisions that recognized the importance of western forests for watershed conservation and as eventual stores of timber that would be needed once private lowland forests in the east were all gone. In Canada, forests were held by the Crown, with responsibility for management eventually turned over to Provincial governments. In the United States, the federal government turned public forest management over to what is now the US Forest Service (USFS), originally formed as the Division of Forestry in 1891. It was renamed the Bureau of Forestry in 1901, and in 1905 it became the US Department of Agriculture Forest Service (Steen 2004). The agency was placed under the leadership of Gifford Pinchot, who had studied classical forestry in France and Germany, but recognized that the vast forests of the western United States could not be managed under the same intensive silviculture paradigm as then prevailed in Europe. In the first decades of the twentieth century, there was little demand for timber from these forests, and no way to get access to the trees in any case. As a result, the USFS was initially established as a forest protector, and a key element of protection was fire control. This was especially the case after a major fire, known as the 'Big Burn', occurred in western Montana and Idaho in 1910, devastating millions of hectares of forested land (Pyne 1982).

By the mid-1940s, the USFS had management responsibility for over 29 million hectares across the western United States. It was primarily focused on controlling livestock grazing, building access trails and establishing a fire patrol system (USFS 1948). The Great Depression of the 1930s resulted in a large influx of funding and labour, allowing the US Forest Service to build major recreation facilities like Timberline Lodge on Mount Hood in Oregon, as well as campgrounds and trails. But timber management remained a small part of the programme (Bergoffen 1976; Steen 2004).

This changed during and immediately after the Second World War. By then, private forests had been heavily exploited, and the post-war suburban construction boom exponentially increased demand for timber. The USFS had planned for this moment, and shifted quickly into a new role as a provider of timber. This change also happened in Canada, though at a slower pace due to the much lower level of population and construction relative to the amount of forest available.

Forest land cover in the western states has been remarkably stable since Euro-American settlement. Rocky Mountain Forests still cover 26% of the total land area, whereas they once covered 28%. In the Pacific Northwest, 40% of the total land area was forested prior to Euro-American settlement, with the current amount reduced only to about 37%. But the nature and condition of these forests have changed substantially as they have been subjected to **fragmentation**, human-caused and natural **disturbances**, biological **invasions**, artificial fire exclusion and land development. There have been shifts from agriculture to forests and vice versa, while some forest land has been converted to more intensive uses, such as urban areas. Since 1991, there has been an increase in the ratio of forest growth to removal for the Pacific coast and Rocky Mountain regions as a result of decreased harvesting on public lands and increased tree growth on timber stands that were regenerated after harvest during the twentieth century (USFS 2001).

13.3.1 Pacific Northwest forest restoration

Restoration of forests in Cascadia began in the 1990s as a response to the listing of the Northern spotted owl (*Stryx occidentalis*) as an **endangered species**. This species of owl is highly dependent on old-growth forest conditions, and had been monitored for years as an indicator of forest conditions (FEMAT 1993). The historical amount of mature or old-growth forest fluctuated between 25% and 75% of the entire forested area,

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under the influence of natural disturbances including insect outbreaks, wildfire and windstorms (Wimberly *et al.* 2000). Only about 10% of the temperate rainforest within western Oregon and Washington is presently in old-growth conditions (Forest Ecosystem Management Assessment Team (FEMAT) 1993). An estimated 80% of the original old growth in large valleys along the mainland coast of British Columbia has been logged (Ministry of Forests 2003). Generally, there is more unlogged rainforest in the north, and progressively less in the southern and eastern parts of the region.

Relatively large patches of never-logged rainforests persist and do not require ecological restoration. These forests have infrequent fires despite naturally high levels of fuel accumulation. They lack roads, and do not have invasive species. The main risks to these remaining old-growth forests are from activities on nearby or adjacent lands, particularly fires that originate elsewhere, or from windstorms that blow unimpeded across adjacent clearcuts.

Previously logged forests of Cascadia today are characterized by dense conifer plantations, or young mixed hardwood and conifer stands where replanting did not occur. Managed forests often have dense road networks and can be highly impacted by invasive species. Unplanted clear-cuts sometimes have dense shrub growth that inhibits tree regeneration for decades. Older clear-cuts that were not replanted (replanting was uncommon until the 1950s) tend to be dominated by hardwoods, particularly alder and maple. Maple is long-lived and shade-tolerant, and can also inhibit regeneration of conifer trees if left untreated. A big concern in the Pacific Northwest is forest fragmentation – the reduction of the size of forest patches – particularly in old, late-successional forest (Altman & Hagar 2007).

The main restoration issues for previously logged forests of the Northwest are:

- Low complexity of forest structure in young, even-aged, hardwood or shrub-dominated forest stands.
- Excessive numbers of roads, some of which are poorly built.
- Invasive species, particularly in or near urban areas.
- High tree density in older multilayer forests impacted by fire exclusion.
- Fragmentation of remnant forest patches.

Active restoration is increasingly common on public forest lands where old growth conifer conditions are desired. The Pacific Northwest Forest Plan of 1993 was created to protect and recover old-growth forest dependent species, most notably the Northern spotted owl (FEMAT 1993). A typical restoration approach entails thinning dense young stands in a variable manner so as to create openings, reduce competition and encourage more rapid tree growth. A goal is to establish more vertical and horizontal diversity as well as patchiness of spatial **heterogeneity** at both the stand and landscape scales (Tappeiner *et al.* 1997; Carey *et al.* 1999; Franklin & Norris 1999; Franklin *et al.* 2002; Muir *et al.* 2002; Apostol & Sinclair 2006). Existing roads are used for thinning operations, and may be removed or decommissioned after one or more thinning operations are completed.

Road removal and decommissioning are important aspects of forest restoration in Cascadia. Many logging roads were built on steep mountain midslopes, with soil material cut from the high side and deposited on the low side. Frequent culverts cross these roads. The culverts are often undersized and are not well maintained. Fill slopes are subject to failure due to weight and lack of compaction, resulting in numerous washouts and debris flows that have badly damaged formerly productive salmon streams (Apostol & Sinclair 2006). Full restoration involves removing drainage structures and pulling the fill material back up onto the road bed to match the pre-existing contours as much as possible. This is a very expensive operation, often costing US$6700 or more per linear kilometre (Napper 2006).

More commonly, roads are 'stabilized' by pulling out the undersized culverts and replacing them with surface drain dips. This prevents debris build up and catastrophic failures. Roadbeds are ripped and reseeded or planted (Bagley 1998). Where continued access is needed, culverts are replaced with larger, 'salmon-friendly' stream crossings. New roads are kept narrow, and are regraded to allow water to run directly across them rather than alongside them. This eliminates the need for ditches and culverts, and reduces maintenance costs.

Variable thinning is designed to create a more heterogeneous forest structure and composition, reduce susceptibility to insect, disease and fire-induced mortality and accelerate the rate at which remaining trees grow by removing competition. Conventional forest thinning attempts to maximize wood fibre development, while restoration thinning maximizes structural complexity and, presumably, biological diversity.

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Hardwoods are a natural early-successional stage in the forests of Cascadia. In some cases, hardwoods are much more dominant today than they were historically. Bigleaf maples can form long-lived near-monocultures in some forests, because they sprout from stumps after disturbance and quickly form a canopy that shades out conifer seedlings and inhibits their regeneration. Forest restoration in maple-dominated forests therefore typically includes thinning and herbicide use to prevent additional stump sprouts. Alder, another important northwestern hardwood, is short-lived and not shade tolerant. It is also a nitrogen fixer that prepares the way for subsequent conifer and understorey growth. Consequently alder-dominated stands are often seen as a successional condition that does not need to be managed if restoration is the goal. However, in some cases land managers have thinned alder to make space for planted conifers to speed the regeneration and development of conifer trees, particularly in riparian areas where large trees that eventually fall into streams are important for stream restoration and the **reinforcement** of salmon populations.

Oak savannas and woodlands are an important ecological and cultural component of Cascadian forests. They range from southwestern British Columbia, into southern Oregon and California, with increasing species diversity in the south. The native oaks are fire-adapted and fire-dependent species. They need fire to keep competing vegetation at bay, and in its absence, they can be overtopped and out-competed by both Douglas fir and grand fir. Oak woodland and savanna restoration projects are occurring across Cascadia. Generally restoration includes cutting or killing in place competing conifer trees, removing invasive, mostly non-native brush, reseeding or planting the understorey with native bunchgrasses and forbs, and in some cases reintroducing fire (Apostol & Sinclair 2006).

There are no comprehensive data available on the extent of conifer and oak woodland restoration taking place within Cascadia, but it is widespread and expanding. The two US federal agencies that control much of the forest land in the region are actively engaged in restoration at a scale of tens to hundreds of thousands of hectares a year (US Department of Agriculture and US Department of Interior (USDA and USDI) 2011). Over 1700 km of roads have been removed or stabilized on National Forests of the Pacific Northwest in 2008 alone (USFS 2009). Oak woodland restoration is being done by local governments, by nongovernmental organizations such as the Nature Conservancy and by private landowners.

13.3.2 Interior Western forests

Dry temperate forests of interior western North America are also the focus of restoration work, but the dominant issues there are forest health and fire ecology. Most interior forests are fire adapted and fire dependent. Ponderosa pine is the single most widespread tree in western North America (Burns & Honkala 1990). It currently occurs on circa 16 million hectares in the western United States (Arno 1996), and is extremely well adapted to fire. It develops a thick protective bark even at a very young age. Typically ponderosa pine forests were on a 7–25-year fire cycle, with fires originating by either Indian burning or lightning. The fires kept tree spacing wide and understorey vegetation (known in North America as brush) at a minimum (Arno 1996). Elimination of the historic pattern of frequent low-intensity fires in ponderosa pine and pine-mixed conifer forests has resulted in dense thickets of small trees and are experiencing insect and disease epidemics and severe wildfires (Arno 1996).

It is estimated that hundreds of millions of hectares of interior western forests are currently outside their natural range of variability due to the relative absence of fire (Nature Conservancy 2010). In some cases, such as mixed *fire regimes* in large wilderness areas, restoration of these forests can be accomplished by guiding or managing naturally occurring fires. However, in many other areas restoration requires more active management, particularly thinning, to help create a more natural forest spacing and structure before it is safe to bring fire back into the system. Thinning can be a temporary strategy eventually replaced by fire alone, or it can be a continuous tool where reintroducing fire is not practical or desired (Arno & Fiedler 2005).

The first recorded efforts to use both cutting and burning to restore interior pine forests was in 1984 at the Lubrecht Experimental Forest, managed by the University of Montana (Arno & Fiedler 2005). Since that time, this approach has become widespread, and federal agencies in particular have been diligent about reducing fuel loads. Since 2001 over 14 million hectares have been treated to reduce fuels. In 2009, the Forest Service provided a breakdown between restoration

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and fuel reduction. About 1 million hectares are shown as having had 'restoration', with 1.6 million having had fuel reduction only. About 73 000 hectares were placed under 'stewardship contracts', which tend to cover multiple activities that are restorative, including road stabilization or decommissioning, invasive species control, prescribed fire and replanting (USDA and USDI 2011).

Much of the work of restoring interior, fire-adapted forests is being done through the efforts of a multi-agency collaboration called the *Fire Learning Network*, started in 2002 by the US Forest Service, the US Department of the Interior, and the Nature Conservancy. According to a 2009 analysis, approximately 80% of ecosystems and major habitat types are moderately to highly departed from their respective **reference** conditions as identified by people working with each type of ecosystem (Blankenship *et al.* 2009). This includes **ecosystems** that have experienced too little fire, as well as those that are experiencing too much.

In most cases, the Fire Learning Network focuses on land areas of 400 000 ha or more, which means that land ownership and management responsibility are mixed, and consensus building and collaboration are necessary (see Chapter 22). Altogether, across the United States, over 32 million ha of land have been brought under the aegis of the network. In 2009, the focus was on the eastern slope of the Cascade Mountains in Washington and Oregon, western Montana, the Siskiyou Mountains of northern California and forest land in New Mexico. The Nature Conservancy estimates that managers will have to treat 64 000 ha per year for decades to come, in order to work their way through the 'backlog' of forests that need restorative work.

The Fire Learning Network brings **stakeholders** together, establishes shared goals and develops an information database. It supports implementation projects that can range from a few hundred acres to much larger. Typical projects include tree thinning, brush removal, prescribed burning, livestock exclusion fencing and reseeding with native grasses and forbs. Each individual project is planned within a larger **landscape**-level strategy. Because this work is unproven, an **adaptive management** framework is used, which allows learning and improving practices over time. Projects are integrated with local economies, and by-products of restoration are put to use wherever possible.

A similar approach to collaborative forest restoration was established by the US Congress (under Title IV of Omnibus Public Land Management Act of 2009 – Public Law 111-11, Sec. 4001-4004; US Congress 2009) as the Collaborative Forest Landscape Restoration (CFLR) Program. The purpose of the CFLR Program is to encourage the collaborative, science-based ecosystem restoration of priority forest landscapes. It provides a means to (1) encourage ecological, economic and social **sustainability**, (2) leverage local resources with national and private resources, (3) facilitate the reduction of wildfire management costs, including through re-establishing natural fire regimes and reducing the risk of uncharacteristic wildfire, (4) demonstrate the degree to which various ecological restoration techniques achieve ecological and watershed health objectives and (5) encourage utilization of forest restoration by-products to offset treatment costs, benefit local rural economies and improve forest health.

The CFLR Program provides funding authority for up to US$40 000 000 annually for fiscal years 2009–2019, up to 50 percent of the cost of carrying out and monitoring ecological restoration treatments on National Forest System land, up to $4 million annually for any one project, up to two projects per year in any one Forest Service region and up to 10 projects per year nationally. In 2010, 9 of 10 projects selected for funding were in the western United States. In Box 13.1, we present the Upper South Platte Watershed Project as a case study that illustrates many of the points raised thus far.

13.4 PERSPECTIVES

Restoring forests across a large part of a continent is a daunting prospect. Events are changing quickly, and there is much we simply do not and cannot know. It is challenging for forest managers and restoration ecologists to stay up-to-date with current methods and technologies. The authors have worked in the arenas of ecology, restoration and natural resource management for decades. Our perspectives include private and public practice, research, teaching, writing and facilitating restoration efforts. We would like to offer a few observations on the prospects and perspectives for restoring temperate forests in western North America by way of a synthesis of our experiences.

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Box 13.1 Case study: Upper South Platte Watershed Project, Colorado, United States

The Upper South Platte Watershed Protection and Restoration Project is implementing restoration actions at a landscape scale. It is located in the foothills of the Rocky Mountains near Denver, Colorado (Figure 13.2). This area is dominated by a mixed ponderosa pine–Douglas fir forest. Much of Denver's water supply comes from this watershed. The South Platte is also a recreation area, highly regarded for its trout fishery, wildlife, and trails. And it is susceptible to severe wildfires that can threaten homes and communities.

The current landscape does not reflect historic conditions and is not sustainable (Kaufmann *et al*. 2000; Romme *et al*. 2003). Historically, wildfire visited this area every 30–50 years, maintaining a patchy crown structure in the forests, with small to moderate openings. Fire suppression, logging and livestock grazing gradually allowed smaller, thin-barked trees to proliferate. This has resulted in a dense forest and increased risk of large, high-intensity fires. The Buffalo Creek (1996), Hi Meadow (2000) and Hayman (2002) fires burned at least 64 280 hectares of forest and 196 built structures in and around the Upper South Platte.

The Upper South Platte Project was initiated in 1998 to address sedimentation and other issues resulting from the Buffalo Creek fire. A primary goal was to establish more sustainable conditions based on the historic character of the ecosystem, within the constraints of existing human needs. The project was made possible thanks to an interagency partnership between the US Forest Service, Colorado State Forest Service, Denver Water Board and other agencies. These partners adopted watershed restoration as a framework for overall management and specific project planning. They began with a landscape-scale assessment, completed in 1999. This assessment helped identify and prioritize restoration opportunities aimed at maintaining or restoring important watershed functions.

Restoration approach

Projects on National Forest lands combine thinning, gap creation, and prescribed fire to restore a mosaic pattern that reflects historic conditions (Plate 13.1). Open areas and thinned forest serve as firebreaks and buffers around or between remaining areas of dense forest. Some existing roads are obliterated after use. Off-road equipment reaches logs not accessible from roads. Where the use of off-road equipment is not desirable, logs are left on the forest floor.

The overall Upper South Platte Project plan is to treat 13 600 ha over a period of 10 years. Most Upper South Platte Project treatments consist of tree thinnings, with the remainder being small clear-cuts, ranging from ½ to 6 ha in size. Thinning procedures are intended to retain larger, more mature trees, particularly ponderosa pine. Some larger Douglas fir trees are removed where they compete with the pine.

Following logging, and a period allowing cut wood and brush to dry out, treated areas are subsequently burned. The goal is achieve a fairly open canopy, with circa 25% canopy cover, which is thought to be the level that predominated in the historic period taken as the reference models. In general, managers anticipate the need for prescribed burns every 10–30 years, in order to maintain the desired conditions of relatively open canopy.

Other restoration interventions include:

- Planting riparian areas that have exposed soils.
- Placement of woody debris and boulders in stream channels.
- Reshaping existing sediment deposits in riparian zones to facilitate plant re-establishment.
- Re-establishment of ponderosa pine in previously burned upland areas.
- Selective dredging to remove accumulated sediments.
- Closure and reclamation of roads.

Altogether about 9600 ha were treated between 1999 and 2010. Long-term stewardship contracts cover a 10-year period. They encourage removing as much wood as possible to help sustain local businesses. Between 2012 and 2015, about 2800 ha will be treated.

The Upper South Platte Project plan includes an adaptive management component, with six areas of monitoring prescribed:

1. Threatened, endangered, and sensitive wildlife and plant species
2. Forest vegetation and fuels
3. Noxious weeds
4. Oil erosion
5. Water quality
6. Off-highway vehicle use

Monitoring to date has shown that desired conditions have been met for fuel ladders, crown cover, tree size

Continued

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Box 13.1 *Continued*

class distribution, tree density, noxious weeds and the endemic Pawnee montane skipper butterfly (*Hesperia leonardus montana*), which has increased since project implementation. Measurements show that a significant reduction in crown fire risk and large scale high intensity fires has already been achieved (Johnston 2005).

Restoration of forests in the Upper South Platte Watershed are representative of other efforts in dry forests of the Intermountain West. These projects show great promise as ways to restore forest conditions similar to those that existed prior to Euro-American settlement, with composition and structure that are thought to be much more sustainable than current, overly dense forest conditions.

One concern is how these forests will be maintained once extractive timber removal is completed. Managers will need to conduct periodic burns, scout for and remove invasive species, prevent damage from recreational use and otherwise keep a close watch on the Upper South Platte and many other public forests across the West. This will cost money, and it is not yet clear whether there will be political support for long-term restorative management of this type over such a vast area.

First, because such a great amount of western North American forests are owned and managed by federal and provincial governments, restoration has been and will continue to be driven largely by government policies and funding. Up until the mid-1990s, the focus of these public land policies was on extracting resources such as timber, grazing for livestock, water, fossil fuels and minerals, while also attempting to **mitigate** environmental impacts of these industries insofar as possible. This focus on extraction was driven by two key factors: politics and agency culture. Elected representatives in this part of the world gain political advantages by facilitating the exploitive use of resources on public lands and subsequent job creation. Or to put it another way: more jobs equal more votes. Countervailing political pressure and strengthened environmental laws eventually overcame this factor, particularly in the United States. The second important factor was the internal culture of the agencies in charge of public lands. Forest management agencies in the United States and Canada were, until recently, largely led by resource professionals who personally favoured an extractive approach to public forest management, a tradition dating all the way back to Gifford Pinchot (see section 13.3). But over time, in response to public pressure and the emergence of a new generation of land managers, the culture of resource agencies has changed. The new managers are better schooled in ecology, and tend to have a more *holistic view* of their responsibilities than did the generation before them. Since the mid-1990s, public land management decisions have given increasingly more weight to noncommercial, non-extractive **ecosystem services** and increased community engagement in land management planning. The emphasis has largely, though not completely, shifted from resource extraction to sustaining ecosystems. This has led to a steady increase in interest in using **ecological restoration** as both a land objective and a set of management tools. We can see this shift playing out over vast areas of western North America. Much more is now being spent, particularly in the United States, on removing forest roads than is spent on building new ones. Large-scale clearcut logging on public forests is by and large a thing of the past. Restoration, while not yet the dominant paradigm, has taken its place as a serious alternative that is increasingly employed by forest managers. It has become a new tool in the manager's toolbox.

But as if land managers needed more challenges, **climate change** has now added a new level of *uncertainty* that brings into question the efficacy of restoration activities in temperate forests of western North America. In many cases **reference ecosystems** are based or constructed on the best available information concerning historical ecosystem structure and function. However, as will be discussed in Part 4 of this book, there is often uncertainty in the relevance of using historical conditions to guide restoration efforts, given for example the growing influence of climate change. Additionally, there are few tools to guide the selection of strategies that will restore the ecosystem resiliency needed to adapt to climate change. As one example, opportunities for proactive forest restoration that account for anticipated climate change may be

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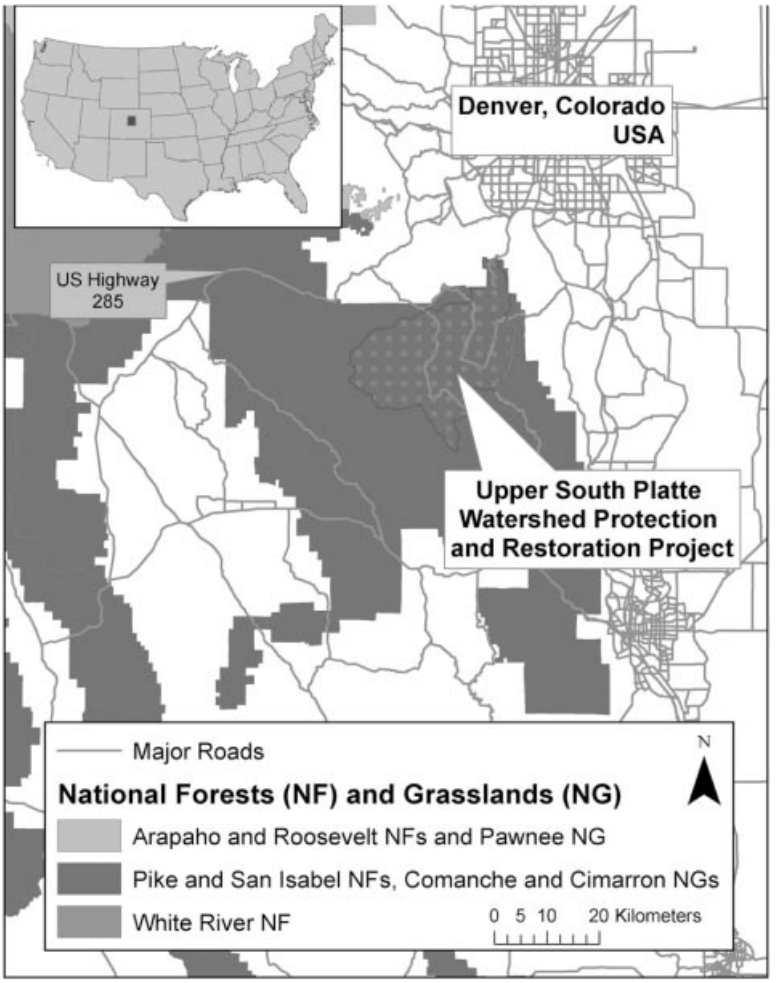


Figure 13.2 Location of the Upper South Platte Watershed Protection and Restoration Project, Colorado, United States.

limited by the availability of suitable planting stock from tree nurseries. In general, most nurseries are not actively incorporating information about climate change into their stocking choices, and may be unable to provide appropriate planting stock due to policies that use seed zones designed to protect locally adapted genetics (Tepe & Meretsky 2011). Since forest distribution and composition in western North America are highly correlated to the availability of annual moisture, small changes in precipitation could have significant changes in determining what type of forest, if any, can grow where.

Lastly, the current practice of restoration on public forests in western North America remains more reactive than proactive. Planning and projects are driven by priorities to protect **habitat** for wildlife species on the brink of extinction, or to head off potentially catastrophic fires. Goals are modest, mostly to sustain endangered or threatened species at or just above *minimum viable population* thresholds, or protect homes and property from fire at the wildland–urban interface. While recent initiatives, such as the public–private US Fire Learning Network and the CFLR Act, suggest a shift toward landscape-level restoration, public forest

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managers have yet to embrace or push for a more forward-leaning strategy that establishes restoration as a central practice. Large landscape-level, multipartner projects focused on both **ecological restoration** and **human well-being** are needed to truly sustain whole ecosystems across geographic extents that matter to both nature and people. However, while restoration still remains somewhat on the periphery of forest management, it is continuously gaining acceptance and advancing towards the centre.

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Chapter 14

RESTORATION OF DRY GRASSLANDS AND HEATHLANDS

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14.1 INTRODUCTION: CHARACTERISTICS OF DRY GRASSLANDS AND HEATHLANDS

Inland and coastal dry grasslands and dry heathlands harbour characteristic plant and animal communities on mesotrophic or oligotrophic soils. We focus on these communities in Europe, with its industrialized and densely populated countries. As similar problems exist to a certain extent elsewhere, we will also pay attention to grasslands in North America. For Europe, we follow the European Nature Information System (EUNIS 2006). This is a supranational instrument providing for a common framework for the conservation of plant and animal species and their natural habitats within the 27 member states of the European Union. This classification is the basis for the creation of a European network of Special Areas of Conservation, a major constituent of Natura 2000. We will be concerned with EUNIS habitat types E1 Dry grasslands, F4 Temperate shrub heathland and B1 Coastal dunes and sandy shores. Note that we consider the EUNIS categories as **reference** communities for purposes of conservation, and their defined species assemblages as appropriate targets for restoration programmes in **grasslands** and **heathlands** anywhere.

These EUNIS reference communities are of course heavily influenced by human activities, as it is assumed that human impact was a major factor increasing the area of dry grasslands, dune grasslands and heathlands, primarily as a result of agricultural exploitation during the past millenia, in what is nowadays referred to as low-intensity farming systems (Bignal & McCracken 1996). This is particularly the case in Europe where almost all dry grasslands, dune grasslands, and heathlands are **seminatural landscapes** (Thompson *et al.* 1995). Such systems can only be maintained by low-intensity farming or proxy land management techniques, as either intensification or extensification (i.e. the abandonment of any kind of management) will change the communities. One key question for restorationists to explore is whether such changes are reversible or not.

Sites where low-intensity agriculture is no longer economically feasible are at risk, from both intensification, in some areas, and abandonment, in others. Intensification often leads to eutrophication of the soil. In contrast, agricultural abandonment triggers secondary succession from open grasslands or heathlands to shrublands and, eventually, woodlands or forests. Both result in the disappearance of the characteristic species of open, oligotrophic ecosystems. The main task of restoration under these conditions is to achieve the right nutritional soil conditions in order to enable and facilitate the persistence and/or re-establishment of target species and communities. Primary constraints for restoration of these ecosystems are (1) the high nutrient status of the soil and (2) limited seed longevity and seed dispersal abilities of species targeted for reintroduction.

Dry grasslands, and heathlands, as well as dry coastal dune grasslands, can be characterized from a hydrological point of view as infiltration areas, fed by rainwater. Here, restorationists do not have to deal with complicated groundwater management issues as is the case for mires (see Chapter 16). The traditional view is that after the last glacial period, natural communities of dry grasslands and heathlands occurred on rocky inland outcrops, for example as chalk grasslands, along coasts (heathlands on rocks and dune grasslands on mobile sands), in river floodplains and at the edge of bogs. Their area was restricted to marginal habitats with extreme abiotic conditions such as shallow soil with subsequent low nutrient availability.

In Europe, an agricultural farming system was introduced from the Middle East after about 7000 BP and spread quickly. In north-western Europe, agriculture started at about 5000 BP in the northern part of the Netherlands (Spek 2004) and Germany (Behre 2008). Apart from arable fields, common grazing lands were exploited and resulted in the extension of grasslands and heathlands in the Atlantic part of Europe (i.e. from southern Norway to northern Portugal, and up to about 200 km inland). Domestic livestock has most likely dispersed many plant species from the Middle East into Europe (Bonn & Poschlod 1998). **Transhumance**, the seasonal movement of livestock to another region, must have played an important role in the long-distance dispersal of diaspores (Poschlod & Bonn 1998; Ozinga *et al.* 2009).

Dry grasslands and heathlands developed under a grazing system with common grazing rights, based mainly on cattle and sheep. The practice of hay cutting developed only during the last 2000 years, to provide winter forage for animals such as oxen and horses used for traction in pulling farm instruments such as ploughs. The removal of biomass from the fields resulted in a reduction in soil fertility, which is a characteristic phenomenon of low-intensity farming systems. Although good examples of low-intensity grassland

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with high nature conservation interest are still found in Europe, it is increasingly difficult to maintain them as a result of changes in land use (Veen *et al.* 2009).

North American tallgrass *prairies* expanded greatly beginning about 5000 BP (Knapp *et al.* 1998). From that time until about 3000 BP, the region's climate was hotter and drier than at present, favouring grassland development as woodlands retreated. The origins of tallgrass prairies and the roles of climate, grazing animals and human activity are still not completely understood. Humans have been part of the prairie biome on that continent ever since before the last glaciers retreated from the Midwest. Prairies were home to Native Americans for thousands of years prior to European settlement. The Native Americans managed the prairies according to their needs and abilities, and deliberate fires played an important part in shaping prairie vegetation. Fire was used to facilitate travelling and hunting, to stimulate new plant growth for game and to reduce fuel loads near habitations. Nowadays, large areas of former prairie that were destroyed through conversion to agriculture, intensive grazing or urbanization, have been degraded through fire suppression, drainage or other alterations (Knapp *et al.* 1998).

Having indicated the main characteristics of the relevant low-intensity farming systems, in the next section we will discuss the changes in land use, namely, intensification and abandonment. Then, we will discuss the results of techniques to overcome the constraints for restoration. Some such as growing crops deal with only the nutrient status of the soil; others such as mowing, grazing, burning, sod cutting and topsoil removal have effects on both reduction of nutrients and prevention of succession to shrubland. Finally, we will discuss whether such techniques must be carried out by nature conservation agencies in designated reserves or also outside reserves carried out by farmers according to agri-environment schemes.

14.2 THREATS

Grasslands and heathlands have been subject to at least two different types of change that reduce their conservation value. The most obvious change is where *land use* is changed through so-called 'reclamation', actually exploitation, where the aim is to increase the agricultural productivity of the area via 'agricultural intensification'. This process resulted in (1) habitat loss and fragmentation, (2) an increase in soil fertility and (3) reduction in plant species richness as a result of seeding agricultural crops, fertilizer application and soil homogenization. Further increase in soil fertility is the result of background **eutrophication**, which is derived from surrounding fertilized agricultural areas and atmospheric deposition, especially of nitrogen (Verhagen & van Diggelen 2006). This has been demonstrated clearly in the United Kingdom through the analysis of long-term land use surveillance data (Smart *et al.* 2005). Indeed background eutrophication was identified as one of the drivers leading to biotic homogenization at a regional scale (Smart *et al.* 2006). Plant communities that occur on very nutrient-poor soils, such as those of dry grasslands and heathlands, are particularly vulnerable to this indirect nutrient addition (Bobbink *et al.* 1998). This atmospheric deposition, which has increased since the 1980s (Smart *et al.* 2005), makes it harder to (1) maintain the communities on nutrient-poor soil where they already exist and (2) restore these communities after exploitation (Marrs 2002).

The second type of change occurs where marginal agricultural areas either have been **abandoned** with no active management or now receive reduced management in one way or another. On such sites, **succession** occurs with shrub and tree encroachment and hence a decline in the area of grassland and heathland. Well-documented examples of the decrease of habitats of the type covered in this chapter include heathlands (Webb 1997), calcareous grasslands in north-western Europe (WallisDeVries *et al.* 2002), wooded meadows in Sweden (Mitlacher *et al.* 2002) and tallgrass prairies in the United States (Samson & Knopf 1994). In addition, European coastal sand dune grasslands have also decreased as a result of the decline of the natural herbivores, namely, rabbits in the 1950s (Jones *et al.* 2008), agricultural abandonment and urbanization. Abandonment coincides with bush encroachment accompanied by a decrease in plant species richness. For instance, on the alvar grasslands in Öland, Sweden, the number of plant species characteristic of the alvar community has declined continuously as cover of *Juniperus communis* shrubland increases to become the dominant species (Rejmánek & Rosén 1992). Associated fauna is also affected. In Sweden, insect species dependent on plant species of nutrient-poor soils declined, whereas those dependent on plant species growing on nutrient-rich soils increased during the past 20 years (Öckinger *et al.* 2006). Up to 20% of European butterflies are threatened (Bourn & Thomas

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2002). Not only rare habitat specialists, but also some common, widespread butterfly species declined during the past 20 years in the Netherlands and Belgium. They maintained their populations in nature reserves such as dunes, heathlands and seminatural grasslands as a result of management practices, but they strongly declined in farmland and urban areas (van Dijck *et al.* 2009). In the Netherlands, 10 and 5 bird species, respectively, breeding in open grasslands and in dunes, have disappeared from these ecosystems between the periods 1973–1978 and 1998–2000 (Saris *et al.* 2002). At the same time, six bird species of dense shrubland on sand dunes showed an increase. This implies that shrub encroachment has strongly influenced the breeding bird population in dunes (Sierdsema & Bonte 2002).

14.3 CONSTRAINTS FOR RESTORATION

The aforementioned shows that species have disappeared after changes of the ecosystem by exploitation, enrichment of soil nutrient status or changes in land use intensity. What is needed for restoration of these modified ecosystems is reduction in nutrient availability and re-establishment of now-absent species, through either re-emergence from the soilborne seed bank or else dispersal of propagules (seeds, fruits or vegetative parts) from the surrounding area into the site to be restored. Hence, we will discuss the issues of nutrient status of the soil, dispersal capacity of target species, longevity of seeds in the soil and interactions between organisms as preconditions for succesful restoration. The first step for re-establishment of species is their dispersal to the target site. Once arrived, they can either survive in the soil seed bank, or germinate and establish as an adult plant. During this process of establishment, of course, seeds encounter many limitations resulting in few adults compared to the large amount of arrived seeds (Figure 14.1; Baeten *et al.* 2009). Hence, a large amount of seeds should arrive at the site to be restored for the successful establishment of now-absent species.

14.3.1 Nutrient status of the soil

Plant and animal species have disappeared as a result of agricultural intensification, often as a result of increased nutrient levels. Hence, high nutrient levels are a constraint for re-establishment during restoration. In western Europe, total atmospheric input of inorganic nitrogen ranges from 2–40 kg N ha^{-1} yr^{-1}, which is related to mean species numbers of 22–10, respectively, in plots of 2 m × 2 m in acidic grasslands (Stevens *et al.* 2010). Moreover, a synthesis of experiments all over the world with addition of nitrogen shows a decline in species numbers across a latitudinal range of ecosystems from arctic and boreal systems to tropical forests (Bobbink *et al.* 2010). The magnitude of the potential difficulty can be assessed by comparing these figures with the calculated *critical nitrogen loads*, that is, effect thresholds for atmospheric deposition, which are below 20 kg N ha^{-1} yr^{-1} for heathland and grassland (Bobbink *et al.* 1998) and coastal sand dunes (Jones *et al.* 2004). A 23-year field experiment with addition of 10 kg of N ha^{-1} yr^{-1} on top of the local atmospheric wet deposition of 6 kg of N ha^{-1} yr^{-1} revealed a plant species reduction of 17% in prairie grasslands in the United States (Clark & Tilman 2008). The decline of a number of butterfly species in Sweden is related to the relatively high atmospheric deposition, which is 12 kg of N ha^{-1} yr^{-1} (Öckinger *et al.* 2006).

It is also important to consider interactions among nutrients, especially the balance between the main macronutrients (i.e. phosphorus, potassium and nitrogen). Moreover, when two or more nutrients are limiting plant productivity, the system is less sensitive to temporary rises in the availability of a single nutrient. Sod cutting and topsoil removal can be effective in removing nitrogen but have much less effect for phosphorus (e.g. Bekker 2009; Figure 14.7 in Box 14.2). In the great majority of dry grasslands and heathlands, productivity is only limited by nitrogen availability. Hence, these systems are sensitive to small fluctuations in N inputs. This is especially true where atmospheric deposition can be more than double the critical loads for oligotrophic target communities (Bobbink *et al.* 1998).

14.3.2 Dispersal in space

Plant species that have disappeared and do not have a long-term persistent seed bank must have adequate long-distance dispersal mechansisms in order for them to be able to re-establish themselves in a fragmented landscape. Hence, it is important to know which dis-

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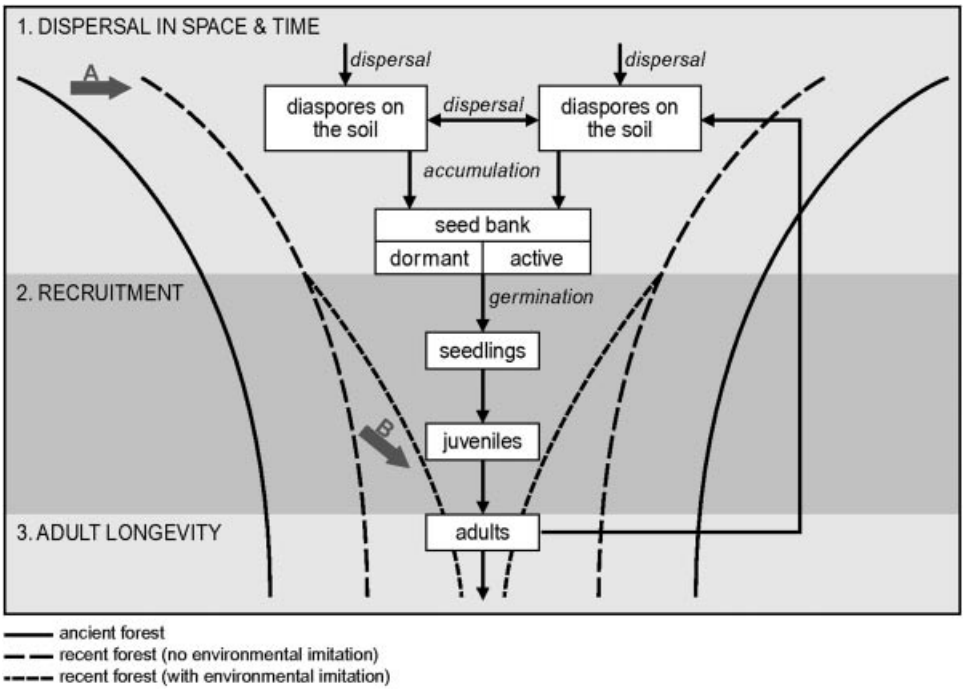


Figure 14.1 Conceptual bottleneck model representing the different successive processes of re-establishment in different types of forest as an example, which can be impeded by a two-stage limitation (dispersal and environmental). The funnel-shaped lines indicate the decreasing number of individuals through mortality and predation. First, dispersal limitation causes lower seed occurrence on the soil in a site to be restored (arrow A), second, environmental limitations can cause the funnel to narrow even more across different life stages (arrow B); it depends on the species and specific land-use history of the site to be restored. Modified from Baeten *et al.* (2009). Reproduced by permission of Wiley-Blackwell.

persal mode mechanisms were predominant in the local community before **fragmentation** of the landscape. Low-intensity farming entailed an enormous dispersal of seeds as a result of livestock grazing, cutting and manure application (Poschlod & Bonn 1998) and from holding barns (Losvik & Austad 2002). Current intensive farming in north-western Europe strongly reduces this seed dispersal pathway as a result of fencing and regulation of rivers and brooks (Poschlod & Bonn 1998). Remnants of the once extensive dry grasslands and heathlands are separated in the highly fragmented landscapes of contemporary Europe, and are no longer interconnected by flooding water and large-scale tending of flocks of livestock for transport of seeds (Ozinga *et al.* 2009; see Box 14.1 and Figure 14.2). Hence, failure of short-distance dispersal through fragmentation, and of long-distance dispersal due to the loss of connecting vectors, has become an important constraint to restoration efforts. This holds not only for seeds but also for gene exchange by pollen between populations (Kwak *et al.* 1998).

14.3.3 Dispersal in time: seed longevity

Plant species that had disapperared from the established vegetation can survive in the soil **seed bank** as a memory of the past. Especially after changes in habitat quality and land use, it is important to know which species have a long-term persistent seed bank. Only those species can re-establish during restoration. Soil seed bank analyses from a range of plant communities in dry grassland and heathland in north-western Europe show that these communities can only partly

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Box 14.1 Dispersal failure contributes to plant losses in north-western European countries

Dry grasslands and heathlands have suffered from habitat fragmentation. For the prediction of successful restoration, it is important to know which species will have difficulties to arrive at sites to under restoration. The importance of long-distance dispersal capacity of plants and the impact of the reduction of dispersal vectors in the current fragmented landscape was studied by Ozinga *et al*. (2009). The ability to track the changes in habitat configuration, through seed dispersal in space (long-distance dispersal by various dispersal vectors) and/or time (formation of a long-term persistent seed bank) appears to be a major determinant of regional species dynamics. The researchers had access to two large, up-to-date databases that enabled them to monitor plant distribution developments on a large spatial scale as well as the presence or absence of individual species at individual sites. The first database contains information on long-term changes in the frequency of occurrence of vascular plants and is based on repeated inventories of over 200 000 grid cells in the Netherlands, Germany and Great Britain, recorded over the twentieth century. The second is the LEDA database containing quantitative information for over 20 plant characteristics of more than 3000 vascular plant species in north-western Europe (also covering the three countries listed above) (Kleyer *et al*. 2008).

Ozinga *et al*. (2009) selected the plant characteristics most useful for discriminating between species with different dispersal traits and hence were able to explain plant species losses according to their dispersal capacity. They found that dispersal traits make a large and significant contribution to explaining interspecific patterns of species losses, of the same order of magnitude as the effect of eutrophication (see section 14.3.1). Interspecific differences in dispersal traits are thus good predictors of the extinction risk for plant species. The results are consistent across all three countries listed above. Species with a high potential for dispersal in the fur of large mammals or by running water are significantly more likely to decline than those using other dispersal vectors (Figure 14.2). Conversely, species with a high potential for dispersal by wind or birds are less likely to decline. The results also demonstrate that species with the ability to accumulate a persistent soil seed bank ('dispersal through time') perform relatively well (Figure 14.2).

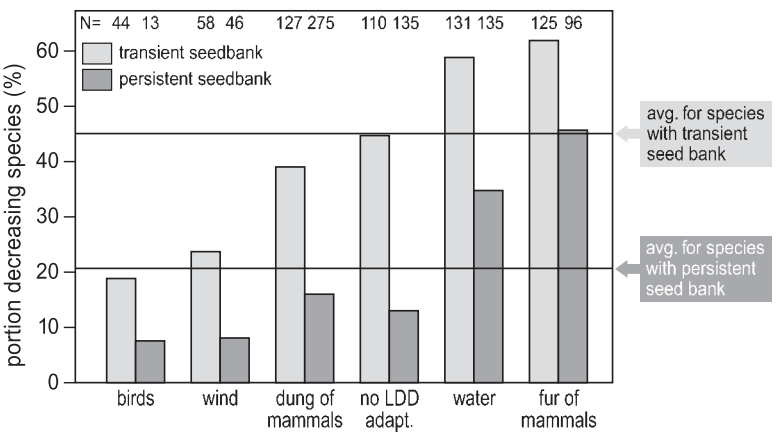


Figure 14.2 Percentages of plant species declining by more than 25% over the twentieth century for five long-distance dispersal (LDD) vectors. Species are divided into two groups for each dispersal vector, according to their ability to accumulate a persistent soil seed bank. Horizontal lines indicate the average percentages (geometric means) for species with a persistent soil seed bank and those with a transient seed bank (data from the Netherlands). (Modified from Ozinga *et al*. 2009.)

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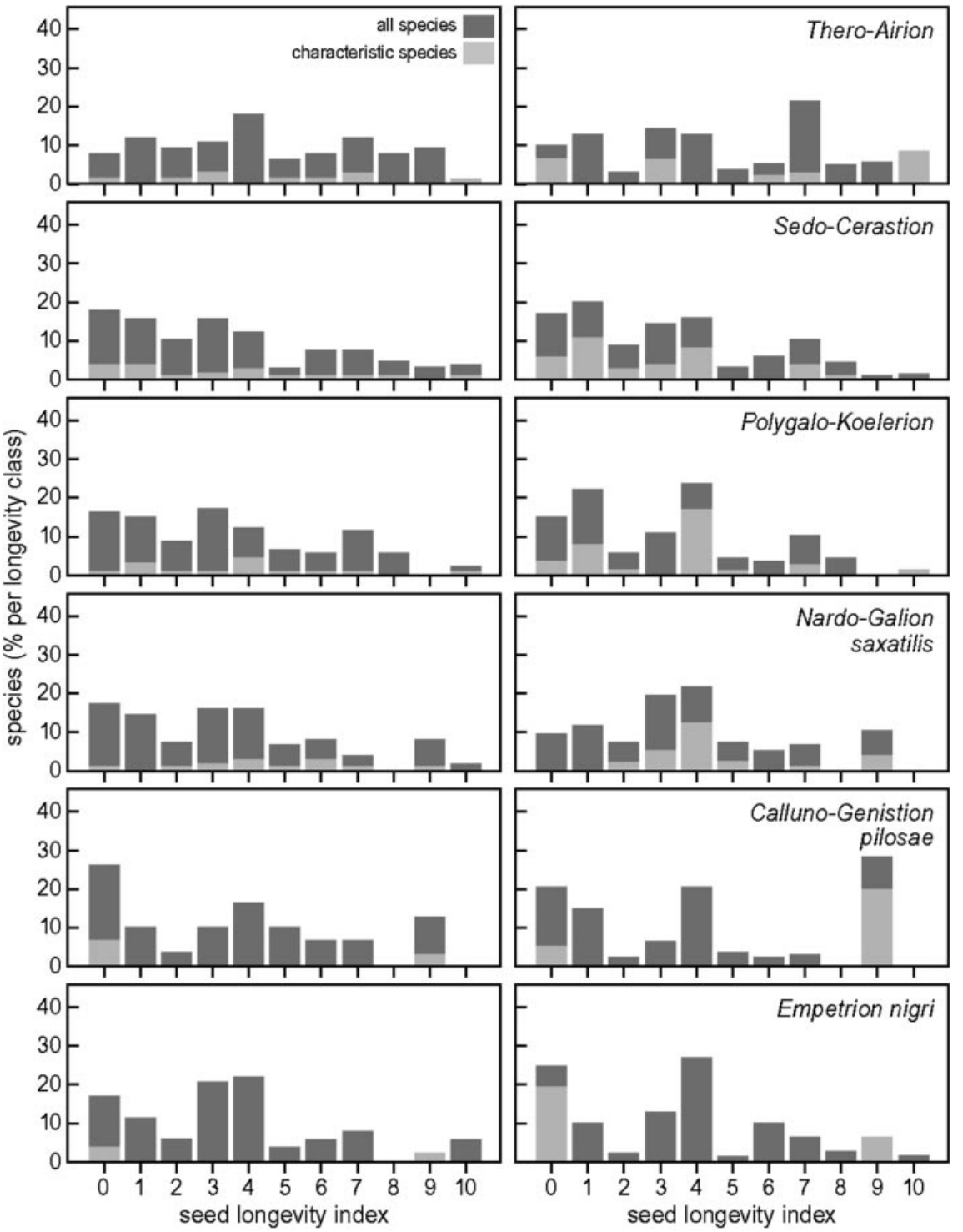


Figure 14.3 Seed bank longevity spectra of dry heathland communities (*Calluno-Genistion pilosae* and *Empetrion nigri*) and dry grassland communities (*Thero-Airion*, *Sedo-Cerastion*, *Polygalo-Koelerion* and *Nardo-Galion saxatilis*). On the *X* axis, longevity classes are indicated by the seed longevity index ranging from 0 (transient) to 10 (long-term persistent) according to data from Thompson *et al.* (1997). The *Y* axis gives the percentage per longevity class of the species in the community. The left-hand panels indicate the proportion of the longevity class within the community for sheer presence of the species, and the right-hand panels indicate the proportion taking into account the frequency of species in reference relevées of the database of the *Vegetatie van Nederland*. (Modified from Bekker *et al.* 2002.)

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rely on the soil seed bank for restoration (Figure 14.3) of grasslands and heathlands (Bossuyt & Hermy 2003) and calcareous grasslands (Fagan *et al.* 2010).

Plant species composition may not change during the first years of woody plant encroachment (abandonment) or of establisment of dominant grasses (eutrophication). As a result of decreasing light availability at soil level, fewer species will flower, set seed and germinate. This implies a depletion of the soil seed bank, especially of species with a transient (<1 year) or short-term persistent (2–5 years) seed bank (Thompson *et al.* 1997). After encroachment had taken place over several decades on the alvar of Öland, Sweden, both the species richness of the soil seed bank and the established vegetation decreased dramatically (Bakker *et al.* 1996a).

14.3.4 Interaction between organisms

Interactions between plants and soil organisms is an important area for intervention when seeking to restoring plant communities on nutrient-poor soil. Even when restoration has resulted in nutrient-poor soil conditions and seeds of nutrient-poor soil conditions are available, re-establishment of certain species can be hampered (van der Heijden *et al.* 1998). The problem may be found in the soil biotic community. However, soil organisms disperse very slowly, and hence their absence can be a constraint for restoration (Frouz *et al.* 2009) in a similar way to seeds. In a microcosm experiment (de Deyn *et al.* 2003), soil herbivores such as nematodes foraged preferentially on grass species such as those that are dominant in early eutrophic successional stages of restoration projects. Once the nematodes have reduced the early successional species, later successional target species in restoration of species-rich mesotrophic grasslands can more easily establish.

Removal of nutrients by taking away soil does reduce biomass, and also removes numbers of bacteria, fungal biomass and nematode abundance. On initially bare soil after, for example, topsoil removal, however, the experimental introduction of soil organisms of the late stage after topsoil removal did not facilitate the establishment of later successional plant species. Apparently, each successional stage of the plant community is related to a characteristic community of soil organisms (Kardol *et al.* 2008).

All these constraints and complexities have different consequences and ramifications that should be considered by restoration practitioners. It is necessary to first reduce the amount of nutrients in the soil to levels appropriate for the re-establishment of communities on nutrient-poor soils. The next step for restoration is the re-establishment of species (Bakker *et al.* 1996b). Once species have disappeared, the manager or practitioner may hope that target species are still present in the soil seed bank, and if not, they must be encouraged to disperse from nearby source sites and meet the soil organisms to build the target community. Active reintroduction of species is a relatively new element in the restoration of dry grasslands and heathlands, and will be discussed in the last section.

14.4 RESTORATION AFTER INTENSIFICATION OR ABANDONMENT

An important issue in the restoration of communities on mesotrophic or oligotrophic soils in old fields that were formerly exploited very intensively is the removal of surplus nutrients, especially nitrogen and phosphorus, or the reduction in their availability in the soil. Several techniques such as growing crops, mowing, burning, grazing, sod cutting (<10 cm) and topsoil removal (>10 cm) can be considered. The target communities of dry grasslands, dune grasslands and heathlands need management to prevent succession towards a community in which just a few herbaceous species dominate that then become shrublands, woodlands or forests. This also applies to sites where sod cutting and topsoil removal have occurred.

14.4.1 Growing crops

When cultivating barley in pots with soil from an old field that was formerly intensively used, or from oligotrophic soil, the nitrogen content of the crop grown on fertile soil was higher than that of the crop grown on oligotrophic soil (Marrs 1993). This suggests that growing crops can help to enhance the process of nutrient removal under field conditions. Marrs *et al.* (1998) started an experiment to remove especially phosphorus to create the right soil conditions for the re-establishement of heathland in a large, field-scale restoration project in Minsmere nature reserve in Suffolk, United Kingdom. They added only nitrogen (as ammonium sulphate) and potassium as inorganic fertilizers, and grew crop plants (mainly cereals) on sandy

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Table 14.1 Average nitrogen content at peak standing crop (yield; mean ± S.D.) and nitrogen removal in the first half of July in different cutting regimes and different years. Nitrogen content: 1975, $n = 1$; 1983, $n = 3$; 1999, $n = 5$; yield all years, $n = 10$. After Bakker *et al.* (2002a).

Year	Cutting regime	N concentration (%)	Yield (g of dw m^{-2})	N removal (kg ha^{-1})
1975	July	1.31	625 ± 92	82
	July and September	1.39	810 ± 97	113
1983	July	1.49	723 ± 64	108
	July and September	1.77	641 ± 69	113
1999	July	1.89	269 ± 23	51
	July and September	1.41	291 ± 43	41

dw, dry weight.

soils that had been used for arable cropping without the application of phosphorus on a sandy loam. The rationale was that the ammonium–nitrogen and potassium would help increase crop yield and hence enforce a greater phosphorus offtake, and the sulphate would help acidify the limed soil. The yields of the above-ground material were lower than under normal agricultural practice, and less nitrogen and potassium were removed than measured inputs. With phosphorus, there was indeed a net removal. However, there was no reduction of extractable (plant-available) phophorus in the soil in 7 years (Marrs *et al.* 1998). There was a slight reduction in exchangeable calcium but not in soil pH in 7 years. On clay soils, it had taken 70 years of cropping to reduce soil phosphorus concentrations to levels suitable for restoration of nutrient-poor conditions (Marrs 1993). Cropping is, therefore, likely to be a useful long-term strategy to modify a nutrient-rich soil so that ecological restoration of communities characteristic of nutrient-poor soil can begin thereafter. Whether the crop can be sold is another matter that needs to be addressed, but that question is outside the scope of this chapter.

14.4.2 Mowing

Haymaking (mowing and removal of the mown grass) is a common technique that prevents succession and removes both seeds and nutrients from the site. A comparison of different cutting regimes showed that haymaking twice a year resulted in a plant community closer to the oligotrophic target grassland community than haymaking once a year in the sandy uppercourse of a brook valley in the Netherlands on a site that had been intensively farmed. Annual or biennual mulching (mowing and leaving the cut grass where it lay) produced a different tall forb community (Bakker *et al.* 2002a).

Although haymaking is a successful restoration practice by reducing standing crop from 800 to 200 g dry weight m^{-2}, it appeared not enough to create the oligotrophic target grassland, which has a lower standing crop. The nitrogen offtake in haymaking is too low to compensate for inputs from atmospheric deposition (Table 14.1; Bakker *et al.* 2002a).

Mulching is generally not successful if the aim is to restore oligotrophic communities in the Netherlands. However, this treatment produced similar results to haymaking in a 25-year experiment in southern Germany (see comparable changes in species composition between 1975 and 1999 for #2 (haymaking) and #3 (muching) in Figure 14.4). High ambient temperatures in late summer may encourage faster decomposition of the litter in Germany compared to the Netherlands where the climate is cooler (Kahmen *et al.* 2002). However, these results confirm the complexity in vegetation management and the pitfall of trying to transfer techniques between sites and regions without testing them previously. This could also hold for other techniques mentioned.

14.4.3 Burning

Burning is a relatively cheap way to remove above-ground biomass and some nutrients. However, the effects on species richness are not positive. Collins (1992) found that in the absence of grazers the application of prescribed fire in North American tallgrass prairie tends to homogenize the vegetation by uniformly removing the above-ground biomass and litter.

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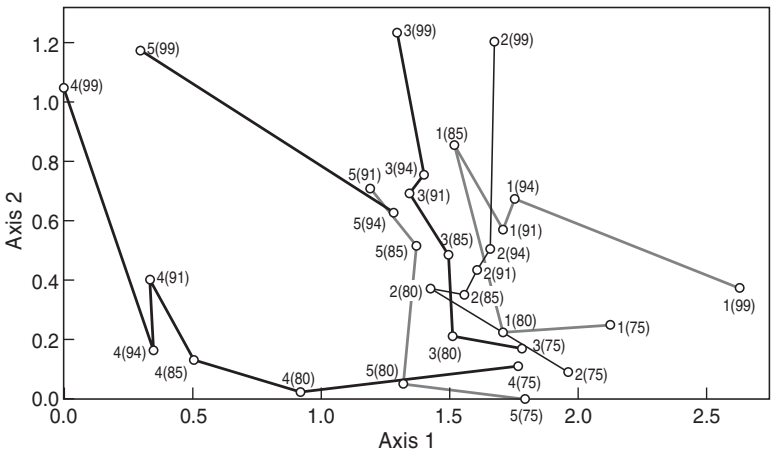


Figure 14.4 Pathway of species composition under five different management regimes from 1975 to 1999 in steps of 5 years presented in an ordination diagram of a detrended correspondence analysis (DCA). Total number of species is 84. Eigenvalues: Axis 1, 0.3; Axis 2, 0.1. At the start of the experiment in 1975, species composition was similar in all plots, but deviated strongly afterwards under the different management regimes. Largest differences occurred between grazing and burning (at the left side) and grazing (at the right side). Treatments: 1, grazing; 2, haymaking; 3, mulching; 4, burning; 5, laissez faire. Years are given in parentheses. (Modified from Kahmen *et al.* 2002. Reproduced by permission of Elsevier.)

Similar homogenizing effects were found in a long-term experiment on calcareous grasslands in Germany (Kahmen *et al.* 2002). The initial results seemed promising. However, after 25 years the grass *Brachypodium pinnatum* became so dominant that the plant community resembled that of a species-poor abandoned field (Fig.14.4; Kahmen *et al.* 2002). In contrast to grassland communities, burning is successful for a dominant heathland species. Prescribed burning is used routinely in the management of upland heaths within the United Kingdom, where it is successfully applied in rotation. The aim is to remove the vegetation and allow the dominant species, common heather (*Calluna vulgaris*), to regenerate for the stem bases. Usually a 6–12-year rotation is practised (Gimingham 1992).

14.4.4 Grazing

After abandonment of old fields, the stocking density adopted is often the one used in mesotrophic or oligotrophic communities. Such a grazing regime is more or less successful in sites that have not been heavily fertilized in the past. Examples show that the development of mesotrophic communities is possible. Apart from the lower costs, grazing is often preferred over cutting because the former induces spatial differences whereas the latter produces a uniform effect across the whole field. Where extensive grazing occurs on areas with plant production exceeding herbivore utilization, vegetation compositional and structural patterns are produced at different scales (Bakker 1989) that cannot be mimicked by cutting. It was also found in North American tallgrass prairie that grazing by bison can generate small-scale heterogeneity (Veen *et al.* 2008).

Grazing by sheep with low stocking rate is often not enough to prevent adverse successional change. For example, in a successional sequence following topsoil removal, ruderal communities with tall forbs established after 3 years in a site with bare soil after topsoil removal in Germany (Stroh *et al.* 2002). Sheep grazing could not stop this trend. Despite their suppression by sheep, many ruderal species were maintained and represented a latent potential for recolonization (Stroh *et al.* 2002).

14.4.5 Sod cutting

To enhance the restoration of oligotrophic grasslands and heathlands, sod cutting (up to 10 cm in depth) is practised. This technique does remove nutrients with

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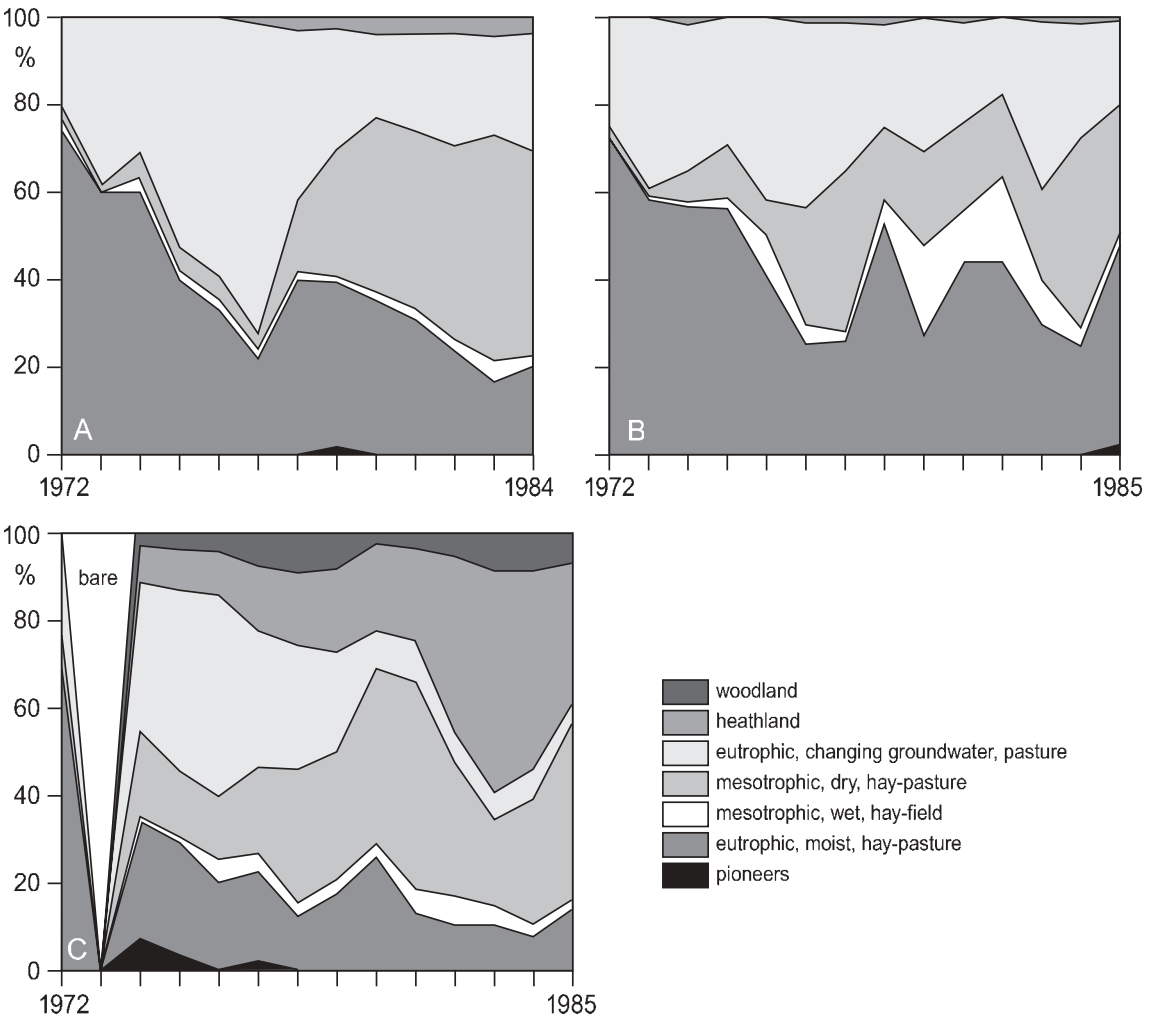


Figure 14.5 Relative changes of cover percentages of ecological groups after (a) grazing, (b) haymaking and (c) sod cutting from 1972 onwards.

the sod and allows the establishment of for example heathland species from the soil seed bank if present (Figure 14.5). The disadvantage of sod cutting is that it also removes most of the soil seed bank, and this will include any present target species. However, shallow sod cutting of up to 10 cm can also activate the seed bank of nontarget species. A headache for many authorities in charge of conservation is the widespread establishment of the common rush, *Juncus effusus*. This species can also show up as a result of trampling by grazing livestock. It is not a local problem for restoration practicioners. Its seeds are represented in most soil samples in old fields and heathlands in northwestern Europe (Bekker *et al.* 1997).

14.4.6 Topsoil removal

Topsoil removal (up to 50 cm in depth) implies definitive removal of the traces and 'footprint' of former agricultural history of a site by removing the long-ploughed and heavily fertilized soil right down to the C horizon

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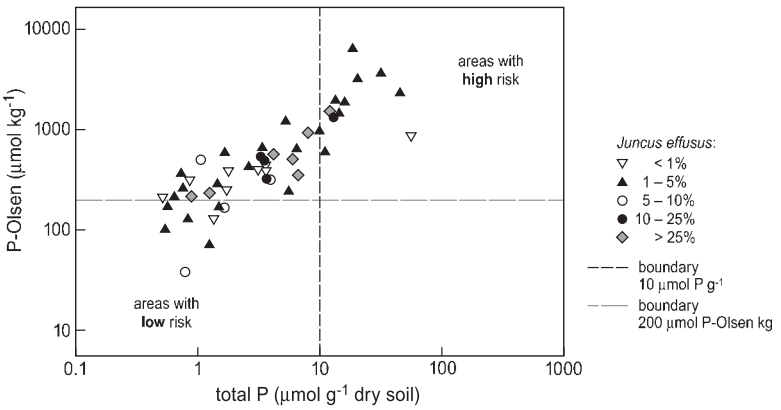


Figure 14.6 Areas of high and low risk for future dominance of *Juncus effusus* based on its current cover abundance and the current level of available and total P in the soil. (Modified from Bekker 2009.)

Box 14.2 Effects of topsoil removal – case studies in the Netherlands

After 20 years of practice, Bekker (2009) evaluated over 300 sites where topsoil removal had taken place in the Netherlands, by reading through plans, databases and status reports of authorities in charge of nature conservation. A subset of 42 sites was selected to be included into a field survey during 2006 and 2007. These sites were monitored for the actual vegetation and soil samples were taken. Thus the relationship between plant cover, species composition and soil nutrient parameters nitrogen and phosphorus could be established.

The abundance of plant species characteristic of nutrient-poor soil conditions was negatively related to the cover of the newly established vegetation. It appears that the longer bare soil is available in the vegetation after topsoil removal, the more chance the target species of dry grasslands and heathlands have to establish. Sites with <200 µmol P-Olsen kg^{-1} and <10 µmol P kg^{-1} were identified as being at relatively low risk for the spreading of *Juncus effusus* (Figure 14.6). The amount of topsoil removed also plays a role. The less nutrients (organic matter) were left after toposil removal, the more successful the vegetation developed. Yet, these sites need a vaste amount of follow-up management to prevent tree species and common rush (*Juncus effusus)* from dominating the vegetation within a few years.

Topsoil removal is not only important for plant species. Fifteen out of 16 butterfly species characteristic of plant communities on nutrient-poor soils managed to colonize sites after topsoil removal. Some, mostly Red List species, populated the stripped sites at much lower abundancies than the surrounding nature reserves. However, over 75% of the species pool of butterflies in the neighbourhood was found in each of the sites after topsoil removal. The expansion of butterfly species characteristic of oligotrophic habitats was positively related to the size of the site, time after removal and the successful establishment of plant communities characteristic of nutrient-poor soil conditions. For rare species, the distance to source populations poses an additional constraint.

It can be concluded that successful restoration of communities of nutrient-poor soil conditions is only possible when phosphate levels after removal are low. Characteristic butterfly species can only establish when the target plant community has established.

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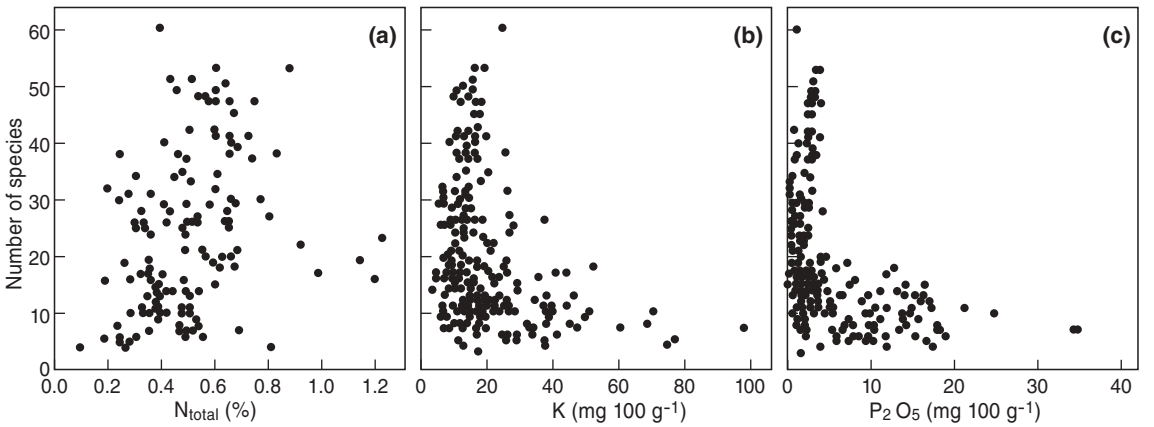


Figure 14.7 Distribution of total nitrogen, percentage of soil-extractable potassium, soil-extractable phosphorus against the number of species per 100 m^2 in 281 grassland sites in western Europe. (Modified from Janssens *et al.* 1998.)

(the undisturbed parent material) and to 'reboot' with oligotrophic soil conditions. The seed banks of target species are depleted or removed, but so are those of the nontarget species. The results after 10 years (Verhagen *et al.* 2001) show that nutrient removal is possible. However, in some sites a considerable amount of phosphorus is found in the C horizon as a result of heavy fertilizer inputs in the past (see Box 14.2 and Figure 14.6). Together with a continuous input of nitrogen from atmospheric deposition, this may cause problems for the future development of oligotrophic communities (Verhagen & van Diggelen 2006) through environmental limitations (Figure 14.1; Baeten *et al.* 2009). A high phosphorus level can be such a limitation. The highest plant species diversity in grasslands over north-western Europe is more related to low phosphorus levels in the soil than to the levels of potassium and nitrogen (Figure 14.7; Janssens *et al.* 1998).

After topsoil removal, vegetation studied by Verhagen *et al.* (2001) revealed a range of 0–30% similarity with target plant communities of oligotrophic grasslands and heathlands. Many target species for restoration occurred within 1 km. However, after nearly 10 years, many target species were still absent. This again indicates that dispersal is a limiting factor for restoration. When host plants are lacking, the re-establishment of target butterfly species is also limited (WallisDeVries & Ens 2010).

In a study of potential restoration techniques (Marrs *et al.* 1998) on a sandy soil that had been used for arable production, at the Minsmere bird reserve in Suffolk, United Kingdom, which was already mentioned above, a high available soil phosphorus concentration and high soil pH were identified as the most difficult soil constraints for the restoration of heathland. Surface topsoil removal and burial were both tested. Unfortunately, the site had been under agricultural production for much longer than initially thought and there had been substantial additions of lime and marl. The result was that the soil properties did not change over the upper 2 m, during the period of the study, and surface topsoil removal would clearly have been ineffective. Hence, we can conclude that the decision to carry out topsoil removal should be made with care, as its potential usefulness differs between restoration situations. This holds especially when the target site has archaeological interest.

14.5 PERSPECTIVES

Restoration of communities on oligotrophic soil can be achieved by reduction of nutrients, especially nitrogen, in the soil. However, enrichment of nitrogen by atmospheric deposition counteracts the intended reduction. As the highest numbers of plant species in grasslands in north-western Europe occur on soils very poor in phosphorus, the latter must also be reduced. Even when the appropriate abiotic conditons have been restored, the restorationist may face the problem that the target species do not re-establish without direct assistance or intervention. Knowledge of the longevity

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of seeds in the soil, and the poor dispersal capacity of many organisms, is needed in order to set realistic targets in restoration of dry grasslands, dune grasslands and heathlands. Otherwise, the need for deliberate reintroduction of species should be taken into account while recalling that spontaneous establishment of certain plant species may pose problems by outcompeting species targeted for reintroduction.

14.5.1 Nutrient reduction

As mentioned at the outset of this chapter, one of the main constraints for restoration of grassland and heathland ecosystems derive mainly from the excessively high nutrient status of the soil of abandoned agricultural fields and pastures. Modelling the effects of management and atmospheric deposition on *Calluna vulgaris* on lowland heaths in the United Kingdom revealed important interactions. More frequent cuttings of this emplematic species were required with high rainfall when atmospheric deposition was also high. These regional variations must be taken into account when defining critical loads of nitrogen in atmospheric depositition or designing management prescriptions (Britton *et al.* 2001). Long-term haymaking can remove nutrients up to the level of mesotrophic communities. Further *oligotrophication* is only likely to be achieved using sod cutting or topsoil removal. It certainly enhances the transformation of plant communities towards the targets in habitats when the requirements for other abiotic conditions are met. Grazing can only be successful to reach oligotrophic conditions when the herbivores are introduced after several years of frequent haymaking or after sod cutting or topsoil removal.

14.5.2 Dispersal and re-establishment of species

The other major constraint we have considered is related to limited seed longevity and seed dispersal abilities of target species. Solutions must therefore be sought. As mentioned above (Figure 14.2), grazers can disperse seeds through their dung (Mouissie *et al.* 2005a) or in their fur (Mouissie *et al.* 2005b). Grazed sites often include a mosaic of eutrophic and mesotrophic sites to be restored and still-existing dry grassland and heathland communities on oligotrophic soils to allow dispersal. Unfortunately, herbivores may enrich the sites by depositing their dung, while the seeds they introduce in this way seem to originate mainly from species in the sites with the highest nutrient levels, which harbour better forage quality for the herbivores (Mouissie *et al.* 2005a). Indeed, dispersal occurs, but in the wrong direction.

Even when nutrient-poor abiotic conditions are achieved, the restoration of dry grassland, dune grassland and heathland communities is limited by dispersal of target species (Bakker & Berendse 1999) and subsequent germination and establishment (Baeten *et al.* 2009). The importance of the 'moving ecological infrastructure' such as free-ranging animals (Ozinga *et al.* 2009) and humans (Strykstra *et al.* 1996) is underestimated. Experiments with the introduction of seeds or hay show that poor dispersal can be overcome. A solution could be the introduction of hay from nearby reference communities (see Chapter 8), which enhances the chance that seeds with similar genetic backgrounds are introduced from the local species pool.

When spontaneous re-establishment of species does not occur, deliberate **reintroduction** can be considered. Many authors advocate the advantages of spontaneous re-establishment as a strategy instead of actively introducing species (e.g. Prach *et al.* 2001) but there are also large seed production programmes routineously used in grassland restoration programmes (Jongepierova 2008; see also Chapter 15). Notwithstanding differences in opinion, all experts agree that there are certainly dangers involved in a widespread application of deliberate reseeding. Not only may propagule addition determine future developments and block alternative developments but it may also enhance the dispersal of nonlocal genotypes (see also Chapter 7). It depends on the breeding type of individual species whether this is a problem. Plants establishing from propagules of local or regional populations often show better performance than genotypes from elsewhere (Vander Mijnsbrugge *et al.* 2010) and using the latter may result in decreased restoration results. Because of these potential dangers, conservation agencies in some countries, such as the Netherlands and Switzerland, have formulated rather strict guidelines concerning the conditions under which species introduction is allowed (Rometsch 2009). In the Netherlands, nature conservation agencies deal with the following considerations for plants that have disappeared from the established vegetation. It should be clear from historic records that the species previously occurred in the

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region. Further, species proposed for reintroduction must be shown not to have a long-term persistent seed bank or adaptations for long-distance dispersal (>100 m) such that they could re-establish at the site spontaneously. When a species for a certain region matches the aforementioned criteria, reintroduction can be considered. Nowadays, information on the crucial life history traits can be derived from large databases (Kleyer *et al.* 2008). However, there is always the caveat that the target site should have the right abiotic conditions. Additionally, as a result of global climate change, what was present in the past at a site may have little relevance to what occurs there in future, come what may!

In an overview of species introduction projects in grasslands in central and north-western Europe, Kiehl *et al.* (2010) discuss the effects of various techniques. They deal with seeding of site-specific seed mixtures, transfer of fresh seed-containing hay, vacuum harvesting of seeds and transfer of turves or seed-containing soil. In fact, seed limitation can be overcome successfully by most of the aforementioned measures for species introduction. Old field sites with bare soil resulting from tilling or topsoil removal, or both, or abandoned soils, for example in mined areas, have proven most successful for seeding experiments, whereas species-poor grassland without soil disturbance and older arable fields with dense weed stands were less successful (Kiehl *et al.* 2010).

14.5.3 Invasive species

It is likely that some plant species from southern Europe will spread into north-western Europe as a result of global and continental **climate change**. Some of these new species may become **invasive** and outcompete the currently, and historically, **native species**. In order to understand the mechanisms playing a role in this process, knowledge must first be gained on the interaction of the exotic invasive plant species and the soil communities with which they interact. Inderjit and van der Putten (2010) suggest three kinds of interaction. First, plant–soil feedback interactions may be neutral to positive, whereas native species suffer from negative feedback effects. Second, exotic species can manipulate local soil communities by enhancing pathogen levels or disrupting communities of root symbionts, while suffering less from this than native species. Third, exotic species may produce allelochemicals toxic to native species that cannot be detoxified by local soil communities. For the future, research programmes are needed to unravel interactions between native and invasive plant species, and their interactions with native and invasive animal species and with soil communities. Otherwise, measures for counteractions against dominant invasive species remain trial and error.

14.5.4 Conflicting targets

Dry grasslands, dune grasslands and heathlands with most or at least part of the characteristic species still present and connected to similar areas can be managed by the continuation or reinstatement of practices inherent to the former low-intensity farming systems, such as mowing, sod cutting, grazing and burning. However, it is possible that more detailed knowledge of former agricultural practices should be known for successful restoration. In Europe, this implies continuation of the still-existing low-intensity farming system in countries such as Greece, Spain, Portugal, parts of France and the United Kingdom (Bignal & McCracken 1996) or eastern European countries (Veen *et al.* 2009). Here, characteristic grasslands and heathlands still exist outside nature reserves, and are exploited by farmers. In order to maintain these systems, farmers can be compensated financially for the continuation of their current practices, and intensification can be avoided. Here, agri-environment schemes can be extremely successful. In other European countries and regions with intensive agriculture, dry grasslands, dune grasslands and heathlands with nature conservation interest are often protected inside set-asides or nature reserves. Here the administration and personnel in charge of restoration and management have more or less to take over the former farming practices or provide some proxy to replace them. Agri-environment schemes outside nature reserves perform poorly (Kleijn & Sutherland 2003).

Sites targeted for restoration and conservation management should be monitored before and during the establishment of target species of plants, invertebrates – such as butterflies, grasshoppers and carabid beetles – and vertebrates, including those present in adjacent reference sites. This will help elucidate background and on-site rates of dispersal and re-establishment of different groups of organisms and suitability of target sites. Many species of invertebrates, birds, mammals

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and reptiles have quite narrow habitat preferences in terms of vegetation structure, especially with regard to the spatial configuration of bare soil, short turf, tall forbs, shrublands and forests. This means that conflicts between different restoration targets can arise. Large-scale sod cutting and haymaking are positive for a number of plant species – although not all – in view of the removal of nutrients, but negative for many animal species. The latter may require tall stands or litter accumulated for shelter, oviposition and the development of juveniles. Restoration efforts should therefore aim to develop complete communities and not just plant communities of dry grasslands and heathlands (Mortimer *et al.* 1998). Summing up, the design of mosaics including different successional stages and different scales should be part of integrated restoration and long-term management. This will require close cooperation with all stakeholders.

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Chapter 15

RESTORATION OF ARCTIC–ALPINE ECOSYSTEMS

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15.1 INTRODUCTION

Arctic–alpine ecosystems as used here include the Arctic and all alpine mountain ranges in the world. These high-latitude and high-altitude ecosystems occupy circa 10% of the Earth's surface. They vary geographically, meteorologically, geologically and historically, in terms of human land use and resource extraction during the Holocene. Despite their heterogeneity, they nevertheless have certain features in common. For example, the single most important ecological characteristic of Arctic–alpine environments is the absence of trees, due primarily to their low mean air temperature during the growth period, which does not allow tree growth. The vegetation is thus typically composed of dwarf shrubs, sedges, grasses, mosses and lichens and is commonly referred to as Arctic and alpine tundra. The term 'tundra' comes from the Kildin Sámi word tūndâr, describing the 'uplands', and 'treeless mountain tract' found in north-western Russia where this small ethnic group occurs. Worldwide, there is in fact a very high diversity of Arctic–alpine ecosystems. Several overlapping classification systems categorize comparable ecosystems into zones according to temperature conditions and vegetation types. Table 15.1 compares analogous terms for zones commonly found in the literature (Walker *et al.* 2005; Ellenberg & Leuschner 2010) among which are those used in this chapter. Plate 15.1 illustrates characteristic examples for each zone. Because of the similarities that exist in the floras and the vegetation types of tundras, not only in the Arctic but also on equatorial and midlatitude mountains, there has been a tendency to equate them and to overlook their dissimilarities (Billings 1973). Since people are now increasingly using these climatically 'last frontiers', we should be aware that differences do exist and that many regrettable errors may arise from wrongly extrapolating conclusions reached elsewhere.

15.1.1 Specific Arctic characteristics

The bioclimatic definition of the Arctic does not correspond with the geographic zone delimited by the Arctic Circle (66.5° N). One reason for this is that cold waters in ocean currents flowing southward from the Arctic bring down the ambient temperatures in Greenland and the eastern Canadian Arctic, whereas in Europe, the northward-flowing Gulf Stream warms the northernmost landmasses. Thus, at the extremes, polar bears and tundra are found at and beyond 51° N in eastern Canada, whereas agriculture is practised in Norway as far north as 69° N. Consequently, for Arctic regions there is no general latitudinal temperature gradient comparable to the altitudinal gradient generally found in alpine regions (see below). In contrast to alpine environments, mean temperatures during the warmest month never exceed 10°C, with the exception of the subarctic zone (see also Figure 15.1).

In the Arctic and subarctic regions, temperature regime is a key factor for all above-ground and below-ground biological processes. Due to temperature-inhibited nutrient cycling within Arctic soils, plant growth is usually limited by nitrogen and phosphorous availability (e.g. Shaver & Chapin 1980). Permafrost is also a common feature. However, the generally low summer temperature of Arctic environments is partly compensated by favourable light conditions due to the 'midnight sun', which refers to the period where the sun permanently stays above the horizon and thus may provide light for plant growth for 24 hours a day. At 70° N, the midnight sun shines for about 2 months each year, while at 80°N it lasts for approximately 4

Table 15.1 Comparison of analogous terms for zoning of Arctic and alpine environments according to Walker *et al.* (2005) and literature within Ellenberg and Leuschner (2010).

Zones		Commonly used synonyms and typical vegetation forms
Arctic	**Alpine**	
High Arctic	Nivale	Polar desert, fragmented patches of cryptogams, perennial grasses and herbs
Middle Arctic	Alpine	Arctic and alpine tundra, dwarf shrubs and grasslands
Low Arctic	Low alpine	Arctic and alpine tundra with possible single trees, grasslands and dwarf shrub heaths
Subarctic	Subalpine	Taiga, patches of forest, single trees, dwarf shrub heaths

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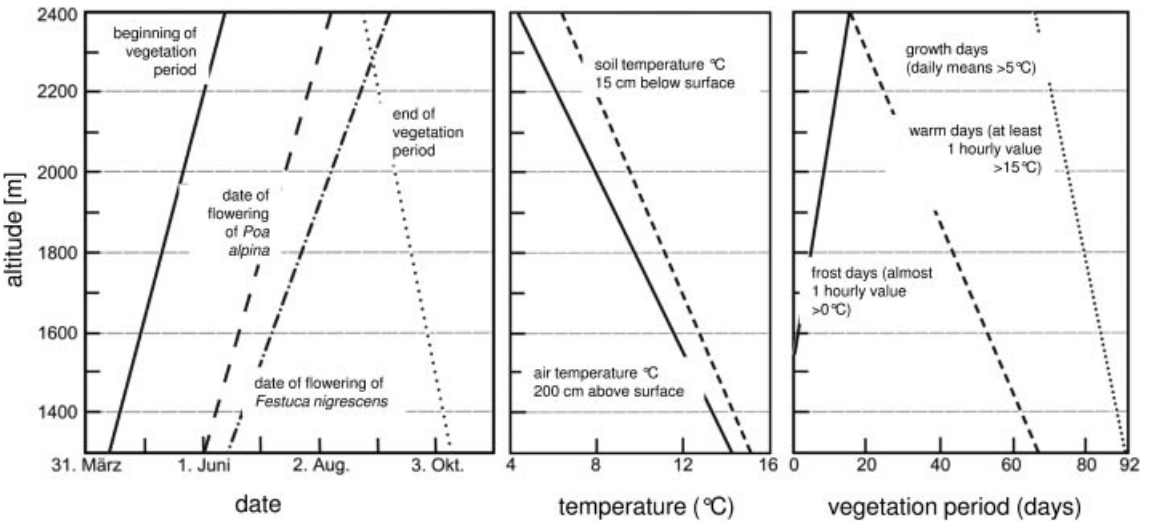


Figure 15.1 Average changes of important phenological and climatic parameters according to altitude. (Modified from Krautzer *et al.* 2003.)

months. During winter, Arctic regions have a comparably long dark period, in which the sun remains permanently below the horizon. Accordingly, the Arctic has not only a distinct temperature climate but also a markedly seasonally light climate. Mountains also are frequent in the Arctic regions, which creates altitudinal climatic gradients similar to those in alpine regions. As a result, Arctic environments are often characterized by a fine-grained mosaic of local altitudinal and regional latitudinal climatic gradients.

15.1.2 Specific alpine characteristics

Plants at high altitudes are often subject to frequent and often rough changes of climatic factors. The transition from one season to the next often takes place very quickly. With increasing altitude, the vegetation period is around 1 week shorter per 100 m of rising altitude (Reisigl & Keller 1994). The differentiation of the macroclimate from the microclimate, dependent on altitude and location is important. The most important differences depending on altitude can be briefly characterized by the factors described below (see also Figure 15.1).

Air temperature generally decreases by 0.6°C per 100 m of altitude. Frost may occur at all times of the year in high altitudes; at the beginning and end of the vegetation period, an interchanging frost climate generally predominates (Arenson 2002). The relatively low soil temperatures in alpine environments strongly reduce the rate of soil microbiological activity and thus also nutrient cycling. Decomposition of dead organic mass, and thus the provision of basic mineral nutrition to plants, is thereby inhibited. The subterranean habitat is thus limited – contrary to the warmer, lower zones – to the most strongly warmed, humus-rich and generally acidic and intensively rooted upper layers of the ground.

Precipitation generally increases with altitude, while evaporation rate also rises. Critical situations in the water balance of plants, however, are rare, other than in special locations like those exposed to strong radiation, high temperature or strong winds. In general, wind speed and frequency also increase with altitude. Wind influences alpine plant growth not only directly but also indirectly due to its impact on snow distribution pattern during winter. Snow depth may have a significant impact on, among other things, the length of the vegetation growth period, soil temperature and soil humidity. Various inclinations of the sun's radiation create differing degrees of heat. The ecological significance of differences between a northern and southern exposition generally increases with altitude.

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The influence of microclimate, however, can surpass that of the macroclimate and altitude (Ellenberg & Leuschner 2010).

According to overall prevailing climatic conditions (Veit 2002), alpine vegetation may be divided into commonly corresponding altitudinal specific zones (see Table 15.1.). Altitudinal changes of the above-mentioned factors lead to a vertical sequence in various climatic areas (Ozenda 1988), or life zones (Holdridge 1947), and a corresponding turn-over of biota. The altitudinal zones are separated by borders that are fairly easy to recognize: the subalpine zone is delimited by the upper tree line, whereas the alpine zone is treeless, and the nival zone begins above the climatic snow line. The subnival zone still may contain scattered vegetated areas.

15.1.3 Exploitation and restoration

Many of the world's Arctic–alpine ecosystems are the result of about 10 000–15 000 years of natural **succession** since the end of the last ice age. When predicting the result of human impact on tundra ecosystems, caution is required (Billings 1973). Increased needs for resources lead to steadily increasing exploitation and thus **disturbance** of tundras, many of which are still relatively pristine. Increased exploitation for the demands of winter tourism leads to increased **degradation** up to the subnival zone of alpine areas, where **revegetation** may take decades. However, human interferences may severely damage these systems within seconds. Future use and exploitation of Arctic–alpine ecosystems cannot be totally avoided but any necessary disturbance should be carried out in ways to minimize undesirable environmental impacts and consequences. Thus, ecological restoration often starts prior to the first disturbance.

In principal the main goal of every restoration effort in Arctic and alpine environments is the establishment of a sufficient vegetation cover to prevent erosion. Due to the vital importance of sufficient plant adaptation to growth limiting abiotic factors, we here particularly emphasize the necessity to use site-specific seed and plant material to obtain this goal. In this regard, note that within the restoration ecology community – and the conservation biology community as well – there is often a Babel-like confusion in respect to the term 'site-specific', as well as the related terms 'near-natural', 'seminatural', 'local', 'native' and 'regional'. Here we will use the term 'site-specific' according to the *Rule Book for Ecological Restoration* of the Austrian Grassland Society (Österreichische Arbeitsgemeinschaft für Grünland (ÖAG) 2000): (1) a plant species is considered site-specific when it occurs naturally under given site conditions; (2) a plant community is considered site-specific (a) when it is generally and permanently self-supporting or self-stabilizing following extensive use (or non-use), and (b) when the production of agricultural or forestry products is not its main function; and (3) vegetation established by humans is called site-specific if the ecological amplitudes of species applied match the environmental site factors where restoration takes place and all plant materials used within the restoration process originate directly from the project area or its vicinity, or are obtained from ecologically comparable sites within the natural area, respecting knowledge of local ecological types or subspecies.

In the following we first indicate the major threats and disturbances occurring in Arctic–alpine ecosystems, within an historic perspective, in order to identify priority areas for ecological restoration (section 15.2). Then, in section 15.3, we summarize materials and methods for the ecological restoration and revegetation of Arctic and alpine ecosystems, with special regard to the extreme site conditions generally found there. It is important to note that we do not offer 'recipes' for successful restoration, but rather a set of possible tools, with which positive results have been obtained in several tundra restoration projects to date. Finally, we reflect on future perspectives.

15.2 THREATS AND DISTURBANCES

In Europe, over the last 150 years, agrarian utilization in high altitude zones and other less productive areas has clearly receded, which has in turn led to a corresponding expansion of forested areas (Cernusca *et al.* 1996). As a result, the exploitation of alpine meadows has intensified in some areas or else, in other areas, is completely abandoned. In the subalpine zone, during the transition process from the intensively cultivated alpine meadow areas back to the natural forest vegetation, a creeping destabilization of the ecological systems of high alpine-meadow regions can arise. Surface **runoff** from summertime precipitation increases, and unless corrected immediately **erosion** gullies – such as those that appear in cultivated alpine-meadows

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– can lead to extensive landslides and the formation of shell-shaped erosion-scars (Stahr 1996; Tasser *et al.* 2003). Up to the time at which the natural vegetation is re-established, there is a clear increase of erosion processes, which continuously require more restoration and preventative measures (Gray & Sotir 1996).

In addition to agricultural use, summer and winter tourism in the last few decades has led to extensive opening of alpine locations for recreational hiking and skiing. There are already more than 13 000 ski lifts, cable cars and other transport facilities throughout the European Alps, most of which are used primarily for tourism. Forty thousand ski runs with a total length of 120 000 km have been built during recent decades, of which one third are located in subalpine and alpine zones (Krautzer & Klug 2009). Gradually rising winter temperatures oblige ski resort owners to invest in artificial snow equipment. Based on the most recent calculations, ski runs in Austria alone now cover more than 23 000 ha, of which more than 8000 ha are kept white and 'skiable' in winter with artificial snow (Commission Internationale pour La Protection des Alpes (CIPRA) 2004). All over the European mountain areas, thousands of hectares are bulldozed annually to keep the skiing areas attractive to skiers. Necessary measures for the protection of the facilities (torrent and avalanche barriers) also require large areas each year.

In Arctic areas, awareness of disturbances is a much more recent phenomenon. Pioneering attempts for restoration in North America started only in the early 1970s in connection to the construction of the Trans-Alaskan pipeline (McKendrick 2000), which was built between 1974 and 1977 to exploit the North Slope oil fields. Hand in hand with the increasing resource exploitation of the Arctic (mining and oil and gas extraction), infrastructural interventions like road and railway construction, pipelines, power lines and legal requirements to 'restore' open cast mining areas are the main reasons for interventions.

15.3 RESTORATION TARGETS AND LIMITATIONS

Most Arctic–alpine vegetation types are the result of a long-lasting evolution of plant species and communities operating in relatively intact ecosystems. In most cases, human interferences in Arctic–alpine areas lead to drastic disturbance. Successful restoration and rehabilitation measures therefore demand a clear definition of restoration targets and awareness of limiting factors.

15.3.1 Protection against erosion

Dynamic degradation processes such as soil erosion may often exceed damaging effects of the initial anthropogenic disturbances (Vasil'evskaya *et al.* 2006). **Erosion**, with all of its negative effects, such as loss of vital topsoil, is therefore one of the main challenges in the restoration work of Arctic–alpine environments. Average slope gradients of 30–45% in the area of ski runs, and often steeper (i.e. in the area of natural erosion zones and avalanche barriers), make adequate erosion protection measures and regulation of surface **runoff** a prerequisite for successful restoration. Results of several assessments of **revegetation** indicate that only sufficient vegetation cover exceeding 70–80% stabilizes the topsoil and reduces soil erosion to an acceptable degree (Markart *et al.* 1997; Tasser *et al.* 1999; Peratoner 2003). The achievement of such a vegetation cover within a relatively short time period is crucial. Therefore, an adequate combination of application techniques and adapted seed mixtures, or vegetative propagation material, should be the main primary target for restoration. Under normal conditions, minimum required cover can be achieved in the second season of vegetative growth, but to achieve this requires using techniques that also provide sufficient surface protection during the first 2 vegetation years (see also Figure 15.2). Especially the application of a thin layer of mulch is a common and successful technique (section 15.4.3).

15.3.2 Maintenance of biodiversity

There has been a dramatic change in the attitude of people to their environments in recent years. The maintenance of **biodiversity** has become a special concern of agrarian and environmental policy. Ecological restoration projects with the target of creating a site specific vegetation cover have obtained increased importance in recent years. During the last decade, evidence has accumulated concerning the crucial importance of biological diversity, including genetic diversity at the intraspecific level, for **ecosystem**

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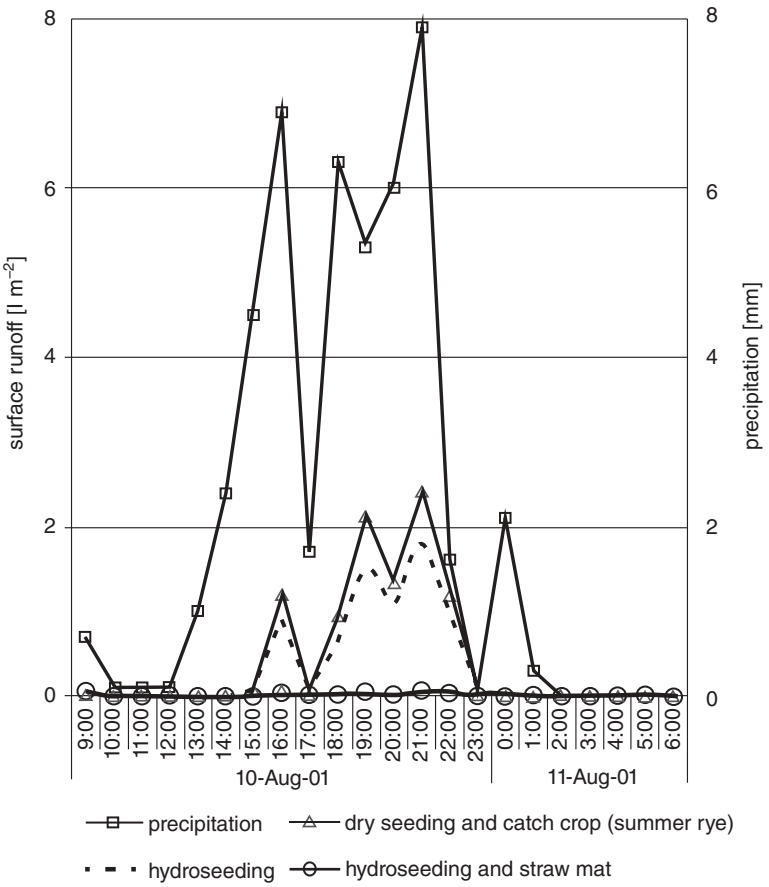


Figure 15.2 Comparative rates of surface runoff under different restoration treatments during a two-day rainfall event; only the organic layer prevents from surface runoff and guarantees sufficient protection from erosion. (Modified from Krautzer *et al.* 2003.)

functioning. Consequently, the maintenance of biodiversity has become a special concern of agrarian and environmental policy (European Commission (EC) 1992; Andersen *et al.* 2003; SCBD 2006). The increasing awareness of the importance of biodiversity is also reflected in the development of material, procedures and treatments used in restoration projects and programmes in Arctic and alpine areas. In general, the range of well-established restoration techniques and knowledge for alpine areas exceeds those available for Arctic areas. However, one has to respect that restoration in Arctic–alpine environments always is subject to biophysical and climatic limits to plant growth.

15.3.3 Key limiting factors

With increasing altitude and latitude, restoration following anthropogenic disturbances requires particular focus on key limiting ecological factors of plant species. Irrespective of the type of disturbances, only a combination of site-specific plant material together with thoroughly chosen and applied restoration techniques can lead to long-lasting restoration success. A major requirement for all plant material used in restoration programmes in Arctic–alpine environments is their ability to reproduce under prevailing site conditions. The altitudinal limit for commercially available site-specific seeds for European alpine environments is

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about 2300–2500 m (ÖAG 2000; Krautzer *et al.* 2004a). Thus, restoration efforts above this altitudinal belt can generally not be accomplished with plant material found in the horticultural trade. Consequently, a good understanding of target species' reproductive behaviour and vegetative growth patterns and the dynamics of initial phases of succession, are essential for development of appropriate restoration methods (Urbanska 1997; Peratoner 2006).

Prevailing environmental conditions within high Arctic and high alpine zones are usually so harsh for plant growth that restoration even with site-specific plant material is nearby impossible. As is the case for Arctic bogs and alpine *Carex curvula* meadows, few vegetation types in these regions can be restored within the period of one human life span and their disturbance should therefore – whenever possible – be avoided. Restoration with site-specific seed and plant material results not necessarily immediately in the targeted vegetation type. Therefore, it should at least promote an ecosystem state from which the planned vegetation type can develop through natural succession within 10–20 years.

Taking account of the targets and limitations of restoration in Arctic–alpine environments and incorporating the knowledge developed during the last decades, we can make some recommendations on how to achieve sustained success.

15.4 RESTORATION APPROACHES

Globally there is a wide range of different vegetation types in the varying vegetation zones, and one has to be careful when attempting to transfer or adapt materials and methods from, for example, middle Arctic areas from Alaska to Norway, or from European alpine areas to South American alpine areas. Restoration with plant material can be successful only within the ecological amplitude of the selected species. The restoration techniques applied have to balance the site-specific plant growth limiting key factors with respect to the selected plant material. At most Arctic or alpine locations, there is no single limiting key factor but rather a combination of several (Figure 15.3). The application of site-specific seed or plant material can be successful only when the appropriate period for application is respected (Figure 15.4). The following presents a short overview of the most commonly used restoration techniques within Arctic–alpine environments. In addition

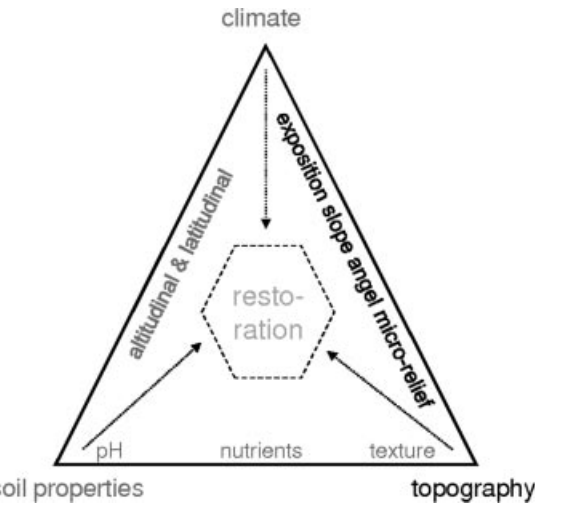


Figure 15.3 Essential key factors for plant establishment and growth within Arctic–alpine environments.

to the use of feasible plant material, improvement of (1) substrate stability, (2) physical and chemical soil conditions for plant establishment and growth and (3) site- specific climatic conditions are essential restoration measures.

15.4.1 Abiotic key conditions

It is essential in restoration planning to meet the required abiotic conditions of a habitat (e.g. nutrient-poor, dry or damp). Particular requirements for the restoration in Arctic–alpine environments are given below.

Substrate stabilization

Substrate stabilization is a particular requirement in restoration of Arctic–alpine ecosystems with (1) a high 'relief energy' (i.e. difference of minimum altitude from the maximum altitude in a sampled area), (2) vulnerability to wind erosion and (3) thawing permafrost. Commonly known methods for substrate stabilization (e.g. Zeh 2007) are generally applicable with the exception of sites with thawing permafrost. When concerning geotextiles, however, the use of nondegradable synthetic fibres and wire netting should be, where possible, avoided. Under given climatic conditions, galvanized-iron netting and synthetic netting degraded

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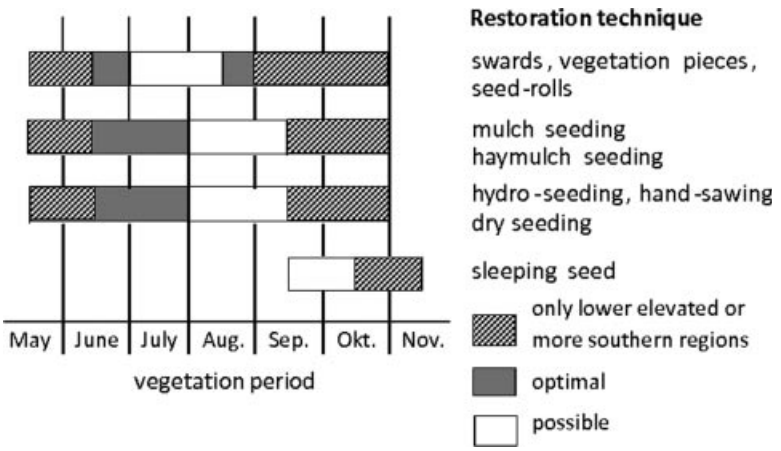


Figure 15.4 Preferential seasonally periods for application of selected restoration techniques within Arctic and alpine environments.

extremely slowly and life spans exceeding 30 years are no rarity. Even biodegradation of organically based textiles like coconut fibre can take decades and may thus act as a hinder for revegetation (Uhlig 2008). If artificial material (e.g. geotextiles) is used for erosion control, it generally should be degradable over a couple of years. Furthermore, organic geotextiles such as coconut or hemp fibre fabrics are naturally poor in plant nutrients and thus do not improve soil chemical properties. Therefore, it has been suggested to develop erosion control mats constructed from 'site-specific organic matter' (Uhlig 2006). The use of textiles with improved biodegradability could increase plant nutrient release and soil organic matter enrichment, and thus promote soil development. Based on our experience we emphasize that many types of erosion control material possess a relative high volume. Costs for transport to remote sites can be reduced by using locally available material such as peat, shrubs or stranded algae in coastal Arctic areas. Contrary to widespread belief, the use of seed mixtures consisting of rapid-growing species has no positive influence on the short-term prevention of erosion (Krautzer *et al.* 2010; see also section 15.4.2).

Improving soil conditions

Effort invested in improving soil conditions prior to planting or sowing is inversely correlated to the quality of the growing conditions for newly introduced plants or seeds (e.g. Johnson & van Cleve 1976). Leaving damaged sites with a soil that resembles the natural landscape in topography, hydrology and other physical and chemical properties is the most important practice for tundra restoration (Forbes & Jefferies 1999). The extent of the changes in the chemical and physical characteristics of substrata caused by human activities often imposes severe limitations on the establishment of plants (Pyvell & Putwain 1996). A problem-resisting solution in restoration of a disturbed tundra site is how to combine revegetation with the re-establishment of a stable thermal regime (e.g. Johnson & Cleve 1976; McKendrick 1997). As mentioned, due to temperature-inhibited nutrient cycling, tundra soils are nutrient poor, specifically in nitrogen and phosphorus (e.g. McKendrick 1991). Nutrients stocked in plant biomass or in the superficial layers of the soil are often exported from the ecosystem during or shortly after the disturbances (Deshaies *et al.* 2009). Beside, as the site for microbial activity and nutrient cycling, the organic layer plays a vital role that depends on site-specific thermal and hydrological properties. Thus, any disturbance of the organic layer can cause a dramatic decline in soil fertility. Therefore, it is important to save all the topsoil displaced and disturbed in the process of building and construction activities for later use in restoration projects. However, removal, storage and reapplication of topsoil should be carefully planned. For example, the drying out of topsoil during storage should be avoided or minimized to preserve substrate

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quality (Chapin & Chapin 1980). An additional benefit to preserving all available topsoil is its possible content of propagules and vital roots fractions. Even after a partial mixing of the topsoil with mineral layers, which are devoid of a **seed bank**, seed densities can be considerable (Diemer & Prock 1993; Peratoner 2003). Whenever possible, topsoil should therefore be stored and returned in association with the removed vegetation type. Where site-specific topsoil from the site to be restored or from an appropriate donor site is not available, an organic slow-release fertilizer, such as well-rotted farmyard manure or certified biological compost, should be used. Inorganic mineral fertilizers with slow but long-term release of nutrients can also be used. A single, moderate dose of fertilizer is generally sufficient to achieve plant establishment (Krautzer *et al.* 2006).

Fertilization with nitrogen and phosphorous will generally promote plant growth; however, for many Arctic plants the specific amounts required are not known. Deshaies *et al.* (2009) invested the effects of fertilization on the performance of three indigenous plant species from subarctic Québec. They found that mineral fertilizer in principal could promote cover of *Lathyrus japonicas* and *Trisetum spicatum* under field conditions. However, under greenhouse conditions effects of mineral fertilizer were negative on both species, particularly at elevated levels. Results suggested that either species performs better when grown in nutritionally poor substrate, at least under controlled conditions (Deshaies *et al.* 2009). Furthermore, several studies show that fertilizer cannot promote growth of plants that are not adapted to cold soil (McCown 1973). Fertilization can in fact favour growth of introduced, nitrophilous species, at the expense of site-specific species that were targeting at the outset. Over-fertilization and fertilization in the wrong season often increase plant susceptibility to pathogens such as fungi (Johnson & van Cleve 1976; McKendrick & Mitchell 1978) and retard winter hardening. Over-fertilization may also cause changes in vegetation composition to the advantage of 'weedy' species or cause an increase in moss cover (Klokk & Rønning 1987). However, phosphorus fertilizer promotes flowering and consequently seed development. It is important to achieve a balanced nutritional relationship (Heer & Körner 2002). Insufficient vegetation cover in the second year of revegetation may demand further fertilization measures (Holaus & Partl 1996). Supplementary fertilizer applications can effectively be combined with over-seeding of a site-specific seed mixture.

15.4.2 Exploitation of site-specific plant material

Ecological restoration requires much more than revegetation. It implies the recognition of a site-specific **reference system**. In general, site-specific vegetation is mainly composed of site-specific species and does not require any management measures, with the exception of different grassland communities that depend on extensive management measures such as mowing, haymaking or grazing. The advantage of using site-specific species is that they are adapted to the site-specific ecological conditions and thus can grow and reproduce without further support. It is important to notice again that even if a species is site-specific, in the broad sense that it grows naturally in the geographical region, it might still not be adapted to the specific conditions of the restoration site itself (e.g. different altitude and pH).

Seeds

Seeding is in general the most commonly used restoration method in Arctic–alpine environments. Conventional, commercially available seed mixtures mainly comprise fast-growing species originally bred for grasslands used for livestock grazing, ornamental purposes, or sport fields. Plant species within such mixtures are commonly adapted to warmer locations with a prolonged growing season and are thus generally not suitable for restoration of ecosystems in Arctic–alpine environments (Urbanska 1986). Introduced plant species from more temperate regions are not adapted to Arctic light conditions and thus will not develop sufficient winter hardiness (e.g. Klebesadel *et al.* 1964). Florineth (1992) indicates that, with the exception of *Festuca rubra*, the common commercially bred grassland species are not persistent under alpine climatic and soil conditions. Light climate, a combination of day length and light quality, is of vital importance for winter acclimatization of Arctic plants.

Introduced species that are bred to maximize biomass production, run counter to restoration goals in Arctic–alpine environments. Such 'commercial' seed mixtures are for example often used in **revegetation** of ski slopes. Beside the necessity for regular cutting, grazing or removal of accumulating biomass, the high nutritional needs of these species can require long-term, costly fertilization measures. Without such supporting measures, these species may not survive when introduced

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to a restoration site (Krautzer *et al.* 2010). Long-term supplementary management of restoration efforts is costly and problematic. In some countries, there is also a conflict between laws related to seed. Use of commercial non-site-specific seed material, as well as the use of cover crop seeds, can also have negative impact on spontaneous **succession** of plant communities with native species. Plant nutrients will be bound up by these plants and only be released slowly to the soil. At the same time, surface litter can prevent site-specific seeds from germinating (Cargill & Chapin 1987; Densmore & Holmes 1987). In subarctic, low-Arctic, subalpine and alpine zones, restoration using cover seeds is only recommended where it is needed for erosion control (Partl 2006). At other sites, revegetation will occur faster without use of cover seeds. Furthermore, effects of sowing new species or ecotypes into local plant communities are often unpredictable and may even displace the extant vegetation or lead to undesirable hybridization with locally adapted ecotypes (Sackville Hamilton 2001; Malaval *et al.* 2009; Vander Mijnsbrugge *et al.* 2010).

In contrast, plants arising from site-specific seeds generate relatively little standing biomass but can rapidly develop extensive, self-maintaining stands with high resistance to subsequent uses for tourism and agriculture (Krautzer *et al.* 1993; Peratoner 1993). When site-specific seed mixtures are used, sowing quantities can be drastically reduced from 200–500 kg ha^{-1}, such as are commonly used for conventional seed mixtures, to 80–160 kg ha^{-1} (Holaus 1997). Unfortunately, as mentioned already, commercially produced site-specific seed material may be difficult to obtain for most of the Arctic–alpine regions, though recently there have been significant efforts in several countries to close this gap (e.g. Rausch & Kershaw 2007; NTW seed project and ECONODA – see the appendix at the end of this chapter). Alternative ways of obtaining site-specific seed material for restoration purposes are the use of vegetative cuttings from the nearby areas, meadow threshings and the hay-flower seeding method (Kiehl *et al.* 2010), all of which will be described in the 'Sources for site-specific seeds' subsection.

Sources for site-specific seeds

The availability of a donor area, which provides ripe seed material for direct use in restoration or for the further multiplication of suitable seed material, is definitely of importance. One should avoid the use of seed material from more distant biogeographical areas.

A widely used method is the mowing of suitable donor sites at the time when most of the desired species are at an optimum stage of seed maturity (June–August). To avoid excessive seed losses, the material is cut preferably early in the morning when it is moist with dew and then immediately taken to the restoration area (receptor site) and spread there. Another possibility is to dry the mowed material and to use it later for restoration. Nevertheless, this method requires increased manipulation and therefore higher costs. In addition, a large part of the seed material may be lost.

The method of meadow threshing (Kirmer & Tischew 2006; Jongepierova *et al.* 2007) collects site-specific seeds from suitable donor sites. To obtain the greatest possible number of mature seeds from the preferred species particular attention has to be paid to harvesting time. Seed mixtures with highest species diversity are generally achieved by consecutive harvesting of donor sites according to species-specific seed maturation rates and schedules. In the Alps, seed yields are usually between 50 and 200 kg ha^{-1}. The relationship of donor area to restoration area thus varies from approximately 1:1 to 1:4. If application of threshed seed material is not possible immediately after harvest, it must be dried and stored in a dry location.

The hay-flower seeding method uses seed-rich remains from threshing floors in hay barns, which often keeps sufficient seed quantities and qualities (ÖAG 2000). In general, seed material should be regained from hay no more than 2 years old. To acquire an appropriately high amount of pure seeds, sieving is helpful. Hay flowers are recommended to be sown in quantities of 0.5–2.0 kg m^{-2} and with their stalks to a maximum depth of 2 cm. To minimize loss through scattering by wind, seeding should only take place on wet soil, or if prompt watering of seeded areas is feasible. If germination capacity of available hay flowers is deficient, site-specific seeds can be purchased and sown as a supplement.

A good method that is currently practised in several countries is the nursery or large-area production of seed of suitable species with the aid of agricultural techniques. Above all, species used often and in large amounts can be produced at comparatively reasonable costs and implemented on appropriately large project areas. This method has been used successfully in the United States, Austria and Switzerland for restoration projects above the tree line (Richards *et al.* 1997;

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Krautzer & Hacker 2006); similar approaches are now being tested in the French Pyrenees (Malaval 2006) and in Iceland (Aradottir & Johannsson 2006).

One common obstacle to widespread acceptance of relatively high-priced, propagated seed material is related to lack of transparency with respect of the area of origin of the material used. To be able to give consumers confidence regarding seed material offered for sale, several countries are working on the implementation of certification procedures for the producers. In this way, the origin or provenance of seed, as well its purity and viability are guaranteed to meet predetermined standards.

Site-specific plant material

As for seed collection, site-specific species with generally high vegetative reproduction potential should be used (Grabherr & Hohengartner 1989). Selected plant material can be cultivated in pots until they have a well-developed rootstock and are then planted into restoration sites. The potted plants can either be grown from vegetatively reproduced mother plants or locally harvested vegetative or seed material. Given an appropriate selection of species, this method can give excellent results, even at sites with extremely harsh climatic conditions.

The 'turf transfer method' transfers partial soil–plant segments from donor to restoration sites. Depending on whether turfs are obtained manually or mechanically, unit size usually varies between 0.15 to 0.50 m^2. To avoid drying, stifling and rotting, turfs should not be stored in pits or stacked on pallets in layers more than 100 cm wide and 60 cm high. Moreover, storage period should not exceed a maximum of 2–3 weeks in summer. Wherever possible, the transplanting of turfs should take place as early as possible at the beginning of the vegetation period or after the start of the autumn vegetation pause, thus just after the melting of snow or directly before the onset of winter. Vegetation turf segments are especially suitable for the rapid site-specific restoration of disturbed sites. Accessible soil vegetation segments are removed before disturbance, stored and returned to the site after levelling. On steep slopes it is recommended to stabilize grass turfs with, for example, wooden stakes or nails. With proper planning, grass turfs from building and construction sites can be directly transferred to restoration sites without intermediate storage (Krautzer *et al*. 2006).

Another possibility is the use of shoots or rosettes from mechanically separated turf segments that are randomly distributed onto the restoration site. At sites accessible to vehicles, distribution can be performed mechanically. In this way, larger areas can be restored than by using the labour-intensive transplanting of turf segments. However, the resulting vegetation cover is usually sparser and as a result, the risk of erosion will be higher. In the eastern Alps, a new approach was developed with the production of ready-made sward (sod rolls) that is well known in conventional horticulture. Site-specific plant species based sod rolls are cultivated for about 12 months, which ensures satisfactory plant development (Gottschlich 2008). According to needs and restoration aims, various plant species mixes can be produced on demand. Sod rolls are then harvested and transported to the restoration site. The sod roll method has the advantage of providing a complete topsoil vegetation cover. However, this method is costly and, as a result, mostly used for **interventions** in small areas and in extremely difficult locations. Turf segments, sod clippings, grass swards and seeds are of course all living materials, and careful handling and expert attention are therefore indispensable.

In practice, a combination of two or more of the above-listed methods is often used, for example the turf transfer method with application of seeds (Wittmann & Rücker 1995). Here, vegetation swards (or sod rolls) are initially arranged in a scattered pattern, for example like a chess board. Subsequently, site-specific seeds are sown into the intervening areas (Figure 15.5). Germinating seeds reduce erosion between vegetation swards, while sward-based plants are allowed to invade intermediate areas. In this way, plant species not available as seeds are able to establish. Combining erosion control mats and seeding is a commonly used method for restoring steep slopes (>30%) where there is a high risk of erosion. The use of combined methods also serves to reduce negative impacts on donor sites and to promote the rapid establishment of a diverse vegetation cover.

15.4.3. Improving site conditions with mulch

Depending on prevailing environmental conditions, the successful re-establishment of plants in disturbed sites is commonly supplemented by a combination of seeding and microclimate improving measures. Such

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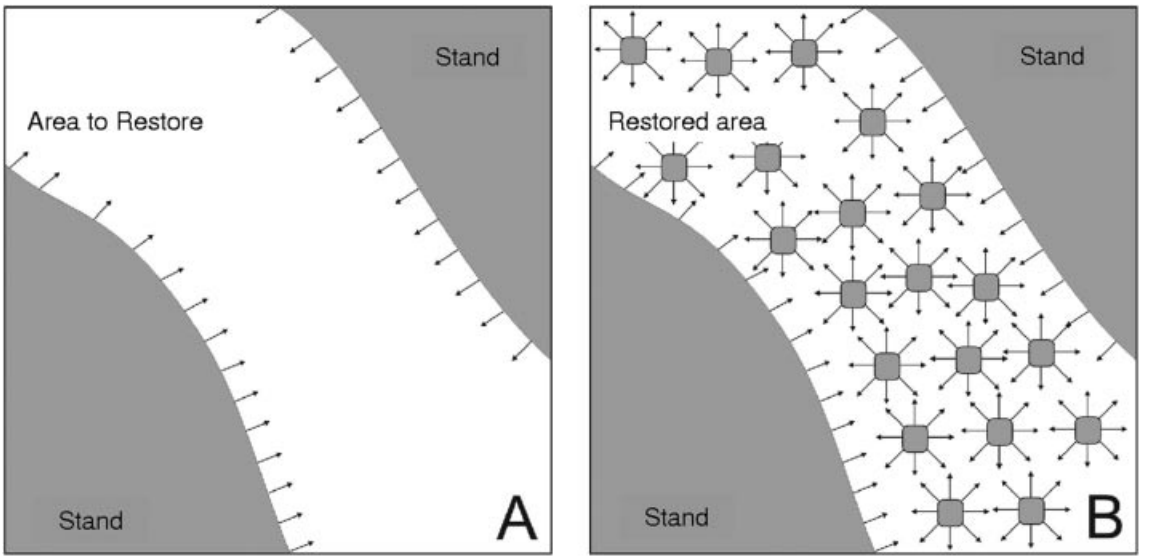


Figure 15.5 The schematic depiction of the principle of the seed–sod combination process: through the grid-like vegetation parts covered – and despite relatively short distribution distances of alpine vegetation – the entire area can be colonized. (From Wittmann and Rücker 2006.)

measures generally consist of applying a thin layer of organic material to improve soil surface microclimatic conditions. This practice, known as *mulching*, is common in gardening in hot, dry areas. It is highly suitable in Arctic–alpine environments where an organic-based soil surface protector can be applied to improve and accelerate restoration results. Mulching reduces erosion, helps retain moisture, and provides nutrients and organic matter that contribute to soil development as it decays. This in turn promotes seed germination and enhanced plant growth. The most commonly used mulch materials in Arctic–alpine restoration projects are hay and straw or fresh-cut plant clippings (e.g. Claridge & Mirza 1981). To avoid the spreading of non-site-specific seeds from mulch, only hay or clippings from the second or third cut should be used. If an appropriate donor site is available, hay-mulch material containing mature seeds can also be useful.

For optimum seed germination and plant development, the applied mulch layer should not be so thick that it blocks the penetration of sunlight. Experience shows that approximately 300–500 g of dry material per square metre is a good average to aim for. Due to thinner stalks and firmer structure, hay-mulch generally yields a more stable cover than straw-mulch. The mulch seeding method is generally used on relatively wind protected, gently sloping sites. At steeper locations (slopes >15–20°), the well-known *black-green seeding method* can be applied. Here the mulch layer is stabilized by a bitumen emulsion sprayed on top. The bitumen normally decomposes within a few months. However, this technique is in most countries not allowed to be used in watersheds providing drinking water; there, light, organic gluten can be used as a substitute for bitumen (ÖAG 2000).

The addition of foreign soil organic substrates (e.g. peat moss from nearby wetlands) can also improve plant establishment (Rausch & Kershaw 2007). However, one should ensure that physical and chemical properties of the supplemented organic matter, for example the pH (Deshaies *et al.* 2009), are complementary to the physiological requirements of the plants used.

15.4.4 Long-term restoration efforts

A certain degree of aftercare is usually required to insure the long-term success of restoration program-

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mes. For example, mowing, additional seeding, carefully dosed post-fertilization or grazing enclosures may all be required. These measures sometimes are essential elements of restoration success.

It is not uncommon that extreme weather events such as prolonged droughts or unusually harsh winters hinder or delay planned restoration activities. Indeed, even at the best of times, most restoration sites in Arctic–alpine environments are difficult to access. Long-term management of a site under restoration is therefore usually time consuming and costly. Any set of methods and materials that minimizes long-term management is therefore to be favoured. Research trials in the European Alps have shown that restoration with site-specific seeds significantly reduces the need for management in the long run (Krautzer *et al.* 2004b; Graiss *et al.* 2005). Despite higher initial costs for site-specific seed material, the overall costs compared to the use of commercial seed mixtures decline due to a reduction of aftercare costs for reseeding, fertilization and frequent cutting (Krautzer *et al.* 2006). The establishment of site-specific plants is also important for creating forage for a range of animals, such as moose (McKendrick 1999). However, also unwanted grazing cattle or wild game seem to be attracted by restored areas and may cause significant site disturbance and soil erosion. Thus, it is recommended that until the establishment of sufficient vegetation cover density, at least over the first two growing seasons, grazing or trampling should be prevented (Klug *et al.* 2002), if necessary or possible by the use of temporary fencing. However, in many Arctic–alpine areas, fencing is not practical and the selection of restoration materials and methods should respect this limitation.

15.5 PERSPECTIVES

Arctic–alpine environments are under increasing pressure due to increasing human exploitation, not to mention climate change. Additionally, the number of methods that are successfully applicable decline with increasing latitude and altitude (Krautzer *et al.* 2006). Even with the most sophisticated materials and methods, it is not possible to restore every vegetation type within a human life span. It is therefore advised to avoid disturbances in the high Arctic and alpine zones wherever possible.

15.5.1 Evaluation of success

Ecological restoration is still in its early stages in the greater part of the alpine ecosystems and the circumpolar North. Several of the approved material and methods from lower latitudes and altitudes have failed when applied in the more difficult environments we have discussed in this chapter. At various sites in Arctic–alpine environments, successful restoration efforts may require many years or even decades (Streever *et al.* 2003; Rydgren *et al.* 2011). A single late-spring frost event, unexpected lack of snow cover or prolonged summer drought may turn apparent success into failure. Thus, one can only learn from mistakes and gauge success if methods and measures are evaluated over a sufficiently long period of time of at least 20 years.

In general, it is neither ecologically or economically feasible, nor even necessary, to fully restore a disturbed site to its 'original', pre-disturbance state. In many circumstances, it will be an acceptable solution to stabilize the site and thus avoid self-accelerating erosion processes, and consequently create beneficial conditions for site-specific succession. The establishment of an adequate vegetation cover (as mentioned in this chapter, 70–80%) has generally proved to be sufficient to achieve protection from erosion. However, in many high-alpine and Arctic areas, vegetation cover may not naturally attain or exceed such a high rate of cover. Consequently, vegetation cover targets may differ accordingly; for the North Slope of Alaska, the cover performance standards varied for example between 10% cover within 10 years and 60% cover in 3 years (Streever *et al.* 2003). Thus, monitoring and evaluation should match the individual vegetation type found naturally at the restoration site.

Although establishing plant cover as quickly as possible is an important goal of most high-altitude restoration projects, natural succession may subsequently lead to vegetation similar to the surroundings (McKendrick *et al.* 1997). Once again, the long-term view is critical to success.

15.5.2 Towards the future

As mentioned, ecological restoration of Arctic–alpine ecosystems is relatively new, and as a result there

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are still considerable gaps in our knowledge and know-how. Approaches to the technical aspects vary considerably, and the development of special restoration methods for high elevation areas is far from sufficient. The legal requirements and limitation to extensive restoration methods for Arctic and alpine landscapes also vary greatly from one country to another. What is commonly accepted in some countries is strictly forbidden in others! Above all, despite prohibitions and restrictions written into various nature protection laws, the use of non-native plant species in Arctic and alpine restoration work is often ignored or overlooked due to lack of the knowledge about alternatives or ability to properly identify plant material being offered for sale or used on site. Although permission for building projects at extreme sites is obligatory in almost all of the countries concerned, the protection laws are less than strictly controlled. There is also a lack of information among the authorities concerning what is technically possible. The drawing up of binding guidelines for ecological restoration, which reflect the latest awareness of technological advances, is urgently needed.

Changing climate, with expected increases in temperatures will seriously impact Arctic–alpine ecosystems in the coming years and decades – that is certain. However, it is unclear to what extent the affected flora and fauna will be able to withstand and adapt to rapidly changing environmental conditions. To cope with rapid and profound changes will be one of the biggest challenges in the coming decades, for the life forms concerned as well as for science. Nowhere is this more true than in the Arctic and alpine regions of the world.

APPENDIX: WEBSITES

ECONADA: Ecologically sustainable implementation of the 'Nature Diversity Act' (Naturmangfoldloven) for restoration of disturbed landscapes in Norway. http://www.bioforsk.no/ikbViewer/page/tjenester/prosjekt?p_document_id=86296.

NWT seed project: Northern Native Plant Development Collections in the Northwest Territories of Canada. http://data.nwtresearch.com/entry.aspx?licence=17e1fd5e-830b-465d-95fa-751b767c3e36.

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Chapter 16

RESTORATION OF MIRES

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16.1 INTRODUCTION

Mires are peatlands where peat is currently being formed (Joosten & Clarke 2002). A *peatland* is land with peat, that is, with a superficial layer of partially decomposed organic material that is at least 20–30 cm thick. Mires are ecosystems that produce peat and include *bogs* and *fens*. Bogs are mires raised above the surrounding landscape and solely fed by precipitation, especially rainwater, whereas fens are situated in depressions and, in addition to precipitation, they are also fed by ground- or surface water. Bogs are always acidic (pH < 4.2; Siegel *et al.* 2006), whereas fens are often base-rich or slightly acidic or neutral (pH > 5.5; Succow 1988; Wheeler *et al.* 2002).

Along with the term 'mires', we will also use the generic term **wetland** to describe any area of land that is sometimes or always covered by shallow water, and supports vegetation adapted to saturated soil conditions. A wetland may or may not be a peatland; it can also occur on mineral soil.

It is estimated that on a world scale the natural extent of mires was more than 4 000 000 km^2 (Joosten & Clarke 2002), of which 2 500 000 km^2 is situated in North America and Siberia (Plate 16.1). Human exploitation has altered 500 000 km^2 in such a way that peat accumulation has been stopped. Mire losses are highest in Europe (>50%) due to intense human population pressure and the climatic suitability for both agriculture and forestry. Losses are particularly great in western and southern Europe, where less than 10% of the natural mire area has remained (Joosten & Clarke 2002). About 80% of the mire losses here are related to agriculture and forestry. Finland and Russia in particular have drained large areas of peatland for forestry (50 000 km^2 and 38 000 km^2, respectively); this accounts for more than half of the global destruction of mires for forestry (Joosten 2009a). In most eastern European countries, between 10% and 50% of the former mires remain. In South America and Africa, peat losses are low in absolute values, but that is because these continents do not have large stocks of peat. In Africa, for instance, some 140 000 km^2 was originally present, but 20% of that is now already lost (Joosten 2009b). In South America, losses amount to 10%, but peat extractions are expanding, particularly in Tierra del Fuego (Argentina and Chile), where unique bogs have developed with a cover of only one *Sphagnum* species (*S. magellanicum*).

In this chapter, we discuss restoration of damaged mires worldwide, but with a particular focus on Europe. We will first describe some pristine mire types that can serve as a source of information and inspiration for restoration projects. However, they are not necessarily the appropriate **reference systems** for all **ecological restoration** projects (e.g. those in densely populated areas whose hydrological systems have often been irreversibly changed). Accordingly, we will also discuss **rehabilitation** prospects of mire remnants within strongly human-influenced **landscapes** (see also Chapter 5). The vegetation of such mire remnants may resemble that of natural mires, but **hydrologically** such systems are very different. The vegetation composition of relic mires can sometimes be used as a reference in rehabilitation projects.

16.2 UNDISTURBED MIRE SYSTEMS

The classification of mires is based mainly on species composition, often supported by stratigraphical and palaeo-ecological data (Brinson 1993; Grünig 1994). Succow and Joosten (2001) integrated hydrological features with the genesis of mires and linked that to nutrient status and vegetation composition. Here we focus on the following five types: rainwater-fed bogs, groundwater-fed percolation fens, terrestrialization fens, spring fens and floodplain fens.

16.2.1 Rainwater-fed bogs

Bogs are fed by rainwater although some peripheral parts – the so-called lagg zone – can be influenced by water from surrounding areas that has been in contact with mineral soil (Plate 16.2a). Most bog systems originate from lakes and groundwater-fed mire systems, over which a developing rainwater lens allows *Sphagnum* moss species to grow. In this way, *Sphagnum* 'escapes' the influence of groundwater and may form a domed-shape peat body that grows above the immediately surrounding area. Groundwater flow to the bog system remains essential for the functioning of the bog system by keeping water levels stable. The living top layer of a bog consists of a loosely structured layer, called *acrotelm* (Ingram 1983). It consists of living mosses (predominantly *Sphagnum* species), intermin-

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gled with phanerogams adapted to very wet and nutrient-poor conditions. There is a distinct gradient in hydraulic conductivity in this situation. The underlying, more firm and decayed peat layer called *catotelm* can store a large amount of water, thus maintaining the required wet conditions for the typical bog species. Excess water flows to the periphery of the bog through the acrotelm. In dry periods, the water level in the acrotelm drops, and reaches peat layers with much lower hydraulic conductivities. Water flow in these layers then becomes very low. This regulating feedback mechanism prevents a rapid loss of water from the bog during dry periods (Joosten 1993; Succow & Joosten 2001).

Various types of bog have been distinguished on the basis of their morphology (Glaser 1992; Glaser *et al.* 1997). 'Blanket bogs', which cover the undulating landscape like a blanket, are common in Ireland and Scotland. 'Plateau bogs' are large bogs with a flat top that used to be common in north-western Europe, but are now – as living mire systems – very rare. Still larger bog systems occur in Canada (Warner 2005), Russia (Yurkovskaya 2005), Scandinavia, the Baltic states and Belarus, as well as in Tierra del Fuego, in southernmost South America (Coronato *et al.* 2006).

16.2.2 Percolation fens

These groundwater-fed fens are large peat-forming gently sloping systems, sometimes semiforested, but often almost treeless, in which case they are dominated by sedges and bryophytes (Plate 16.2b). These fens occur in mountain areas and lowland river valleys, in situations where the groundwater comes from the surrounding catchment area. As in natural bogs, the uppermost peat of natural fens is loosely structured and permits a rather rapid flow of water during wet periods of the year. This type is referred to as percolation mire since, in contrast to other peatland types, a substantial part of the groundwater flow in this case occurs through the rather permeable peat in the upper layers of the mire (Succow 1988). Large natural fen systems of thousands of hectares occur in Canada (Warner 2005), Scandinavia (Lindholm & Heikkilä 2005), the Baltic States (Pakalne & Kalnina 2005), Russia (Yurkovskaya 2005), Tierra del Fuego (Coronato *et al.* 2006), Tibet (Tsuyuzaki 2006) and South Africa (Grundling & Grobler 2005). Such large peat-forming, groundwater-fed mires were also widespread in north-western Europe, some centuries ago, but at present only remnants of percolating fens occur there, which no longer form peat (Succow & Joosten 2001). In the best-preserved fen systems, such as those in the Biebrza Valley, Poland, typical fen species co-occur with a large number of fen meadow species that mark the transition towards grasslands. Locally peat formation can occur, but many such fen systems no longer accumulate peat, and in most systems regarded as fens the peat is actually degrading. One of the largest fen systems in the world, the Everglades in Florida, United States, is a large calcareous fen that originally occupied more than one million hectares (Kadlec 2009). At present more than half of it has been reclaimed for agriculture (Richardson 2008). In section 16.4.2 we will discuss attempts to restore damaged parts of the Everglades.

16.2.3 Terrestrialization fens

Terrestrialization fens occur almost everywhere where peat formation can occur, and they are abundant under natural conditions. In human-dominated environments, however, most terrestrialization mires are artificial. In the lowlands of north-western Europe, for instance, the natural mires (fens and bogs) are long gone (Plate 16.2a and 16.2c) and secondary terrestrialization has taken place in former peat extraction sites. Most of these newly formed terrestrializing mires ('floating mats') are small, ranging in size from less than 1 ha to a few hundred hectares, such as the Norfolk Broads in England and the Dutch Weerribben or Wieden (van Wirdum *et al.* 1992; van Diggelen *et al.* 1996). In the Mississippi River delta plain in Louisiana, United States, there is a very large, floating freshwater system of circa 3000 ha (Sasser & Gosselink 1984).

Terrestrialization mires are ecologically very diverse. Eutrophic plant communities, such as reeds, form floating rafts on which in later stages mesotrophic or even oligotrophic plant communities can develop when the peat layer is sufficiently thick to allow the formation of rainwater lenses (van Wirdum *et al.* 1992). When groundwater supply is insufficient or the surface water contains too many nutrients and sulphates, these terrestrializing fens are rapidly overgrown by shrubs and acidify rather quickly (van Diggelen *et al.* 1996).

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16.2.4 Spring fens

Spring fens are almost exclusively fed by groundwater discharge (Plate 16.2c). They generally occur in landscapes with rather complex geological and hydrological conditions. Usually they occur in places where groundwater flowing through an artesian aquifer bursts through a rupture in the overlying confining layer and discharges at the land surface. Such a rupture is often the result of changes in the original stratification of sediments (e.g. where tectonic movements have occurred) (Wilcox *et al.* 1986; Grootjans *et al.* 2005). Spring systems can be found as elevated spots, in lowlands in the middle of a sloping landscape or even close to a hilltop. In all these settings, spring fens occur at the inflection point where local groundwater flow systems intersect the land surface (Almendinger & Leete 1998).

In calcareous substrate areas, the regular discharge of groundwater may accumulate large amounts of $CaCO_3$ (*travertine*) up to a height of 30 m (Grootjans *et al.* 2005; Pentecost 2005). When groundwater, supersaturated with $CaCO_3$, comes into contact with the atmosphere, CO_2 escapes and $CaCO_3$ precipitates. Spring mire plants, and mosses in particular, stimulate this process by using the CO_2 in the discharging groundwater as a source of carbon. The result is that $CaCO_3$ precipitates on plant leaves, and when they die off and decompose, $CaCO_3$ is deposited. Under favourable climatic conditions, peat formation may occur. Peat formation in spring mires is sensitive to changes in landscape hydrology and climatic conditions that trigger changes in *groundwater discharge* leading to the *decomposition* of the peat layers. Strongly decomposed peat has a high resistance to water flow, thus blocking water transport in the spring mound. The discharging groundwater will then force its way out somewhere else in the spring system, thereby creating new opportunities for peat or travertine formation (Wolejko *et al.* 1994). Some of the best-preserved spring-mire systems anywhere can be found at the base of the Alps and the Slovakian Tatra Mountains, and in Latvia (Pakalne & Kalnina 2005). Outside Europe, spring mires occur in the United States (Komor 1994; Glaser *et al.* 2004; Middleton *et al.* 2006), South Africa (Scott & Vogel 1983), Siberia (Schipper *et al.* 2007) and Australia (Whinam & Hope 2005).

Most spring mires in western Europe have disappeared due to decreased inflow of groundwater from surrounding areas as a result of changes in land use. In north-western Poland, however, many spring systems are still present and their infiltration areas have not been hydrologically disturbed. Yet most of them have been damaged by drainage in downstream lake areas (Plate 16.3c; Wolejko *et al.* 1994). Decreasing lake levels in the nineteenth century have triggered erosional processes that have washed away most of the peat that has accumulated around these spring systems.

16.2.5 Floodplain fens

In hydrological terms, floodplain fens (Plate 16.2d) are very dynamic systems. In winter and spring, intensive flooding may deposit large amounts of sand, silt or clay. In summer, water tables may drop to 1 meter or more below the soil surface. Under such conditions, nutrient availability can be very high (Olde Venterink *et al.* 2003) resulting in high productivity of floodplain vegetation. On a geological time scale, rivers frequently change their course, leading in turn to modified flooding frequencies and sedimentation rates. Eutrophic floodplains may change into mesotrophic fens and existing fens, or even bogs, may become flooded with surface water. Examples of large floodplain mires in Europe include the Danube floodplain in Romania (Vadineanu 2009), the Oder floodplains on the border of Poland and Germany, the Narev floodplain in Poland and the Rhône River delta in southern France (see also Chapter 17). Large floodplain mires outside Europe are the Okavanko Delta in Botswana (McCarthy & Ellery 1998) and the Mesopotamian marshes in Iraq (Maltby 2009).

16.3 CAUSES OF DISTURBANCE OF NATURAL MIRES

The main causes of destruction of and disturbance in natural mire systems vary from direct peat extraction for fuel to indirect changes in landscape hydrology and atmospheric nitrogen deposition due to changes in *land use* by agriculture, forestry or urbanization. The indirect hydrological changes and their effect on nutrient availability in the peatland may be subtle, but can lead to natural mires changing into systems that no longer accumulate peat, but instead actually release carbon into the atmosphere. The change from natural mires to disturbed ecosystems is illustrated in Plate 16.3, which

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shows typical remnants of natural mire types after large changes in land use during the past few centuries. The time period in which such land use changes began may differ greatly, but the outcome is usually similar.

16.3.1 Peat extraction

Peat extraction is responsible for circa 10% of global mire losses, with new peat extraction sites being established at a rate of 10 km^2 annually (Joosten & Clarke 2002). Countries with large peat extraction activities for energy are Finland, Russia and Ireland. In Ireland, in particular, this use of peat for energy is criticized by national and international organizations because burning peat is very inefficient as compared to burning coal or gas. In other countries, like Germany, the Baltic states and Canada, peat is primarily extracted as a raw material for horticultural growing media. Even when peatlands are no longer used for peat extraction, the peat losses continue. Deeply drained peatlands suffer from peat loss through shrinkage and mineralization (Oleszczuk *et al.* 2008). This process may cause losses as great as 2–3 cm yr^{-1} (Joosten 2009a) and trigger the release of enormous amounts of greenhouse gases into the atmosphere (ca. 40 kg of N_2O $ha^{-1}yr^{-1}$ and 10 t $ha^{-1}yr^{-1}$ of CO_2; Armentano & Menges 1986). Altogether, these processes have significant impacts on global greenhouse gas cycles. On a global scale, peat losses due to agriculture, forestry and wildfires amount to circa 500 million tons of carbon per year (Joosten 2009b, see also Box 16.1 on Indonesian peatlands). In contrast, global peat accumulation is estimated to at least five times less than that. This makes it clear that global peatlands have switched from being carbon sinks to carbon emission sources (Couwenberg *et al.* 2010).

16.3.2 Indirect changes in hydrological regimes

Most fens and bogs in north-western Europe have been converted into intensively used agricultural land or commercial forest plantations. These land use changes have altered groundwater flow patterns and groundwater composition, which of course has negative consequences for remaining fens and bogs. Ecohydrological research in Poland and the Netherlands has shown that large drainage works in a landscape have fragmented the former regional flow systems into smaller local cells. This fragmentation of hydrological systems has resulted in significant hydrochemical differences, which can be observed even within a single small fen (Wassen *et al.* 1996). In the Biebrza catchment in eastern Poland, for example, the hydrochemical and associated trophic gradients in the vegetation are still very smooth and gradual over large distances (Wassen *et al.* 1996). This relative spatial uniformity is related to slow but continous flow of groundwater in the mire that keeps it saturated with mineral-rich groundwater. Fen systems in the Netherlands resemble Polish fens with respect to vegetation, but their hydrological systems are much more variable. In areas with a large precipitation surplus, drainage promotes **acidification** in peatlands because calcium- and iron-rich groundwater is replaced by rainwater (Schot *et al.* 2004). Such processes can even trigger bog formation, when sufficient precipitation water is present.

In order to compensate for water losses due to drainage, surface water is often supplied to agricultural areas during summer. This artificial water supply tends to reverse the natural fluctuation pattern such that low water levels occur in winter and spring and high water levels occur in summer. Most of this water originates from large rivers with much higher nutrient and sulphate content than groundwater. A higher nutrient availability in the water leads to **eutrophication**. But in organic soils, high sulphate levels may also trigger eutrophication. This process is called *internal eutrophication*. Under anaerobic conditions, the availability of alternative electron acceptors, such as sulphate, may strongly stimulate the breakdown of organic matter and increase the availability of nutrients (Smolders *et al.* 2006). During sulphate reduction, sulphide is produced, which in relatively high concentrations is toxic for most vascular plants (Lamers *et al.* 2002). In most groundwater-fed fen soils, sulphide will not reach toxic concentrations since it is chemically bound by iron. When sulphide production, however, exceeds the availability of iron, free sulphide concentrations increase (Caraco *et al.* 1989). When iron availability in the soil becomes limited, for instance when groundwater supply to the fen has stopped, phosphate concentrations in the pore water can increase to high levels. Such changes in nutrient cycling can be very harmful for phosphorus-limited fens (Koerselman & Verhoeven 1995; Richardson 2008). In general, anoxic iron-rich groundwater tends to slow down nutrient cycling,

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Box 16.1 Peatlands in Kalimantan: Destruction and hopes for restoration

Although precise data are absent, it is estimated that Indonesia may have 27 Mha of peatland, the largest area found in any tropical nation. In 1995, the then president Suharto initiated the so-called 'Mega-Rice project', which was intended to drain one million hectares of peatland in central Kalimantan for rice production. The aim was to produce two million tons of rice per year in order to keep Indonesia self-sufficient in rice production and at the same time redistribute people from the over-populated islands (Java, Bali, Lombok; each with around 700 people km^{-2}) to less populated areas, such as Kalimantan. The total area of the mega-project was almost 1.5 Mha, including 0.9 Mha of peat swamps, which represents 41% of the total peat swamps in central Kalimantan. In order to make the area suitable for rice production, primary tropical forest had to be cleared and an extensive drainage system had to be dug. The main drainage channel was 110 km long, 25 m wide and 6 m deep. The secondary, tertiary and quaternary channels had a total length of more than 4500 km. The canals were dug without sufficient knowledge of the hydromorphological properties of peatlands. Many peatlands were drained too deep, resulting in subsidence, peat oxidation and acidification, and greatly increased risk of wildfire. Indeed, the biomass residues from logging activities provided fuel for immense, uncontrollable fires in 1997 and, to a smaller extent, in consecutive years. More than 500 000 ha of land was intentionally or accidentally burned in 1997. Many fires were lit by companies and farmers as a cheap way of clearing land for agriculture, especially oil palm and rubber plantations. In the affected areas, the surface-drained peat that was supposed to support crops, burned away. In 1997, more than 40 000 people suffered from respiratory diseases, and over 1000 people died, from smog-related illnesses. Neighbouring countries including Malaysia, Singapore, Brunei and even Thailand, suffered the consequences as well. Schools were closed, airline flights cancelled and thousands of people wore face masks for weeks on end. Environmental costs were also extremely high. Page *et al*. (2002) estimated that in 1997 alone 810–2570 Mt C was released to the atmosphere as a result of burning peat and vegetation. This is equivalent to 13–40% of the mean annual global carbon emissions from fossil fuels. The haze and fires during August–December 1997 cost the region an estimated US$4.4 billion. Within two years, it became apparent that the project would never achieve its objectives and the new president of Indonesia, President B.J. Habibie, reversed the decision of the former president Suharto, and stopped the project. By then around US$500 million had been invested, but little had been achieved. Most of the forest, however, had been destroyed. Habibie soon decided to convert the peat areas into agricultural land to grow other food crops than rice and also to further development of oil palm and rubber plantations. Although the new plans stress the need for wise-use principles for using peatlands, the main emphasis was and still is on economic development. The presidential decree was criticized by environmental groups because it lacked consideration of the ecological functioning of tropical peatlands and ignored their environmental values. Areas that were designated for peat and wildlife protection in this new policy were highly fragmented and therefore not suitable for conservation objectives as they are situated too close to extensively drained development areas. Most importantly, carrying out these new plans did not stop the fires. In the last decade; new, and somewhat more integrated plans have been made to restore the area, paying more attention to conservation and integral water management. However, little actual implementation has yet taken place. CO_2 emissions from drained peatlands in Indonesia still amount to more than 500 Mton CO_2 per year, and this excludes emissions due to fires. The emissions from Indonesian peatlands are almost half of the global CO_2 emissions per year from drained peatlands (Joosten 2009b). European coutries and Australia are now investing many millions of dollars in projects that aim to block the drainage channels and rewet the peat again, but the successes are still very modest.

Based in large part on Rieley (1999) and Joosten (2009b).

while oxic surface water tends to stimulate nutrient cycling. For further reading on the effects of oxidizing effects of nitrate- and sulphate-rich water on internal eutrophication in wetlands, we refer to Smolders *et al*. (2010).

16.3.3 Atmospheric N deposition

Agricultural areas with intensive cattle breeding emit high amounts of NH_3 into the atmosphere, which also reaches nature areas through dust particles and pre-

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cipitation (*external eutrophication*). Atmospheric nitrogen and sulphur deposition have a very negative effect on almost all low-productivity wetland ecosystems. The concept of critical N load has been developed to indicate the annual amount of N deposition above which there is a realistic risk that essential functions of an ecosystem may be impaired (Achermann & Bobbink 2003). *Critical nitrogen loads* for bogs are 5–10 kg of N $ha^{-1}yr^{-1}$, and for mesotrophic (unmanaged) terrestrialization fens they are 20–35 kg (Bobbink *et al.* 1998). When the deposition of N increases, the *Sphagnum* species start to accumulate N in amino acids, or mineral N is no longer absorbed and becomes available for vascular plants such as *Molinia caerulea* and *Betula pubescens* (Lamers *et al.* 2000).

16.4 RESTORATION APPROACHES, SUCCESSES AND FAILURES

There is a growing awareness that *rewetting* (i.e. increasing water levels) in drained peatlands not only is beneficial for protecting **biodiversity** but also reduces greenhouse gas emissions. New economic uses of peatlands, such as biomass cultivation for biofuel, are now emerging, since many peatlands have become unsuitable for modern agricultural production (Pfadenhauer & Grootjans 1999). In many peat areas, in Europe in particular, the maintenance costs and subsidies paid by taxpayers are simply too high, and the revenues too small, to allow this type of land use on peat soils to continue.

For biodiversity conservation and other environmental objectives, rewetting should preferably be done with anoxic, unpolluted groundwater, because this will conserve the peat and prevent further emissions much more than rewetting with surface water (Smolders *et al.* 2010). Rewetting can be achieved by constructing dams or filling in drainage ditches. Terminating groundwater abstraction activities will also lead to rewetting.

When restoration to the natural state is no longer possible, **rehabilitation** of some wetland functions is a more appropriate and realistic goal (e.g. Wheeler & Shaw 1995). When a wetland is damaged beyond a certain **threshold** of repair, rehabilitation efforts may lead to remodelling the system towards a state that probably never existed before, but is far preferable to sheer abandonment. In areas that have been abandoned by farmers, industries or other land users, most nature development projects now in fact explicitly aim at designing and creating an entirely new wetland ecosystem.

In what follows, we will discuss restoration experiences, and lessons learned, in western Europe and elsewhere, with a focus on damaged nature reserves or abandoned peat extraction areas.

16.4.1 Restoration of rainwater-fed bogs

In north-western Europe and in North America, many restoration and rehabilitation efforts include attempts to restart peat growth in large bog complexes where peat has been extracted for commercial use (Wheeler *et al.* 2002; Money *et al.* 2009). Reinitiation of *Sphagnum* growth in such flat surfaces has proven to be very difficult (Vermeer & Joosten 1992). Essential for succesful bog restoration is to re-create a new functional acrotelm (Money *et al.* 2009). Without that, peat formation cannot occur. So, the first step is to create good conditions for very active *Sphagnum* growth. In degraded bog remnants, these conditions are unfavavourable due to (1) too-high water table fluctuations (>25 cm), (2) high atmospheric N deposition and (3) low dissolved inorganic carbon (DIC) concentrations in the pore water.

Too-high water table fluctuations

Water table fluctuations in degraded bog remnants are usually too large for *Sphagnum* growth, due to the too-low storage capacity (specific yield) of the remaining peat layers and because of water losses to surrounding (drained) agricultural areas. Restoration measures in such cases usually consist of increasing water levels in the bog to over the surface by building large dams in and around the bogs. Water table fluctuations can be largely reduced by such measures, but large parts of the bog may become permanently inundated, which can limit *Sphagnum* growth due to light limitation and lack of carbon dioxide. Humic acids from the remaining peat substrate lead to a condition known as dystrophic (i.e. water that is poor in nutrients and contains a high concentration of humic acid, with limited penetration of light). Light limitation can thus hamper the growth of submerged *Sphagnum* when water depth exceeds 0.5 m (Wheeler & Shaw 1995). Shallow flooding, however, often results in strong fluctuations of the water level and the drying out of the

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topsoil in dry years (Price 1998). Increasing groundwater levels in surrounding agricultural areas will improve the restoration success in the bog remnants considerably, but this is an option only when these drained areas can be purchased, or otherwise compensation can be arranged for the relevant farmers or landowners.

Experimental research has shown that good restoration results can be achieved when the peat either swells up to the newly created water table or becomes buoyant, in both cases creating a favourable substrate for *Sphagnum* mosses. Floating of *Sphagnum* vegetation is usually caused by high methane production from underlying substrates (Lamers *et al.* 2002; Tomassen *et al.* 2003). Buoyancy of *Sphagnum* mats is stimulated when poorly humified *Sphagnum* peat is still present (Tomassen *et al.* 2004), or when slightly or somewhat calcareous groundwater enters the peat base, thus stimulating decomposition (Malmer & Wallén 1993; Smolders *et al.* 2003). Some field experiments are presently underway in which small amounts of lime are added to the peat before rewetting and less degraded peat from other areas is added in order to stimulate decompostion processes and methane production (van Duinen *et al.* 2011).

High atmospheric N deposition

Limpens *et al.* (2003) showed that high atmospheric N deposition (30–35 kg of N $ha^{-1}yr^{-1}$) reduces the growth of rainwater-fed *Sphagnum* species and favours the growth of *Molinia caerulea* and *Betula pubescens*. Above 18 kg of N $ha^{-1}yr^{-1}$ *Sphagnum* species cannot take up all the NH_4^+ from the soil solution and the nitrogen becomes available for vascular plants, which start to shade the *Sphagnum* plants, thereby reducing their growth considerably.

Low dissolved organic carbon concentrations

Initial stages of bog formation usually consist of a dense vegetation of submerged or floating *Sphagum* species, like *Sphagnum cuspidatum* or *S. fallax*. Carbon dioxide availability is crucial to the growth of submerged *Sphagnum* species (Smolders *et al.* 2001). In general, such species are only able to reach buoyancy when carbon dioxide concentrations in the pore water (i.e. the water filling the spaces between grains of sediment) are higher than 500 µmol l^{-1} (Smolders *et al.* 2003). Carbon dioxide in bogs is derived mainly from decomposition processes. As a result, carbon dioxide concentrations are highest just above the inundated peat soils. Therefore, shallower waters will present not only more favourable light conditions but also higher carbon dioxide concentrations for submerged *Sphagnum*. Once submerged or floating *Sphagnum* species have established, a structure may be formed on which true bog species can establish and form a new functional acrotelm. Key species for acrotelm development are *Sphagnum magellanicum*, *S. papillosum*, *S. imbricatum*, *S. fuscum* and *S. rubellum*. These typical 'hummock' and 'lawn' species are usually very slow colonizers compared to the wetter 'hollow' species such as *S. cuspidatum* and *S. fallax*. Introduction of key species in carpets dominated by hollow species or on bare substrates appears to be very successful, indicating that the main constraint is colonization (Smolders *et al.* 2003).

Several recent studies suggest that in the first stages of peat regeneration, *Sphagnum* plants may also need support from tussock-forming species, such as *Eriophorum vaginatum*, or from perennial species such as relatively tall *Carex* species that can form many erect shoots, without shading the *Sphagnum* plant too much (Ramseier *et al.* 2009). In Canada, mulching with straw has been used for protection against evapotranspiration losses and to provide a support structure for young *Sphagnum* plants (Rochefort *et al.* 1995).

16.4.2 Rehabilitation of groundwater-fed fens

Repairing the hydrological regime of a wetland is more complex than just raising water levels. In groundwater-fed fens, in particular, increasing water levels may lead to **acidification** when the discharge of base-rich groundwater cannot be reinstated. Therefore, successful management of groundwater-fed fens should be approached at a broader scale that includes the landscape-scale management of groundwater systems. Not only quantitative aspects are important but also qualitative aspects. Leaching of nitrate to the groundwater, for instance, can cause large-scale mobilization of sulphate from geological pyrite or gypsum deposits and the immobilization of ferrous iron (Smolders *et al.* 2010). A *landscape-scale approach* often implies changing land use in the entire surrounding catchment

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area. This requires stakeholder participation. Without that support, fen rehabilitation is almost unachievable because of conflicting land use claims from farmers, foresters, city dwellers and so on (Klimkowska *et al*. 2010b).

One of the largest rehabilitation projects in the world is the well-known project in the Florida Everglades (Kadlec 2009), where large-scale hydrological measures are being executed to reinstate insofar as possible, the original flow patterns of this large fen system. Much effort is given to reduce phosphorus loading to the protected fen areas of the Everglades National Park. A substantial amount of phosphorus stems from agriculture, and therefore this sector should logically contribute substantially to the cost of rehabilitation. If farmers do not meet the goals of phosphate reductions, as formulated in *Best Management Practices*, they are required to pay extra taxes to the state of Florida. The total cost of the actions intended to maintain and restore the ecological character of the Everglades is currently estimated at more than US$10 billion, and the figure is rising (Kadlec 2009).

16.4.3 Restoration of terrestrialization fens

In western Europe, terrestrialization fens in lake areas are often the last refuge for nutrient-poor fen plants that were once widespread in natural groundwater-fed fens. With increasing eutrophication of surface waters, the lakes also became polluted and, as a consequence, nutrient-poor fen species in the terrestrialization fens have become rare (van Wirdum *et al*. 1992). Restoring such nutrient-poor fens has to start with improving the water quality of the lakes in which the fens occur. Technical solutions, such as sewage treatment plants, can decrease nutrient concentrations. In densely populated areas, however, sewage treatment may not be suffcient, since nutrients from diffuse sources may enter a protected nature area via canals or via groundwater flows from surrounding agricultural areas. A proper way to deal with the complex relationships in the water systems and human exploitation of water (e.g. for drinking water, navigation and tourism) is integral water management. In other words, all the interrelated hydrological problems in a watershed – including pollution of underwater sediments, local and regional input of pollutants, shoreline management, water level management, groundwater extraction for drinking water and industrial use – should ideally be addressed simultaneously and in an integrated fashion.

Not all terrestrialization fens need management. In oligotrophic lakes, small bog hummocks or low-productive fen vegetation can develop soon after the formation of a floating mat of reed or large sedges. In eutrophic lakes, terrestrialization can lead to monocultures of reed (*Phragmites australis*) with little value for nature conservation. In such cases, cutting can reduce the vitality of the reed and increase biodiversity. Summer mowing reduces the vitality of *Phragmites* more than winter mowing (van Diggelen *et al*. 1996). Excavating new peat ponds is a measure to restart the terrestrialization process to provide new habitats for rare and endangered fen species (Beltman *et al*. 2001). Excavation should be practised only when the new peat ponds can be supplied with very clean water, preferably groundwater.

16.4.4 Rehabilitation of spring mires

Most degraded spring-mire systems can no longer be restored since the original peats and sediments have disappeared and the water discharge sites have shifted to lower sections of the spring system and cannot be directed upwards. The replacement communities, consisting of plant and animal species adapted to low temperatures and constantly flowing water, are also highly endangered in western Europe (Wolejko *et al*. 1994). Rehabilitation measures should aim at stabilizing water outflow in springs and preventing pollution in infiltration areas. When the discharge of groundwater has diminished or the spring water has been polluted in surrounding infiltration areas, the most obvious measure is to protect the direct catchment areas and abolish drainage and fertilization practices. In efforts to rehabilitate a severely damaged spring mire complex (6 ha) in the Sernitz region of north-eastern Germany (Koska & Stegmann 2001), several measures were taken concurrently to raise the water table. Measures included (1) constructing a series of wooden dams in the largest drainage ditches, (2) completely filling ditches with peat, (3) reflooding parts of the mire with spring water and (4) perforating the impervious gyttja layers at the base of the mire. The best results were obtained with complete filling of drainage ditches. Flooding parts of the mire with spring water that had

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accumulated behind wooden dams could not prevent severe desiccation during summer. The series of wooden dams in the main drainage ditch were also ineffective, since they only slowed down drainage, rather than preventing. Their impact remained very local. Perforating the impervious layers to enable spring water to discharge at the top of the spring mire also had a very limited effect and did not contribute to the rewetting of the mire.

16.4.5 Restoration of floodplains

Stimulating flooding in eutrophic flood mires can be an effective measure to combat acidification and can, under certain conditions, compensate for the influence of drainage (see also Chapter 17). Nutrient levels and sulphate levels should be very low to prevent rapid eutrophication. Remnants of former extensive flood mires are often surrounded by agricultural areas with much lower water levels. Former discharge areas have turned into infiltration areas and **acidification** of the topsoil has degraded the fens and fen meadows to the extent that iron levels have become critically low (van Duren *et al.* 1998; Lamers *et al.* 2002). Reflooding with surface water, even when pre-purified by **helophyte filters** (reed swamps that reduce the nutrient content of the surface water), does not always restore the iron concentrations to higher levels, since surface water usually contains very little iron. If iron is fixed as FeS_2 (*pyrite*), flooding with surface water may lead to a higher pH during winter and spring, but during summer, when groundwater levels drop, the topsoil acidifies again due to oxidation of FeS_2 (Lamers *et al.* 2002). Permanent flooding could prevent acidification, but will also increase the availability of nutrients in the soil, leading to very productive plant communities (Lucassen *et al.* 2004). Such restored wetlands, however, regain the capability to capture nutrients from the surface water system (Olde Venterink *et al.* 2003; Richardson & Hussain 2006), and thus provide habitats for large populations of waterfowl (Middleton *et al.* 2006). Flooding is also important for the redistribution of seeds within restoration sites (Wheeler *et al.* 2002; Jansen *et al.* 2004). Flooding does not automatically restore peat formation. Many species that respond positively on renewed flooding, such as *Glyceria maxima*, *Acorus calamus* and *Phalaris arundinacea*, do not form peat. For peat formation, the vegetation should consist of wetland species with stiff or fibrous tissues that degrade slowly, such as *Phragmites australis* and various tall sedges (*Carex* spp.; Richert *et al.* 2000).

16.5 PERSPECTIVES

In densely populated areas, **ecological restoration** of mires is almost impossible since hydrological conditions of natural mires are usually dependent on the larger hydrological systems of the surrounding landscape. If restoration implies restrictions to regional water use, support from society will often be lacking entirely. Targets for restoration projects should therefore be set carefully and clearly in order to obtain political support (Swart *et al.* 2001). In practice, mire ecosystems can only be restored on a very local scale, and although features of natural mires may return, the new ecosystems will differ from the ones that have been destroyed in former times. Successful projects have in general been executed at sites little affected by intensive agriculture and drainage.

Successful restoration in densely populated areas often implies repairing damage at high costs. From an economic perspective, conservation of still-existing undisturbed ecosystems is much more cost-effective. However, there are increasing numbers of situations where pressures and motivations are sufficient to trigger – and economically justify – mire restoration elsewhere. Failures to repair damaged elements of mires are as numerous as the successes, but they are usually not well documented. Failures are often caused by an incorrect diagnosis of the restoration prospects of the site (Grootjans *et al.* 2006), lack of knowledge on ecological processes affecting the site negatively, and expectations that are too high or unrealistic.

Reduction of the amount of N deposition remains a prerequisite for successful restoration of many nutrient-poor ecosystems, such as bogs, fens and several types of fen meadow. In some European countries, atmospheric N and SO_2 deposition has declined considerably during the past 20 years, due to more strict environmental legislation. Freshwater ecosystems have benefited considerably from drastic reductions of phosphorus emissions in the surface water, but in many streams and rivers the amount of sulphate is still much too high and causes eutrophication in terrestrial mire systems when they are flooded.

Additionally, leaching of nitrate to the groundwater should receive much more attention, especially for its potentially large-scale mobilization of sulphate from

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geological pyrite deposits and the immobilization of ferrous iron. Many water managers still ignore that sulphate-induced eutrophication and sulphide toxicity can strongly affect the biodiversity of wetlands that are directly – or indirectly, via surface water – fed by sulphate-rich groundwater (Lamers *et al.* 2002; Smolders *et al.* 2006). The reduction of nitrogen loads to the groundwater should be a major objective in programmes designed to tackle this problem.

Happily, the prospects for **rehabilitation** of damaged ecosystems are relatively good in most developed countries, since (1) much experience is now available to repair or even rebuild damaged ecosystems, (2) due to new legislation some environmental stress factors, such as high nutrient loads in surface waters and atmospheric nitrogen deposition, are decreasing and (3) public and political support for restoration is increasing. In developing countries, by contrast, the situation is less clear. Since environmental laws are less strict or less strictly controlled, environmental problems may be imported from the West. Public and political support for restoration activities is largely lacking. However, the quality and the number of relatively undisturbed wetlands are still very high in many parts of the world, and the costs to repair the damage in such systems are still low. It could be very beneficial to develop projects that combine economic development and maintenance of (semi)natural mires and wetlands (Wichtman & Succow 2001). With modern technology, mires can be destroyed relatively easily. But in most cases the economic benefits of such actions are temporary, because once destroyed, mires can no longer supply services to society. Societal costs for restoration of damaged mires are very high, and very often the damage is so severe that full restoration is no longer possible. To summarize the prospects of mires, we could say: the future of mires is in conservation.

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Chapter 17

RESTORATION OF RIVERS AND FLOODPLAINS

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17.1 INTRODUCTION

Natural river systems are dynamic features in terrestrial landscapes that change continuously as a result of their inherent physical conditions such as slope, bedrock geology and the complexity of the drainage network. Yet, their characteristics are also influenced by external factors including climatic conditions, precipitation and human activities such as afforestation, deforestation, urbanization, land drainage, pollutant discharges and flow regulation; it is the combination of the inherent river processes that occur over time (Brunsden & Thornes 1979; Schumm 1979; Darby & Sear 2008), and often uncontrollable external influences, that ultimately determine the form of a water course. Recognition of these two aspects – inherent processes and external influences – is key towards sustaining a healthy river system, in which both natural relationships are maintained, pollutants are absorbed, wastes decompose and sediment is redistributed during floods (Postel & Richter 2003).

From a geological point of view, the continent of Europe, on which this chapter primarily focuses, is relatively young and this has resulted in a large number of river catchments that tend to be small, compared with much of the rest of the world. Only about 70 rivers in Europe have catchment areas exceeding 10 000 km^2. Of these the largest is the Volga (1 360 000 km^2; compared with 3 349 000 km^2 for the Nile) and this river, together with the Danube and the Dnieper, drain a quarter of continental Europe. Furthermore, the rivers of Europe account for only 7% of the world's rivers, with a total annual discharge of approximately 3100 km^3 of fresh water into the sea each year (Kristensen & Hansen 1994). Although this is a relatively small amount (8%) of the total discharge worldwide, the overall impact is not insignificant. The temperate humid climate together with a high percentage of extremely erodible limestone means that the amount of dissolved solids in European rivers is considerable, and its impact is exacerbated by a heavily populated continent and associated agriculture, resulting in an intense concentration of minerals within the rivers.

Rivers and floodplains have internal physical, chemical and biological properties that are fundamental in determining the types, abundance and spatial distribution of organisms that occur there. But they are also affected by the landscapes within which they are located. Land type and land use determine water quality, but it can also be altered by the action of vegetation in the riparian interface on both sides of the river (Osborne & Kovacic 1993). Naturally, rivers and floodplains support a wide variety of interacting terrestrial and aquatic flora and fauna and are an essential component in creating pathways or corridors between other habitats such as woodlands. For example, fish show highest diversity within the main channel, but many species need both the main flowing river channel and backwaters to complete their life cycle. Upland, boulder-strewn streams can, for instance, provide spawning grounds for salmonids which, once hatched, move downstream to slower moving and larger sections of river systems where they are dependent on the food supply provided by aquatic and bankside invertebrates. In addition to the river, many backwaters, cut-off channels (natural and human-made) and pools can provide permanent and semipermanent habitat for a range of wetland and sheltering species (e.g. in seasonally connected backwaters, damsel- and dragon-flies can occur, amphibians may migrate to floodplain areas to deposit eggs and aquatic plant species richness increases when compared to a river system that is disconnected from its associated floodplain).

Like any **ecosystem**, rivers and floodplains contain characteristic communities of species that are interconnected through shared habitat use, food resources and refuge from predation. They also have a fundamental interdependency through transfers of organic material, minerals and nutrients between and among different trophic groups. Each type of organism has natural functions within the ecosystem: for example, green plants photosynthesize, some invertebrates shred and break down coarse organic matter transported by the river from upstream, bacteria decompose organic matter and so on (Menezes *et al.* 2010). If river habitats of interacting species – so-called **keystone species** in particular – are disconnected, then there will be a disruption to normal ecological functioning within the river. There are two basic categories of ecological disconnection: (1) spatial – whereby specific habitats and/or species become isolated, and (2) temporal – where connections are broken at crucial times of the year. Increasing isolation can have dramatic negative effects on **biodiversity** within the river system, and break down food web structure in particular (Shulman & Chase 2007). Once the river habitats become degraded or disconnected, then restoration may not provide the whole answer; the complexity of the system and the interconnections must be

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considered. For example, the installation of in-stream structures and large wood to improve or increase the area of fish habitat may lead to local improvements in fish numbers but unless other factors, such as lack of spawning habitat or poor water quality, are addressed population recovery may still fail to come (Stewart *et al.* 2006).

The main purpose of this chapter is to present a broad understanding of the state of river restoration, rehabilitation and enhancement with a European focus. For the purposes of this chapter, these three terms are all referred to as restoration since the distinction between each is often difficult to specify; the level of river **intervention** feasible for ecological benefit is often determined by local, regional and global factors, of social, economic, financial and infrastructure dimensions, along with the historical management practices of the river and associated floodplain as depicted in Figure 17.1. The chapter discusses the impact of such factors, including **disturbances**, as well as the importance of economics, public policy and scientific understanding in terms of best practice to achieve optimum, holistic river restoration outcomes.

17.2 HISTORICAL CONTEXT TO EUROPEAN RIVERS

Wherever rivers are not confined, they continually change their course in response to the specific range of environmental conditions acting upon them. In other words, fluctuating climatic and other drivers mean that rivers and their floodplains are always adjusting to both local changes that affect annual variability of flood frequency and the size of flow events, and global variation that can result in major shifts in river planform pattern (i.e. the characteristic path of the channel) and transform their natural geomorphological state. The precise mechanisms of geomorphological change in rivers cannot be explained within the confines of this chapter, but many textbooks already cover these issues (see e.g. Callow & Petts 1992; Knighton 1994; Gregory 1997; Thorne *et al.* 1997). Nevertheless, the importance of understanding *geomorphic processes* cannot be over-estimated. It can both hold the key to explaining the changes that have occurred in a riverine landscape as a result of anthropogenic intervention and help to predict how specific restoration methods will enhance degraded rivers.

17.2.1 Natural impacts

Although rivers and floodplains have constantly been shaped by changes in climate over time (see Table 17.1), the riverine topography we have inherited today owes many of its features to the impacts of the last major Ice Age that ended some 10 000 years ago. This formed not only many of the rivers themselves but also the valleys and entire catchment basins. In northern

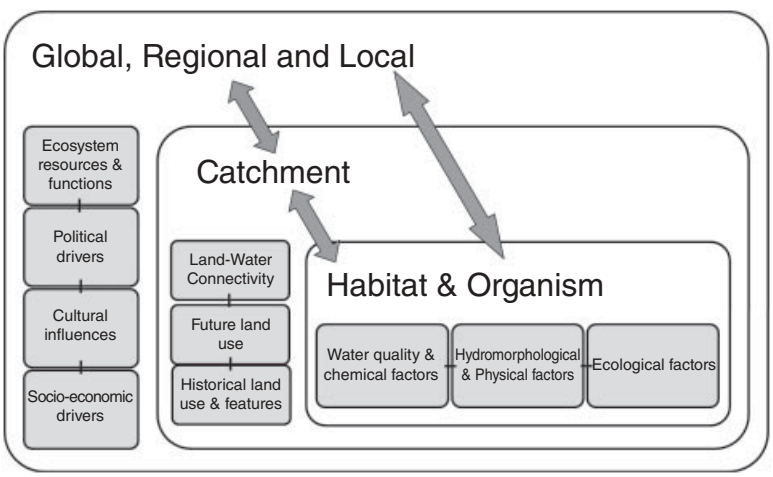


Figure 17.1 The essential elements of river restoration science. The complex, scale-based, hierarchical dependencies between elements essential for successful river restoration are shown.

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Table 17.1 Historic climate change and associated channel processes in Europe. Adapted from Gregory and Lewin (1987).

Years BP	Climate	Precipitation	Temperature	Vegetation	Hydrology	Channel processes
15 000	Glacial	Snow	Low	None	Summer flood	Multithread
15 000–10 000	Early part of the late Glacial	Snow	Ameliorating – cold winters	Grass and sedge succeeded by birch woodland	High peak discharge, but decreasing as forest spread	Multithread
11 000–10 000	Late Glacial	Mainly drier	Extreme cold	Herb rich grassland	Runoff reducing, but high sediment supply	Fluvial deposition – unstable
10 000–4000	Holocene	Rain	Rising	Mixed oak forest with some clearance	Run off lower than today	Fluvial erosion dominant with singe thread meandering channels
4000–present	Holocene cont.	Rain	Reducing but fluctuating; presently rising	Deforestation	Seasonally fluctuating discharge	Lowland cut-offs and floodplain accretion of sediment

Europe, the ice pack covered large areas, rounding off mountains and scouring out wide 'U'-shaped valleys far larger than could have been shaped by watercourses alone. This large-scale process had impacts on both flora and fauna, and areas once below the ice now have less genetic diversity than those that survived further to the south; they relied on colonization by plants and animals able to travel large distances. Where the ice failed to advance, new rivers developed and old rivers were displaced to drain the meltwater. The River Thames in England moved miles further south, discharging into a new estuary where London is now located. The valley of the River Skjerne in Denmark, which drains 11% of the Jutland region's soil, was gouged out by torrents of meltwater and, even beyond the immediate influence of the ice, deposition of eroded rock and sediment occurred, creating lakes and deltas, thus helping to shape the course of rivers and streams.

The Medieval Warm Period, which lasted for a few centuries around 1000–1200 CE, resulted in another significant shift in the riverine regimes of Europe. This period was represented by hotter, drier summers north of the Alpine areas and, although the winters did not differ substantially from today's climatic conditions, the outcome was more convective rainfall in the summer months, resulting in high-intensity but short-duration rainfall events. As a consequence of this climatic change, the character of the rivers in Middle England shifted from a single-thread channel to a braided system, then anastomosing (multithread) systems, and finally back to single-thread channels as river profiles adjusted to accommodate larger flash floods, and generally more unpredictable flood conditions (see Benito *et al*. 1998 for more details). In northern Italy, however, the rivers remained unstable whereas further south they tended towards single-thread systems with frequent out-of-bank flows resulting in large deposits of sand and silt on floodplains. Ultimately, the effects on the rivers and floodplains, therefore, depended on a combination of precipitation, local antecedent conditions and the infiltration rate of the substrate.

Since the Medieval Warm Period ended, the rivers of Europe have been continually subjected to minor changes in climate. Perhaps the most notable of these was the Little Ice Age that occurred between the twelfth and seventeenth centuries CE. Documentary evidence suggests that the River Thames, in London, often froze over during this period although it is not completely

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clear if this was related solely to climate change or else exacerbated by the hydrodynamic effects of the numerous bridges constructed during this period. Nevertheless, the effects of the Little Ice Age were not restricted to the United Kingdom and records across Europe show a similar pattern, with many lakes and rivers freezing over and evidence of glacier expansion. Furthermore, records of this period imply that this was also a time of dry weather and hence intermittent riverine activity (Benito *et al.* 1998).

17.2.2 Human impacts

Climate and local weather are instrumental in driving the form of Europe's rivers, but these have gradually been matched in importance by an increase in the degree of human intervention. Although distinctive phases of human activity that ultimately affect our river systems can be identified since the early Holocene, circa 10 000 years BP, with simple woodland clearance, it remains difficult to disentangle anthropogenic impacts from nonhuman determinants. Take for instance the impact of human interference through deforestation compared to natural decline in forest cover as a result of periods of glacial activity. Immediately it becomes apparent that trying to distinguish the relative impacts of each of these is problematic. Furthermore, especially in northern Europe, many riverine areas are still recovering from the Little Ice Age, while others have been widened and deepened to drain the land for farming or else for purposes of navigation. It is important to recognize the additional difficulties associated with a long period of human intervention and constraints when evaluating degraded rivers with a view to restoration. The identification of a pristine riverine state to start with is difficult, if not impossible, and in many cases, as expressed by Macklin and Lewin (1997), today's rivers are often 'climatically-controlled but culturally blurred'. Thus, the identification of a **reference system** is complicated and necessarily somewhat arbitrary.

Deforestation in particular has had a major impact on river systems in Europe, and elsewhere, especially during the last 4000 years. Estimates of forest decline along the Rhine vary widely, but all literature indicates a significant decrease resulting in increased sediment availability and deposits on the river bed, both directly – by means of **runoff** – and indirectly, via systems of field and land drains. During the medieval period, rivers throughout much of Europe were harnessed as a source of energy to drive mills for a range of activities from cloth to flour-making industries. Thus began a long period of major human constraint to, and control over, river courses. The impact of these mills cannot be overestimated. An entry from the Domesday Book of 1086 (Martin 2003), for instance, shows that in southern England alone there were 5624 watermills, which equates to one mill for every 50–60 head of population. Further manipulation of the water courses occurred during the fourteenth–eighteenth centuries as water meadows became popular as a way to increase food crop production by keeping water on the floodplain over winter, which in turn prevented the ground from freezing, thereby allowing the grass and crops to start growing earlier in the spring. These systems subsequently became redundant and fell out of use after the introduction of fertilizers and intensive farming methods in the late nineteenth century.

During the 1930s, dredging and straightening became the primary management activities in many lowland European Countries with a view to improve field drainage of agricultural land with little thought about the impact of this on river **biodiversity** or **hydrology**. The removal of hedgerows, which acted as buffer strips, increased the amount of soil load being washed into river systems. Further arterial drainage schemes were implemented during the 1960s in many countries, partly as a push towards ensuring self-sufficiency of food after World War II; in Austria, for example, 30 000 km of river have been regulated in the last 50 years. At the same time, an increase in housing development and associated infrastructure resulted in further straightening and deepening of rivers, disconnection from their associated floodplain areas and water abstraction to support the increased development. Many of the rivers of Europe today have effectively been turned into carriers of floodwaters in an attempt to move water from both rural agricultural land and from urban areas as quickly as possible, with little or no consideration of biodiversity or the natural flow dynamics and morphology of river systems (see Brookes 1988; Petts *et al.* 2002). These changes often result in a far more varied flow regime, including more flash floods, than would occur otherwise.

Deepening of channels prevented waters from reaching floodplains under high flow events. The negative impacts of these historical activities, as outlined in Table 17.2, are now beginning to be addressed, both in

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Table 17.2 The main human activities that have influenced river systems in Europe.

Activity	Reason	Impact
Land drainage	Agricultural	Loss of floodplains and wetlands, increased sediment supply to the river, increased flood peak through decreased storage; Disconnection.
Flood protection	Urban and economic	Isolation and loss of floodplains, loss of biodiversity; Increased discharge.
Reservoirs and dams	Water supply and hydro-electric power	Ecological deterioration downstream river; Fundamental change upstream, river to lake; increase in contamination; disruption to the transfer of sediment from upstream change.
Weirs	Mill systems	Prevents fish passage to upstream reaches; reduces access to spawning grounds, causing sedimentation locally.
Channelization	Erosion prevention; Flood control; Drainage of surrounding land; Navigation; Infrastructure.	Disrupts the physical equilibrium of the watercourse; Reduced riparian vegetation and increased water temperature (range of temp. change too); Increase in flow velocity and hence reduces habitat and biodiversity.
Dredging	Gravel and sand extraction increases capacity. Spoil heaps and levees.	Over widening and deepening of the river; instability and bank collapse; Removal of natural bed material; Raised bank full height; reduced spillover.
Water abstraction	Drinking water and agriculture	Lowering of river water levels and the floodplain water table.
Urban expansion	Increased populations and economic growth	Increase in hard surfaces, greater and faster runoff; Loss of riparian corridor and floodplains; Poor water quality; sewage, spillages.
Water quality	Population increase; Increased industrialization; Intensive farming, increases use of fertilizers.	Poor water quality, increased sedimentation, reduced riparian vegetation.

terms of economical viability and potential ecological gain. This has created the opportunity for river restoration to be taken more seriously as a viable alternative to present management practices, as there is an increasing acknowledgement that it is not always possible or acceptable to channelize and/or regulate rivers (see Petts 1984).

17.2.3 Disconnection of European rivers and their floodplains

No river system should be considered in isolation from its floodplain and yet throughout Europe there have, historically, been high demands on these areas; as a result many are now left with a legacy of land management and flood defence strategies often based on unnecessarily over-engineered solutions. The result is disconnected floodplains which, in a natural riverine environment, would not only have been of much higher value ecologically but would also have increased the storage capacity of the rivers in times of high flow, thus reducing the need to mitigate against flood impacts downstream.

17.3 CURRENT DISTURBANCES AND THREATS

Today the rivers and floodplains of Europe have importance for a wide range of plants and animals, however, very few of them can be truly defined as natural and this has serious implications for the associated ecosystems. The naturally diverse physical and biological habitats of Europe's river systems have declined in quality and area, particularly over recent decades.

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Floodplains, an integral part of the river system, have often been disconnected from the river channels, leading to reduced natural flood storage function and linkage to low floodplain and wetland areas. As mentioned, this linkage is essential for sustaining the species that make up the ecological communities, some of which are now under conservation protection. Similarly, in river ecosystems across Europe there have been dramatic changes in water quality, for example through excessive nutrient inflow leading to **eutrophication**. As mentioned, interventions such as canalization, dredging, draining and vegetation removal have also caused damage and **degradation** to river systems in Europe and elsewhere. Fish and invertebrate habitats, for example, have been destroyed by these measures, and the construction of dams and siltation of spawning grounds means that many native species are now threatened with decline or localized extinction or **extirpation** (see Halaham 2000).

Urbanization has had multiple impacts beyond watercourses simply being constrained in concrete channels or culverted. The input of effluent from sewage works and industrial sites and the runoff from roads has led to serious degradation in water quality. Habitats of plant and animal species along the river corridors within Europe have gradually declined in response to increased urbanization and the decrease in floodplain forest. Many of Europe's rivers now have little natural floodplain habitat with restricted riverine corridors, and a thin strand of open water is often all that remains to act as wildlife corridors. As these habitats have shrunk, 'Biodiversity Action Plans' have been introduced across Europe with the aim of rectifying habitat loss and other environmental damage. Within these plans, specific species associated with rivers and streams have been identified (for the United Kingdom, these are listed at http://www.ukbap.org.uk/Broad59.htm; similar lists exist for other countries).

Historically, the floodplain was a wet area avoided by industry and homeowners until drained, but with new improved flood protection techniques in urban areas, some of this reticence has been forgotten. A flood protection scheme is only as good as its design specifications, and even those designed to withstand a 1 in 50, or even a 1 in 100 year, flood scenario are, by definition, not guaranteed to keep every flood at bay. These engineered schemes are therefore unlikely to be sustainable economically in the long term; hence, there is now widespread recognition that reconnecting the floodplain and working with the river's natural processes should be considered as part of any flood risk management scheme.

17.4 RIVER AND FLOODPLAIN RESTORATION

As indicated in Figure 17.1, river restoration is a complex subject that affects not only the local situation and users of a particular watercourse, but also the wider **landscape** within a river catchment. All but a few rivers and floodplains within Europe have been severely degraded over a prolonged period, which means that restoration projects cannot simply aim for a return to some previous form. There is a growing awareness in the scientific and political worlds that naturally functioning riverine environments are vital to biological and ecological diversity at the landscape scale and also provide ecosystem services to human society. Spending on flood risk management that works with the rivers natural processes and aims to reconnect rivers to their floodplains is seen as one way to alleviate current often unsustainable flooding problems and indeed EU-wide policy recommends this approach (see Zöckler 2000; Department for the Environment, Food and Rural Affairs (DEFRA) 2005; Environment Agency 2010).

Restoration programmes need to focus on (1) the re-establishment of a *self-sustaining system* exhibiting dynamic equilibrium that can allow both the hydromorphological form and function of the river and its floodplain to develop as naturally as possible under the present and future climatic regimes, and (2) the interdependent **habitats** and organisms to properly interact and utilize available habitat and resources provided by a natural river. This in turn will help to deliver the **ecosystem services** that are essential within society. However, very few societies are, at present, in a position to achieve this, and hence individual needs and objectives must be acknowledged. This can considerably influence the outcomes of restoration schemes. Furthermore, although lessons can be learnt from other counties, such as the United States (FISRWG 1998; Bernhardt *et al*. 2005) and Australia (Rutherford *et al*. 2000), the techniques applied there may be wholly inappropriate for European rivers because of differences in climate, species assemblages or river typology.

At its most basic, *de-culverting* (or 'daylighting' in the United States) can equate to a huge increase in the biodiversity value of a watercourse. For example, in Switzerland over the last 130 years, approximately

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90 km of Zürich's streams were culverted during the last 100 years or so, but since a federal law was introduced in 1991 imposing the separation of clean water from combined sewer systems, engineers have restored over 14.5 km of surface streams in this city alone (Pinkham 2000).

In essence, the factors limiting natural function of the river ecosystem need to be identified and then the system restored in a manner that will move it away from the current degraded state and past the controlling biotic and abiotic **thresholds** (*sensu* Hobbs & Harris 2001, and see discussion in Mainstone & Holmes 2010). Only by surpassing the thresholds is it possible for the ecological **conditions** to improve (Hobbs & Harris 2001). It is also important to recognize that whilst complex, river restoration has to be **adaptive** and aim towards **resilience** of the system in light of the anticipated changes to local climate conditions (Harris *et al.* 2006) – it is not simply a matter of restoring a facsimile of what was there before.

17.4.1 Economic and legislative justification of restoration

Various EU directives now in place are aimed at implementing measures at the continental level that advocate conservation of sites that are under pressure from development and associated pollution; see especially the EU Habitats Directive 92/43/EEC (EC 1992a) and the more recent Water Framework Directive (WFD) 2000/60/EC (EC 2000). The WFD requires a more *holistic approach* by considering the interconnected elements that constitute an aquatic ecosystem and determine its ecological status and health (see Chave 2001). Nonetheless, each country has inevitably started from a different point, depending on the historical use of its rivers, with issues ranging from water quality to inappropriately engineered rivers. Luxembourg, for example, has only inland rivers and thus waste water (water quality) is the main problem; Ireland has spent over €15 million on fisheries restoration measures (see O'Grady 2001; see also Figure 17.2); and southern Spain's main concern is improving in-stream flows where intensive water extraction for irrigation has caused severe degradation (Cachón de Mesa 2001). Furthermore, any restoration must be appropriate to the specific landscape and the historical heritage. In the United Kingdom, the government document Planning Policy Guidance 25 (PPG25 2001), revised to Planning Policy Statement 25 in March 2010, states that planners should make the most of the benefits of green infrastructure for flood storage and conveyance, re-create functional floodplains and set back flood

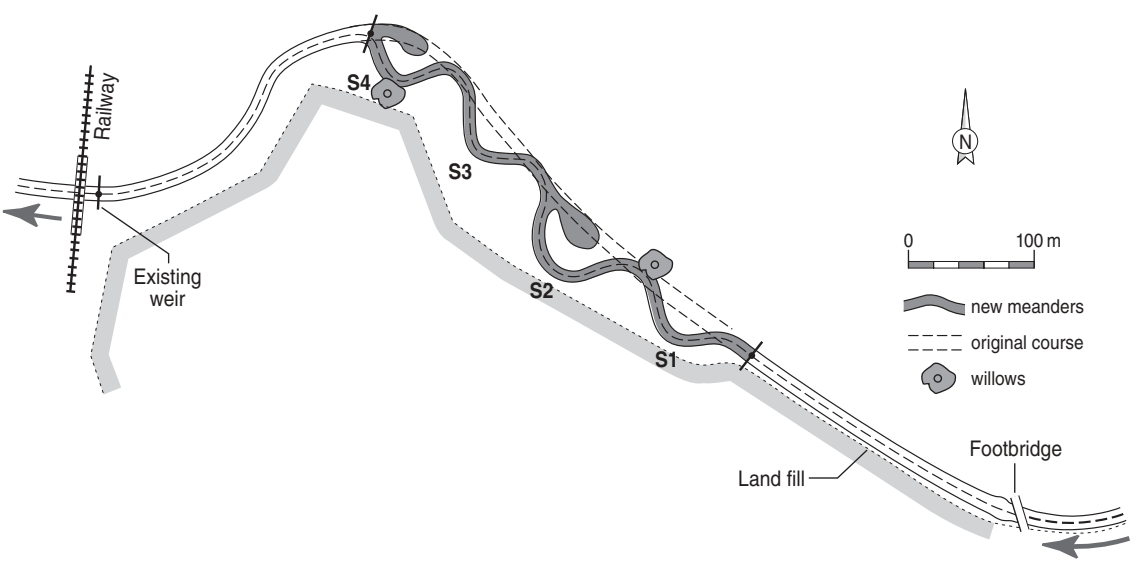


Figure 17.2 Diagram of re-meandered section of a previously straightened river.

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defences, whilst the EU's Floods Directive (2007/60/EC) aims to reduce flood risk in the context of human health, the environment and cultural and economic issues. However, in many countries, the scientific evidence that new urban developments will not increase flooding in vulnerable highly urbanized areas is still not available. In continental Europe, the pressure not to change traditional flood defence ways is exacerbated by the transboundary nature of rivers. Those countries where the precautionary principle of highly engineered rivers and flood defence systems is widely applied are often at the downstream end of the river. The Netherlands is just one example where the government has little control over what water is received from the Rhine and Meuse. Whilst the River Basin Management plans drawn up for the Water Framework Directive potentially provide a more uniform catchment-wide view to the management of the rivers across country boundaries, it will take some time before associated programmes of measures can all be implemented, and until such time individual countries will inevitably remain cautious about altering existing approaches.

However, without reliable and complete estimates of the *costs and benefits* of river restoration, much work is undertaken on a piecemeal and opportunistic basis. Directly comparing the cost of a road improvement scheme and the value of floodplain woodland is still, for example, very difficult. Legislation has assisted restoration objectives such as the EU Habitats Directive 92/43/EEC (EC 1992a) that requires member states to protect rare habitats and improve to 'favourable condition' habitats supporting rare species. Similarly, in England, the Wildlife and Countryside Act 1981 and the Countryside and Rights of Way Act are examples of acts which can encourage river restoration actions. There are now moves to include cost–benefit analyses which focus on the services that ecosystems provide rather than just actions to conserve specific species or features. To date, inadequacies remain in the interpretation of biodiversity, aesthetic, public enjoyment and natural heritage issues in the ecosystem services approach.

17.4.2 European River Restoration in action

There is no simple solution to restoring and rehabilitating rivers and their floodplains, particularly in terms of long-term **sustainability** of a project and meeting the aspiration of **ecological restoration**, as defined by the SER Primer (Society for Ecological Restoration International (SER) 2004; see Chapter 2). The success of a project will depend on the **reference** conditions against which it is measured. Projects have to consider how conditions at a site relate to not only the historical attributes but also the contemporary and future context. Therefore, a variety of integrated elements (see Figure 17.1) and needs have to be considered on their own merits. It is not simply about putting things back to the way they were a number of years ago. In some cases, a previously straightened reach may be restored to a meandering form (see Figure 17.2) bringing with it the added benefits of increased biodiversity, but this is by no means always the most appropriate method. The recovery of an ecosystem may, for example, be assisted by smaller scale restoration principles, such as re-profiling river banks and creating wet berms to rehabilitate habitat and re-invigorate natural processes along existing river sections (Figure 17.3). The following section provides some examples of the types of issues impacting on rivers and floodplains and also outlines those factors that are driving river restoration in various countries across Europe. The following examples are by no means comprehensive and many more examples can be found in other textbooks (including Ward *et al*. 1993; Middelkoop & van Haselen 1999; Klijn & Dijkman 2001; Nijland & Cals 2001) and the River Restoration Centre's (RRC) *Manual of Techniques* (RRC 2002).

United Kingdom

In the United Kingdom, rivers have been substantially altered over the past few centuries, with at least 80% of lowland river reaches having had at least part of their channel modified (Raven *et al*. 1998). Degradation has been particularly severe in the last 50 years through intensive management. Programmes of draining, dredging and straightening have altered almost all rivers. Since 1990, various groups and government agencies have been working to change the perception of river managers and to promote a more sustainable approach to river and floodplain use and river management, rather than purely as flood defence drivers.

In the 1980s, conservation and river enhancement was restricted to voluntary bodies and was seen as an 'add-on' to works under the statutory duties of flood

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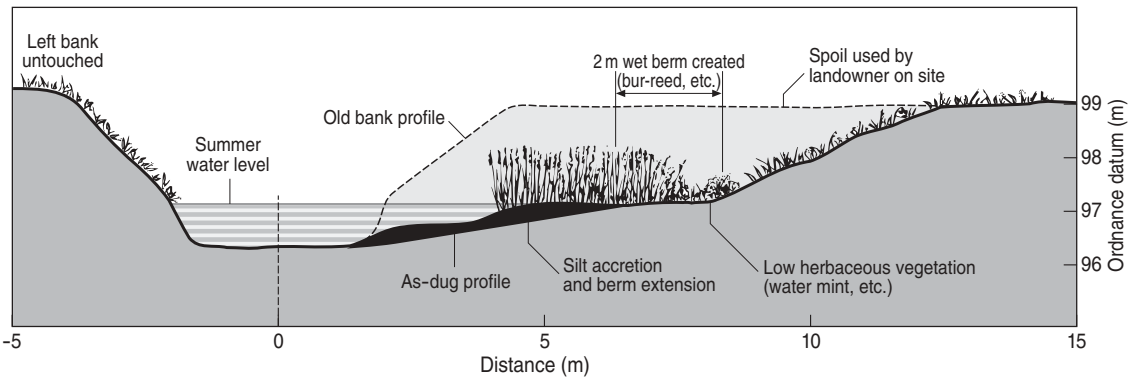


Figure 17.3 Creation of online bay by reprofiling an old bank of a previously trapezoidal channel. Herbaceous – herbaceous vegetation; water mint – *Mentha aquatica*; as-dug profile – refers to the designed dug profile for the specific project; and ordnance datum (m) – height above sea level.

defence, fisheries and water quality. Many rivers were still seen as efficient conduits for the evacuation of troublesome water. In the early 1990s, concern for the United Kingdom's rivers led to the formation of the River Restoration Project, and the design and implementation of two RRP demonstration projects on the rivers Cole and Skerne. This work, funded by an EU LIFE grant and in conjunction with works in Denmark (e.g. the River Brede), acted as a catalyst for change, supporting a rising number of restoration and enhancement projects in the last 10 years. The RRC is now well established in the United Kingdom with the principle aim to provide information and advice on river management for restoration and enhancement. The RRC holds the National River Restoration Inventory of over 2000 river restoration projects and has produced a manual detailing 47 river restoration techniques from 17 UK projects (RRC 1999, 2000; Centro Italiano per la Riqualificazione Fluviale (CIRF) 2001). One example of restoration to 're-meander' a river in the United Kingdom is presented in Box 17.1 and depicted in Figure 17.4.

The aspiration to restore rivers continues, but the focus is now on delivering individual projects within the context of linking projects benefits at a catchment scale. The London Rivers Action Plan (http://www.therrc.co.uk/lrap.php) is an example of this approach, through improving urban watercourses, and includes examples of restoration work within the River Thames catchment, such as de-culverting (River Ravensbourne at Norman Park), re-meandering (River Quaggy at Chinbrook Meadows, River Brent at Tokington Park, River Roding at Ray Lodge Park), the removal of tidal sluice gates (Rainham Creek) and the creation of wetland habitats (Watermeads Island on the River Wandle).

Denmark

It is estimated that 97% of Denmark's 40 000 km of natural rivers have been altered in their physical form (Brookes 1984). In addition, another 30 000 km of human-made watercourses exist; these channels were designed to drain wetlands and floodplains and to increase agricultural production. Much of the work to drain Denmark was undertaken in the twentieth century, together with fish farming and industrial and urban expansion. Channelization was also frequently accompanied by mills and other structures, effectively denying free passage to fish and macro-invertebrates. Through legislation and changes to the administration of Danish watercourses, management improvements and river restoration have been implemented since the mid-1980s. Twenty-four such schemes are detailed in Hansen (1996). Many of these are intended to naturalize the physical form after water quality standards have been achieved. In 1996, arising from a joint Danish–UK collaboration, Denmark became the first base for the European Centre for River Restoration. Since that time, the directorate of the centre has passed through various member states and is currently housed in the Netherlands. Two effective examples of restoration in

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Box 17.1 An example of river restoration in the United Kingdom

PROJECT NAME: River Skerne in Darlington, United Kingdom

BACKGROUND:

- A straightened and realigned river due to a combination of industrialization and urbanization over some 200 years.
- A 2 km reach was chosen for restoration.

AIMS:

- Re-create a more naturally functioning watercourse.
- Develop an attractive local community landscape and encourage local public engagement throughout the project to ensure project 'ownership' (Figure 17.4)

TECHNIQUES USED:

- In-channel deflectors to re-create sinuosity and flow diversity, bank reprofiling, channel narrowing, spoil disposal, landscaping, surface water outfall rationalization, backwater creation, soft revetment engineering (i.e. bankside protection to prevent erosion by using plants), increasing floodplain storage, extensive marginal planting of native species and the creation of wetland scrapes.

PROJECT FUNDING:

- EU, statutory government environmental agencies and the landowner (local council).

BENEFITS:

- A more natural river system with improved self-regulatory capacity.
- Improved flood management.
- Increased wildlife and improved water quality.
- Amenity and landscape appeal – 'a piece of countryside in a town'.



Figure 17.4 River Skerne, Darlington, United Kingdom: (a) before restoration, (b) log toe revetment (i.e. support at the bottom of the bank using tree trunks) during construction on the river (courtesy of Northumbrian Water, United Kingdom) and (c) after restoration.

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Figure 17.4 *Continued*

Denmark are given in Boxes 17.2 and 17.3 and Figures 17.5 and 17.6.

The Netherlands

The Netherlands has a long history of managing its rivers for settlement and farming. Being at the downstream receiving end of strategically important rivers of continental Europe such as the Ruhr, Meuse, Rhine and Emscher, to name just a few, it also has a similarly long history of protecting itself from the results of the river management practices of other countries upstream. At present, the main function of much of the floodplains in the Netherlands is agriculture. As a result, the floodplain area available to store and attenuate major floods is limited compared to the large flat wetland area which would naturally have been available prior to intensive farming. For this reason, floodplain restoration is now of high priority, encouraging the maintenance of landscapes that have

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Box 17.2 An example of river restoration in Denmark

PROJECT NAME: River Skjern, Denmark
BACKGROUND:
- A channelized and dredged river between 1962 and 1968 with approximately 4000 ha of floodplain, wetlands, reedbed, meadows and marshlands drained to allow agricultural production on its fertile soils.
- Peat soils became desiccated, lowering the entire farmed area.
- Continuous and expensive updating of the pump systems was required to drain the low-lying ditch systems into the river.
- Farmlands were a major source of sediment into the river, causing severe water quality pollution and major deposition along Ringkøbing Fjord.

AIMS:
- To restore the lower reaches of the Skjern system, re-creating over 2200 ha of typical floodplain and the sinuous course of the once multithreaded river (Figure 17.5). In 1998, the Danish Parliament, with a huge majority, passed a Public Works Act for the work.
- To restore the natural functioning of the system to once again provide a rich variety of habitats for some of Europe's endangered species such as the bittern, otter, black tern and corncrake.

TECHNIQUES USED:
- Restoration of 4 km of river and the movement of 2.7 million cubic metres of soil.

PROJECT FUNDING:
- The project was budgeted at approximately €319 million (National Forest and Nature Agency 1999).

BENEFITS:
- The project was completed in 2002 and by 2009 after 3 years of agreeing land acquisition deals for farmers.
- The river has naturalized with shallow waters supporting a range of migratory waders.
- In addition educational facilities, nature trails, and picnic facilities have been developed for people; the area is in the process of being designated a national park.

Box 17.3 A second example of river restoration in Denmark

PROJECT NAME: The Houting Project, Denmark
BACKGROUND:
- The Houting (*Coregonus oxyrinchus*), a protected species of fish, was once distributed throughout the freshwaters that flow into the Wadden Sea.
- Now only 6 rivers support this species, while industrialization has severely limited the Houting's migration and spawning areas.

AIMS:
- To restore and maintain favourable conservation status for Houting on the rivers Varde, Sneum, Ribe and Vida.

TECHNIQUES USED:
- 13 in-channel obstacles (mainly weirs associated with fish farms and hydro-electric power generation) need to be removed.
- One specific example on the River Vida is shown in Figure 17.6; 2 m high weir was removed and the old millpond was separated from the river. A gravel bed and banks installed.

PROJECT FUNDING:
- The 13.4 million Euro project was funded by the EU-Life spawning areas for the fish.

BENEFITS:
- 130 kilometres of river channel habitat and 500 hectares of new nursery.
- New spawning areas have been developed for the fish.

more **heterogeneity**, including wetland hollows and floodplain woodland, and can support an increase in biodiversity. From a species perspective, the enhancement of poorer quality, still-water bodies, which are created as a result of historical gravel and sand extraction, and the reinstatement of secondary channels are also very beneficial, acting as refuge areas for fish and macro-invertebrates. The long history of flood defences, multiple raised embankments and pollution from upstream has meant that today those floodplains that

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Figure 17.5 River Skjern, Denmark, (a) before and (b) after restoration diagrams. (Adapted from the Skjern River Restoration Project 1999.)

have been frequently inundated are covered with a layer of clay or sandy clay. The expected diversity of floodplain topography, soil type and vegetation has often disappeared. The solution being adopted today is both giving 'room to the river' and lowering the floodplain to allow more natural **connectivity** regimes (RIZA 1996; Smits *et al.* 2001). Any sustainable flood protection measures will necessitate imposing limits on the amount of floodplain land that may be used for purposes that are not directly river related, and the most sustainable flood defence measures are likely to be those that are tied in with the natural processes of rivers. In addition, lowering the floodplain by removing the clay deposits on the floodplain down to the original profile (economically viable through its use in brick manufacturing) provides an increase in habitat

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Figure 17.6 (a–b) The River Vida, Denmark, where a weir was removed and new fish habitat and connectivity improved.

diversity as well as renewed storage capacity (Wolters *et al.* 2001).

Italy

At the end of the twentieth century, a growing need for energy supply drove the implementation of hydroelectric industrial systems and storage devices throughout the Alps and Apennines regions of Italy, culminating in 495 plants with a total capacity of 14 312 MWh mostly located about 2000 m above sea level. Furthermore, the combination of extensive mountain ranges, urbanization and development along valley floors and floodplains meant that natural river dynamics were

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Box 17.4 An example of river restoration in Italy

PROJECT NAME: River Zero, Italy
BACKGROUND:
- This project concentrated on implementing a catchment strategy to protect key freshwater and estuarine habitats associated with the Venice Lagoon.

AIMS:
- Reduction of nutrient (nitrogen and phosphorus) by identifying the areas at risk in the catchment.
- Create buffer zones to reduce pollution entering the rivers within the catchment at strategic points.

TECHNIQUES USED:
- Buffer areas were created through riverine lakes, large reeded bank margins, floodplain lakes and large areas of riparian woodland all supporting a range of habitats.

PROJECT FUNDING:
- Locally funded.

BENEFITS:
- Creation of 16 km of restored river channels.
- 30 hectares of riverine and floodplain lakes.
- 10 hectares of reedbeds (Figure 17.7).

considered to be a hydraulic risk within river corridors (i.e. unacceptable risk of flooding in urban areas). As a consequence, many rivers suffered the same fate as much of the rest of Europe, resulting in concrete channels, engineered infrastructure, extraction of gravel and sand, intensive agricultural use of soil and a loss of biodiversity for all but a few rivers. By the end of the 1980s, the Italian government produced important normative actions concerning the water management policy that led to the introduction of River Catchment Authorities that no longer followed administrative borders and of systems of *Integrated Management of Water Resources* that follow flow regimes from source to discharge. In this context, the Italian Centre for River Restoration (CIRF 2001) was established in 1999 as a nonprofit association that aims to promote an innovative approach to water and territory management through pilot projects. See Box 17.4 and Figure 17.7 for an example in Italy.



Figure 17.7 River Zero, Italy, after restoration. (Courtesy of CIRF, Italy.)

Transboundary systems

Some central European rivers have the added complication of flowing through a large number of countries, all with a vested interest in the river. Some may see (or may previously have seen) it as a conduit for waste and flood waters, and others downstream may see it as the bringer of pollution and floods. Often interpreting national policies on the sustainable management of rivers is a difficult enough task, without having to come to international agreement. However, some good examples do exist that take into account the requirements of local inhabitants, improve biodiversity and ensure that the economic needs relating to flood defence are met. In this context, good schemes are those that aim to create a sustainable river and floodplain solution, which function as naturally as possible within the constraints of today's increased pressures on the surrounding land.

Within northern mainland Europe, the Rhine is one of the most important rivers and, whilst its source is in Switzerland, it flows through France, Germany and the Netherlands to the North Sea. It has been the

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foundation of settlements and commerce for many centuries, and hence human impact has been considerable. One of the earliest recorded impacts was in 1449, when over-fishing and pollution led to declines in fish population. Even at this point, the international 'Strasbourg Regulations' were adopted to improve the Rhine, yet further deterioration was still to come. Between 1817 and 1874, considerable straightening occurred due to major engineering works in an attempt to improve navigation, reduce flooding and recover alluvial areas for farming. By 1950, Atlantic salmon (*Salmo salar*) in the Rhine had disappeared as habitats diminished and physical barriers increased. Since 1952, the Rhine Commission has worked toward improving water quality, river ecology and pollutant emissions. Many individual and large programmes of works have been and are being undertaken, including flood retention in Germany and embankment removal in the Netherlands (Figure 17.8).

17.5 PERSPECTIVES

We conclude this chapter by reflecting on a number of problems regarding the prospects for ecological restoration of degraded rivers and floodplains. Although the projects covered here are forward thinking and have resulted in examples of best-practice river restoration, not all European countries are at present in a position to implement such ideas. Nonetheless, many are already accepting that naturally functioning river systems are intrinsic to our future **human well-being**. But despite this, there continue to be widespread disturbances and profound threats to river ecosystems that must be highlighted and dealt with appropriately.

In central and eastern Europe, *water quality* remains a crucial factor to the success of river restoration, but there is little or no money for improvement. In the Russian Federation, for example, 60% of existing sewage treatment works are overloaded and 40% need

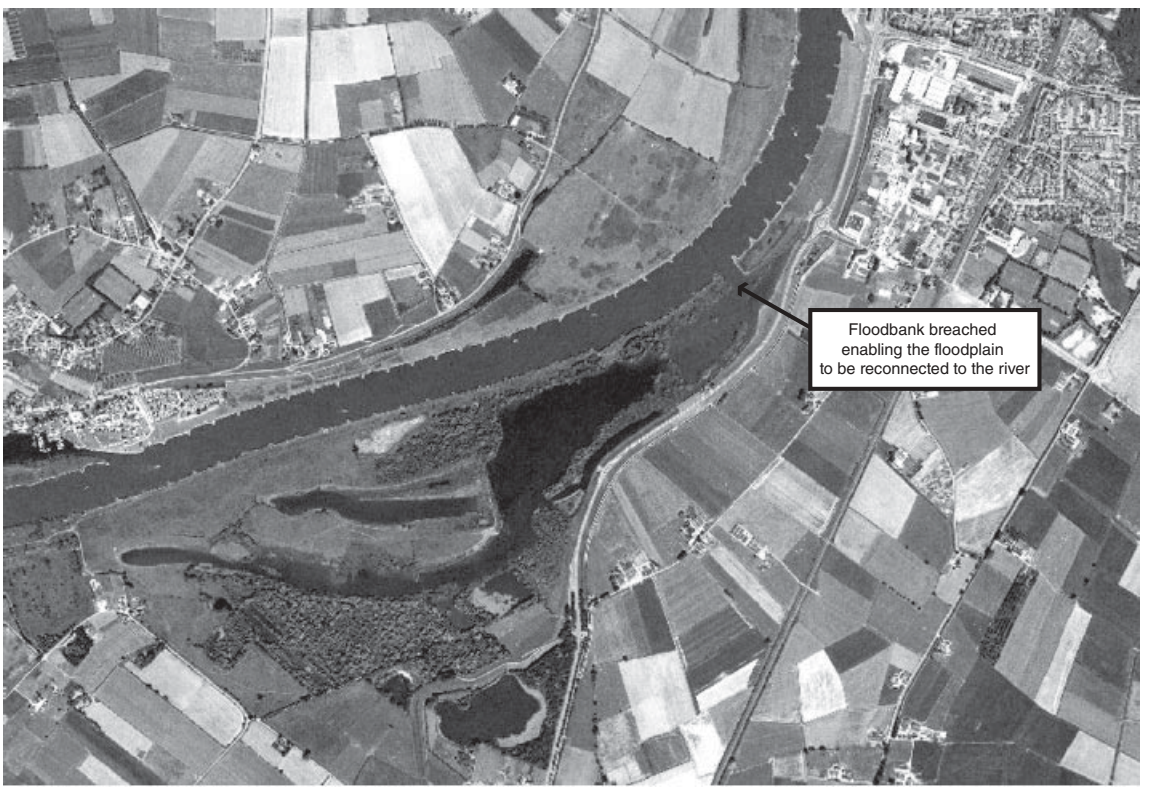


Figure 17.8 Flood bank removal on the river IJssel, the Netherlands. (Courtesy of Ute Menke, ECRR.)

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repair. This has serious implications for contaminated land, and most migratory fish, such as sea trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and sturgeon (*Acipenser sturio*), are virtually extinct.

The idea that river restoration is important remains a divided issue among EU member states. Spain has an active Restoration Centre, but the country is still grappling with over-use of and over-reliance on river water for irrigation and increased urbanization, especially in southern parts of the country. This has gone hand in hand with continued building of major dams and an increase in pollutants both of which have been detrimental to the ecological status of many Spanish rivers. In comparison, the Netherlands already has a suite of government policies and subsidies in place, aimed at putting river restoration high on the national agenda. Many river restoration centres throughout Europe are now promoting the importance of rivers and floodplains to support ecological diversity and sustainable options for flood management. To date, the United Kingdom, Italy, Denmark, the Netherlands, Spain, Norway, Romania and Russia all have such centres, with an overarching *European Centre for River Restoration* acting as coordinator and clearinghouse. Furthermore, the World Wildlife Fund project *Europe Living Rivers* is also championing the idea of restoring rivers and wetlands across Europe. This project is working to protect and restore over 65 partnership river projects within 25 European countries.

In the United Kingdom, there is growing acceptance that any flood control measure should ensure that there is no net loss of **biodiversity** and that, wherever possible, environmental enhancement should be promoted; to this end, the UK government (DEFRA 2002) has published guidance on the environmental appraisal of flood defence to help ensure that the implications for flood prevention and management are fully considered in decision making. Such schemes remain in their infancy, yet as many existing flood defence schemes will soon no longer be viable to maintain on economic grounds alone, the justifications for more ecologically friendly options are likely to be considered more seriously, as sustainable and long-term cost-effective alternatives to raising existing flood wall defences. Developments in urban landscape planning and design, inclusion of sustainable urban drainage systems in national and local authority planning guidance and better integrated solutions (from engineers, ecologists and landscape architects working together, amongst others) to old problems all add to a wide knowledge base readily available through Europe-wide collaborations.

There is now also much discussion about future **climate change** and the impact on biodiversity (Gitay *et al.* 2002) and how best to manage our rivers to **mitigate** habitat stress (Palmer *et al.* 2008). By extension, this has implications for river systems and their future flow regimes. This in turn could have an adverse effect on ecological status and hence any future restoration initiatives should build in some design flexibility to account for changing scenarios and appreciate that rivers are very sensitive to change (see Downs & Thorne 1998). More recently, Durance and Ormerod (2008) have concurred with these views, showing that macroinvertebrates are extremely sensitive to small temperature changes, but conversely, restoration measures can offset some of the negative impacts.

Inevitably, any river restoration put into practice will be subject to a degree of risk and *uncertainty* (Darby & Sear 2008). By ensuring that new schemes are fully appraised, both pre- and post-project, in terms of their impact on the river geomorphology, ecology and public perception, those charged with restoring rivers today can learn from each completed scheme. To put this into perspective, it is essential that new projects be monitored against initial specific and measurable objectives, such as habitat enhancement or increased channel morphological diversity. New methods to achieve this are being discussed (England *et al.* 2008), and it is recognized that monitoring has to be cost-effective and linked to the size and risk of a specific project. Only by including appropriate levels of monitoring can we be certain of the extent to which any scheme can be classified as either a success or a failure and allow scientists to ascertain what types of schemes are best suited to different environments and for various requirements. We can then build on a growing evidence base to provide for a future of sustainable river systems that work with natural processes and functions.

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frequency and magnitude of flooding in Scotland. Thanks also to Jelte van Andel for his patience and help in editing this chapter.

APPENDIX: WEBSITES

European Centre for River Restoration (ECRR) (http://www.minvenw.nl/rws/riza/home/ecrr/)

Italian River Restoration Centre (CIRF) (http://www.cirf.org)

River Restoration Centre (RRC) (http://www.therrc.co.uk)

United Kingdom Biodiversity Action Plans (UKBAP) (http://www.ukbap.org.uk)

Wise Use of Floodplains (WUF) (http://www.floodplains.org)

World Wildlife Fund (WWF) (http://www.wwf.org)

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Chapter 18

RESTORATION OF FRESHWATER LAKES

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18.1 INTRODUCTION

The development of modern society, including the demographic explosion and intense industrial and urban developments of the past 150 years, but especially of the last half a century, has caused inland surface waters to become heavily enriched by agricultural fertilizers and toxic substances. The human-made alterations to freshwater aquatic ecosystems worldwide – not only lakes but also reservoirs, various kinds of wetlands and rivers of all sizes – have been severe and destructive. Despite recent attempts to restore some lakes and other bodies of freshwater, these ecosystems are arguably among the most damaged and vulnerable of all (Schindler 2006, among others). In the western world, lakes and reservoirs are recreational sites and tourist attractions (for swimming, boating, fishing etc.). In addition, they are major sources of water for drinking, irrigation, industry and transportation, and sink areas for floodwater storage. Whereas lakes and lagoons also act as final sinks for many of the waste products of human activity, rivers carry human and animal wastes, and other wastewater effluents (urban, industrial and agricultural), down to the sea. For better or worse, this is a service that society demands of lakes, lagoons, wetlands and rivers. Increasing demand for fresh water has also led to the creation of storage reservoirs in the floodplains of many river systems (Moss 1998). All too often, conventional management plans for these aquatic ecosystems ignore their regional watershed context, their hydrology, and the socio-economic systems of which they are part.

For sustained and long-term use, many aquatic ecosystems should be not only protected by abatement of pollution, but also restored or rehabilitated. Several restoration studies have been carried out in the United States and Europe on how to facilitate or accelerate the return of disturbed wetland ecosystems to functionality similar to the conditions prevailing prior to major disturbance (e.g. National Research Council (NRC) 1992; Cooke *et al.* 2005). The goal of **ecosystem restoration** is to emulate or reconstitute a more or less natural and self-regulating system that is integrated within its ecological landscape (SER 2004; see also Chapter 2). In practice, however, what is often called 'lake restoration' is in fact **rehabilitation**. It tends to focus on improvements in *water quality* (using parameters such as water clarity, dissolved oxygen conditions and the amount and species of algae present) to improve lake conditions designated for human use and health such as recreation, fishing, water supply, nature conservation and biodiversity protection. As is done throughout this book, we use the term 'restoration' in a general sense, while recognizing that most lake restoration projects aim primarily at improving the most important functional attributes rather than a hypothetical return to some kind of pristine ecological condition. In practice, most such attempts focus primarily on eliminating undesirable consequences of human-induced disturbances.

Restoration is steadily becoming a critical part of national and international efforts to improve both water quality and the ecology of freshwater ecosystems (NRC 1992), especially in western Europe, the United States and Canada (Cooke *et al.* 2005). Lake restoration work in the United States and western and northern Europe started in the early 1970s (e.g. Bjork 1972). By 1975, the US Environmental Protection Agency had initiated the Clean Lakes Program by amending the Federal Pollution Control Act. Subsequently, more federal funds were provided to clean more than 300 lakes in 47 federal states. Restoration of acidified lakes by liming, as in the north-eastern United States, became a relatively common practice in Scandinavia. In Europe, the Water Framework Directive (WFD) was established in 2000 (European Union 2000). It requires that in European member states all inland and coastal waters within defined river basin districts achieve at least a 'good ecological status' by 2015. Moreover, an important aim of the WFD is to initiate water pollution control by reducing emissions of harmful substances into waters (see papers in Solheim & Gulati 2008).

Since 1975, some 25 lake restoration measures and techniques have been developed worldwide and tested for their effectiveness, cost per unit area, required frequency of employment, range of applicability, etc. (see in Cooke *et al.* 2005). Since the early 1980s, **lake biomanipulation** as a tool for lake restoration has often been used, both in Europe and in North America (see section 18.3.2). Lake restoration is now one of the key topics of water management (Gulati & van Donk 2002; Nienhuis & Gulati 2002).

In this chapter, we present an overview of published results of ongoing studies of aquatic ecosystem restoration and rehabilitation projects of the past four decades, especially those in north-western Europe and North America. Particular emphasis is paid to shallow lakes, which are particularly susceptible to eutrophica-

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tion. First we shall assess the major types of disturbances of lakes, identifying the problems and main symptoms, and then discuss lake restoration strategies and techniques in use. Finally we draw some conclusions and discuss research and development prospects for the future.

18.2 DISTURBANCE FACTORS AFFECTING LAKES

Continuously rising inputs of nutrients, organic matter, silt and still more toxic contaminants, have led to sharp deterioration of water quality in many lakes and reservoirs over recent decades. This entails increased growth of algae and aquatic plants, and accumulation of organic matter, including detritus, leading to reduced water transparency. Water transparency is considered an indicator of lake and reservoir health. The most persistent and widespread water quality problem related to human use of lakes and reservoirs is **eutrophication**, but **acidification** remains a problem in some parts of the world. Here we discuss both problems, presenting their main causes and symptoms. This will set the stage for discussing restoration strategies in the following section.

18.2.1 Eutrophication

Eutrophication is a natural ageing process of lakes that causes a steady increase in production of biomass due to a gradual accumulation of nutrients and a slow decrease in lake depth. In classical terms, eutrophication is the enrichment of water by inorganic plant nutrients, especially N and P. Increasing eutrophication in the early 1970s of the Great Lakes and many other lakes and reservoirs in the United States and Canada, along with many lakes in western Europe, raised widespread public concern. In view of P-enrichment in lakes and related problems of eutrophication, many state agencies funded large-scale research projects, such as the Experimental Lake Area in Winnipeg, Canada (e.g. Blanchfield *et al.* 2009). The eutrophication models thus developed provided insight into the quantitative relationships between *nutrient loading* rates and algal biomass and production (Vollenweider 1987). What emerges clearly is that the main causal factors for eutrophication are direct, point discharges of human and animal wastes, as well as diffuse agricultural **runoff** from catchment areas into lakes. Accordingly, the rates of algal production and nutrient accumulation in lake sediments rise and the effects of eutrophication will persist and accumulate over time (Rast & Thornton 1996).

In temperate regions, increases in light and water temperature in eutrophic lakes, especially in the months of spring, generally result in increased algal growth rates and production, dominated by cyanobacteria. Consequently, the underwater light conditions deteriorate. In eutrophic lakes, many genera of cyanobacteria (e.g. filamentous genera: *Planktothrix* (*Oscillatoria*), *Anabaena*, and *Aphanizomenon*; and the cosmopolitan, colony-forming species *Microcystis aeruginosa*) gradually come to dominate because they form blooms and scums. The ability of cyanobacteria to dominate phytoplankton over a wide range of nutrient levels, as well as to fix atmospheric nitrogen, together with their relatively low palatability to zooplankton, allows them to attain high densities and biomass. Thus, they can persist and dominate the phytoplankton of shallow, eutrophic lakes throughout the main growth period (spring–autumn), and even overwinter. Lastly, several species of cyanobacteria can produce potent toxins, which constitute a menace to both human and animal health (Codd 2000).

Rast and Holland (1988) provide a decision-making protocol for developing and implementing eutrophication control measures in lakes and reservoirs (Figure 18.1). This scheme addresses the various concerns and cost-effectiveness to be considered when selecting feasible, remedial measures. A practical framework for the management and control measures of lakes and reservoirs is to (1) assess the available information, (2) identify eutrophication problems, (3) analyse costs and expected benefits of the alternative management strategies and adequacy of institutional and regulatory frameworks for implementation of a given strategy and then (4) select a control strategy and publicity measures and evolve mechanisms to minimize the recurrence of eutrophication problems.

18.2.2 Acidification

Fortunately, acidification problems in lakes and reservoirs in Scandinavian countries and the United Kingdom are less grave today than they were in the late twentieth century. In the United States, however, acidification is still an important environmental hazard in

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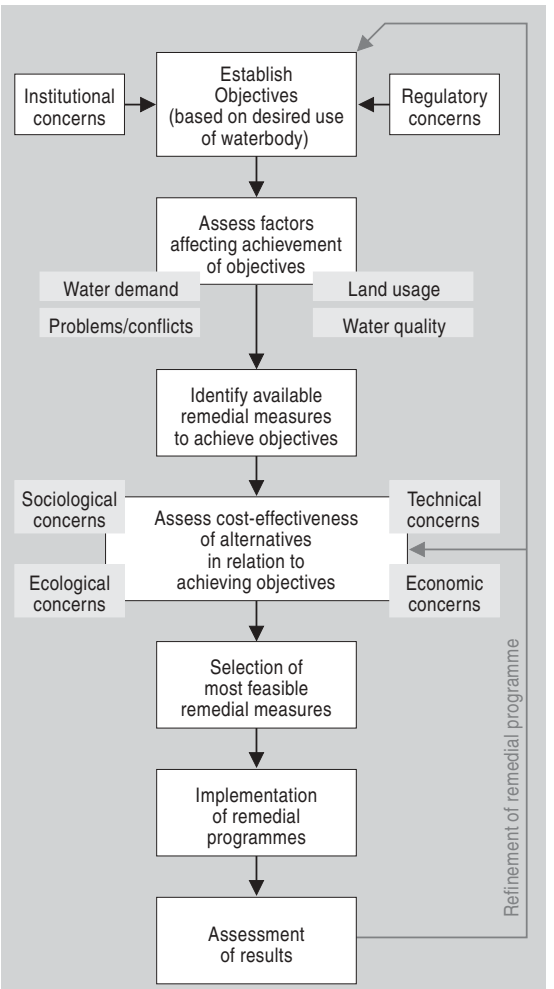


Figure 18.1 Schematic representation of a recommended decision-making process for the selection and implementation of eutrophication control programmes in lakes. (From Rast and Holland 1988. Reproduced by permission of Ambio.)

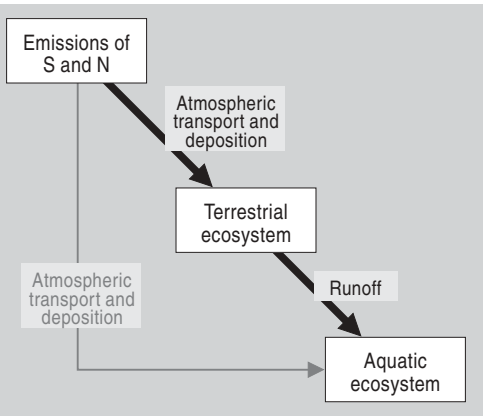


Figure 18.2 The direct and indirect steps linking emissions of SO_2 and NO_x and deposition to aquatic ecosystems. Note that the catchment area (terrestrial ecosystem) and the runoff into lakes are more important causes of lake acidification than direct, atmospheric deposition. (From Steinberg and Wright 1994. Reproduced by permission of John Wiley and Sons Ltd.)

lakes, second only to eutrophication. The hyperacidity of rainwater ($pH < 4.7$) in the affected areas is due mainly to polluted air masses containing S and N compounds (SO_2 and NO_x), released from the burning of fossil fuels, and their transport by winds often originating at great distances from the place of deposition. These compounds are transformed by photo-oxidation to sulphuric acid (ca. 70%) and nitric acid (ca. 30%) before they eventually fall to Earth as 'acid rain'. These emissions are linked via runoff from terrestrial ecosystems and through direct transport and deposition in aquatic ecosystems (Figure 18.2). In farms with intensive cropping and/or animal husbandry, nitrate is formed from the large amounts of ammonium emitted. The overall nitrification reaction leading to nitrate formation ($NH_4^+ + 2O_2 \rightarrow NO_3^- + H_2O + 2H^{++}$) then acidifies the watercourses. The buffering capacity of lake water against acidification is determined by the concentration of bicarbonate ions. The acidification process in lakes occurs in three main steps, related to the decrease in pH caused by lowering of the buffering capacity of water (Mason 2002). In the first main step, bicarbonate (HCO_3^-) buffers the input of strong acids ($H^+ + HCO_3^- \rightarrow H_2O + CO_2$). The pH remains generally above 6, and the plant and animal communities remain stable as the lake loses alkalinity. In the second step, transition lakes, the bicarbonate buffer may be lost during long periods of acid inputs, resulting in large fluctuations in pH and periodic fish kills. In the final stage, acid lakes, the loss of alkalinity is complete and the lake retains a low but stable pH, usually below 5, while metal levels, especially aluminium, may be elevated, resulting in the extermination of fish populations. Lakes that have a high buffering capacity will never reach the permanent acid state. Limestone in a drainage basin may help prevent acidification consid-

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erably; regions with a calcareous geology are not sensitive to acidification.

Acidification causes marked biotic changes in communities of lake organisms. Shifts in the competitive relationships of the algae or the disappearance of **keystone species** can alter community structure (Eriksson *et al.* 1980). When acidified, the solubility of many metals (aluminium, iron, copper, zinc, nickel, lead and cadmium) in water increases, but that of some other metals (mercury and vanadium) decreases. Adverse effects on organisms are invariably attributed to the increased solubility of aluminium and its shift to the toxic Al^{3++} form, which on its increased mobilization also causes precipitation of P and humic substances. The decreased availability of PO_4–P thus leads to a decreased phytoplankton production. Such acid lakes tend to become oligotrophic.

Ecosystem processes such as ion regulation, osmoregulation, acid–base balance, nitrogen excretion and respiration are adversely affected by an increase in acidity (Steinberg & Wright 1994). Great damage to fish populations in lakes in Scandinavia has occurred already from the 1960s to the late 1980s (Henriksen *et al.* 1989). In Norwegian lakes, Atlantic salmon (*Salmo salar*) was wiped out in the early 1900s and brown trout (*Salmo trutta*) had already disappeared in mountain lakes as early as the 1920s and 1930s. In Finland, roach (*Rutilus rutilus*) disappeared from many bodies of water in the 1980s. Hardy species like whitefish (*Coregonus peled*) and perch (*Perca fluviatilis*) experienced high mortality of eggs. Similar harmful effects on fish populations are reported from eastern provinces of Canada. In conclusion, acidification leads to periodic mortality of fish during the early stages of development and growth and causes populations to decrease and disappear.

18.3 LAKE RESTORATION MEASURES

Building on applied research programmes, management and restoration technologies for lakes and resevoirs developed rapidly during the 1980s in the United States, Canada and Europe, especially in the Netherlands and Denmark, but also in Germany and the United Kingdom (Moss *et al.* 1996). The restoration and management measures applied depend on users' interests (i.e. the economic and recreational uses of the body of water in question). Lake restoration strategies combine the social aspects and available technology,

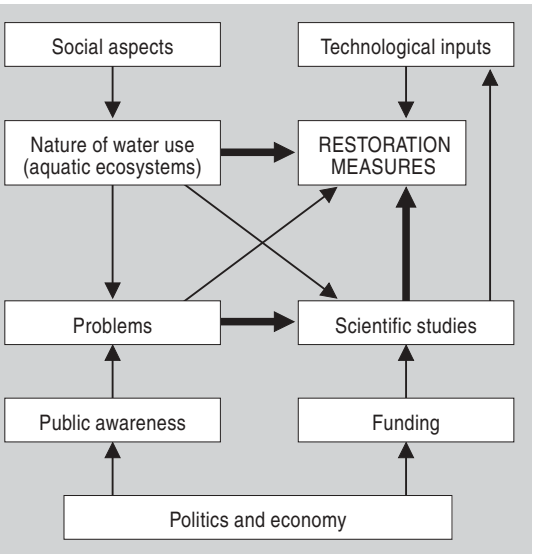


Figure 18.3 Strategic principles of lake restoration. The choice of restoration measures will depend on both direct and indirect factors related to the nature of water use, problems relating to water quality, and scientific studies (thick arrows). (From Gulati 1989; see also Vollenweider 1987.)

that is, the nature of water use, and public awareness of the problems on the one hand, and funding, scientific knowledge and desirable restoration measures on the other (Figure 18.3). Most lake restoration techniques are directed at reducing external P inputs (e.g. papers in Ryding & Rast 1989; Cooke *et al.* 2005), and they can be divided into two main types, namely, external and in-lake control measures (Figure 18.4). External measures focus on diverting sewage and wastewater inputs intended to prevent nutrient-rich inputs into the lake or reservoir (section 18.3.1). The in-lake measures are designed to decrease internal P loading (P released from retention in lake sediments) by various physicochemical means, biomanipulation of the lake's food web structure and functioning, or both (section 18.3.2). In section 18.3.3 we refer briefly to a few other science-based measures of lake rehabilitation.

18.3.1 Reduction of external nutrient loads

During the 1970s–1980s, both in western Europe and in North America, tertiary treatment of sewage and

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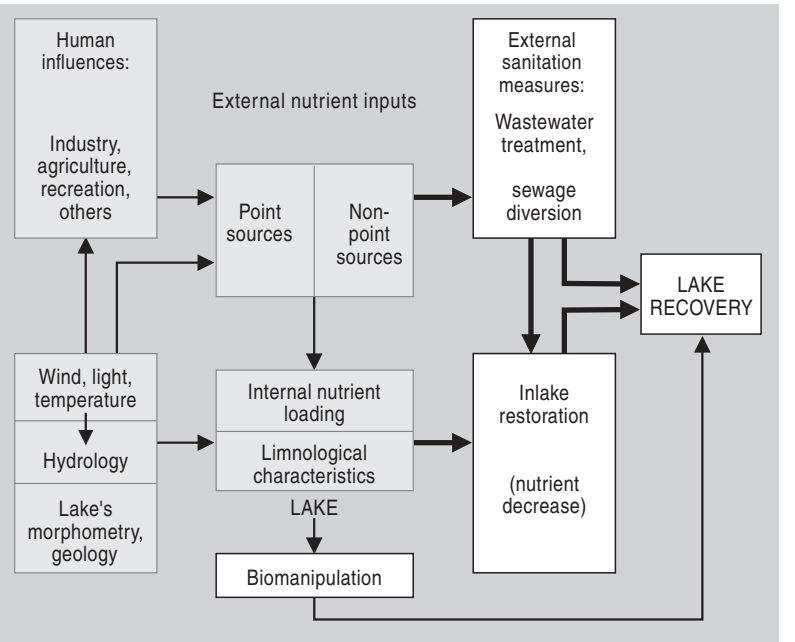


Figure 18.4 Schematic representation of factors causing an increase in nutrient loading via external inputs, which also result in an increase of internal loading, and restoration measures (white boxes) leading to lake recovery. (From Gulati 1989.)

animal wastes (>95% P removal) was the main P-control measure. Most importantly, P-containing laundry detergents were replaced by P-free detergents in most western countries. This led to about 50% reduction of P input into some lakes in the United States. In Barton Broad, Norfolk, United Kingdom, about 90% of the annual P load in the effluent from sewage treatment works was reduced by adding ferric sulphate (iron binds P and the Fe–P product precipitates to the bottom). However, because the bottom contained so much residual P as a result of decades of eutrophication, this P started to mobilize from the bottom into the water column blocking the hoped-for improvement in water quality (Phillips *et al*. 1994).

The response of algae to restoration measures can greatly differ among lakes: whereas some lakes improve in water quality (i.e the water transparency depth increases because of a reduction in concentration of algae), the others exhibit a small reduction of algal biomass, and still others show no reduction at all in algal biomass. In lakes in the Netherlands and Denmark, the P-reduction measures undertaken over recent decades have generally reduced concentrations of both P and chlorophyll (indicating algal biomass), and thereby improving water transparency. However, P retention in lake sediments, and its subsequent release (internal P loading), retarded the lakes' response to P reduction measures (Ibelings *et al*. 2007; Jeppesen *et al*. 2007a; Figure 18.5). Thus, the observed variation in responses of lakes to P-reduction measures depends on the amount of P that is stored in the sediments.

Phosphorus from external inputs may also be removed by first passing P-rich effluents into treatment ponds, where much of the P is adsorbed on to sediments and settles there. Also, most of the P released due to lysis and death of algal blooms will be taken up by the sediment. Regular harvesting of aquatic vegetation (e.g. duckweeds, *Lemna*; water fern, *Azolla*; and other floating plants) can significantly reduce P (e.g. Viessman & Hammer 1993). To reduce nonpoint P loading, agricultural farming practices in a lake's catchment area need to be altered radically by preventing erosion, and rationalizing the frequency, amount and timing of fertilizer applications. In addition, creation of pasture land and planting of buffer strips between farmland and watercourses may help reduce P.

The route to recovery or restoration of lakes (i.e. from eutrophication back to nutrient-poor conditions) takes

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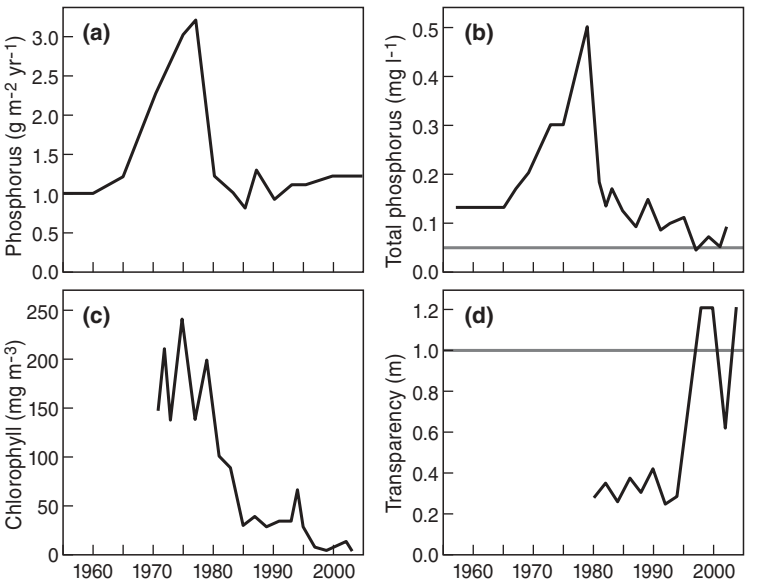


Figure 18.5 Long-term monitoring of the effects of various P reduction measures in the shallow Dutch Lake Veluwe almost immediately after the lake's formation. Note the marked increase in Secchi-disc transparency in the mid-1990s. The fluctuations in transparency, especially the decrease during 2001, are caused by wet winter periods. (Courtesy of M.L. Meijer *et al.*, unpublished results.)

much longer than, and differs from, the initial route of degradation and eutrophication. This discrepancy is called **hysteresis** (Scheffer 1998). For example, in Lake Veluwe (the Netherlands) macrophytes disappeared due to ongoing eutrophication at total phosphorus (TP) levels above 200 µg L^{-1}, whereas the return of macrophytes during the lake's restoration or *re-oligotrophication* occurred only at a TP concentration below 100 µg L^{-1} (Ibelings *et al.* 2007). In this case, the presence of bottom-dwelling fish and their interaction with wind promoted sediment resuspension causing high turbidity of water, which reduced the light intensity and thus prevented the return of macrophytes. Most lakes experiencing ongoing re-oligotrophication approach a new equilibrium (macrophyte presence, changes in algal composition and decrease in their abundance) in 10–15 years (Anderson *et al.* 2005; van Donk *et al.* 2008). Some researchers (Mooij *et al.* 2005) expect global climate changes will counteract the effects of nutrient reduction in lakes and delay the recovery process. Indeed, heavier rainfall may lead to higher runoff of nutrients from farmland into surface waters and higher temperatures to earlier and more release of nutrients from the sediments into the water column.

18.3.2 In-lake techniques for P-reduction

External P-load reductions do not guarantee improvements in water quality of lakes in the short term (van Liere & Gulati 1992), primarily because of accumulated P in lake sediments. In shallow lakes high stocks of benthivorous fish (foraging at the bottom of the lake), like large bream (*Abramis brama*), resuspend the sediments and therefore contribute to P mobilization from sediment to the water column. Apparently, this recycled P from the sediments increases if P loading in inflows is reduced. Therefore, high P concentrations, often observed in lakes during summer, and algal photosynthesis and production can go on unabated despite external control measures. Thus, our experience is that high levels of internal P loading may keep lakes in a eutrophic state for years after the reduction of external P loading.

Preventing P loading from lake sediments

The cycling of P between the sediments and water is complex and poorly understood. The P release from sediment depends on both redox and pH and involves

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bacterial decomposition of organic matter, including algal blooms. Several techniques have been applied to inactivate sediment P. Oxidation of organic matter enhances P binding in the sediment complexes. 'Sealing' or stripping inactivates the sediment P, using the salts of Ca, Fe or Al, to precipitate all P species to sediment as a flock (see Cooke *et al.* 2005). The process removes up to 90–95% of P. In the Netherlands, Boers *et al.* (1992) applied $FeCl_3$ solution (about 5 mg Fe^{3+} l^{-1} d^{-1}) for P stripping by mixing the solution with lake water and surface sediments using a water jet. However, high external loading of P nullified the positive effects. Although Al immobilizes P more efficiently than Fe, it is potentially toxic and its use for P reduction in public water supplies is generally avoided. Recently some researchers have attempted to treat lake water with chemical compounds including Phoslock®, a commercial bentonite product coated with lanthanum, to reduce P concentration in lake water. For example, Egemose *et al.* (2010) treated water from three Danish lakes with Phoslock® and evaluated the effects on P concentration. Although this compound took several days to reduce P levels, the sediment stability increased by 265%. Moreover, this compound improved sediment consolidation and removed colouration from the water, thereby improving light penetration, which in turn improved conditions for macrophyte colonization.

Wind-induced resuspension of organic matter and nutrients and mixing with the water column can also be reduced by creating deeper pits in shallow lakes. Penning *et al.* (2010) carried out a model study in Lake Loosdrecht, a shallow (Z_{mean} 1.8 m) and peaty lake in the Netherlands. They calculate the effect of creating three deep pits (*c.* 12 m), covering 10% (120 ha) of the lake's total surface area (~1200 ha). The study predicts a decrease in the concentration of organic detritus by 25%, and in the light attenuation coefficient (α) from 2.5 m^{-1} to 2.2 m^{-1}. Together with the P load reduction measures and decrease in chlorophyll-a level, α is anticipated to decrease to 2.0 m^{-1}, and to 1.6 m^{-1} if combined with the deepening of the lake. Such improvements of the underwater light climate are the first steps for the recovery of a submerged macrophyte community. Such studies are extremely useful in shallow, eutrophic lakes where wind-induced mixing (and mixing reinforced by benthivorous fish) and constant resuspension of nutrient-rich sediments delay the lake recovery processes (Gulati & van Donk 2002).

Sediment dredging leads to a reduction of the internal P loading. Field studies concerning sediment removal by dredging are rare, however, because they are relatively expensive. Moreover, the sediment dredging eliminates the toxic and hazardous compounds and rooted aquatic plants, in addition to P removal. Nevertheless, sediment removal has three disadvantages: (1) during dredging, P from the sediments is released into the water column, (2) finding disposal sites for the extracted sediments is a major dilemma for the lake restorers and managers and (3) new underlying sediment layers exposed to the water could even enhance P release.

Dilution and flushing of the lake with nutrient-poor water

Lakes can be replenished with water from extraneous sources or from lakes with lower nutrient levels but preferably rich in Ca^{2++} and HCO_3^{--}. Dilution as a restoration tool, therefore, implies reducing per se the nutrient levels in lake water to limiting concentrations (i.e. flushing rate with diluted water exceeds the algal growth rate). Cooke *et al.* (2005, 149–64) cite several examples where this technique was successfully applied in lakes in the United States and in Europe. The winter period is the best for flushing since both the dilution water and the lake to be diluted have less suspended material and algae than in other seasons. Because good-quality dilution water is generally scarce and expensive, due to the logistics of its transport, the technique has not gained great popularity. Flushing may also be done with bicarbonate-rich water. In two lakes in the Netherlands, winter flushing with bicarbonate-rich (and P-poor) dilution water since 1979 resulted in a pronounced drop in P-release. The increased bicarbonate is supposed to cause a better binding of P to the sediments through buffering and lowering of the pH (Hosper & Meijer 1986; Hosper 1997).

Lake biomanipulation

1. The theoretical aspects

Lake biomanipulation or food web manipulation has become routine for improving water quality of shallow lakes and reservoirs. It both has an ecological basis (Reynolds 1994) and complements the restoration methods involving nutrient reduction. In conjunction, these two measures can speed up lake rehabilitation. Two important hypotheses have enhanced our insights into food web relationships: (1) the *size–efficiency*

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hypothesis (Hall *et al*. 1976) and (2) the *cascading trophic interactions hypothesis* (Carpenter & Kitchell 1992). These two hypotheses, but especially the latter, elucidate ecosystem functioning and structure, and intertrophic feedback effects. Whereas the first hypothesis enhances our insight into the fish–zooplankton dynamics (i.e. fish tend to prey on large-bodied zooplankton), the trophic cascade hypothesis shows how intertrophic effects cascade down the food chain. In other words:

Piscivorous fish
↓
Planktivorous fish
↓
Zooplankton
↓
Algae

In short, the lake food web is influenced by nutrient inputs (bottom-up control) on the one hand, and zooplankton grazers and predatory fish (top-down control) on the other (Figure 18.6). Intense predation by piscivorous fish will lead to a decrease in the biomass of planktivorous fish and an increase in that of larger zooplankters, especially *Daphnia* spp. These changes cause a reduction of phytoplankton biomass, improve water clarity and promote diverse biological communities (Jeppesen & Sammalkorpi 2002). In shallow lakes, the development of macrophytes is the most striking side effect of these changes in the food chain. The macrophytes compete for nutrients with phytoplankton and further limit the latter's growth during spring and early summer, leading to clear water. Biomanipulation is applied as an ecological restoration method in which the strategy is to induce a drastic reduction of the fish stock.

For shallow lakes, application of biomanipulation is based essentially on the knowledge that top-down manipulations in the food web, especially reduction of planktivorous fish biomass, can lead to desirable changes at lower trophic levels. The theory relies on the hypothesis of **alternative stable states**: a turbid state dominated by phytoplankton blooms, and a clear state dominated by macrophytes (Scheffer *et al*. 1993; Moss 1998; see also Chapter 6). There is ample evidence to support the existence of alternative stable states in lakes (Gulati & van Donk 2002), but it is important to recognize that the **hysteresis** effect (see section 18.3.1) retards recovery or restoration from a turbid to a clear state. For a lake to shift from a turbid state to a clear-water state, substantial reductions of the planktivore and bottom-dwelling benthivore fish stocks are needed before macrophytes can establish and multiply.

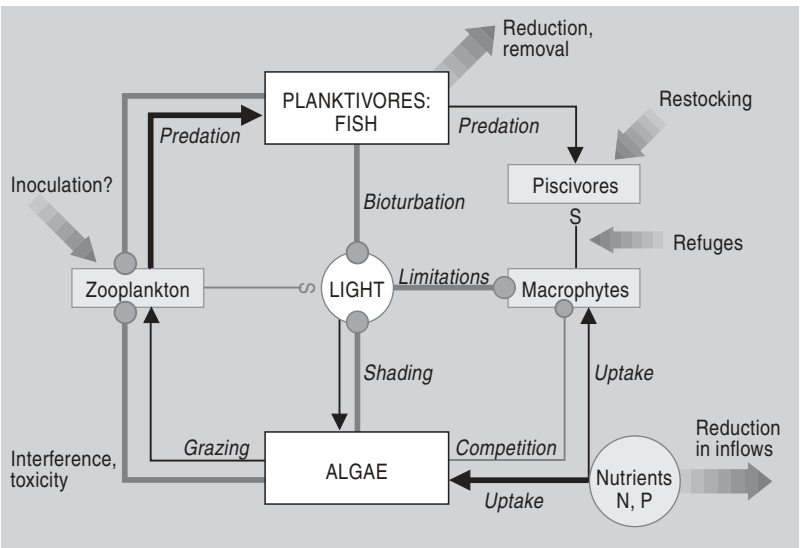


Figure 18.6 A simplified diagram of top-down and bottom-up control measures in the food web of shallow lakes. Nutrient reductions in the inflows and major biomanipulation measures are indicated with arrows. (From Gulati and van Donk 2002.)

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Measures to reduce these fish stocks need to be repeated to prevent re-establishment of their populations. An improvement in the underwater light climate (i.e. more visibility) indicates that the reduction of planktivore and benthivore fish is succesful and that the top-down cascading effects are re-established (Hosper 1997; Meijer 2000): phytoplankton biomass is controlled by zooplankton which in turn are not heavily predated by planktivores because piscivores control them.

2. Historical overview

Lake biomanipulation as a restoration measure started in the early 1970s. State-of-the-art reviews are given by Gulati and van Donk (2002) and Jeppesen *et al.* (2007a). From these studies, it becomes clear that in almost all biomanipulated lakes in Europe, the standing stock of planktivorous fish was effectively reduced but *Daphnia* populations did not increase in the years thereafter. Both poor food quality (high cyanobacterial densities) and/or predation by remaining planktivores probably contributed to the failure of the daphnids to develop high population densities. Northern pike (*Esox lucius*), which was introduced to control the planktivorous fish, mainly bream, was rarely a success. These studies showed that the size-selective predation on larger zooplankton by the planktivorous fish led to a decrease of daphnids and to their grazing on phytoplankton, so that water quality did not improve (Gulati & van Donk 2002). In other words, the *trophic cascade* between phytoplankton and zooplankton was largely decoupled (Kasprzak *et al.* 2007). In both Denmark and the Netherlands, the effect of fish removal was less obvious because lakes tended to return to the turbid state unless fish removal was repeated annually. Other factors that caused biomanipulation to fail were (1) insufficient reduction in external P loading (e.g. Benndorf *et al.* 2002), (2) continuation of internal P loading and (3) the failure of macrophytes to appear.

There are more cases of long-term failure than success for lake biomanipulation, mainly because the nutrient input effects on the pelagic food web tend to persist even after the top-down manipulation measures (McQueen *et al.* 1986). Thus, reduction of nutrients from the lake's catchment, rather than in-lake only, is an important prerequisite for success of biomanipulation. In deeper lakes the failure of biomanipulation measures is also caused by high P loading (Benndorf *et al.* 2002). Because sediment–water interactions differ with depth, the nutrient dynamics and the efficacy of restoration measures are also likely to vary with lake depth (see Moss 1998). In addition, because shallow lakes are more likely to be colonized by macrophytes, a shift to a clear-water state in these lakes will occur earlier than in the deeper ones.

3. Lessons learned

Gulati *et al.* (2008) attribute the failure of lake biomanipulation measures to one or more bottlenecks, including (1) ineffective biomass reduction of planktivorous and benthivorous fish and the inability to sustain fish at low levels, (2) inadequate reduction of external P and a concomitant increase of P release from sediments, (3) poor edibility of cyanobacteria to zooplankton, (4) reduction of macrophytes by fish and waterfowl and (5) recurrent failure of introduced northern pike (piscivorous fish). Among these, bottlenecks (1), (2) and (4) are crucial to overcome for lake biomanipulation to be successful (see also Gliwicz 2005). Below, we highlight the importance of selected biotic factors for applying biomanipulation as a lake restoration measure.

Importance of fish

In shallow lakes, it is relatively easy to manipulate fish (Lammens 1999) and produce rapid effects through fishing on the planktivores and benthivores. After fishing, the standing stock usually ranges from 150 kg FW ha^{-1} to 20 kg FW ha^{-1} (Lammens *et al.* 2002). Maintenance of a fish stock at low densities is desirable but generally hard to achieve. This is because there is less competition between fish individuals for food leading to higher growth. Furthermore, because the amount of P per unit body weight in fish is quite high, P recycling by fish seems to retard lake restoration (Sereda *et al.* 2008). Studies on Loosdrecht lakes showed that the P regenerated from fish was about 140% of the external P loading (van Liere & Janse 1992). Thus, nutrients and algal concentrations are expected to decline upon removal of planktivores. For fish removal to be successful, a substantial reduction of the fish stock must take place.

Role of macrophytes

Macrophytes stabilize lakes after biomanipulation (Coops & Hosper 2002). They influence various processes in shallow lakes (Figure 18.7). Firstly, macrophytes can accumulate relatively large amounts of N

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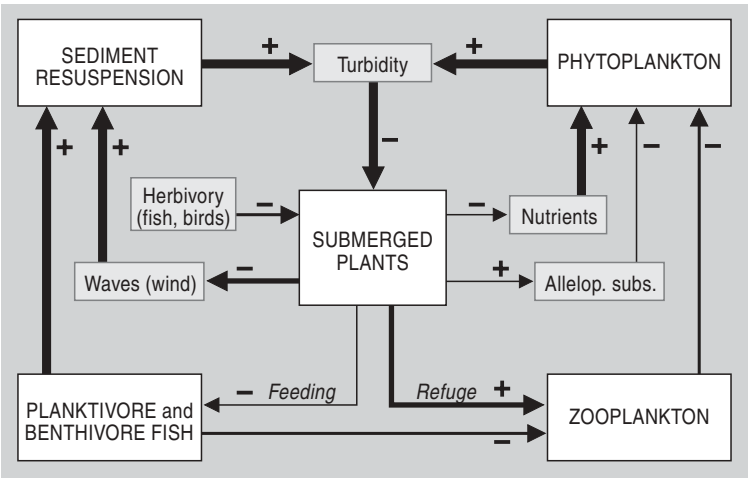


Figure 18.7 A diagrammatic representation of the mechanisms and factors causing sediment resuspension and turbidity in shallow lakes in relation to macrophytes (submerged plants). Different feedback mechanisms and their relative intensities are indicated with arrows (Allelop. subs. = allelopathic substances). (From Gulati and van Donk 2002.)

and P from both water and sediments (Barko & James 1998), reducing bioavailability of these elements for algae (van Donk & van de Bund 2002). Moreover, the algae (periphyton) adhering to macrophytes act as major nutrient sinks. Secondly, the macrophytes provide refuge for larger bodied zooplankton and young fish against fish predation (Moss 1998), and thus promote zooplankton grazing. Thirdly, macrophytes consolidate bottom sediments and reduce their resuspension by fish and wind. Finally, both denitrification in the macrophyte beds and the release of allelopathic substances by macrophytes are reported to adversely affect phytoplankton (Figure 18.7), although the mechanisms for such negative feedbacks are as yet unclear (van Donk & van de Bund 2002). Thus, all these characteristics related to macrophyte development and growth lead to improved underwater light climate in lakes. For macrophytes to be able to stabilize lakes after biomanipulation, it is important that they can develop into a stable population. This depends on the amount of light reaching the bottom, the presence of propagules (plant material) in the bottom, predation by waterfowl and the softness of the sediment (Scheffer 1998).

Role of zooplankton

In lake restoration studies, the standing stock of planktivorous fish is always reduced so that predation on large-bodied zooplankton decreases. The decreased predation effects cascade in the food web and lead to a marked increase in larger-bodied zooplankton, especially daphnids, as well as their grazing pressure on algae (Potthof *et al.* 2008) leading to a clear-water phase. Clear-water conditions have been reported for several lakes in western Europe following reductions of planktivorous fish (e.g. Gulati 1990; Jeppesen *et al.* 1999) and in the United States (Schrage & Downing 2004). It can thus be concluded that reduction of the planktivorous fish stock helps to restore the large-bodied zooplankters, particularly those comprising *Daphnia* species. Such a change will lead to a reduction in algae biomass and improvement of water transparency.

Role of zebra mussels

The zebra mussel, *Dreissena polymorpha*, a bio-invader in many lakes in temperate regions, is a potential tool for lake management (Dionisio Pires *et al.* 2010). Because zebra mussels are not found everywhere in the world, the use of these bivalves is less general than other techniques, like external P reduction, which apply universally. Use of zebra mussel in lake management therefore only applies to temperate regions. Dionisio Pires *et al.* (2004) demonstrated that adult mussels can act as biofilters: the mussels clear the lake from cyanobacteria at much higher rates than other particles in the water (Figure 18.8). In some shallow

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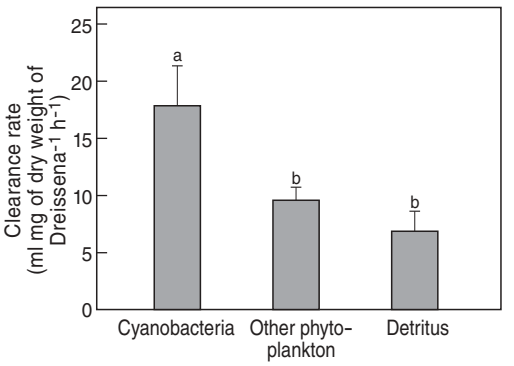


Figure 18.8 Clearance rates of adult zebra mussels (*Dreissena*) on different food particles from Lake Zwemlust, the Netherlands. The clearance rates on cyanobacteria are significantly higher than those on other phytoplankton and detritus as indicated by the letters a and b above the bars. (From Dionisio Pires *et al.* 2004. Reproduced by permission of Blackwell Publishing.)

Dutch lakes the areas colonized by zebra mussels are clearer, even to the naked eye, than the other lake parts.

In contrast to the practice in some European countries, in North America, zebra mussels, and their congeners the quagga mussels (*Dreissena rostriformis bugensis*), are eradicated from the lakes they have invaded, instead of being used as biofiltrators (Strayer 2009). Both the zebra mussel and the quagga mussel have caused much economic and ecological damage by settling on hard substrates where they clog pipes of the cooling systems. These mussels strongly compete with other filter feeders and disrupt lake food webs. **Eradication** programmes in North America will have difficulties in achieving success because these mussels reproduce readily and fast.

18.3.3 Other measures

There are several other measures available for lake restoration. In this section, we will highlight only three that are science-based, aimed at counteracting acidification, excessive water level fluctuations and oxygen-poor conditions, respectively.

Restoration of acidified systems

Actions to reduce acidifying emissions in Europe, the United States and Canada began in the mid-1970s, when emissions of SO_2 and NO_x peaked. By the mid-1980s, there was a perceptible decrease in emissions (Mason 2002). By the year 2000, two thirds of surface waters in Europe, where long-term monitoring (n = 56) had been carried out, showed reductions in acid deposition. Additionally, modelling studies of acidification in Norwegian surface waters indicate that these waters will continue to recover slowly (Larssen *et al.* 2010). By 1983, almost all countries had committed to reduce their SO_2 emissions by 30% within a decade, and to decrease by 70–80% by 2010 (United Nations 1994). However, contrary to these emission reductions, the NO_x emissions have tended to increase, for example in the United Kingdom. Therefore, acidification related to N is still a grave problem.

Liming is the most common technique for restoring acidified lakes, for example in Scandinavian countries, the United Kingdom (Scotland and Wales) and eastern Canada. Limestone, which includes calcite ($CaCO_3$) and powdered dolomite, is the most commonly used compound. Also, quicklime (CaO) and slaked lime ($Ca(OH)_2$) have been used in addition to alum ($(Al_2SO_4)_3 \cdot 14H_2O$). Liming produces longer lasting buffering effects and pH generally does not rise above 7.0. The liming of Loch Fleet, Galloway, southwest Scotland, facilitated the introduction and sustenance of a trout population.

Both in Sweden and in Norway, large-scale liming is used as a national strategy for preserving species threatened by acidification (Henrikson & Brodin 1995). In Sweden alone, between 7500 and 11 000 km of streams were limed annually to raise the pH to >6.0 in order to help indigenous fauna and flora to survive. Nearly 90% of the acidified bodies of surface water have thus been restored.

Adjusting water level fluctuations

Shallow lakes are particularly sensitive to rapid changes in water level. Therefore, water level fluctuations (WLF) may have an overriding effect on shallow lake ecosystem functioning and management (Coops & Hosper 2002). Water levels in shallow lakes naturally fluctuate both seasonally and annually depending largely on regional climatic conditions and past and current human activities (Beklioglu *et al.* 2001). WLF can also be disastrous for submersed plant communities. Extremely high water levels in the vegetation period reduce light availability, and low water levels may damage plants due to ice and wave action during

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winter and to desiccation during summer. The plans by water managers in the last 20 years, to allow more dynamic water levels in set-aside nature areas, especially, entail extending the upper and lower limits of the permissible annual water level fluctuations (Coops & Hosper 2002). Near-natural water levels that allow wider fluctuations than the current 'fixed' levels are considered the best option by most water managers.

A good case study on WLF management is that of Lake Okeechobee (Florida, United States, headwaters of the Everglades). As a subtropical lake ecosystem, it exhibits large seasonal and interannual variation in rainfall and high evapotranspiration. This can result in large and unpredictable variations in water level that can affect ecosystem dynamics. In response to this, as well as to other environmental concerns, a 30-year plan was initiated to construct structures to restore the quantity, quality, timing and distribution of water (Havens 2002). This overall programme is called Comprehensive Everglades Restoration Program (CERP). CERP is expected to reduce the occurrence of damaging high and low WLF and to increase the occurrence of spring water level recessions that benefit native biota. Johnson *et al.* (2007) studied the response to hydrological variations in Lake Okeechobee of both vegetation and fisheries. Their findings indicate that lakes with a high water level and prolonged flooding are likely to show substantial losses of aquatic and wetland plants as well as a negative impact on fish populations, as is the case at Lake Okeechobee. In contrast, shallower lakes with moderate water level variations were reported to have widespread stands of emergent and submerged aquatic vegetation in most years. Consequently, habitat structure was improved and food resources increased for largemouth bass (*Micropterus salmoides*) and other fish species, alligators, wading birds and snail kites (*Rostrhamus sociabilis*).

Mixing of the water column

Oxygen-poor water conditions can be counteracted by artificial mixing, which involves aerating or oxygenating lakes using pumps, jets and bubbling air at the lake bottom. The technique has been used in the United States to prevent fish dying during ice cover (Cooke *et al.* 2005). Aeration oxidizes substances in the water column, allows removal of Fe and Mn from the water into the sediments more rapidly and reduces internal P loading from sediment. Aeration seems to prevent cyanobacteria from exploiting the optimal light conditions in the upper mixed layers, so that the dominant phytoplankton shifts to noncyanobacterial forms. In the Netherlands, artificial mixing is used to disrupt stratification of the water column (i.e. a water column that is divided into an upper and a lower layer due to the increase in spring and summer temperature) to prevent bloom formation by cyanobacteria (Huisman *et al.* 2004). Thus, mixing or circulation, unlike nutrient reduction, produces instantaneous improvements in water quality, and without decreasing the nutrient concentrations or loading. However, the technique seems to be more effective for lakes in which stratification of the water column occurs.

18.4 PERSPECTIVES

Although in many European countries freshwater lakes and reservoirs constitute only a small fraction of the land area, their importance for human health, recreation and national economies is considerable. There is obviously an urgent need to further curtail, divert and treat the unwarranted inputs into the lakes and reservoirs of nutrients, organics, silt and contaminants from the watershed. Despite more than a quarter century of nutrient reduction measures in runoff waters, many lakes still have poor water quality. The principal cause for the delay of responses to corrective measures is the large stockpiles of P in lake sediments. The slow release of this element allows eutrophication symptoms to persist and even proliferate. Secondly, inadequate nutrient reductions in the runoff waters and the virtually unabated and diffuse inputs from the agricultural grounds in the lake catchment areas act as a major bottleneck to lake restoration. It is, therefore, difficult to predict the response of an ecosystem under restoration. Thus, further manipulations of both chemical and biological processes are needed to sustain the positive effects of the corrective measures. However, monitoring of water quality and restoration of the in-lake processes alone will be a futile exercise if not carried out in a watershed context. This latter involves documenting the entire **landscape** setting, including habitat type, hydrological regime, soil properties, topography and invasive species, which all can hamper restoration measures. Moreover, chances of improving a lake are often better if the chosen measures complement each other.

It is difficult to draw any conclusions on the effects of **climate change** on lake restoration. At present, we

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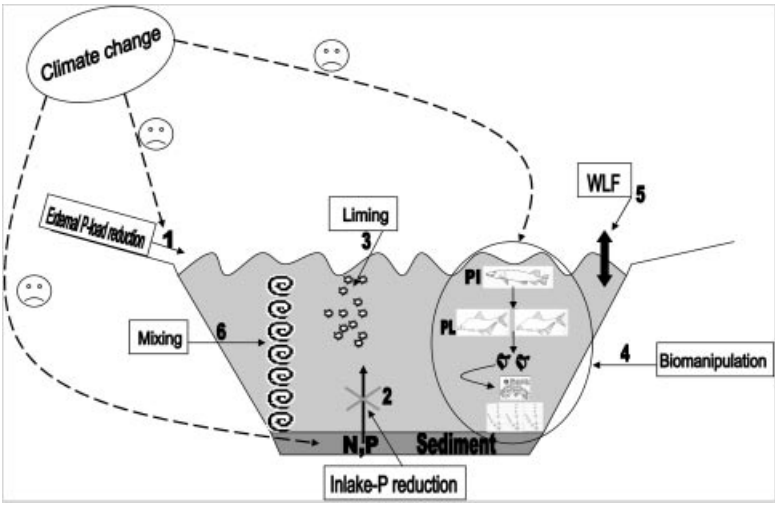


Figure 18.9 Diagrammatic depiction of different restoration methods applied to lakes, illustrating also the predicted effects of climate change on lake restoration measures. The possible restoration measures (as discussed in the text) are shown in boxes and numbered. The circle on the right side of the figure shows how biomanipulation operates: it leads to reduction of planktivorous fish (PL) and increase of piscivorous fish (PI). See text for its effects on the food web. Climate changes are likely to negate effects of some of the restoration measures, especially nutrient reduction (increase in both nutrient release from the bottom and external nutrient loading) and on the food web (positive effects on planktivore fish and inedible phytoplankton and negative effects on piscivore fish in temperate waters), hence hampering biomanipulation efforts. These negative effects of the climate change are portrayed as the three unhappy smileys.

know little about long-term climate change and its consequences for hydrology and water management practices (e.g. the impact of flooding or droughts, or both, as well as of human water use on ecosystems). However, several model studies predict that warming will act as a catalyst for higher growth of cyanobacteria in lakes at higher temperatures than other phytoplankters (Paerl & Huisman 2008). According to Jeppesen *et al*. (2007b), global warming is expected to intensify eutrophication and its symptoms, via nutrient loading, increased rates of evaporation losses and changes in water levels. For example, the fish community structure could be affected by increases in temperature, eutrophication and salinity. Both the life history traits and the feeding behaviour of many organisms are likely to be affected: changes in life history of many fish species (like a shorter body size and life span) will lead to changes in fish community compositions in lakes. As a result of this, less predators will be present which will benefit herbivores, planktivores and omnivores and, hence, a disruption of the food chain may take place (see section 18.3.2). Together with increasing temperature, these changes will lead to greater predation pressure of fish on zooplankton and macro-invertebrates. Such a scenario seems to be especially valid for temperate lakes where temperature rises are perhaps relatively easier to predict. Successful biomanipulation will therefore probably be more difficult under a changing climate. Finally, the predicted climate changes expected to intensify the negative impact of eutrophication on water quality in temperate waters (Mooij *et al*. 2005). Figure 18.9 illustrates the different restoration measures as discussed in the text, and shows which of these measures are negatively impacted by climate change. Regarding tropical waters, we do not have at present the basic information, especially on biological aspects of lake restoration, let alone predicting the climate change effects for these waters.

Lake restoration plans nowadays typically envisage *near-natural restoration*, that is, allowing nature to take its course, and emphasizing that a lake is an integral part of a landscape comprising other aquatic, semi-aquatic and terrestrial ecosystems (see papers in Nienhuis & Gulati 2002) and taking climate change into

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account. First, such a measure includes reinforcing the shoreline vegetation of lakes to prevent wind- and wave-induced erosion and improving the propensity of the land–water transition to develop a natural biodiversity. Secondly, excavating deeper pits within the shallower lake parts offers a viable control measure to isolate and bury the organic matter shifted by wind to these pits. The burial of the nutrient-rich lake sediments will retard in-lake nutrient release rates from the sediments. Thirdly, more exploratory work is needed for creating artificial islands in small and shallow lakes. Such an island within a lake, facing the commonly prevailing winds, will reduce the wind fetch factor and slow down shore-line erosion on the leeward side of the island. Fourthly, feasibility plans are also under way to deploy water level management, to encourage the shoreline macrovegetation and develop greater natural evolution of the aquatic and semi-aquatic ecosystems.

Sustainability of the positive effects on water quality is central to the remedial measures. The experience gained from the failures and occasional successes of the last two decades should make it possible to develop more enduring strategies for a more sustainable restoration of our lake ecosystems. Lastly, the long-term aims of water management should be to create and maintain sustainable and healthy aquatic environments that possess optimal properties for their assigned functions.

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Chapter 19

RESTORATION OF SALT MARSHES

Jan P. Bakker

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19.1 INTRODUCTION: THE HISTORICAL CONTEXT

This chapter deals with tidal salt marshes adjacent to intertidal flats. Salt marshes and intertidal flats occur along the edges of shallow seas with soft sediment bottoms where the tidal range is considerable, at least a meter or so (van de Kam *et al.* 2004), but also in the absence of tides, as in the Baltic Sea. Low-lying intertidal areas are inundated at least once a day, and make a place for more irregularly inundated areas of salt marsh higher up. In tropical areas, and even some benign temperate areas such as northernmost New Zealand, the upper parts of intertidal areas may be covered by mangrove forests rather than salt marsh. Such mangroves have the tendency also to cover the regularly inundated parts of intertidal soft sediments, thus reducing the extent of mudflats in many tropical areas. No intertidal deposits or salt marshes occur at high latitudes (further north than 70–73°N). Here coastlines are either ice-covered for most of the year or disturbed by moving ice too frequently for soft sediment deposits or vegetation to build up. Hence, *salt marshes* are mainly found in the temperate zone.

Salt marshes and intertidal flats are under complex natural controls. The main external controls for the tidal lands are the sea level and sediment supply regimes. Upward sea level movements and autocompaction – that is, diminishing of the volume of the sediment – combine to provide accomodation space within which marshes build upwards. Mineralogenic marshes consist of a vegetated platform dissected typically by extensive networks of blind-ended, branching tidal creeks. The flow-resistant surface vegetation both traps and binds tidally introduced mineral sediment, but also contributes an organic component of indigenous origin to the deposit. When the sea level next to mineralogenic marshes becomes stable or falls, however, in response to century- or millennium-scale fluctuations, the organic sediment component becomes dominant and mineralogenic marshes are transformed into organogenic ones. Because peat is such a porous and permeable sediment, and there is little or no tidal inundation, organogenic marshes in north-western Europe typically lack surface channels for intertidal drainage (Allen 2000). At present very little peat marsh occurs in Europe, except for the Baltic Sea (Dijkema 1984). In contrast, the north-eastern coast of North America features large coastal peat deposits (Niering 1997). Along the south-eastern coast of North America, the vertical accretion rate of salt marshes is directly related to the accumulation of organic matter, rather than to inorganic matter (Turner *et al.* 2000).

Global sea level rise after the last glacial period caused a poorer drainage of the coastal hinterland and a subsequent rise of the groundwater table in the adjacent low-lying inland zones which became marshy, allowing peat formation over the underlying Pleistocene subsurface. As a consequence of increased marine influence, the freshwater marsh transformed into areas of tidal salt marshes and intertidal mudflats, or brackish lagoons. As a result, the basal peat layers were covered by marine sediments, and with continuous sea level rise the area became totally submerged. This transgressive process continued until the mid-Holocene, after which the coastline stabilized more or less at its present position. As a result of the decline in sea level rise, sedimentary processes became increasingly dominant (Esselink 2000).

Coastal regions around the world are not only affected by natural processes. In north-western Europe, the coastal zone became increasingly shaped by human activities undertaken to increase agricultural land area, transport links and urbanization and coastal defence. Most human activities in and exploitation of intertidal flats were relatively unintrusive for a long time, consisting primarily of small-scale fishing and the taking of shellfish by hand. With the advent of industrialization, however, over the twentieth century, and the use of large nets and dredges, human exploitation patterns of intertidal flats have come to influence the natural processes a great deal indeed. It is not entirely clear whether the same can be said for salt marshes, where, embankments aside, grazing by domestic animals has been the main human factor. Loss of extent has had a significant impact on salt marshes, resulting in truncation of the upper zone. Canalization and dredging of estuaries resulted in widening and deepening of channels and loss of the pioneer zone. Both resulted in loss of associated species. It is quite possible that the grazing by domestic animals has replaced the grazing that took place before human times by wild large herbivores. The Baltic and southern European coasts have been less affected by coastal defence works. See Davy *et al.* (2009) for an overview on embankments and land claim along the European coastline.

In Europe, the concepts of 'natural' and 'seminatural' salt marshes have been defined for the international Wadden Sea (Esselink *et al.* 2009). Natural salt

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marshes feature undisturbed **geomorphological** conditions and have no history of direct management. They show a natural drainage system with meandering creeks and levees with higher elevation than the adjacent depressions and no agricultural exploitation (Plate 19.1). Grazing can occur with natural grazers such as geese and hares. Natural or pristine salt marshes are very rare, and occur in Europe in sandy back-barrier conditions or in parts of former Wadden Sea bays along the mainland coast. Two groups of **seminatural** marshes can be considered. Some seminatural marshes are similar to natural marshes with natural draining creeks, but include livestock grazing or mowing (Plate 19.1). An other group of seminatural marshes features artificial ditches, sedimentation fields, defences against erosion and often land use. The sedimentation fields are areas surrounded by 200 m × 200 m brushwood groynes that reduce water velocity, with subsequently higher sedimentation of suspended material. These marsh types are affected in their geomorphological conditions by artificial drainage and/or by measures to enhance livestock grazing or cutting (Plate 19.2). Seminatural marshes are found on barrier islands, in foreland clay marshes and in marshes with sedimentation fields and an artificial drainage system (i.e. ditches) (Table 19.1). Characteristic salt marsh plant species can be present in all three salt marsh types. However, their abundance in typical salt marsh communities and their spatial arrangement in the vegetation structure can be affected by *land use*. Intensive livestock grazing results in homogeneous short sward, whereas abandoned salt marshes are often characterized by uniform tall vegetation. Moderate grazing features most variation in vegetation structure by combining short and tall canopy.

Understanding the historical context of the development of tidal salt marshes along intertidal flats is a prerequisite for any fruitful discussion about the perspectives of nature conservation and restoration in these systems. In this chapter, I focus on concepts, which makes it easier to understand salt marsh systems and the possibilities for restoration than by presenting many examples of restoration from all over the world. Because of my familiarity with western Europe, many cases will be from that continent.

Table 19.1 Outline of the different landscape types from natural to seminatural landscape features and examples for land use.

Drainage type	Erosion protection	Type of landscape	Land use
Creeks	No groynes	Natural	No
Creeks	No groynes	Seminatural	Grazing/ cutting
Ditches	Groynes	Seminatural	Grazing/ cutting/no

19.2 CHARACTERISTICS OF SALT MARSHES

Abiotic conditions, especially elevation, affect the duration and frequency of inundation by sea water. Hence, they affect the **zonation** along the *elevational gradient* of salt marsh ecosystems. The **succession** of the communities on estuarine marshes is driven by vertical accretion. However, the succession of the communities on sandy marshes is nutrient-driven (de Leeuw *et al.* 1993; Olff *et al.* 1997). However, salt marsh vegetation is governed not only by bottom-up physical factors, such as tidal inundations, salinity and soil nutrient concentations, but also by top-down processes such as grazing animals.

19.2.1 Abiotic conditions, zonation and succession

The driving bottom-up control in salt marsh development is the tidal amplitude, causing inundation and subsequent sedimentation of silt. The mean spring-tidal range in Europe varies from 12.3 m in estuaries to 1.6 m in the Wadden Sea (Allen 2000), to nearly zero in the Baltic Sea. Transplant experiments in Alaska have demonstrated that the abiotic conditions drive plant communities at low elevations and higher inundation frequency and duration, whereas at higher elevation interspecific competition drives plant communities (Snow & Vince 1984). Therefore, grazing may strongly affect plant communities at higher elevation by removal of biomass and subsequent spreading of communities of the low marsh towards higher on the elevational gradient (Bakker 1985).

The pioneer zone of salt marshes consists of annual plant species, and they do not trap sediment. The perennial grasses *Spartina anglica* and *Puccinellia maritima* at the low salt marsh catch sediment, whereas **erosion** can take place of unvegetated soil (Langlois *et al.*

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2001). In the *Festuca rubra* zone, higher up the salt marsh with less inundation, the rate of sedimentation is lower than in the *P. maritima* zone (Andresen *et al.* 1990). A typical salt marsh zonation along the east coast of the United States shows from the pioneer zone towards higher elavation: *Spartina alterniflora*, *S. patens*, *Juncus gerardi* and *Iva frutescens* (Bertness *et al.* 2009). Sedimentation patterns show spatial variation. Over comparatively wide marshes, a landward decrease of sedimentation was found in seminatural mainland marshes in Sussex, United Kingdom (Reed 1988), along the Westerschelde, the Netherlands (Temmerman 2003), in a back barrier marsh at Skallingen, Denmark (Bartholdy 1997) and in seminatural marshes with sedimentation fields in Germany (Schröder *et al.* 2002) and in the Dollard, the Netherlands (Esselink *et al.* 1998). Superimposed on the large-scale differences from low to high marsh, the rate of sedimentation also declines away from creeks and ditches (Figure 19.1). Moreover, higher rates were

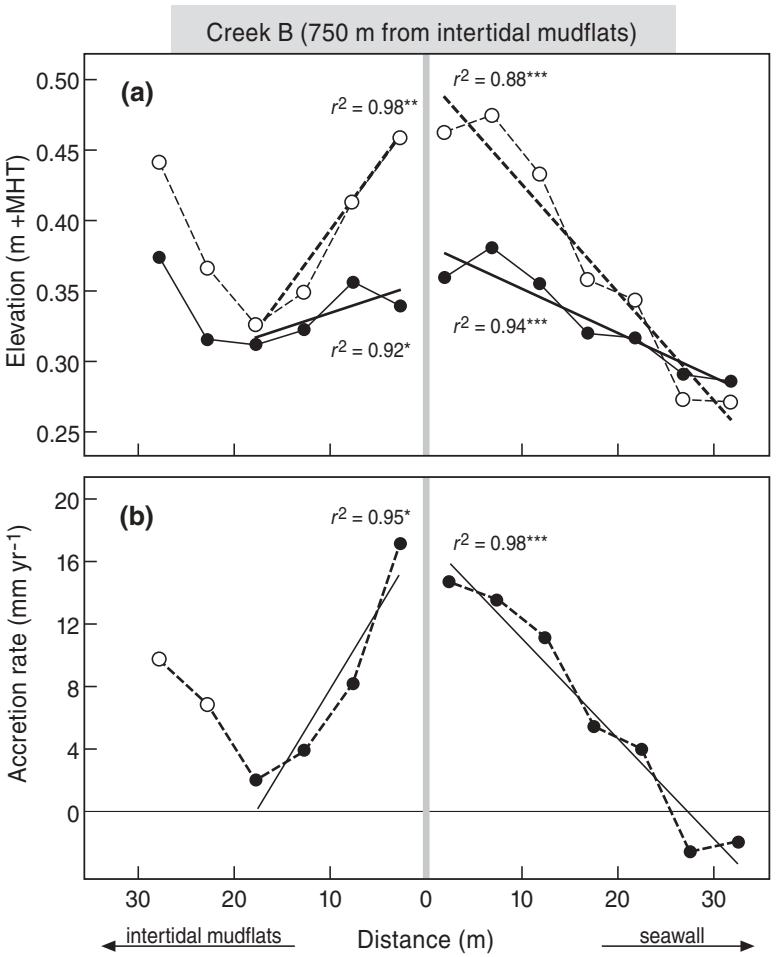


Figure 19.1 (a) Levee development near a minor creek at a distance of 750 m from intertidal mudflats and (b) annual vertical accretion rate (means ± S.E.M.) at different distances from a main creek as a function of the distance from the intertidal mudflats. In (a): ●, 1984; ○, 1991. Points in the left-hand panel at higher elevations were located on the neighbouring levee of the next minor creek. MHT, mean high tide. (Modified from Esselink *et al.* 1998. Reproduced by permission of *Journal of Coastal Research*.)

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found on ungrazed than on heavily grazed seminatural marshes with sedimentation fields in the Dollard (Esselink *et al.* 1998). Dense, tall vegetation positively affects the rate of sedimentation (Leonard *et al.* 1995). Detailed measurements have revealed vertical accretion during winter periods, but shrinkage during the dry summer period (Erchinger *et al.* 1994).

The vertical accretion results in succession from pioneer communities, via low-salt marsh communities to high-salt marsh communities. This successional sequence, derived from aerial photographs, is mirrored in the spatial zonation from pioneer to low and high marsh in mainland estuarine marshes in the southwestern Netherlands (de Leeuw *et al.* 1993). In contrast, long-term permanent plot studies revealed different successional patterns at the low and high marsh of the barrier island of Terschelling, the Netherlands, where low-marsh plant communities did not transform into high-marsh communities (Leendertse *et al.* 1997). Hence, the zonation does not mirror succession in back barrier salt marshes, but reflects the underlying **geomorphology** of the sandy base elevation (de Leeuw *et al.* 1993; Olff *et al.* 1997). At many older ungrazed marshes in north-western Europe, the tall grass *Elytrigia atherica* is taking over gradually. With increasing age of the salt marsh, *E. atherica* is spreading downwards along the elevational gradient. It appears that the grass can cope with the salinity stress at lower elevations when more nutrients are available (Olff *et al.* 1997). Salt marshes are nitrogen-limited systems (see references in Davy *et al.* 2009). Nitrogen supply can affect the competitive relations of marsh plants and hence has important consequences for the abundance and distribution across marsh landscapes (Levine *et al.* 1998). The lower tidal boundaries of marsh plant distributions are generally set by physical stress, whereas the upper boundaries of plants are set by competitive exclusion (Snow & Vince 1984).

The influence of fresh water in mainland estuaries, discharged by rivers from the hinterland, creates a gradient of decreasing salinity inland. The vegetation features *Scirpus maritimus* and especially *Phragmites australis*, as in estuarine marshes of the Wadden Sea (Esselink 2000) and the Baltic Sea in Europe (Dijkema 1990), and the Atlantic coast in the United States (Bertness 1999).

In tropical regions, *mangrove forests* and *salt marshes* compete for space along a latitudinal gradient. In north-east Queensland, Australia, mangroves may be up to 30 m, but in southern Victoria they take the form of low shrubs about 1 m tall (Thomson *et al.* 2009). Salt marshes can occur where mangrove growth is inhibited, which often occurs by cutting the trees. Mangrove cutting results in increased soil salinity and hence bare intertidal flats or herbaceous vegetation (Costa *et al.* 2009).

19.2.2 Plant–animal interactions

The barrier island of Schiermonnikoog, the Netherlands, extends eastward, thus featuring a chronosequence from east to west. This phenomenon provides an opportunity to study salt marsh development over a period of some 200 years. A positive correlation is found between the thickness of the clay layer and both the nitrogen pool (Olff *et al.* 1997) and the availability of nitrogen for plants (Bakker *et al.* 2005). Hence, the *chronosequence* represents a *productivity gradient* featuring low-statured plants in early stages and tall grass in later successional stages with thicker clay layer, and a decrease in the number of plant species (Bakker *et al.* 2002b). As a result, the forage quantity for natural herbivores such as spring-staging geese and resident hares increases, but the quality, expressed as the leaf–stem ratio, decreases (van de Koppel *et al.* 1996). Hence, geese and hares are 'evicted' by vegetation succession, namely dominance of the tall forb *Atriplex portulacoides* and the tall grass *Elytrigia atherica*. Exclusion experiments revealed that geese can forage on the salt marsh only when hares occur and eat the tall plants, hence hare facilitate for geese, and they can retard the succession with a few decades (Kuijper & Bakker 2005). Indeed, back barrier island marshes without hares – such as on Mellum, Germany – appeared to be completely dominated by tall stands of vegetation (Kuijper & Bakker 2003).

Salt marsh ecosystems have long been considered as being controlled by physical bottom-up factors such as salinity, tidal inundations and soil nutrient concentrations. The above-mentioned studies with natural herbivores stress the importance of consumers and food web characteristics of salt marshes. Hence, top-down control is an essential element in understanding salt marsh ecosystems (Silliman *et al.* 2009), including human exploitation of salt marshes by livestock grazing. The role of livestock grazing is further discussed in section 19.3.

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19.3 THREATS AND DISTURBANCES

Embankment is the most definitive threat for the occurence of salt marshes, and occurs worldwide. Other threats are erosion, reduction of the tidal amplitude and decrease in salinity of inundating water. Intensive livestock grazing is considered a threat in many parts of the world. Overgrazing results in short unifom swards without tall vegetation for plant and animal species to survive. Also, the potential for sediment capture and wave attenuation has reduced. Moreover, evaporation and salinization take place. However, in Europe most salt marshes have always been exploited for either grazing or cutting. As most salt marshes are agriculturally exploited, the cessation of exploitation is a sudden change in long-term management and thus causes disturbance. After **abandonment**, a single plant species can become dominant with subsequent losses of characteristic halobiontic species (i.e. groups or organisms tolerating saline conditions). However, some exceptions wil be discussed below.

19.3.1 Embankments

In Europe, the first seawalls were constructed against the increased risk of flooding in the tenth century in the northern Netherlands (Oost & de Boer 1994), and during the eleventh century in adjacent Germany (Behre 1995). The entire North Sea coastline of the Netherlands and Germany was protected in the thirteenth century. The first seawalls were constructed in the salt marshes above the level of mean high tide, and hence, in most places, a strip of unprotected salt marsh remained in front of the seawalls. New marshes developed after the construction of the first seawalls, especially in sheltered bays (Oost & de Boer 1994). The new marshes, which originated during the twelfth–fourteenth centuries, may have evolved without human intervention. However, human **intervention** was very likely from at least the seventeenth century onwards. Several techniques have been applied to promote both vertical accretion and horizontal expansion of salt marshes. At present, the majority of mainland salt marshes are seminatural, resulting from sedimentation fields with intensively engineered ditching for drainage, such as those currently found in Denmark, Germany, the Netherlands (Dijkema 1984) and the United States (Pye 2000). Back barrier marshes developed in the shelter of dunes, but also in the shelter of artificial sand dikes during the twentieth century (Dijkema 1987). These marshes always had a natural drainage pattern with creeks.

19.3.2 Erosion, reduction of salinity and tidal amplitude

Salt marshes have been eroding rapidly in southwestern England during the past 150 years, and particularly in the past few decades. The mechanisms of **erosion** include landward recession of the marsh edge, wave erosion of the marsh surface, internal dissection due to enlargement and coalescence of tidal creeks and mud basins and direct removal due to human activities. Increased wind and wave energy is supposed to contribute most strongly to erosion. Increased mean sea level and tidal range are underlying factors leading to coastal 'squeezing' of salt marshes between the sea and seawalls (Pye 2000). Establishing seawalls on the intertidal flats makes them more vulnerable to erosion. In seminatural marshes with sedimentation fields, the abandonment of accretion works results in retreating of the marsh edge (Esselink 2000).

As one result of future rising sea levels caused by global climate warming, widespread salt marsh erosion is predicted. A long-term experiment was carried out on this subject, at the Wadden Sea island of Ameland, the Netherlands, in a seminatural marsh system with drainage assured by natural creeks. As a result of gas extraction, soil subsidence of 10 cm was observed over a 15-year period, affecting both the low- and high-salt marsh (Dijkema 1997). The net elevation of low-marsh plots did not change, indicating that sedimentation kept pace with subsidence. In contrast, net elevation of the high-marsh plots decreased by 10 cm, indicating that no extra sedimentation took place. Neither in the lower nor in the upper plots of the salt marsh did vegetation change (Dijkema 1997).

Another important cause of losses of salt marshes is coastal protection by shortening the coastline of estuarine coasts. Desalinization causes the transformation of salt marsh communities into communities adapted to freshwater conditions. Continued grazing by livestock retards the losses of halophytic plant species (Westhoff & Sykora 1979). Moreover, grazing benefits short turfs that are favoured by winter-staging geese, as in the former salt marshes. Undisturbed succession results in scrub and forest with characteristic bird species (van Wieren 1998).

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Not all estuaries are dammed. In 1986 a sluice–gate barrier was completed in the mouth of the Oosterschelde estuary, the Netherlands. It can be closed during storm surges. Although the barrier allows tidal exchange, the tidal flow has been restricted. This caused a 26 cm decrease of the mean high tide and hence a decreased inundation frequency of the marsh. Most plant species had moved down along the elevational gradient (de Leeuw *et al.* 1994).

More small-scale processes took place in northeastern United States. During the twentieth century, about 2000 ha (30%) of Connecticut's tidal marshes were degraded or lost through coastal development. Tidal flow to many marshes was restricted by the construction of impoundments, producing microtidal environments in which the non-native haplotype of *Phragmites australis* or, less frequently, *Typha angustifolia* became established at the expense of typical tidal marsh communities. In addition to these human influences, *P. australis* has also invaded brackish tidal marshes in the lower Connecticut River system where salinity levels are often reduced by freshwater inputs (Fell *et al.* 2000).

19.3.3 Exploitation

Salt production is one of the most ancient estuarine industries. The oldest indication is a Bronze Age salt-evaporating hearth (1400–1130 BCE) in Essex, United Kingdom, and there were many Iron Age, Roman and medieval salterns around the English coast (Fleming 2004). The first colonists on salt marshes in the northwest European mainland settled on the highest parts of the marsh, on levees along watercourses, in the seventh century CE. Farmsteads were initially built on the marsh bed. In response to increased risk of flooding, people started to build their dwellings on artificial mounds. The number of mounds along the northern coast of the Netherlands suggests intensive exploitation of the salt marshes (Figure 19.2). When salt marshes extended seaward, new settlements were built

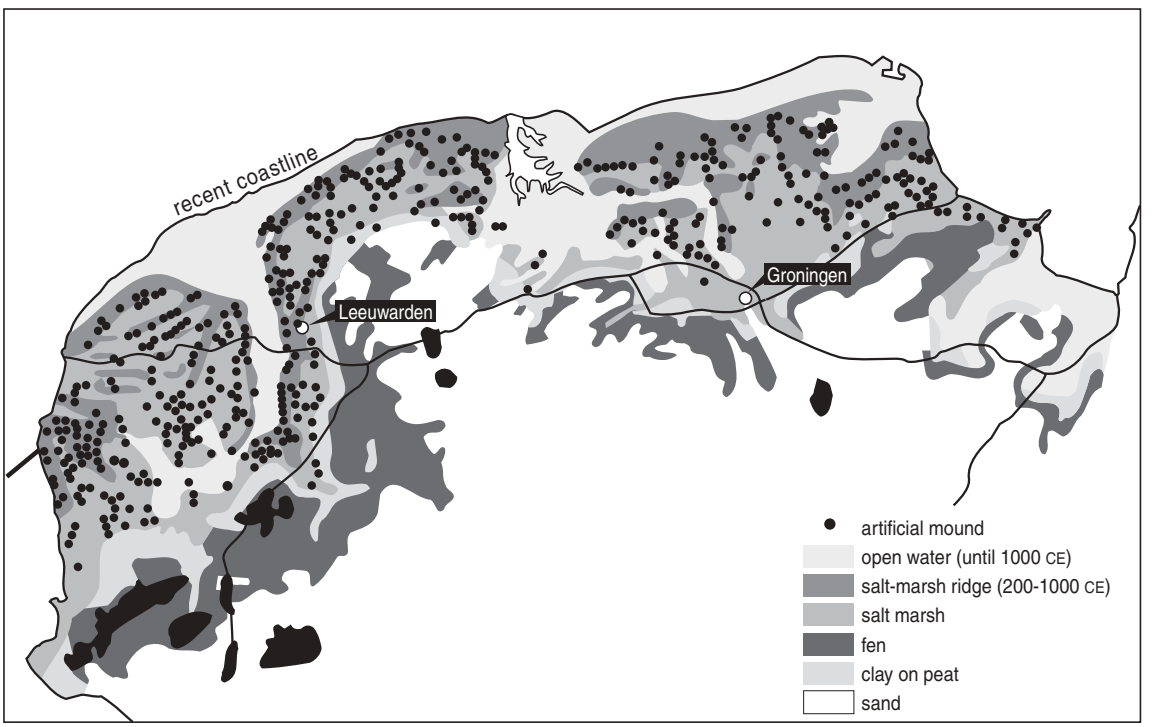


Figure 19.2 Landscape types and the occurrence of artificial mounds along the northern coast of the Netherlands about 1000 CE. Copyright Cultural Heritage Agency, Amersfoort, The Netherlands.

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on the younger marshes until the entire coastline was protected by seawalls in the thirteenth century. Initially arable crops were grown on the levees, but ditching and the construction of embankments, dated from the first century BCE to the second century CE, allowed crops to be grown on the salt marshes. The majority of the marshes were exploited for livestock grazing from the early settlements onwards, and haymaking from the first–third centuries onwards. The high frequency of subfossils of *Juncus gerardi* and the low frequency of *Elytrigia* spp. found in artificial mounds led to the conclusion that unexploited salt marshes were scarce during most of the occupation period (Esselink 2000). Nowadays salt marshes in the Wadden Sea that have never been grazed by livestock are of recent origin, found only at the eastern point of the Wadden Sea islands; the oldest one, since 1930, is found on the island of Terschelling, the Netherlands.

Marshes that had accumulated enough sediment were embanked. The incentives for embankments have gradually changed during the twentieth century from land claims for agriculture to coastal protection. During the early twentieth century, large-scale accretion works with sedimentation fields have been started to create salt marshes that were to be reclaimed for agriculture, but some decades later this was no longer economically feasible due to changes in both socio-economic conditions and agricultural policies. From about the 1970s, there has been a growing recognition that the remaining salt marshes, though largely 'developed' as a result of human intervention, have an important nature conservation interest (Esselink 2000). Increasing areas of seminatural salt marshes with sedimentation fields were designated as nature reserves in Denmark, Germany and the Netherlands, and were included in national parks. Erosion is not allowed because of coastal defence, and new sedimentation fields are not promoted, as they reduce the area of intertidal flats. Hence, existing salt marshes are squeezed between the seawall or artificial sand dikes and the intertidal flats. The existing marshes undergo a process of maturation, and pioneer and young marshes become lost as a result of decreased dynamics. This process is still enhanced when livestock grazing on the marshes ceases. Nowadays only about 40% of the salt marshes of the Wadden Sea support livestock grazing (Esselink *et al.* 2009).

Long-term (>25 years) livestock exclosures in seminatural back barrier marshes in the Wadden Sea revealed that the variation in plant communities along the elevational gradient decreased. Especially at the mid- and higher marsh, plant species diversity declined (Bos *et al.* 2002). Similar changes were recorded in long-term ungrazed seminatural marshes. At sites with fast colonization of *Elytrigia atherica* in a seminatural salt marsh, the typical zonation of entomofauna communities along an elevational gradient disappeared (Figure 19.3) and characteristic halobiontic species were replaced by common inland species of tall forb communities (Andresen *et al.* 1990). In contrast, the invasion of *E. atherica* in salt marshes in western France did reveal an increase in noncoastal spider species, web-building and cursorial spiders, but did not interfere with resident species distibutions, finally resulting in higher species densities and species richness (Pétillon *et al.* 2005). The grazing intensity of winter-staging geese was less in long-term ungrazed than in grazed salt marshes in the Wadden Sea (Figure 19.4; Bos *et al.* 2005). Although goose numbers declined, especially in autumn, in the 10-year-ungrazed part of the Hamburger Hallig, Germany, the numbers of some breeding birds increased (Stock & Hofeditz 2002).

North American salt marshes have a different history. Along the eastern coast, tidal marshes formed within the last 3000–4000 years as sea level rise slowed to about 1 mm yr^{-1}, favouring the establishment of the initial colonizer *Spartina alterniflora*, a 1–2 m tall grass (Niering 1997). The accumulation of organic matter controls the accumulation of inorganic matter, not the reverse. Below-ground plant material is very important in maintaining salt marshes once they are established. During the seventeenth to nineteenth centuries CE, salt marshes were mown, grazed, ditched and embanked in order to make them more suitable for agricultural exploitation. In conjunction with these early activities, some ditching and diking were done to regulate tidal flooding, and increase the profitability of cattle grazing and hay production. However, these impacts were minor compared to those that followed the Industrial Revolution (1850s) when, with increased mechanization, marshes were dredged for marinas, filled for development, ditched for mosquito control, filled with dredge spills and tidal-gated in order to prevent upland flooding. The subsequent invasion of *Phragmites australis* in disturbed coastal wetlands resulted in outcompeting of the native plant species and desiccation as a result of strong transpiration out of its habitat (Bertness *et al.* 2009). Wetland protection laws since the 1970s, and no-net-loss policies, have led

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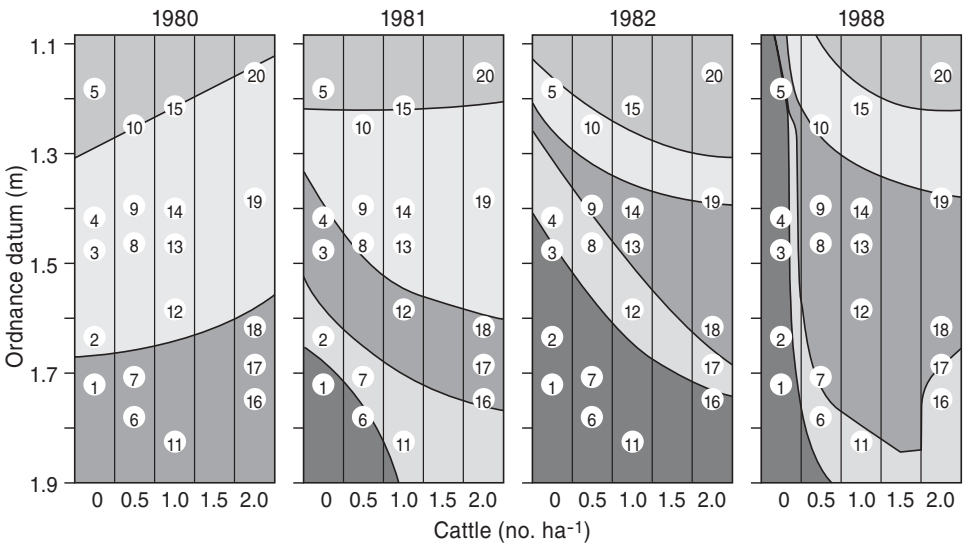


Figure 19.3 Changes of the invertebrate fauna along an elevational gradient (ordnance datum) by cluster analysis of 20 pitfalls for the different stocking rates installed in 1980 and continued during subsequent years on the salt marsh of Leybucht, Germany. The darkest colour indicates non-halobiontic communities. (Modified from Andresen *et al.* 1990.)

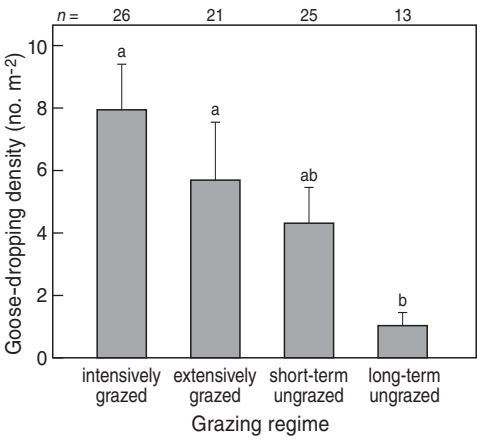


Figure 19.4 Average goose-grazing pressure at transects in the entire Wadden Sea from the seawall to the intertidal flats in relation to livestock-grazing regime for all transects that were paired within the same site. Different letters indicate significant differences ($P < 0.05$). (Modified from Bos *et al.* 2005.)

to restoration efforts. Moreover, with the past decade *Open Marsh Water Management* has been widely practised using biological control, which favours small fish to control mosquitos and simultaneously promotes restoration (Niering 1997).

South American (Costa *et al.* 2009) and Australasian (Thomson *et al.* 2009) coastal salt marshes have a natural **geomorphology**. They are not intersected with an intensive ditching system. The main human impact is heavy exploitation. The effect of intensive livestock grazing, resulting in short swards and possible erosion, in combination with drought is regarded as a disturbance.

19.4 RESTORATION OF SEMINATURAL SALT MARSHES

19.4.1 Targets for restoration of salt marshes

A list of structural attributes that best indicate the status of restored salt marshes was given by Zedler and Lindig-Cisneros (2000): (1) vegetation structure: species composition, stem densitiy, percent cover and biomass or total stem length are probably the most

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widespread descriptors of salt marsh structure, and a tall canopy is regarded as important for birds and invertebrates; (2) soil attributes: texture, nutrients and organic matter are regarded important as far as they contribute to a tall canopy of *Spartina* spp.; (3) invertebrate and fish assemblages: the presence of species alone is not very useful, and abundance and some measure of functioning in the foodweb are preferred; and (4) complex topography: tidal creek networks are important to the distribution of plant species. Creek density and the relative distribution of creeks of different order (first, second and third) can be measured. It is hoped that relatively easily measurable structural attributes can be related to functional attributes.

Apart from abiotic and diversity targets, other **ecosystem goods and services** may play a role in setting targets for salt marsh restoration. Some of the goods and services that salt marshes provide are considered to be 'high' importance by an expert panel (Jones *et al.* 2011; see Table 19.2). Salt marshes were estimated to

Table 19.2 Goods and benefits provided by ecosystem services from (semi)natural salt marshes (after UK National Ecosystem Assessment; http://uknea.unept-wcmc.org) (see Jones *et al.* 2011) and interpretation for restored salt marshes by an expert team (see Jones *et al.* 2011) and the author of this chapter. Class (high, some, none) indicates importance of each good and benefit.

Ecosystem service P:provisioning R:regulating C:cultural	Goods and benefits	Salt marsh (semi) natural	Salt marsh restored
(P) Crops, plants, livestock, fish, etc. (wild and domesticated)	Meat: sheep/cattle/ fish	High	High
	Wild food: Salicornia/other plants/ fish/wildfowl	Some	Some
	Wool (sheep)	Some	Some
	Genetic resources of rare breeds, crops	Some	Some
(P) Trees, standing vegetation and peat/other resources	Turf/peat cutting	Some	None
	Military use	Some	None
	Industrial use: pipeline landfall	Some	None
(R) Climate regulation	Carbon sequestration	High	Some
(R) Hazard regulation –vegetation and other habitats	Sea defence	High	High
	Preventing soil erosion	High	Some
(R) Waste breakdown and detoxification	Immobilization of pollutants	High	Some
(P,R) Wild species diversity including microbes	(P) High diversity, or rare/unique plants, animals and birds, insects	High	Some
	(P) Ecosystem-specific protected areas	High	High
	(R) Nursery grounds for fish	High	High
	(R) Breeding, over-wintering, feeding grounds for birds	High	High
(R) Purification	Water filtration: groundwater, surface flow, seawater	?	?
(C) Spiritual/religious + cultural heritage and media	Sites of religious/cultural significance; World Heritage Sites; folklore; TV and radio programmes and films	Some	—
(C) Aesthetic/inspirational	Paintings, sculpture, books	High	Some
(C) Recreation/tourism	Many opportunities for recreation: incl. sunbathing, walking, camping, boating, fishing, birdwatching etc.	High	Some
(C) Physical/mental health + security and freedom	Opportunities for exercise, local meaningful space, wilderness, personal space	Some	Some
(C) Education/ ecological knowledge	Resource for teaching, public information, scientific study	High	High

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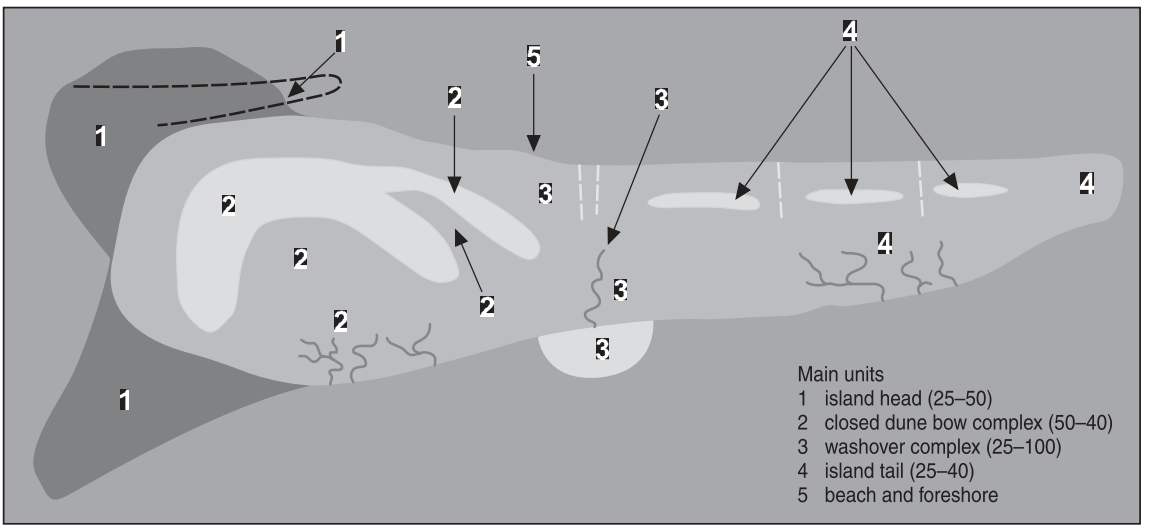


Figure 19.5 Geomorphological model of a barrier island with its characteristic main units and traits. Values in parentheses refer to expected longevity of main units (years). (1) Island head with temporal green beaches, (2) old dune and salt marsh systems disconnected from the beach, (3) wash-over complexes and salt marshes with a wide gradient from high elevation with fresh water from the dunes to intertidal flats with saline water, (4) island tail with young dunes and salt marshes connected to the beach and intertidal flats and (5) beach and foreshore with temporal green beaches. The model represents the full dynamics and zonation of salt marshes, and is a reference model for restoration. (Modified from Esselink *et al.* 2009.)

provide more economic value per unit area than most other ecosystems if tourism, carbon storage and coastal defence were combined. An attempt is also made to indicate to which extent these services can be regained along with salt marsh restoration (Jones *et al.* 2011).

The salt marsh harbouring all these conditions features (1) tidal inundation with salt water and drainage of fresh water from the hinterland, (2) zonation of communities from pioneer zone towards high salt marsh, (3) sufficient width from low intertidal flats towards high elevation to include creeks, creek bank levees and depressions and (4) geomorphological dynamics (i.e. continuous building of young marsh, or periodic erosion followed by building of young marsh) (Esselink *et al.* 2009). Such salt marshes show the highest richness of characteristic saline and brackish plant and animal species, and the habitat types and characteristic plant communities to be protected or restored in the Natura 2000 system (EUNIS 2006). This is a supranational instrument providing a common framework for the conservation of plant and animal species and their natural habitats within the 27 member states of the European Union. This EUNIS classification is the basis for the creation of an European network of Special Areas of Conservation, a major constituent of Natura 2000 (see also Chapter 14). Whereas the EUNIS classification deals with the 'ideal' vegetation, the 'ideal' situation or **reference** of a natural salt marsh, from a **geomorphological** point of view, is shown in Figure 19.5. Although this represents a scheme of an island, it can hold for a mainland marsh when points 1–4 (discussed in this paragraph) are taken into account.

The 'ideal' system may not be achievable in many restoration projects. The best option for restoration is to create variation in abiotic conditions with respect to inundation and drainage, and allow the plant and animal species to find their way. However, it is possible that despite proper tidal inundation, plants may not establish as a result of too-low sediment redox potential (Mossmann *et al.* 2011). Other functions of salt marshes, such as carbon storage and wave attenuation (Table 19.2), will be fulfilled both in a homogeneous and a heterogeneous marsh. There seems to be a contradiction in the fixed classification of EUNIS and the dynamics of the geomorphology. Also here, priority should be given to the dynamic abiotic conditions. Most plant and animal species will establish, as there

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seems no big constraint in dispersal of organisms along the coastline (see below). After all, the composition of communities may change in the future as a result of increasing temperature and CO_2 enrichment of the atmosphere.

Restoring salt marshes requires less intensive management to get somewhere near the targets and is essentially about reinstating dynamic physical processes. Because of the additional functions that salt marshes provide, however – such as coastal defence and carbon storage – above more general **biodiversity** provisioning, the importance of successful restoration is high.

Although there are many similarities in approaches for restoration applied in various parts of the world, some striking different accents can be recognized. In North America, examples are given of removal of fill, amendment of the soil, sowing target species and use of herbicides to remove dominant *Phragmites australis* or *Typha angustifolia*. Sometimes, this happens at a large scale. However, a plea is made for restoration through an *adaptive approach* by subdividing the site into modules to be restored in phases. The most urgent question should be matched to the first module. An early question might be, which species need to be planted and in what assemblages? A second question could be, how should the soil be amended or the topography be manipulated to achieve the project goals (Callaway & Zedler 2009)? **Mitigation** projects, including raising a site and planting *Spartina* spp., should not be considered restoration, as there is no balance between tides, elevation, drainage pattern, substrate type and vegetation, hence it is not a gradually self-organizing system. In Europe, de-embankment and increase of tidal amplitude are mainly practised without further assistance for the development of a self-organizing marsh. The same holds for changes in livestock grazing. The latter is the option to be used in South America and Autralasia.

19.4.2 De-embankments and other measures to repair geomorphological conditions

Embankments interrupt not only salinity gradients but also sediment deposition. It is obvious that continuous rise in net surface elevation occurs on the unembanked marsh in front of the newly created polder after embankment. Differences in soil level in front of and behind the seawall or summer dike will be greater when the polder is intensively drained for agricultural purposes. This will also hold for coastal systems with accumulation of peat where great shrinkage can take place (Roman *et al.* 1995). For the sake of coastal protection and the costs of seawall maintenance, it is assumed that a well-inundated tidal marsh with a good rate of sedimentation in front of the seawall or summer dike is better than a low-lying polder without sedimentation. Coastal defence and nature conservation might be combined by de-embankment of polders and subsequent restoration of these former tidal marshes, described as 'managed retreat' or 'managed realignment' (Boorman 1999). In such cases, a new seawall is necessary inland of the present coastal defence that will be knocked down or breached.

After de-embankment of a summer polder, renewed contact with the sea results in rapid re-establishment of abiotic conditions (Erchinger *et al.* 1994). A restoration is also expected to be quickly successful for birds during high tides, as they have few dispersal problems. It can take a long time before a site is appropriate for foraging on the proper type of food, or breeding in the proper vegetation structure. However, there might be dispersal constraints for plants. Are tidal plants still available in the community **species pool** as persistent seeds in the soil **seed bank** as a historic record of the former marsh vegetation? A study in natural salt marshes indicated that most salt marsh species have a transient or short-term persistent seed bank (Wolters & Bakker 2002). This suggests that restoration cannot rely on a persistent seed bank of salt marsh species. Percentages of target species, as related to the regional species pool, established in 70 de-embanked sites in north-western Europe, may amount to 70%, but most sites show lower figures (Figure 19.6; Wolters *et al.* 2005). The reason is often the constricted elevational zone for all possible salt marsh communities. Nearly 100% of the newly established species originated from the adjacent salt marsh in the de-embanked sites. Apparently, dispersal of diaspores to de-embanked sites may not pose a problem.

On barrier islands in the Wadden Sea, the restoration of dynamics by (partly) removing artificial sand dikes (see Plate 19.1) is in the phase of planning. Along the mainland coast of the Wadden Sea, it is hoped that the intensive ditching pattern in seminatural marshes will transform into natural drainage patterns with current rates of sedimentation. However, an experiment with excavation of 1.5 m of clay for seawall

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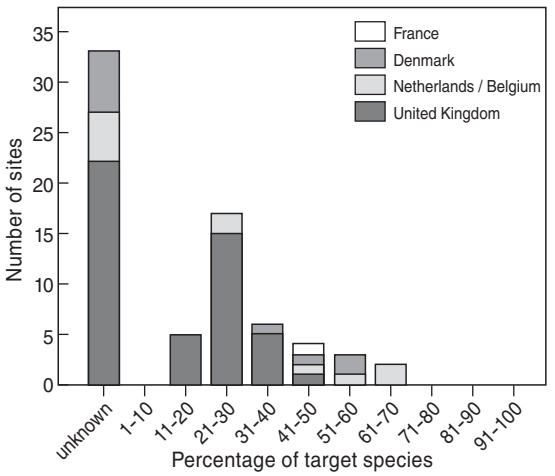


Figure 19.6 Frequency distribution of scores of percentage of charteristic salt-marsh plant species related to the regional species pool of over 70 de-embanked sites in north-west Europe. Note the absence of monitoring in about 50% of the sites. (Modified from Wolters *et al.* 2005.)

reconstruction, from an area of 300 m × 300 m in an intensively ditched salt marsh in Germany, revealed that the claypit refilled with a rate of 15 cm yr^{-1} during the first 2 years to less than 4 cm yr^{-1} after 8 years, when it exceeded Mean High Tide. In the mean time, a meandering creek pattern had developed (Karle & Bartholomä 2008). Of course, all de-embankment measures and plans for removal of artificial sand dikes are carried out within the framework of maintaining adequate coastal defence for the hinterland.

In organogenic coastal areas such as along the Baltic Sea, embankment resulted in lowering of the polder because of agricultural exploitation and oxidation. Hence, removal of the summer dike might result in permanent stagnant pools containing slightly brackish water without any vegetation, after die-off of the freshwater community. This sequence of events was indeed observed at Karrendorfer Wiesen on the German Baltic Coast (Müller-Motzfeld 1997). De-embankment of an estuarine summer-polder in the south-western Netherlands revealed that *Phragmites australis* took over in the absence of livestock grazing, whereas *Plantago maritima* became dominant in a grazed site, and the lower lying pools remained without vegetation (Bakker *et al.* 2002b). These differences emphasize the effect of management regime on the outcome of de-embankment. This is in fact a widespread phenomenon. The sites that were revealed to be most successful with respect to the re-establishment of halophytic plant species after de-embankment were all grazed (Wolters *et al.* 2005). This can be attributed to breaking up monospecific swards and reducing competition. In fact, these restored marshes 'behave' as aforementioned existing salt marshes.

19.4.3 Increase of tidal amplitude

In Connecticut, United States, tidal flows were reinstated by placement of a 1.5 m diameter culvert in an impoundment. Restoration targets were expressed in terms of inundation, salinity, productivity and community structure. Vegetation integrates a number of factors; however, food chain support as manifested by macro-invertebrates, fish and birds was also taken into account. In 1988, 10 years after the start of the restoration, the existing freshwater species *Typha angustifolia* had declined from 75% to 15%, whereas *Spartina alterniflora* had increased from <1% to 45%. In addition, high-marsh species had re-established and covered 20% of the site, but *Phragmites australis* had also spread. After 1988 *Phragmites* declined and salt marsh vegetation had increased to cover 85%. Although the restoration exhibits a striking result, the restored marsh only moderately resembles the pre-impoundment marsh (Fell *et al.* 2000). Monitoring between 5 and 20 years of nine sites after increased tidal amplitude along the coast of Connecticut revealed different results for various parameters. Rapid recovery of vegetation was related to sites with low elevation, greater inundation and higher groundwater tables as a result of greater colonization potential. Recovery of other organisms was not always related to that of the vegetation. A viable population of the native, high-marsh snail *Melamopus bidentatus* took 20 years to recover in a site where the vegetation recovered much faster. Characteristic fish species assemblages were found in creeks and ditches within 5 years. Populations of breeding birds typical of salt marshes had established after 15 years in the restored sites (Warren *et al.* 2002). Hence, within 20 years, successful restoration by the increase of tidal amplitude is possible in this site with these conditions. However, possibilities and time scales for other salt marsh functions, such as carbon storage and wave attenuation, are not known.

The polder Beltringharder Koog, Germany, was embanked in 1987 in order to have a reservoir to

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control drainage of the hinterland. It consisted of intensively grazed salt marsh and intertidal flats. The tidal range was reduced from 3.4 m to zero immediately after embankment. Former salt marshes were colonized by tall fresh forb communities and former intertidal flats by salt marsh species. In order to compensate for the losses, a lagoon system was established allowing reduced tidal influence through two sluices. From 1990 onwards a 0.3 m tidal amplitude was established with stormflood simulations of 0.8 m tidal amplitude twice a month in the nonbreeding period of birds. The restoration was successful in the lower inundated parts where a typical salt marsh zonation established. However, the highest parts remained fresh grassland, and started to get overgrown by shrub species, in the absence of livestock grazing (Wolfram *et al.* 2000).

19.4.4 Changes in the grazing regime

Cessation of livestock grazing can result in a decrease of the number of plant and animal species, as discussed above. In an experiment of resuming livestock grazing in a formerly grazed back barrier salt marsh in the Wadden Sea, the changes in the vegetation after **abandonment** turned out to be reversible within 10 years at a relatively high stocking rate of cattle (Bakker 1989). At the larger scale of the entire elevational gradient, the number of plant communities increased, whereas at the small scale of each elevational level, the number of plant species per unit area increased, mainly because of the removal of the tall grass *Elytrigia atherica* in saline marshes and of *Phragmites australis* in brackish and fresh marshes (Bakker 1989; Bakker *et al.* 2003). However, at the low marsh the number of species decreased. The soft, frequently inundated substrate is trampled by cattle and only annual pioneer species can be maintained. It is estimated that the numbers of brent geese in the entire Wadden Sea in May can be a factor of 4–8 higher if all salt marshes were to be grazed by livestock, than in the absence of grazing (Bos 2002).

19.5 PERSPECTIVES

Targets for the successful restoration of salt marshes include changes in the **geomorphology** and **succession** of plant communities. Squeezing of salt marshes between seawalls or artificial sand dikes in the hinterland and intertidal flats can be prevented by realigning landward. This should not be carried out by the extension of new sedimentation fields into the intertidal flats, because this would imply a reduction of the area of intertidal flats with their characteristic conservation issues such as waders. Along the mainland coast of Europe, seawalls and summer dikes have successfully been removed and new salt marshes have developed in former polder areas. On barrier islands in the Netherlands, removal of artificial sand dikes is planned, but experiments are needed. Increase of the tidal amplitude in embanked polders through sluices is not always successful, and especially the higher parts of the elevational gradient may be lost for salt marsh development when only part of the tidal amplitude can be reinstated. Intensive ditching patterns in salt marshes with sedimentation fields or mosquito control do not transform into meandering creeks. Consequently, reduced abiotic variation may establish, and hence habitats for plant and animal communities.

Increased *sea level rise* caused by global warming might have a drowning effect on salt marshes. However, the salt marsh elevation may follow the level of Mean High Tide without negative consequences for increased sea level rise. Is current vertical accretion enough for salt marshes to keep their relative position in the tidal frame? The current sea level rise in western Europe is about 3 mm yr^{-1}. Recent modelling studies suggest the overwhelming importance of tidal amplitude and concentrations of suspended sediment (Kirwan *et al.* 2010). At future sea level rise of about 10 mm yr^{-1} salt marshes in regions with a tidal range greater than 1 m and suspended sediment concentration greater than 20 mg L^{-1} will not be permanently submerged. When future rates of sea level rise beyond 20 mm yr^{-1} occur, only salt marshes in regions with tidal ranges over 3 m and sediment concentrations above 30 mg L^{-1} are expected to keep pace with future sea level rise. In the latter case, many marshes will permanently submerge despite their tendency to accrete more quickly (Kirwan *et al.* 2010). Knowledge on vertical accretion rates at the scale of catchment areas (creeks with their drainage area) in salt marshes is poorly developed. Back barrier marshes with a low vertical accretion might suffer earlier than mainland marshes with a higher vertical accretion.

Mangrove forests occur lower in the **zonation** than salt marshes. Sea level rise will increase the inundation frequency, reduce soil salinity and increase transport

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of seeds on mangroves into more elevated zones, and mangrove forests will migrate landward at the expense of salt marshes (Costa *et al*. 2009).

In future, global temperatures and CO_2 levels will also rise, just as sea levels will. In Europe, temperate and northern salt marshes might change through changing competition between plant species. Interspecific competition experiments revealed that *Puccinellia maritima* responds more positively to combined increase of temperature and CO_2 than *Spartina anglica*. Although both species will extend their range northward from 57°N, *Puccinellia* will outcompete *Spartina*. It is also suggested that *Puccinellia* under the new regime of both higher temperatures and CO_2 enrichment will extend its lower limits further downshore in existing marshes at latitudes below 57°N (Gray & Mogg 2001). Note that the broad-leaved *Spartina anglica* was introduced to trap more sediment than the native species (Davy *et al*. 2009). Mangroves are restricted to (sub)tropical regions because their leaves cannot survive frost. Increasing temperatures may result in spreading of mangrove forests at the expense of salt marshes towards higher latitude (Saintilan & Willems 1999).

It is not clear how to deal with the trade-offs between vertical accretion and biodiversity issues. Highest vertical accretion can be accomplished on salt marshes with tall and dense canopy, hence without livestock grazing. However, the diversity of plant and animal communities including characteristic halobiontic organisms is better preserved or restored in grazed marshes with lower vertical accretion than in abandoned salt marshes. Highest diversity will be achieved with stocking densities that create patterns of short grazing lawns alternating with patches of tall vegetation. Particularly long-term ungrazed marshes have low diversity of plant and animal communities. Short-term abandonment may result in flowering plants attracting pollinating insects, breeding birds foraging on them, and plants setting seed and attracting granivorous birds.

There are more general trade-offs between functions of salt marshes, and hence targets for restoration. Long-term monitoring on different spatial scales in restoration sites (*Long-Term Ecological Research sites*) of changes in geomorphology, hydrology, vertical accretion, plants, fish, birds, mammals and invertebrates, in a foodweb context, will be helpful as decision tools for future projects. An important issue is to learn at what time scale the different elements of the ecosytem can be restored.

In parts of the world with intensive grazing such as South America and Australasia, experiments with removal of cattle are needed to assess their impact on salt marshes. In north-western Europe, abandonment of livestock grazing and mowing of salt marshes has already taken place with negative results for diversity of characteristic plant and animal species. Recovery of mono-species stands (resulting from abandonment from agricultural exploitation) is successful after reintroducing livestock grazing. Experiments are needed with respect to stocking density and rotational grazing for the benefit of various groups of organisms in their food web context such as plants, invertebrates and breeding and migrating birds. In general, the scientific basis for management based on experiments is largely missing.

Summarizing, restoration of salt marshes, and hence their functioning with respect to sediment trapping and coastal defence, is possible after de-embankment of (summer) polders, but to a limited extent after the increase of tidal amplitude through sluices. Natural drainage systems are hard to restore in salt marshes with intensive ditching. The area of salt marshes may decrease by the spread of mangrove forests as a result of future increase of temperature. The effects of sea level rise depend on the local conditions such as tidal range, suspended sediment concentrations and density of the vegetation. The composition of the community and the structure of the vegetation depend on both the elevation of the salt marsh and its management, especially livestock grazing.

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Part 4

Restoring to the Future

Restoration Ecology: The New Frontier, Second Edition. Edited by Jelte van Andel, James Aronson.
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EDITORS' INTRODUCTION

We started this book on restoration ecology with Part 1, intended to set the scene for a long discussion and voyage of discover. We asked: 'Where do we start, and with what unifying concepts?', 'How do we cope with uncertainty and unpredictability, in view of climate change and other big issues?' And, 'What are some tried and proven options for planning and implementing successful restoration projects, at the local scale, and restoration programmes at the regional scale?' In Part 2 we explored fundamental ecological knowledge in search of conceptual and methodological tools and insights from this specific branch of science that could be useful for the transdisciplinary science and practice of ecological restoration. The chapters in Part 3 illustrated, biome by biome, how ecologists working in the field have learned what is – or could be – effective ecological restoration, collating input from past and ongoing experiments and experiences around the world.

Now, in Part 4, it's time to explicitly address future scenarios and perspectives, in which restoration ecologists will be working together with professional and amateur practitioners, and all the stakeholders who make up a restoration project. This means looking squarely at the ongoing processes of biological invasions by alien species in ecosystems around the Earth, the effects of climate change on ecosystem and socio-ecological system development, emerging markets and mechanisms for rewarding resource and land managers for rendering ecosystem services and, finally, the various ways in which some nations and NGOs have begun to search for sustainability. Here, in what can be called sustainability science, the landscape, ecosystems and biodiversity perspectives to ecological restoration all meet and merge.

Some of the take-home lessons readers should have retained from Part 3 concern general recommendations and guidelines for projects and programmes of ecological restoration to be successful. To wit, there is always and everywhere a need to translate general insights into applications that 'fit' the constraints and opportunities for restoration, locally. There is a clear need to respect the conditions for negotiations and consensual decision making including all the major stakeholders. This requires several steps: (1) identify the causes of degradation in an historic perspective, based on understanding of social and biophysical processes, (2) negotiate among stakeholders to achieve agreement on the level of ambition in terms of common values, goals and trajectories, recognizing the available resources (e.g. financial, labour and seed sources), (3) identify and design the technologies to be applied, (4) arrange long-term management and monitoring to evaluate progress and, if necessary, adapt and fine-tune the strategy chosen in light of changing conditions and (5) initiate research alongside the restoration programme to improve the understanding of the results.

As compared to the first edition, all three chapters in Part 4 are new. We are indebted to Mirijam Gaertner, Patricia Holmes and David Richardson for contributing a chapter on problems related to biological invasions, in which they explore the concept of resilience in relation to ecological restoration (Chapter 20). We also thank Katharine Suding and Elizabeth Leger for their chapter on shifting baselines in a changing world, focusing on the dynamics of evolutionary changes in biotic communities (Chapter 21). We call the reader's attention to their statement that 'although many future changes may not have historical analogues, a historical perspective can help design or steer emerging systems to encompass a greater spectrum of natural variability inherent in the system or under future climate change'.

Finally, we, the initiators and editors of this multi-author book, finish off the journey in our Chapter 22, where we reflect together on all that has been presented thus far. We view ecological restoration as a critical part in society's search for sustainability, at national, regional and international scales. We ask specifically 'How can our current knowledge and insights in restoration ecology help find the way towards sustainable use, development, conservation and restoration of terrestrial, aquatic and coastal ecosystems?' Onward.

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Chapter 20

BIOLOGICAL INVASIONS, RESILIENCE AND RESTORATION

Mirijam Gaertner, Patricia M. Holmes and *David M. Richardson*

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20.1 INTRODUCTION

The idea that biological invasions are one of the major causes of ecosystem degradation is currently under debate. Many authors consider biological invasions to be important drivers of ecosystem degradation, whereas others suggest that they are, in many cases, just 'passengers' – capitalizing on other anthropogenic disturbances (MacDougall & Turkington 2005; Gasso *et al.* 2009). While some authors consider invasive alien species to be a substantial threat to biodiversity and ecosystem stability, and hold them responsible for the decline in native species richness and the local extinction of certain species (Richardson *et al.* 1989; Wilcove *et al.* 1998; Simberloff *et al.* 2011), others point out that net species diversity, in most cases, increases following biological invasions, at least over short time scales (Sax & Gaines 2003).

Consequently, opinions about approaches for managing **invasive alien species** differ; some authors call for the acceptance of invasive alien species in some situations, for example where they provide economic incentives or where they are integrated into native ecosystem networks (Davis *et al.* 2011; Vince 2011). Some studies even call for the use of alien species to restore areas that have been heavily degraded, since alien species grow faster and can provide a canopy under which slower-growing native species can (re-)establish (Ewel & Putz 2004). On the other hand, invasion biologists argue that focused management is necessary because invasive species can cause severe impacts on ecosystems including species extinctions and major economic losses (Simberloff *et al.* 2011). We argue that impacts of biological invasions differ from situation to situation depending on the ecosystem that is invaded and the particular invader. In our chapter we focus on those biological invasions that have undeniably negative impacts on ecosystems, and exclusively on impacts of invasive plant species. We seek to link the topic of invasion ecology and the practice of ecological restoration.

Biological invasions are increasing in importance worldwide as drivers of ecosystem **degradation** and transformation. Invasive species have many impacts: some operate at the level of populations or communities (Hejda *et al.* 2009), while others interfere at higher levels, disrupting fundamental processes that affect entire ecosystems (Parker *et al.* 1999). Alterations to ecosystems can lead to a shift to an **alternative stable state** which may not be amenable to restoration, utilizing standard **interventions** (Suding *et al.* 2004). In section 20.2 we review the many ways in which invasive plant species can potentially change ecosystem composition, structure and functioning, looking at underlying mechanisms and processes of alien plant invasions.

It has been acknowledged that clearing of invasive species alone is often not sufficient for re-establishing native communities; some form of restoration is increasingly seen as vital when dealing with alien invasions (Esler *et al.* 2008). However, restoration efforts are challenged by numerous obstacles caused by the alien species such as altered ecosystem properties and ecosystem functions. Consequently, restoration efforts often have unexpected outcomes or even unforeseen negative consequences. In section 20.3 we summarize the most important challenges that restoration ecologists have to face when dealing with alien invasions and give examples of successes and failures.

To successfully plan and prioritize restoration efforts after alien invasion, a fundamental step is to determine the *degree of ecosystem degradation*. To identify the degree of ecosystem degradation resulting from invasion is a major challenge for researchers and managers. In section 20.4 we evaluate how different types of impact can influence the **resilience** of ecosystems, using the concept of ecosystem **thresholds** to determine ecosystem degradation. In the context of ecosystem restoration, resilience is defined as the ability of an ecosystem to recover from **disturbance** without human intervention (Westman 1978). The concept of *ecosystem thresholds* has been identified as a useful tool for determining the degree of ecosystem degradation (Groffman *et al.* 2006). Briske *et al.* (2006) described a threshold as the point at which the dominance of the negative (regulating) feedbacks that maintain ecosystem resilience is replaced by the dominance of positive (supportive) feedbacks that lead to losses in resilience. Invasive species may dominate an ecosystem to the extent that structural and functional changes to biotic and abiotic processes occur in concert, resulting in turn in supporting feedbacks that further promote the spread of the alien species.

To demonstrate the implications of the ecosystem threshold approach for management and restoration, we present case studies of *Acacia* and *Pinus* invasions in South African *fynbos*. Australian species of *Acacia* (known in Australia as wattles) are particularly suitable as study species for the ecosystem resilience concept as they have huge invasive potential and have been well

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studied. Nine Australian wattles have been classified as major invaders in South Africa and are widely distributed in different parts of the country (Nel *et al.* 2004). Another group of highly invasive species in South Africa is the genus *Pinus*, including the three most widespread invaders in the fynbos biome: Aleppo pine (*Pinus halepensis*), cluster pine (*P. pinaster*) from the Mediterranean region and Monterey pine (*P. radiata*), introduced from California (Richardson 2000).

Management of invaded ecosystems is an increasingly complex problem worldwide (e.g. Roura-Pascual *et al.* 2009). Motives for the restoration and revised management of invaded ecosystems include the desire to deal with (1) loss of **ecological integrity** (e.g. species loss) (Richardson & van Wilgen 1986), (2) impact on **ecosystem functioning** (e.g. changes in nutrient cycles) (Yelenik *et al.* 2004), (3) impaired **ecosystem services** (e.g. reduction in river flow that leads to lower water supply for human use) (Le Maitre *et al.* 1996), and (4) loss in agricultural productivity (Born *et al.* 2005). In many contexts, the goal of management interventions will be **ecological restoration** (i.e. to return a degraded or impaired ecosystem to some historic trajectory) (SER 2004). However, in some cases, other options will have to be considered, especially when significant biological invasions have taken place. Three key questions need to be addressed by managers of invaded ecosystems: firstly, is restoration feasible, secondly, is it desirable, and, thirdly, what are appropriate restoration goals? Answers to these questions need to feed into a *decision-making framework*. In the last section of this chapter, we will apply the concept of ecosystem resilience to describe an approach for decision making in ecological restoration, focusing on plant invasions in native ecosystems. We address questions concerning the feasibility of ecosystem restoration (i.e. will removal of the alien species be sufficient to facilitate autogenic recovery of the ecosystem?) and questions concerning the desirability of ecosystem restoration (i.e. is restoration desirable where the alien has become integrated into socio-ecological systems and provides a valued ecosystem service for local people?).

20.2 HOW DO INVASIVE ALIEN PLANTS IMPACT ECOSYSTEMS?

The establishment of a new plant species often changes the structure and functioning of an ecosystem. Restoration ecology studies often focus on the consequences of invasions for populations and communities (i.e. changes in community composition or changes in species richness). Underlying processes and mechanisms are much less frequently addressed. This has in some cases led to unexpected results, or outright failure of efforts aimed at restoration. As a basis to our framework for the restoration of ecosystems impacted by alien plants (see below), we will therefore differentiate between (1) the processes and mechanisms underlying the invader impacts (e.g. competition or allelopathy), and (2) the outcomes of invasion on the native ecosystem, called 'native ecosystem response' (e.g. decline of species richness). Another factor central to plant invasions, and also important in our restoration framework, is **disturbance**. Natural disturbances (e.g. due to fires or floods) and anthropogenic disturbances (e.g. due to over-grazing or vegetation removal) provide an invasion window for alien species to establish (Richardson *et al.* 2007) and may trigger processes leading to ecosystem degradation.

20.2.1 Processes and mechanisms underlying impacts of invasions

The processes and mechanisms underlying impacts of alien invasion are numerous and complex, including the displacement of resident plants, the inhibition of native plant establishment and the modification of physical and chemical resources (e.g. water and nutrient availability) and native ecosystem processes (i.e. changes to fire regimes and nutrient cycling). Successful alien plants can also make use of existing ecosystem networks to facilitate their establishment (e.g. local pollinators and dispersal agents). We will firstly review the different biotic and abiotic processes underlying impacts of alien plant invasions and secondly refer to the native ecosystem response (i.e. the impacts on plant population and community levels).

Competition

Invasive alien plants can replace already established species in a community, prevent the establishment of new individuals (Yurkonis *et al.* 2005) or both. Displacement of already established plants can occur through competition for resources (Werner *et al.* 2010), changes in physical or chemical soil properties (Yelenik *et al.* 2004), an alteration of soil microbial

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feedbacks (Callaway *et al.* 2004) or allelopathic effects. Garcia-Serrano *et al.* (2007), for example, investigated the replacement of a native *Senecio* species (*S. malacitanus*), native in the south-east of the Iberian Peninsula and Maghreb, by two alien *Senecio* species (*S. inaequidens* and *S. pterophorus*, both from South Africa) in a greenhouse experiment. They found that the alien *S. inaequidens* was the most competitive species for all moisture conditions and that the native *S. malacitanus* was more competitive than the alien only under conditions of water stress.

Establishment limitation of new native individuals can be triggered if alien propagules occupy germination niches or through decreased resource availability, such as for light or nutrients (Davis *et al.* 2000), but also by increased resource availability. A further cause for reduced establishment is the development of a thick litter layer by the alien which creates a barrier for emerging native seeds (Marchante *et al.* 2004).

Nutrient accumulation

Invasive alien plants with a major impact on ecosystem processes can be called 'transformers' (*sensu* Richardson *et al.* 2000). Some transformers alter ecosystem processes by adding resources that are generally limited in the native ecosystem, for example by nutrients. Many invasive plants accumulate nitrogen through increased biomass and net primary production (i.e. through production of litter with higher decomposition rates than native species) (Ehrenfeld 2003). Especially in nutrient-poor ecosystems, an increase in nitrogen can have significant impacts, ameliorating the conditions for invasive alien plants (Vinton & Goergen 2006) and preventing the re-establishment of native plants (Marchante *et al.* 2008). Prominent examples for nitrogen increase in nutrient-poor habitats are Australian wattle invasions in South African fynbos, invasion on young volcanic soils in Hawaii by fire tree (*Morella faya*), native to Macaronesia (the Azores, Madeira and the Canary Islands), and invasion of black locust (*Robinia pseudoacacia*), native to south-eastern North America, into north-eastern American pine–oak ecosystems. Invasion by Norway maple (*Acer platanoides*) and tree of heaven (*Ailanthus altissima*) in temperate forests of the north-eastern United States considerably accelerated nutrient cycling rates and increased soil nutrient levels, with the magnitude of the impact increasing with soil fertility (Gomez-Aparicio 2009). Phosphorus enrichment following alien plant invasions has also been demonstrated in several ecosystems (e.g. Fisher *et al.* 2006). Invasions may also change other aspects of ecosystem biogeochemistry. For example, some plants change soil chemical properties by accumulating certain minerals, such as salt (NaCl), in the soil, leading to changes in plant density and species composition, such as those following invasion by ice plant (*Mesembryanthemum crystallinum*) (Vivrette & Muller 1977).

Water use

Invasive alien species can absorb substantial amounts of water and other limited resources and thus affect plant communities by reducing soil water availability for native species. Furthermore, some invasive alien plants gain competitive advantage by extracting soil water at different times or from soil depths not exploited by native plants. In semi-arid regions of the western United States, for example, Kulmatiski *et al.* (2006a) showed that winter-active alien annual grasses inhibit the establishment of native perennial grasses by early season and deeper use of water resources. Other studies report increased *evapotranspiration* rates in invasive alien compared to native plant species (Zavaleta 2000). In riparian ecosystems, invasions may have wider implications: invasive alien trees often use significantly more water than native riparian species and can therefore substantially reduce water flows (Dye *et al.* 2001). In South Africa, invasive alien trees from Australia (mainly *Acacia* and *Eucalyptus* species) have reduced natural river flows by 20% or more (Le Maitre *et al.* 1996).

Altered fire regimes

Invasive alien species may suppress or promote fire, thereby driving rapid ecosystem transformation (Brooks *et al.* 2004). Examples of increases in fire frequency are common among grass invasions in areas naturally dominated by woody plants (Rossiter-Rachor *et al.* 2008). Even in fire-prone ecosystems, plant invasions can have severe impacts if they alter the natural fire regime to produce a different selective environment (Keeley *et al.* 2005). Besides altering fire frequency, aliens can also alter fire intensity, especially if they produce a greater biomass and hence larger fuel loads than native species (D'Antonio *et al.* 2000). Aliens can also decrease fire frequency and/or intensity, if they

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produce lower biomass or less flammable fuels than native species.

20.2.2 Native ecosystem response

The outcomes of alien invasions on the native ecosystem have been summarized in several reviews (e.g. Parker *et al.* 1999; Levine *et al.* 2003) and can be measured at both population and community levels. Invasions can also affect mutualistic plant–animal interactions (Traveset & Richardson 2006).

Impacts on plant populations

Invasions can have immediate impacts on the performance and phenotypic traits of individual plant species. These impacts can manifest in reduced growth or reproduction or changes in native species morphology (Parker *et al.* 1999). Invasions can also have direct genetic impacts on native species through *hybridization* and/or *introgression* (introgressive hybridization; see also Chapter 7). Hybridization of invasive alien plants with native plants can cause a loss in fitness in the latter and even result in local extinction (Parker *et al.* 1999). Prentis *et al.* (2007) found a decline in the native *Senecio pinnatifolius* from east coast areas of Australia, due to hybridization with the introduced *S. madagascariensis*. Small native populations on islands are especially vulnerable to extinction by hybridization (Levin *et al.* 1996). Introgression describes repeated, interspecific hybridization between a new (to a region) taxon and a resident taxon, followed by backcrossing to either or both parental taxa. This influx of new genetic information results in novel phenotypes which could be more robust and have broader ecological amplitudes than either parental type. They tend to occupy disturbed habitats – also called 'hybrid habitats' (Galatowitsch *et al.* 1999).

Furthermore, invasions can have indirect genetic impacts by altering patterns of natural selection within native populations. Native species in old invasions may have become adapted to the altered habitat (e.g. they develop a resistance to potentially allelopathic chemicals produced by the alien species) (Mealor & Hild 2006). Lau (2008) showed that invasion by an alien plant and herbivore species in open grasslands throughout the McLaughlin Reserve in Napa County, California, United States, altered the strength and direction of natural selection on the competitive ability and antiherbivore defences of the native plant *Lotus wrangelianus*.

Impacts at the plant community level

Impacts at the community level follow a common progression from initial impacts (e.g. increased biomass, nitrogen fixation, species displacement and changes in abundance) to secondary impacts (e.g. decomposition processes, and changed seed bank dynamics) to tertiary impacts (e.g. interactions among fauna) (Le Maitre *et al.* 2011). The most frequently reported initial impact of biological invasions at the community level is a decrease in plant species richness or diversity. Such impacts appear to be largely species-specific, with the severity of the impact depending almost exclusively on the identity of the invading species (Hejda *et al.* 2009). Another important influencing factor is the type of native ecosystem undergoing invasion (Gaertner *et al.* 2009). Invasive plants can also negatively affect native community composition and structure (Lenz *et al.* 2003). Jäger *et al.* (2009) investigated the impact of the red quinine tree (*Cinchona pubescens*) on the fern–sedge vegetation of the Galapagos Islands. Invasion of the formerly treeless wetland community by alien tree species had significant impacts on stand structure and environmental conditions and led to decreases in species diversity and cover.

A secondary impact of invasion on plant community composition is the depletion and homogenization of the native soil **seed bank**. Plant invasions can significantly alter richness, diversity and composition of native seed banks, resulting in long-term changes for the plant community (Gioria & Osborne 2009). For example, in South African fynbos ecosystems, invasion by the Australian wattle *Acacia saligna* causes significant reductions in native soil seed bank density and richness (Holmes 2002). Tertiary impacts are characterized by interference of invasive species in native ecosystem networks and are described below.

Impacts on plant–animal and plant–microorganism networks

Invasive alien plants can influence mutualistic plant–animal interactions, such as pollination and seed dispersal, in several different ways (e.g. Traveset & Richardson 2006). Decrease in pollinator visitation to native plant species has been demonstrated as a result of a competitive advantage by an invasive alien plant

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species (Brown *et al.* 2002). By contrast, a study on the competitive advantage of the invasive alien *Impatiens glandulifera* in riparian ecosystems in Spain did not provide evidence that this alien was out-competing native plants for pollinators (Bartomeus *et al.* 2010). This finding was corroborated in a cross-European analysis on integration of invasive alien species into native pollinator networks (Vila *et al.* 2009). Similarly, studies on the impact of alien plant invasions on the pollinator itself have not yielded conclusive results to date (e.g. Severns & Warren 2008).

Invasive alien plants can also impact soil microbes, indirectly changing soil processes (e.g. nitrification) (Ehrenfeld *et al.* 2001). In hardwood forests in northern New Jersey, United States, Kourtev *et al.* (2002) found that microbial communities differed in structure (measured by phospholipid fatty acid (PLFA) composition) and microbial function (described by enzyme activities and substrate-induced respiration (SIR) profiles) in soils beneath two alien understorey plant species, namely Japanese barberry (*Berberis thunbergii*) and Japanese stilt grass (*Microstegium vimineum*), as compared to soils beneath native plant species. Invasive alien *Acacia longifolia* in sand dunes in Portugal had substantial impacts on microbial functional diversity increasing microbial biomass and activity (basal respiration) as well as nitrification and enzyme activity (β-glucosaminidase) (Marchante *et al.* 2008).

This overview shows that invasive alien plants impact native ecosystems in a variety of ways and that the outcomes of invasions vary depending on the type of ecosystem invaded and the alien itself. Plate 20.1 shows a selection of invasive aliens, with differing impacts in Mediterranean-type fynbos shrubland ecosystems.

20.3 RESTORATION AFTER ALIEN INVASION – SUCCESS AND FAILURE

Whether restoration after alien invasion is required or not depends on the degree of degradation (often related to the duration of invasion). If the native ecosystem has only undergone (initial) biotic changes, then clearing of the alien species may be enough to initiate ecosystem *recovery*. If ecosystem functions have been changed, then active restoration after alien clearance may be required. For example, soil nutrient changes caused by invasive species can persist long after their removal, and this persistence may retard the recovery of native communities for a long period. After clearance of N_2-fixing Australian *Acacia* species in Portuguese coastal ecosystems, it can take several years before soil nutrients and processes return to pre-invasion levels. Elevated soil nutrient levels can cause rapid reinvasion of the same alien species or favour other weedy species, thus preventing the re-establishment of native species. Active restoration including removal of N-enriched litter can facilitate ecosystem recovery (Marchante *et al.* 2009). In North American wetlands, *Phalaris arundinacea* invasion prevents establishment of native sedge meadow communities. Control of this alien species with herbicide led to several setbacks, including rapid *Phalaris* recovery, failure in establishment of introduced native sedge meadow species and an increase in alien weedy species richness and cover (Healy & Zedler 2010). However, a greenhouse study showed that lowering of soil organic nitrogen results in a competitive advantage of the native *Carex hystericina* over *Phalaris arundinacea*. This suggests that lowering of soil organic nitrogen can promote the establishment of native sedge meadow communities and suppress *Phalaris* invasion (Perry *et al.* 2004).

If invaders have been integrated into native ecosystem networks, restoration efforts can have unforeseen consequences that exacerbate rather than mitigate the problem (Hobbs & Richardson 2011). For example, invasive trees (*Tamarix* spp.) provide habitat for an endangered bird species, the southwestern willow flycatcher (*Empidonax trailii extimus*), in riparian ecosystems in the arid western United States. Removal of the invader may lead to further reduction of the already diminished population size of the bird species (Zavaleta *et al.* 2001), especially because native tree establishment after *Tamarix* removal is low owing to lowered water tables and saline soils caused by the invader (Harms & Hiebert 2006). Here, the benefits of *Tamarix* trees as bird habitat have to be carefully weighed against the tree's disadvantages.

20.4 INCORPORATING THRESHOLDS IN DECISION MAKING FOR ECOLOGICAL RESTORATION

Invasions can have severe impacts at population, community and ecosystem levels, often causing shifts to alternative ecosystem states and trajectories. Depending on the type and severity of impact, management of invasion may have to include active restoration. But the worst-case scenario is where invaders establish

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strong positive feedback loops that affect ecosystem resilience. We now describe the different ways in which invasions may impact ecosystem resilience and use this as a basis for exploring ecosystem degradation thresholds following alien invasion.

20.4.1 Resilience and biological invasion

Loss of ecosystem **resilience** owing to biological invasions can be triggered by biotic interactions: upon invading an ecosystem, invasive alien species can cause a loss of resilience by changing community composition and structure, leading to changes in ecosystem **functioning** (Richardson *et al.* 2007). Depending on the type of ecosystem invaded and the identity of the invading species, structural changes can be followed and/or accompanied by changes in ecosystem functions (e.g. changes in nutrient cycling). The most frequent scenario, however, is that alien invasions change structural and functional conditions in concert, creating a switch from negative to positive *feedback loops*. Positive, or supporting, feedback loops can be triggered by the competitive superiority of invaders. Reed canary grass (*Phalaris arundinacea*) causes rapid shifts from diverse native vegetation to a monotypic stand of *Phalaris* in sedge meadows across temperate North America. Adams and Galatowitsch (2005) suggest that vegetative growth of *P. arundinacea* facilitates the dominance of this species and that its invasiveness may be related to high rates of biomass production during establishment. Another form of a positive feedback loop is the creation of nutrient cycling patterns that favour the alien (Kulmatiski *et al.* 2008). Other invasive plants alter ecosystem properties to facilitate the establishment of their seedlings by inhibiting growth in other species. Siemann and Rogers (2003) showed that once Chinese tallow tree (*Sapium sebiferum*) is established in grasslands in the southern United States, their own seedlings are indirectly favoured in competition with neighbouring herbaceous vegetation through increased soil fertility and shade. Positive feedback loops can also be initiated by alterations to microbial processes (Díez *et al.* 2010) or changes in fire regimes (Rossiter-Rachor *et al.* 2008). The type of intervention required to restore an invaded ecosystem will depend on whether assisted recovery is possible (i.e. whether the ecosystem is still resilient). To determine the degree of ecosystem degradation, it may be useful to apply the concept of ecosystem thresholds. **Threshold** crossings are the result of several interacting ecosystem components, and identifying when such points are reached is therefore difficult. Some invaded ecosystems may never reach a threshold and therefore never change into an alternative ecosystem state. Others do, and depending on the type of ecosystem invaded and the invader itself may even cross several thresholds and eventually change into an alternative ecosystem state. It is important for restoration ecologists to determine whether thresholds have been crossed or an alternative ecosystem state has been reached. In the next section we introduce the concept of ecosystem thresholds and conclude by presenting the three-threshold model for plant invasion to guide decision making on restoration goals and interventions.

20.4.2 The concept of ecosystem thresholds – a tool for determining the level of ecosystem degradation

The point at which dominance of the negative (regulating) feedbacks that maintain ecosystem resilience switch to a dominance of positive (supporting) feedbacks that lead to loss of ecosystem resilience has been described as a 'threshold' (Briske *et al.* 2006). At this point, the maximum level of ecosystem **resilience** to **degradation** is exceeded (i.e. a threshold is crossed) and the ecosystem will change to an alternative state. Once this has happened, ecological restoration may be very difficult, if not impossible, and other, less ambitious goals may be more realistic. Thresholds can be determined by identifying key disturbances (i.e. disturbances caused by the alien) and/or key response variables (i.e. the response of the native ecosystem to invasion). Both key disturbance and key response variables can manifest themselves at the level of populations, communities or ecosystems. At each level, we can distinguish between structural thresholds and functional thresholds. Structural thresholds are defined by changes in relative growth form and species composition, whereas functional thresholds are defined by alterations of ecological processes. Structural and functional thresholds can occur through either biotic or abiotic ecosystem changes or a combination thereof (Figure 20.1). Once key disturbance (KD) and key response variables (KRV) have been identified, the next step is to determine the state of these variables over time (i.e. to define the trajectory of degradation). Here it is important to distinguish clearly between the

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	Structure	Function
Abiotic	altered soil nutrient availability (KD) altered water availability (KD)	increased fire intensity/frequency (KD) altered nutrient cycling rates (KD)
Biotic	increased invader biomass (KD) high invader seed production (KD) dominance of alien seedlings (KD) altered community structure (KRV) high native seed mortality (KRV) depleted native seed bank (KRV) declines of native species richness (KRV) decrease of native functional groups (KRV)	suppression of native species (KRV) enhanced growth of other alien species (KD) increased competition for resources e.g. light and water (KD) allelopathy (KD) altered microbial systems

Figure 20.1 2 × 2 matrix showing structural and functional thresholds described by biotic and abiotic ecosystem changes and responses. KD, key disturbance; KRV, key response variable.

alteration processes that start immediately after the establishment of the alien (e.g. litter input and water use), and the response of the native ecosystem to these processes, which may occur only after a lag phase.

Figure 20.2 shows the *three-threshold model* for plant invasions which can be a useful tool to determine the level of ecosystem degradation. The model illustrates the trajectory of invasion with three thresholds being crossed in the course of increasing ecosystem degradation. We use ecosystem response (ER) (i.e. outcomes or consequences of invasion on a native ecosystem) as the means of determining the level of ecosystem degradation. The first threshold is reached by a change of structural biotic interactions within the invaded community, and is followed by a second structural threshold, after a longer duration of invasion. This second threshold is harder to reverse and can be caused by amplified biotic interactions, abiotic changes or a combination thereof (Suding & Hobbs 2009; see also Chapter 21). At this point, most of the ecosystem's measurable traits (e.g. nutrient load) are the same as before, but the species composition has changed. In a later stage of invasion, a third threshold (positive feedback threshold) may be crossed. At this stage, changes in structural components result in a change of functional components (e.g. competitive interactions); these changes in functional components initiate positive feedback loops (i.e. the alien alters the ecosystem to its own favour but to the disadvantage of native species, thereby increasing the rate of invasion).

In practice, measuring changes in ecosystem function over time or over a range of sites that have experienced different levels of invasion allows us to define levels of ecosystem functioning that represent thresholds. To identify whether an ecosystem has crossed one or more thresholds, it is necessary to evaluate ecosystem response (i.e. the location of the ecosystem on the Y-axis), which can also be interpreted by determining the degree of invasion (i.e. the location on the X-axis) (King & Hobbs 2006).

The identification of variables that represent thresholds can be illustrated with the example of the well-studied case of *Lantana camara* L. in New South Wales (Australia). Invasion by this vertebrate-dispersed South American shrub reduced native species richness (key response variable (KRV)) significantly in heavily invaded sites (above a level of 75% cover). Below 75% invader cover, native species richness remained stable. The authors therefore suggest that 75% cover of *L. camara* can be defined as the threshold beyond which native species richness declines (Gooden *et al.* 2009).

20.4.3 Case studies from South Africa: *Acacia* and *Pinus* invasions in fynbos ecosystems

Fynbos shrublands are the dominant vegetation of the Cape Floristic Region, a global **biodiversity** hotspot. More than 9000 plant species occur in a relatively

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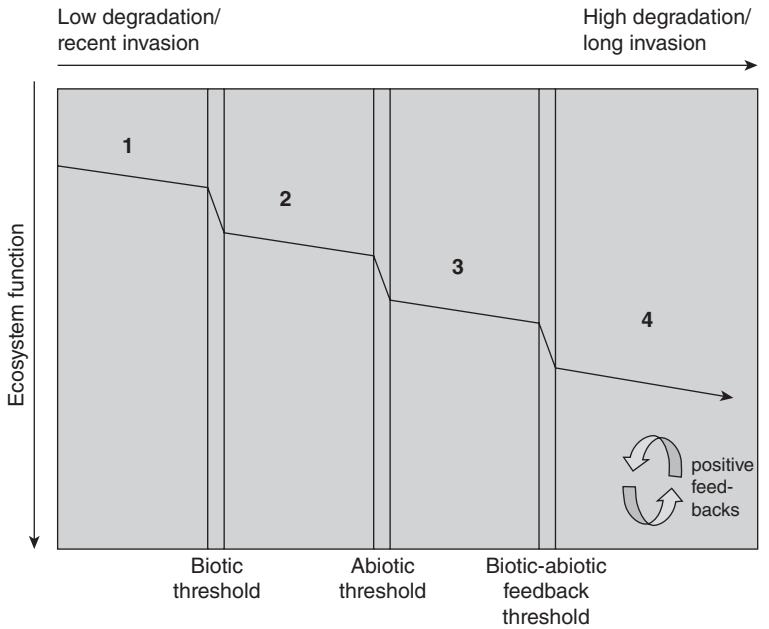


Figure 20.2 Three-threshold model (modified from Whisenant 2002; King & Hobbs 2006) illustrating the concept of thresholds which indicate break points between alternative ecosystem states: (1) native ecosystem state: no threshold is reached (e.g. altered species composition but above-ground vegetation and/or seed banks intact); (2) alternative ecosystem state: biotic threshold is reached (e.g. altered species composition and structure, seed bank depleted); (3) alternative ecosystem state: abiotic and biotic thresholds are reached (e.g. altered water and nutrient availability); and (4) alternative ecosystem state: positive feedbacks trigger threshold to be reached (e.g. changed fire regime favours the growth of invasive species but causes extinctions of native species).

small area (90 000 km^2) wherein approximately 70% of native plants are endemic. **Alien invasions** pose a serious threat to the region, especially Australian wattles in lowland and riparian ecosystems, and Euro-Mediterranean pines in the mountains. Australian *Acacia* species have huge invasive potential and strong persistence due to their capacity to produce enormous amounts of long-lived seeds (Richardson & Kluge 2008). Invasion by these wattles leads to increased biomass and changed fuel properties in fynbos ecosystems (van Wilgen & Richardson 1985). Furthermore, their presence can cause alterations in nutrient cycling due to nitrogen fixation in concert with increased litter production and mineralization rates (Yelenik *et al*. 2004).

Early in *Acacia saligna* invasion of fynbos, changes occur to the biotic structural components (e.g. altered native species composition; Table 20.1, Figure 20.3). With increasing intensity of invasion, these changes in biotic structure result in alterations of biotic functions via the suppression of native species. The dominance of *Acacia* and the decrease in native species density and cover reduces ecosystem resilience. Once invasion is dense, a biotic threshold is passed as *Acacia* excludes the fynbos species and dominates the soil seed bank. Although biotic and some abiotic components have been altered, the system may still be capable of autogenic recovery after *Acacia* control since soil-stored seed banks of fynbos species may remain and seedlings of fynbos species can cope with elevated levels of soil nitrogen (Musil 1993). Dense alien *A. saligna* stands alter ecosystem functioning via elevated biomass, litter production, nitrification and nutrient-cycling rates. This in turn promotes growth of the alien and other competitive (native and alien) species, such as grasses, further boosting their competitive advantage over fynbos species with each ensuing fire cycle. An abiotic threshold is reached after a certain duration of dense invasion (>1 and >3 fire cycles of *Acacia* in lowland and mountain fynbos, respectively). These structural

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Table 20.1 Change in fynbos ecosystem structure and function with *Acacia saligna* invasion indicating key disturbance variables and disturbance response variables.

Transition state (see Figure 20.3)	Description of invasion impacts	Key disturbance variables	Key response variables
1a	Low–moderately dense *Acacia* stand (0–50% canopy cover) – Individual *Acacia* trees establish; high annual production of persistent seeds (10,000 m^{-2} canopy) – Seeds disperse several metres from tree by wind; up to 5 m by ants that bury them safe from rodent seed predation – Rapid *Acacia* soil seed bank accumulation under adults – Adaptation to fire: adults resprout and hard-coated seeds germinate following heat pulse; massive recruitment, densification and coalescence of *Acacia* post-fire (Richardson and Kluge 2008)	Increased invader biomass High invader seed production	Altered community composition (but still relatively intact fynbos community)
1b	Moderate–closed *Acacia* stand (50–100%) – Dense (>75% canopy cover) *Acacia* stand alters plant community composition and structure (shading and other effects) – Dense *Acacia* stand alters faunal community, granivory and dispersal – *Acacias* grow taller than fynbos creating more biomass and leaf litter – Nitrogen-fixing ability results in higher total nitrogen in litter and soil, increased nitrification and nutrient-cycling rates (Holmes and Cowling 1997b), (Musil 1993), (Yelenik *et al*. 2004)	Increased invader biomass Increased competition for resources Altered soil nutrient availability Altered microbial systems	Suppression of native species Altered community composition (but intact fynbos soil seed bank community) Altered community structure Declines in species richness
2	– Fires under hot, dry conditions result in high-severity fires (in both standing and felled *Acacia*) that kill buried seeds and volatilize soil organic material; recruitment of deeper buried seed promoted, especially *Acacia* and other myrmecochores – Indigenous seed banks decline with each fire cycle under dense *Acacia* owing to mortality, germination and lack of replenishment; seed bank decline particularly acute in lowland fynbos (following one fire cycle of dense *Acacia*) (Holmes and Cowling 1997a), (Holmes 2002)	Increased fire intensity Dominance of *Acacia* seedlings	High seed mortality Depleted native seed bank Decrease of native functional groups
3	– *Acacia* dominates ecosystem with only a few weedy, or nitrophilous species co-occurring in the early post-fire period; increased nitrogen promotes competitive species such as alien annual grasses and *Ehrharta calycina* (Yelenik *et al*. 2004)	Increased soil nitrogen levels Enhanced growth of other alien species (or weedy indigenous species)	Loss of all but weedy herbaceous functional group

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Table 20.1 *Continued*

Transition state (see Figure 20.3)	Description of invasion impacts	Key disturbance variables	Key response variables
4	– Alternative stable state maintained by positive feed-backs in nutrient cycling and fire intensity that promote the invader and other weedy species over native species; herbaceous understorey also makes frequent fires possible – Clearance of the *Acacia* in this advanced state will result in weedy and secondary alien species dominating the community. Old fields with similar composition are maintained as weedy herbaceous systems by indigenous fossorial mammals, adding a further level of positive feedback (Authors' personal observations, and Holmes 2008)	Intensification of all key disturbance variables	After *Acacia* clearance, density of fossorial mammals (molerats and gerbils) intensifies

*Data for *Acacia cyclops* which is of similar stature to *A. saligna*.

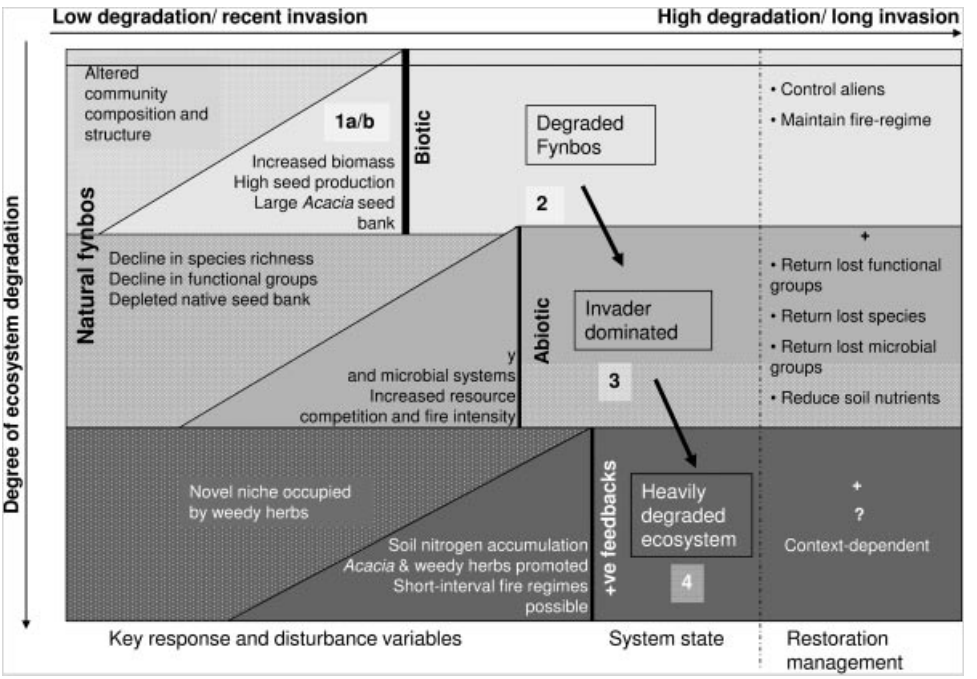


Figure 20.3 *Acacia saligna* invasion of fynbos illustrating different ecosystem states and thresholds as invasion intensifies. The triangles represent invasion impacts by alien *Acacia* and the disturbance variables that lead to each system state; the matrix represents the fynbos ecosystem and its response variables. Thresholds are indicated by the thick black lines. Appropriate management actions to restore the ecosystem are listed in the right-hand column.

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and functional changes to biotic and abiotic components cause positive feedback loops (e.g. increased soil nutrient levels lead to enhanced growth of *Acacia* species, and high biomass of *Acacia* leads to fires of high severity that promote *Acacia* recruitment), and a third threshold is reached: *Acacia* forms monoculture stands that suppress growth of all but the most competitive native and other alien nitrophilous species (Figure 20.4). The latter species form an understorey that may carry near-annual fires. *Acacia* control at this stage results in an **alternative stable state**: grass and alien annual dominance. Another positive feedback loop is evident: grasses promote native molerats and gerbils which disturb the soil and disrupt the regeneration niche of fynbos plant species' seedlings (Holmes 2008).

At this stage, the system has shifted to a highly degraded ecosystem with profound implications for restoration. Restoration of this heavily degraded ecosystem will be very difficult (although not impossible). The high conservation value of the Cape Floristic Region may influence decision making in favour of

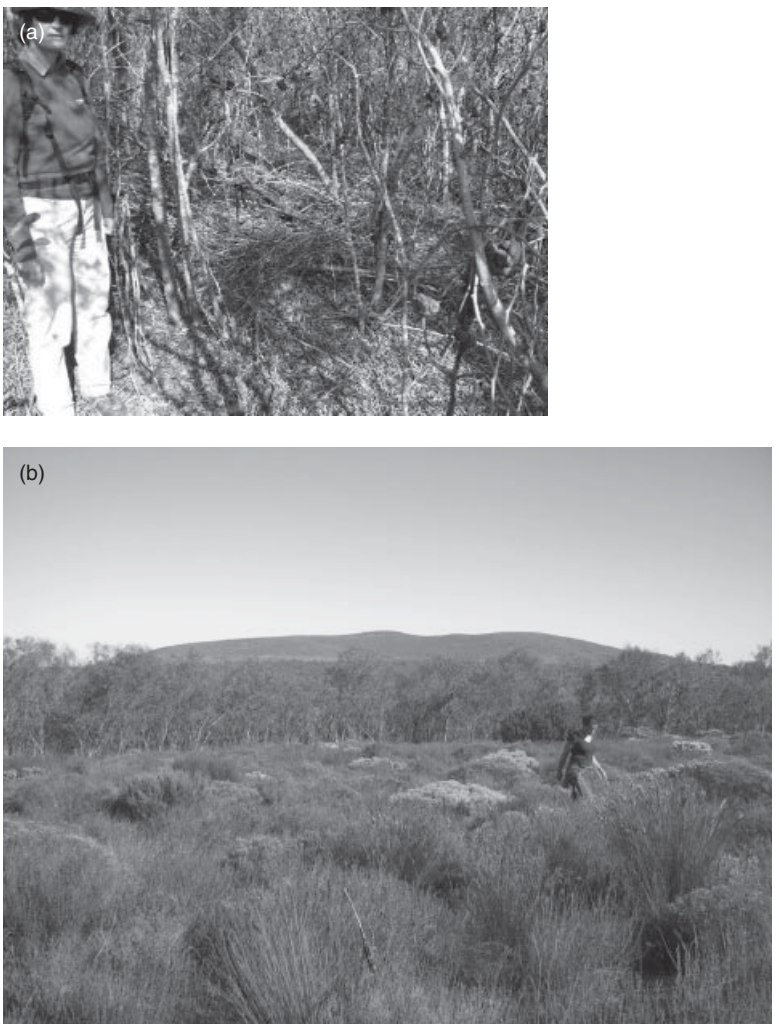


Figure 20.4 (a) Dense stand of *Acacia saligna* with thick litter layer and no native understorey species. (b) Sand fynbos vegetation recovering after removal of a closed-canopy stand of *Acacia saligna*. (Photograph by T. Rebel.)

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restoration, particularly if the site occurs within a protected area. Whether or not restoration is feasible will depend both on the site location in relation to natural vegetation remnants and on available financial resources. If restoration is not feasible, it is important to at least halt further spread of the invasive species. For landscape-scale restoration, biological control is thus essential: a gall .fungus on *A. saligna* which was introduced intentionally as a biological control (biocontrol) agent reduces the life span of *Acacia* trees to 5–7 years (Wood & Morris 2007) and allows the canopy to remain open, thus promoting survival of some native fynbos plants. Restoration of long-invaded sites, characterized by elevated soil nitrogen and lack of native soil-stored seed banks, is very difficult, and to succeed it has to overcome several barriers.

Invasive pines in fynbos have a very different strategy to the wattles. Their key adaptation for survival, persistence and rapid invasion in fynbos, and elsewhere, is their serotinous habit: winged seeds are protected from fires in woody cones which open upon the death-by-fire of the parent plants. This mechanism allows them to germinate rapidly after fire and disperse successfully over large distances. Invasive pines have become highly disruptive, displacing native plant species, altering fire regimes and reducing stream flow from invaded catchments (Le Maitre *et al.* 1996). Pine invasions also differ from *Acacia* invasions in how they degrade invaded ecosystems. Fynbos community structure and composition are impacted by dense pine invasion (Richardson & van Wilgen 1986). However, unlike *Acacia*, pines do not fix nitrogen and they grow more slowly. Whereas in established alien *Acacia* stands canopy closure occurs within 6 months of a fire, this can take several years for pines, allowing coexistence of perennial fynbos species and the opportunity for native seed bank replenishment. As invasion intensifies, pines change the abiotic conditions (e.g. they have a much higher biomass than fynbos and use more water, shade out fynbos and may cause higher intensity fires). Pine invasion does not enhance soil nitrogen levels, so there is no apparent positive feedback loop to reinforce pine or secondary alien species invasion. Rather, pine invasions persist through high propagule pressure and highly dispersible seeds (Richardson & Higgins 1998) (Table 20.2, Figure 20.5). Restoration of long-invaded sites will have to include reintroduction of key native functional groups and possibly microbial groups. Because of the high propagule pressure post-fire, follow-up control will be essential to prevent reinvasion. To date biological control is seldom integrated into restoration projects, either because of a lack of knowledge or because of legal implications. However, especially for landscape-scale restoration, the use of biological control agents would often be essential in slowing the rate of degradation.

The two case studies presented in this section show that different invaders impact ecosystems in very different ways, with resultant implications for restoration. In the *Acacia* example, long-standing invasion results in degradation beyond structural, functional and positive feedback thresholds, causing multiple barriers to restoration. As funding for restoration projects is limited, managers must prioritize sites for restoration. The conservation status of the invaded area as well as its restoration feasibility should be considered. In section 20.5, we present criteria for restoration feasibility and desirability and conclude with a decision-making framework for the management and restoration of invaded ecosystems.

20.5 TOWARDS A DECISION-MAKING FRAMEWORK FOR THE MANAGEMENT AND RESTORATION OF INVADED ECOSYSTEMS

Once the degree of ecosystem degradation has been assessed and the restoration requirements determined, decisions can be made on whether restoration is feasible and affordable and, if so, how the restoration should be approached. Prior to decision making, it is important to establish restoration goals. Depending on the degree of degradation, restoration goals will range from re-establishing a natural ecosystem state, focusing on biodiversity components, to restoring ecosystem processes and functions. Our framework for restoration of invaded ecosystems is based on the three-threshold model (Figure 20.2).

Restoration of a less degraded ecosystem (in our case study, an ecosystem recently invaded by wattles or pines; transition state 1 in Table 20.1) is often feasible because abiotic conditions are relatively unchanged and clearance of the alien plants is the only action required to initiate autogenic recovery towards a target ecosystem state focusing on **biodiversity**. If the structural threshold has been crossed (transition state 2 in Table 20.1), autogenic recovery may have to be facilitated, for example by **reintroducing native species**.

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Table 20.2 Change in fynbos ecosystem structure and function with pine invasion indicating key disturbance variables and disturbance response variables.

Transition state (see Figure 20.5)	Description of invasion impacts	Key disturbance variables	Key response variables
1	– Main impacts of pine invasions results from the increased abundance of trees in habitats where this life form was previously absent or less common.	Shift in life form dominance Increased biomass	Altered composition and structure of above-ground vegetation
2	– Pine invasions reduce native vegetation cover from 75 % to 20% and the total number of species by 58% from 298 to 126 species. Mean plant density reduced from 260 to 78 plants m^{-2}. – Pines are more effective users of resources increasing competition for native species. – Stands invaded by pine have significantly lower species richness, native plant cover and density than pristine fynbos communities. – Dense pine stands suppress fynbos species, threatening many taxa with extinction. – Large fuel loads cause intense fires in dense pine stands, causing increased overland flow and accelerated soil erosion. – Pine invasions might negatively impact on arbuscular mycorrhizal infectivity after long term invasion. – After four decades of pine invasion fynbos seed banks are depauperate (Richardson & van Wilgen 1986, Richardson & Higgins 1998, Holmes *et al*. 2000)	Increased resource competition Increased fire intensity Altered microbial systems	Decline in species richness Decline in functional groups Depleted native seed bank

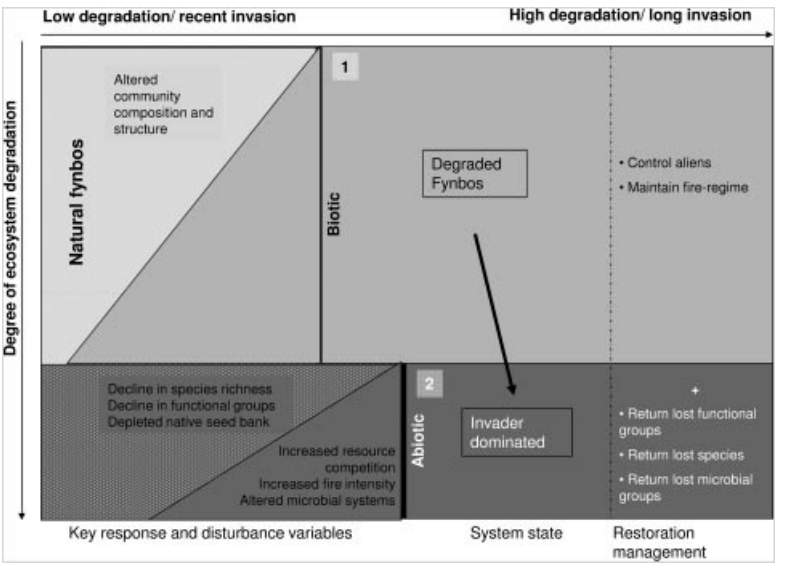


Figure 20.5 *Pinus* invasion of fynbos illustrating different ecosystem states and thresholds as invasion intensifies. The triangles represent invasion impacts by alien *Pinus* and the disturbance variables that lead to each system state; the matrix represents the fynbos ecosystem and its response variables. Thresholds are indicated by the thick black lines. Appropriate management actions to restore the ecosystem are listed in the right-hand column.

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Transition state	Threshold	Management guidelines	Restoration goal
1	Structural threshold **not** crossed	  Alien control and follow-up.....	Target reference ecosystem (focus on biodiversity should be possible)
2	Structural threshold crossed	....AND Re-introduction of native species of at least the most important functional groups. 	Same as above
3	Functional threshold crossed	....AND Address functional changes: • Reduce excess nutrients by burning or removing litter • Prevent secondary invasion by introducing main structural guilds • Restore hydrological characteristics (e.g. remove biomass from riparian zone) • Avoid soil erosion (e.g. removing large fuel or do winter burn)	Establish realistic goals (focus on ecosystem services and functions)
4	Structural & functional feed-back threshold	 Prevent further spread and manage alternative ecosystem state	Same as above

Figure 20.6 Decision-making framework for aid in the restoration of invaded ecosystems.

By contrast, the decision-making process for ecosystems which are heavily degraded (in our case study, ecosystems with long-invaded *Acacia* stands; transition states 3 and 4 in Table 20.1 and in Figure 20.6) is complex and needs careful consideration. Restoration of heavily degraded ecosystems will need major management input and hence substantial resources. Active restoration should therefore only be undertaken once realistic goals have been established.

Several criteria have been identified to guide decision-making process for ecosystems which are heavily degraded:

• If the area is located in a priority conservation region, restoration to at least a structurally representative natural state could be attempted.

• Restoration should, however, also be undertaken if the surrounding landscape is relatively undisturbed as the spread of the invasive species, if uncontrolled, may cause further damage. Maintenance of a natural landscape will provide propagules for the recolonization of neighbouring areas by native species.

• If the invaded area is located in a region of no conservation value and surrounded by transformed lands (e.g. agriculture), **ecological restoration** to a target **reference ecosystem** (focusing on biodiversity) may not be feasible or justifiable. In such cases, **rehabilitation** (i.e. restoring ecosystem processes and functions) may be more appropriate.

• If the alien species has the potential to spread rapidly to invade new areas, the minimum management requirement would be the control of alien species' spread.

• Where a successful biocontrol agent has been established, restoration **interventions** may be relatively localized.

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• The use of limited resources by the invaders (such as water in arid areas) is another important criterion for immediate action.
• In some cases, invasive alien species might have an economic value (e.g. providing fire wood for local communities) or might have become integrated into native ecosystem networks (e.g. pollination networks). In such cases, adverse effects of harmful alien species and the positive impacts have to be balanced, and the main goal could be to prevent further spread of the alien.

20.6 PERSPECTIVES

Further large-scale degradation of ecosystems over large areas of the globe seems inevitable in the coming decades. Ecosystems in 'pristine' or 'historical' condition will become increasingly rare (see also Chapters 2 and 3). Even if we are able to restore highly degraded ecosystems, outcomes might well be unexpected, and the resulting **emerging ecosystems**, although closer to a 'natural' state in terms of some criteria, are likely to differ substantially from any historical condition (Norton 2009). Under such conditions, any and all management activities, including restoration actions, are experiments (e.g. Roura-Pascual *et al*. 2010). Much closer collaborations between managers and scientists are crucial to achieve management goals (including those relating to restoration) for these degraded systems (Seastedt *et al*. 2008). Setting appropriate goals for restoration is thus a task that demands sophisticated planning. Explicit attention needs to be given to the determinants of resilience and the identification of key thresholds. This allows for the level of degradation to be quantified and paves the way for an objective consideration of potential trajectories under a range of management interventions. Referring to two prominent groups of invasive plants in South African fynbos ecosystems, we have described a protocol for improving decision making through explicitly addressing issues relating to resilience. Further work is needed to bridge the gap between understanding the full array of impacts resulting from invasions and knowing how this understanding can be used to formulate plans for restoration. The key lies in further elucidation of factors affecting ecosystem resilience. Implementation of our threshold model in a wide range of ecosystems is dependent upon answering key questions, such as: 'Which ecosystem properties and/or ecosystem functions will give best indication of the target system's resilience?', 'What are the links between resilience and diversity (or species richness) of an ecosystem?', and 'How do we determine whether an ecosystem has reached a threshold and changed to an alternative stable state?'

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Chapter 21

SHIFTING BASELINES: DYNAMICS OF EVOLUTION AND COMMUNITY CHANGE IN A CHANGING WORLD

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21.1 INTRODUCTION: ANTICIPATING THE FUTURE

Ecologists have long recognized that ecological systems are dynamic. Natural disturbances are widespread and essential to the persistence of many ecosystems (Pickett *et al.* 1989). Superimposed on disturbances, changes in climatic conditions have occurred throughout Earth's history (Hessburg *et al.* 2005). Human activities have disrupted natural disturbance regimes either by increasing frequency and intensity (e.g. fire return intervals, extreme climate events such as floods and droughts, and pest outbreaks) or by decreasing frequency and intensity (e.g. damming of rivers, and suppression of fires in grasslands and forests) (Dale *et al.* 2001; Franklin *et al.* 2005). In addition, human activities are affecting the speed at which these changes occur; for instance, climate change is occurring faster than ever recorded, nitrogen pollution has doubled over the last half century and non-native species are successfully establishing in ecosystems across the globe (Vitousek *et al.* 1997; Chapin *et al.* 2006; see Chapter 20).

As its name implies, restoration has traditionally been viewed primarily as a means to reset the ecological clock, with the goals ranging from returning the system to particular reference assemblages to rehabilitating the system to provide a certain level of function or service, such as erosion control or drinking water quality. However, in this period of unprecedented environmental change, the ecological clock is ticking more and more rapidly, whether due to changes in climate, shifts in land use or changes in fauna and floral diversity (see Chapter 3). As restoration often has the aim of directing the target system to a point along a trajectory that allows for self-sustaining population, community and ecosystem processes, it is essential to consider restoration in the context of anticipated future environmental changes (Choi *et al.* 2008; Hobbs & Cramer 2008).

Historical perspectives increase our understanding of the dynamic nature of landscapes and provide a frame of reference for assessing modern patterns and processes (Swetnam *et al.* 1999; Jackson & Hobbs 2009). Although many future changes may not have historical analogues, a historical perspective can help design or steer emerging systems to encompass a greater spectrum of natural variability inherent in the system or under future climate change. For instance, creating new populations in formerly much larger, early historical ranges of declining species has been a viable restoration strategy (Burney & Burney 2007). Understanding the history of the development of the current species assemblage has also helped establish an expectation of the spatial and temporal variation of the vegetation that cannot be accomplished with a static present-day perspective (Lindbladh *et al.* 2007). In some systems, however, even a perspective that encompasses palaeo-ecological time scales may prove unsustainable in the coming decades due to the development of new combinations of environmental factors (e.g. no-analogue climates) or new barriers to species movement. Thus, the expectation of the development of **novel ecosystems**, and the shift in restoration goals for some target systems, from those based on **reference** conditions to ones based on ensuring maintenance of **ecosystem goods and services**, also needs to be incorporated in restoration planning (Seastedt *et al.* 2008; see also Chapter 3).

In this chapter, we address how restoration ecologists and practitioners can apply theory on evolutionary and community dynamics to anticipate and incorporate future – and largely uncertain – environmental changes. We focus on how local and regional processes may influence population and community dynamics over time, in turn affecting how we should manage and restore biodiversity and ecosystem services. Accordingly, we start with the assumption that the initial stages of a restoration project were largely successful – that a particular reference assemblage or a level of function or service in an analogous undisturbed area has been established. With this as a starting point, we suggest additional considerations for restoration projects with the expectation of future evolutionary and ecological change, as well as how to set goals and plan **interventions** for restoration without aiming at a static, and in many cases unrealistic, endpoint.

We first discuss the evolutionary mechanisms that determine whether species persist in altered environments, and secondly, the community-level mechanisms that may shift when species differ in their ability to respond to altered system dynamics. Next, we discuss the potential larger scale processes, specifically gene flow and dispersal, to help or hinder persistence of communities, and finally, the importance of maintaining diversity at all levels – genotypes, species and functional groups – for restoration in a changing world.

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21.2 LOCAL PROCESSES: ADAPTATION AND SELECTION

Motivations for using local genotypes in restoration vary along a spectrum from purely ideological to purely practical (see also Chapters 7 and 8). The ideological perspective is that restoration should maintain the suite of genetic variation historically occupying a particular site; local genotypes and their evolutionary history should be preserved because of their inherent value (Hamilton 2001). The practical end of the spectrum holds that because natural selection can operate to create populations of locally adapted species, restoration using local genotypes should, on average, be more successful than restoration using nonlocal genotypes (McKay *et al.* 2005). While our view leans towards the practical end of the spectrum, both perspectives may need to be refined if restoration is going to address species persistence in the face of rapid environmental change. Natural selection may well have led to populations that are locally adapted under historic conditions, but the persistence and/or superior performance of local genotypes under future conditions are largely unknown (Harris *et al.* 2006).

21.2.1 Maintaining evolutionary potential

Multiple restoration actions in response to changing future conditions have been proposed, including **assisted migration**, wherein species are moved outside their historic range (McLachlan *et al.* 2007), increasing the amount of diversity in populations of restored ecosystems by including genotypes outside the current range (Rice & Emery 2003), the use of artificial selection to create adapted populations (Jones & Monaco 2009) and the use of natural populations from altered sites to restore under similarly altered conditions (Leger 2008). Whichever option is selected, it is important to consider not only the contemporary success of each method, but also the capacity of populations with different genetic composition to respond to future challenges. Rather than reintroducing only a historic suite of local genotypes, or only genotypes with the greatest capacity for success under current conditions, ecologists are recognizing that a new goal may be to create populations that have the capacity to evolve in response to uncertain future conditions. Maintaining diversity in restored systems is the first step towards retaining *evolutionary potential*, as there are direct correlations between population-level response to selection and levels of heritable variation (Fisher 1930).

21.2.2 Disturbance and natural selection

In addition to the amount of genetic diversity present in a restored system, it is important to consider the type of natural selection the population will experience. Certain types of anthropogenic disturbances are likely to result in selection pressures that are consistent and predictable, such as increases in CO_2 concentrations, consistent size selection in harvested populations, or the introduction of new diseases, predators, prey or competitors. Consistent selection pressure can result in directional selection, which occurs when fitness is consistently highest for individuals with traits values that are either larger or smaller than current population means (Futuyma 2005). *Adaptive phenotypic plasticity*, or the ability to modify a phenotype in an adaptive way in response to environmental conditions (Pigliucci 2001), is perhaps the simplest way species can persist under strong directional selection. While selecting genotypes with a high degree of plasticity for restoration projects may allow greater tracking of environmental change, there are limits to phenotypic plasticity, and costs to its maintenance, that may complicate long-term adaptive species responses (Ghalambor *et al.* 2007). For example, Phillimore *et al.* (2010) demonstrate that even though populations of *Rana temporaria* are phenotypically plastic in their spawning time, plasticity alone is likely insufficient to maintain viable breeding populations in Britain under climate change scenarios (Plate 21.1). In cases where phenotypic plasticity is insufficient to maintain viable populations, *additional evolution* (change in gene frequencies) will be necessary to maintain local populations under disturbed conditions. In the case of *R. temporaria*, natural or human-assisted migration of individuals from southern to northern locations could speed the process of evolutionary change in northern Britain, but southern populations border the English Channel, and any migratory process would almost certainly require human intervention.

In a population with sufficient genetic variation, populations might be able to evolve and remain viable without human intervention, even if conditions are shifting rapidly. There is evidence that natural selection can result in the maintenance, rather than extirpation, of some local populations under contemporary (<100

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years) directional selection (Kinnison & Hendry 2001). Examples include evolution of native species in response to invasion (Strauss *et al.* 2006). Many of these examples are native insects adapting to newly introduced host plants, or native species evolving in response to introduced predators, but also include evolution of competitive ability between species in the same guild (Mealor & Hild 2007; Leger 2008). Research into *evolutionary shifts* in harvested animal populations provides some of the best examples of contemporary natural selection. For example, in response to strong and consistent harvest pressure, traits such as decreased body size and decreased time to maturity have evolved in consistent ways in many species in managed systems (Kuparinen & Merila 2007; Allendorf *et al.* 2008). Thus, we should expect that contemporary evolution will occur in restoration projects over time, although the rates and differences among populations or species are uncertain.

Not all novel pressures are likely to be directional in nature. In particular, climate change predictions include increases in variance, as well as changes in means, of major climatic factors (Pimm 2009), and disease or insect outbreaks can be cyclical in nature. Such shifting conditions, where optimal phenotypes vary over time, can result in fluctuating selection (Futuyma 2005). With insufficient genetic diversity, populations can quickly go extinct when experiencing fluctuating selection as a result of compounding losses of diversity and decreasing population sizes over time. Phenotypic plasticity is one evolutionary consequence of fluctuating or unpredictable environmental conditions (de Jong 1995), and has been observed to evolve under contemporary selection pressures. For example, there is evidence of increased phenotypic plasticity in populations of invasive species introduced to new environments (Richards *et al.* 2006), and similar evolution of increased plasticity may be adaptive for native species persisting in changing environments. While native species are not moving across continents, the biotic and abiotic environment may shift around them in dramatic ways, and species and populations with the greatest phenotypic plasticity may be the ones that remain.

21.2.3 Assessing genetic diversity, applying knowledge

Manipulative climate change experiments, reciprocal transplant studies and artificial selection experiments are all useful means to directly assess the ability of populations and communities to persist under novel disturbances (Jump & Peñuelas 2005; Reusch & Wood 2007). Through these experimental methods, one can measure the strength of selection across a range of environments as well as responses to selection, differentiating the potential for adaptive phenotypic plasticity from the need for contemporary evolution (Conner 2003; Etterson 2004). Assessment of the responses of different populations to variable selection pressures could identify a strategy that is likely to maximize initial establishment as well as the likelihood of population persistence in the future. For example, a close examination of size selection among salmonid fry at six introduction sites indicates geographic variation in optimal size, correlated with environmental factors at each site (Figure 21.1; Bailey & Kinnison 2010). In this situation, it is possible that more successful establishment of these endangered populations could be achieved by tailoring the size of released individuals to the direction of selection at each location.

Given the difficulty of measuring the strength of selection across environments, coupled with the difficulty of precisely predicting future climate or invasion scenarios, a restoration strategy employing a highly variable founder population could be used to establish populations in a wide variety of locations, with the assumption that natural selection can favour appropriate genotypes in particular environments. In addition to concerns about outbreeding depression (Chapter 7), another potential problem with this approach is that if the population mean trait values are too far from adaptive peaks, rapid, directional selection may result in selective sweeps, where genetic diversity is lost as genes become fixed in a population due to their physical linkage to gene regions under selection (Barrett & Schluter 2008). In essence, potentially valuable genetic diversity can be lost because it occurs in individuals that possess a single maladaptive trait. These individuals can be quickly purged from a population, leading to the loss of all of their associated alleles, even if some are neutral or beneficial. An alternative to a maximum diversity method is to find natural populations with trait frequencies near potential optima in altered systems, and use an immunization approach to maximize survival of restored populations (Figure 21.2; Schlaepfer *et al.* 2005). This alternative is similar in concept to including genotypes from outside the current climatic zones to prepare populations for climate change (Rice & Emery 2003). Both strategies

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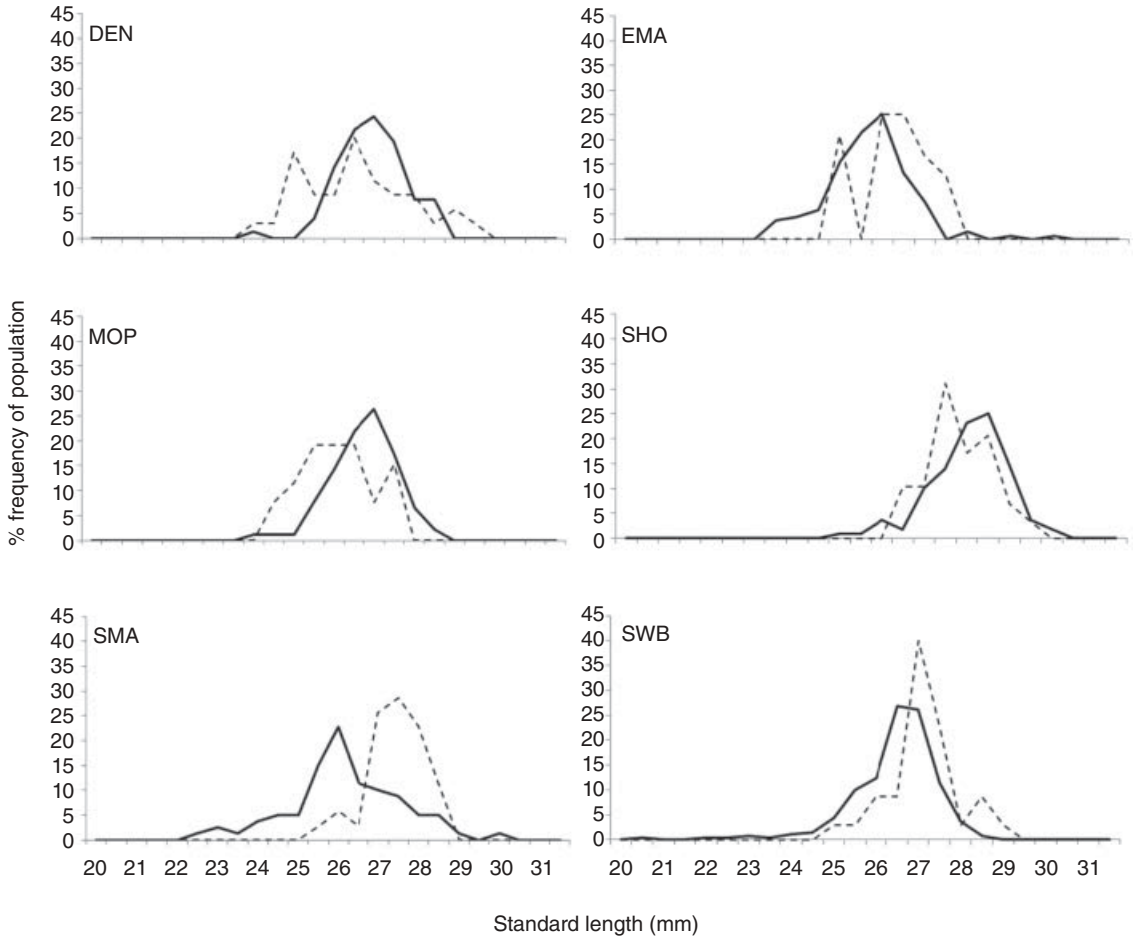


Figure 21.1 Differences in size distribution in stocked populations (solid line) and surviving individuals (dashed lines) at six different release locations of Atlantic salmon (*Salmo salar*) fry in Maine, United States. The size of surviving individuals is significantly different from that of the stocked population in five of six locations, which is evidence of directional selection on fry size. A single size was not optimal across sites, as size of surviving individuals was correlated with variation in stream characteristics. (From Bailey and Kinnison 2010.)

use local genotypes as a source of restoration propagules, but include a way to introduce potentially adaptive genes into populations.

21.2.4 Limits to genetic diversity

Although there are cases where phenotypic plasticity and adaptive evolution may be able to maintain viable populations, these processes cannot be expected to rescue all species or populations in changing conditions. Organisms with particular life history traits, such as long generation times or high incidences of inbreeding, may be at a disadvantage in rapidly changing situations (Barton & Partidge 2000; Kinnison *et al.* 2007). Additionally, even within functional groups or species, some populations will be unable to evolve due to small population sizes, lack of genetic variation or constraints of genetic architecture, wherein selection for optimal phenotypes can be limited by correlated response to selection of genes with very different functions (Walsh & Blows 2009). Finally, the ability of

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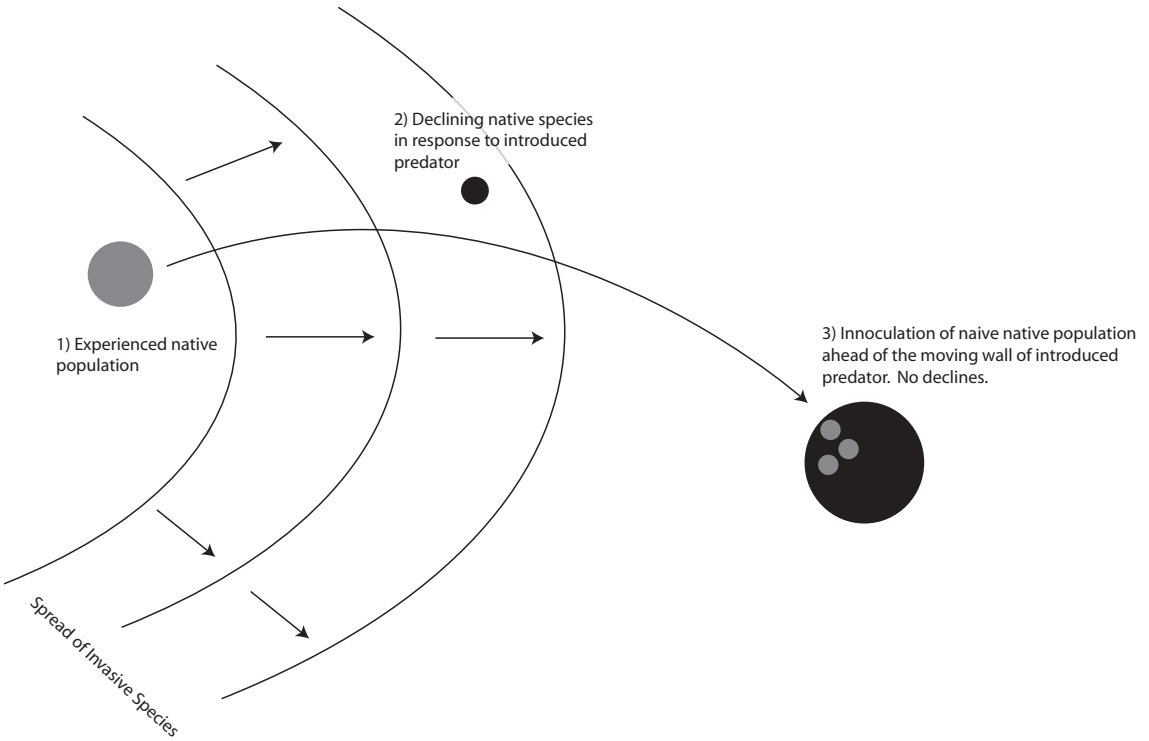


Figure 21.2 A proposed methodology to increase variation in adaptive traits in native populations by introducing genotypes collected from populations that have already experienced a particular disturbance. Transmission of beneficial traits could be through the introduction of genetic variation, or, in the case of animal populations, transmissions of learned adaptive behaviours. The stress in this figure is invasive species, but a similar tactic could be used for other types of disturbances, including disease, N deposition or increased fire frequencies. (From Schlaepfer *et al.* 2005.)

species to evolve in response to single factors may be very different from evolutionary responses to more than one factor, which are difficult to predict, even in laboratory situations (Harshman & Hoffmann 2000). Failure of species to adapt to changing environments is the cause of *extirpations* and *extinctions*, and historic evidence provides many examples of shifts in community composition and species dominance over time. The evidence for these shifts is discussed in detail below.

21.3 LOCAL PROCESSES: SPECIES REORDERING AND TURNOVER

Species reordering (becoming relatively more or less abundant) and turnover (gain or loss) should be expected to occur in a restoration site over time. These shifts could consist of shifts in the dominance of species within a functional group or shifts in the dominance of functional groups, which at their most extreme often can be considered shifts in ecosystem types, such as from forest to grassland. Shifts can be either transient or cyclical, in response to recurring disturbances, for instance, or directional, in response to directional changes in the environment or recovery from infrequent disturbances (Smith *et al.* 2009; Figure 21.3). Anticipating these shifts may help restoration projects track environmental change over time.

21.3.1 Successional dynamics

Classic models of **succession** propose that assemblages are dynamic and progress towards a final state (climax community) along a continuum that is regulated by internal forces such as species interactions.

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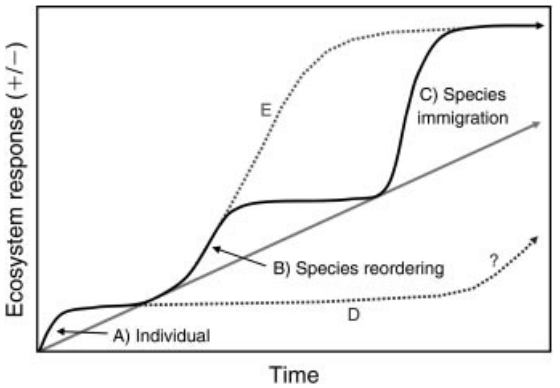


Figure 21.3 A hierarchical response framework suggested by Smith *et al.* (2009) to illustrate how different processes can influence the response of an ecosystem over time to directional environmental change. They distinguish time frames of (a) individual-level change, (b) reordering of resident species and (c) species immigration. In addition, the ecosystem response could be (d) relatively slow in communities with very long-lived species with slow turnover rates and (e) relatively rapid in communities easily invaded by exotic species.

Disturbances can move the composition of the community forwards or backwards along this continuum (Parker 1997). While succession models do encompass dynamics that do not assume a predictable temporal trajectory, such as arrested succession (Lichter 2000; Acacio *et al.* 2007), evaluation of restoration trajectories is often based on the assumption of smooth turnover over time followed by an eventual arrival at a stable 'climax' level that is characteristic of a natural **reference ecosystem** (Matthews *et al.* 2009a). This assumption has been criticized based on empirical evidence (Zedler & Callaway 1999), but it is still widely utilized as a way to gauge success in restoration. In a synthesis of wetland restoration projects, Matthews *et al.* (2009a) found little support for the assumption of simple predictable restoration **trajectories**: different indicators of restoration progress showed different trajectories over time; not all **indicators** of restoration progress showed an increasing trajectory; and in some cases recovery took much longer than the time frame on which **mitigation wetlands** are typically monitored (Figure 21.4). The authors argue for the need to compare restored sites to a naturally variable set of reference sites in order to take into account that multiple restoration trajectories are possible. They also point to the mismatch between technocratic standards of mitigation and ecological dynamics due to the unrealistic policy assumption of simple, rapid and predictable restoration trajectories.

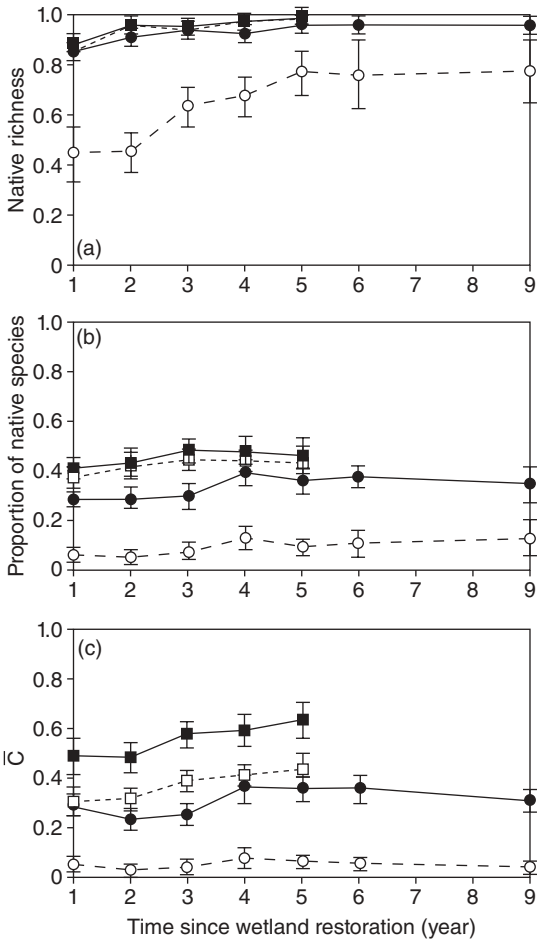


Figure 21.4 Restoration trajectories in Illinois, United States, wetlands, illustrating how different indicators can indicate different restoration dynamics as well as the importance of reference sites. Values are expressed relative to reference wetlands. Solid lines and symbols denote one set of reference sites, dotted lines another set of reference sites. Squares represent values in herbaceous wetlands, and circles represent values in forested wetlands. C (coefficient of conservatism) is an index based on conservation rankings of the native species where a higher value indicates more conservation-valuable native species. From Matthews *et al.* (2009a).

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21.3.2 Thresholds and more dramatic shifts

Disturbances or shifts in environmental conditions can also cause sudden and dramatic shifts in the internal organization of ecosystems that may cause long-term divergence from an intended restoration trajectory and, potentially, a transition to an **alternative state** (Folke *et al.* 2004; Chapter 6). It is important to recognize that trajectories can be nonlinear and sometimes exhibit **thresholds**, where a small change in the environment can cause a large change in structure or function. In a system that has crossed a threshold, the factors that are important for its internal dynamics (i.e. species interactions, abiotic limitations and connectivity) shift and may fundamentally change. Following the shift, restoration that proceeds to re-establish baseline disturbance regimes or composition without taking into account these shifts in internal dynamics may prove largely unsuccessful (Suding *et al.* 2004). While it has proven difficult to verify alternative states in natural systems, particularly in the degraded systems most focused on in restoration, these concepts have proven useful heuristically (Suding & Hobbs 2009). For instance, Firn *et al.* (2010) studied a system in Australia where increased ungulate grazing facilitated the invasion of a problematic grass species. They found that applying management strategies that take into consideration the current dynamics of the novel system, in this case maintaining grazing and increasing the palatability of the invader via fertilization, were more successful than attempting to re-establish the historic baseline conditions (reduced grazing, reduced nitrogen and removal of the invasive).

The presence of positive *feedbacks* – when changes are amplified by ecological or environmental processes – is one mechanism that causes divergent trajectories in a system (Suding *et al.* 2004). This type of feedback is often described as founder, priority or legacy effects. These effects could stem from interactions with other species (e.g. being the first to colonize an area), interactions with mutualists or pathogens (e.g. supporting beneficial or harmful soil organisms) or interactions with the abiotic environment (e.g. ameliorating harsh environmental conditions) (Corbin *et al.* 2004). Restoration projects often have to address existing legacies in a degraded site – be it high propagule pressure of exotic species, changed soil processes or changes in the availability of mutualists, such as mycorrhizal fungi. Restoration efforts can create new founder or legacy effects by their choice of what species to establish first, the preparation of the soil or the introduction of soil mycorrhizae or other organisms (MacDougall *et al.* 2008). It is important to consider how restoration actions may influence the future dynamics of the system, either by their success in ameliorating unwanted past effects or by introducing new effects in the restoration process. For instance, inoculation with a single generalist mycorrhizae taxon may help initial establishment of the plant component in a restoration, but may not function well in times of stress and/or may disproportionately benefit one or two species in the restoration mix (Hoeksema *et al.* 2010). Alternatively, Kulmatiski *et al.* (2006b) found that **exotic species** were associated with strong soil history effects in abandoned agricultural fields in the United States, with evidence indicating that they were able to facilitate their own growth by maintaining beneficial microbial populations and nutrient-cycling rates in these soils. Thus, in cases such as these, restoration addressing exotic species removal also needs to address soil microbial constraints (i.e. through topsoil amendments or removal).

21.3.3 Transient dynamics

It is additionally important to realize the importance of transient dynamics in restoration – when disturbances shift dynamics away from steady state, and result in population dynamics that are either amplified or attenuated in the short term (Stott *et al.* 2010). Legacy and priority effects can also be transient, and not necessarily result in long-term divergence to different end states (Collinge & Ray 2009). While population sizes during these periods may be used to determine restoration success or further management actions, they do not necessarily indicate the long-term status of the population or assemblage (Wiedenmann *et al.* 2009). For instance, van Katwijk *et al.* (2010) demonstrated the importance of considering transient dynamics in the management of eelgrass (*Zostera marina*) populations. While the site was highly eutrophied for several decades, comparisons in the early 1990s showed strong population growth – nearly a doubling in population size. Over the next decade, however, population abundance declined until extinction in 2004. Further studies indicated that microalgae cover was associated with eelgrass mortality prior to seedset. Thus, while the eutrophied location had maximal germination and

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seedling survival rates (and thus high midseason cover), depressed seedbank density eventually caused the population to collapse. The lesson to be learned here is that the timing of compositional change does not necessarily synchronize with environmental change, and might lead to inappropriate management decisions. In this case, the eutrophication process had stabilized long before any large shifts in species were recognized.

Community response to environmental disturbances often depends on traits relating to fecundity, regeneration and dispersal (Neilson *et al*. 2005). Some species may appear to be resilient to change due to their longevity, reducing opportunities for species turnover at the regeneration or recruitment stages until after mortality-causing disturbance (Chapin *et al*. 2004). Lodgepole pine (*Pinus contorta)*, for example, is predicted to expand at its northern limits due to climate changes (Johnstone & Chapin 2003). However, the pine's expansion may lag behind the actual changes in climate because it cannot recruit into the new areas until a fire or disease outbreak occurs. Alternatively, species turnover due to rapid invasions or local extinctions could increase the magnitude or variance expected (D'Antonio & Kark 2002). Species turnover can also depend on temporal variation in environment, with establishment accelerated by prior severe ecosystem disturbance (e.g. due to drought) and limited to transient favourable periods (Swetnam *et al*. 1999).

21.3.4 Tracking environmental change

Lastly, as documented from post-glacial palaeoecological studies as well as from studies addressing more recent time scales, species reordering should be expected to track directional environmental shifts over time (Jackson & Overpeck 2000). As these shifts are expected to be ongoing throughout foreseeable future, with biotic change tracking but never actually catching up with the current environmental conditions, they will likely play out as an additional type of transient dynamic. Large-scale shifts may alter species bioclimatic envelopes for a substantial number of the Earth's biota, thus causing turnover due to extinction and immigration (Jackson & Sax 2010). When the environment shifts closer to or further from population optimum, smaller scale shifts in the abundance of species should be expected as well (Rehfeldt *et al*. 1999). Dispersal limitations, contingent effects of species interactions and novel combinations of environmental factors will add to the complexity of these shifts (Moore & Elmendorf 2006; Suding *et al*. 2008). One way that restorationists can plan for potential future shifts due to directional environmental change is to include species and genotypes from both the core habitats as well as habitats that represent the expected shifts (Vitt *et al*. 2010); species and genotypes in this second group would not be expected to become abundant in the project initially, but patchy establishment in low abundance would still ensure the capacity that the system could track environmental change in the future. Restorationists may also use environmental change to their advantage, for instance by locating projects in areas where projections indicate that problematic invaders will be no longer climatically viable (Bradley & Wilcove 2009).

21.4 REGIONAL PROCESSES: GENE FLOW AND DISPERSAL

Biodiversity at larger spatial scales (from metres to kilometres) ensures that appropriate key species or genotypes are able to arrive after disturbance or when environmental conditions change. Thus, landscape **connectivity** through pollen transfer and propagule dispersal is necessary to ensure that regional processes are in place to anticipate and incorporate uncertain future environmental changes; breaks in this rebuilding capital might cause reduced **resilience** and increased probability of crossing critical **thresholds**. Accordingly, habitat connectivity and **landscape** context are receiving increased attention in restoration projects (Hobbs 2007; Chapters 4 and 5).

21.4.1 Gene flow

Gene flow occurs when there is movement of seeds or pollen or organisms from one population to another. The influence of gene flow on population persistence can be both good and bad; optimal conditions for evolution appear to be present at intermediate levels of gene exchange, although what exactly constitutes optimal levels is likely to vary by species (Lenormand 2002). Too much gene flow can swamp the adaptive change needed to succeed in new environments; this is a hypothesized mechanism for why species fail to adapt to new conditions in marginal habitats (Holt &

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Gomulkiewicz 1997; Bridle & Vines 2007). In situations with too little gene flow, small increases can play an important role in both rescuing populations from extinction, and introducing novel genes that may be adaptive in changing environments (Sexton *et al.* 2009). While experimental evidence on the role of gene flow on the success of restorations is lacking, there are examples in natural systems that suggest that gene flow can play a role in the ability of populations to evolve in response to novel pressures (Kawecki 2008). Population history may play a role in determining the optimal level of gene flow to maintain viable and adaptable restored populations. Species with historically large, interconnected ranges that have recently been fragmented might respond positively to increased gene flow, but caution may be required when manipulating gene flow among populations that have a history of isolation and disjunct distributions (Edmands 2007).

21.4.2 Dispersal

In highly **fragmented** landscapes (see Chapter 5), suitable habitats for native species are often far apart from each other and small in size. This again presents the case where connectivity is a double-edged sword: it is good for **native species** persistence but increases **invasions** from the surrounding matrix. Species abundance is often found to be limited by the amount of seeds that arrive in an area; if more seeds of that species were to arrive, more individuals would recruit and the species would be more abundant (Clark *et al.* 2007). In addition, the degree to which abundances are depressed due to lack of seeds often relates to the extent of landscape dispersal barriers (Seabloom *et al.* 2003). Seed addition in restoration projects can address these barriers, although it often differs from natural dispersal in that it occurs only in the initial stages of restoration. Continued seed input year after year is advantageous because recruitment events often depend on specific weather conditions; interannual variation in recruitment can enhance both genetic and species diversity (Wright *et al.* 2005). In addition, new species or genotype arrival via seed addition may be necessary for the system to track environmental change (Honnay *et al.* 2002).

The type of matrix surrounding habitat patches may also be important to restoration trajectories, particularly in cases where the restoration project is located in a matrix of biotically degraded but abiotically similar habitats (Prevedello & Vieira 2010). For instance, Matthews *et al.* (2009b) found that native species diversity decreased in restored wetlands closer to urbanization, which they suggested was due to increased seed dispersal of invasive species from the urbanized land to the restorations. In these situations, invasive propagule pressure (seed arrival) can overwhelm local interactions and make long-term success of the restoration project difficult to achieve (DiVittorio *et al.* 2007; Reinhardt & Galatowitsch 2008). The latter authors found that wetland restoration was successful when both the propagule pressure of the invasive is minimized and native species seeds are added – neither management technique on their own was successful in establishing a native wetland community. Controlling incoming seeds from invasive species is difficult if the restoration area is surrounded by invaded habitat. In these cases, the scope of the restoration project would need to be enlarged to address the surrounding matrix or a long-term sustained commitment to invasive species control would be required.

21.5 MAINTAINING BIODIVERSITY

Levels of biodiversity (genetic, species and functional diversity) within an ecosystem will undoubtedly be important in influencing the system's sensitivity to change. Diversity of species and functional groups has been shown to influence a range of biogeochemical processes, trophic interactions and resistance to biological invasions (Hillebrand & Matthiessen 2009). Plant genotypic diversity has also been found to have similar effects (Hughes *et al.* 2008). While empirical results are somewhat mixed, species diversity may regulate temporal variability **ecosystem processes** (e.g. productivity and nutrient cycling; Baez & Collins 2008; Isbell *et al.* 2009), making the system more stable. Often increased stability at the ecosystem level due to species diversity is accompanied with increased variability at the population level (e.g. particular species density and biomass), termed 'compensatory dynamics' (Gonzalez & Loreau 2009). Thus, restoration projects with ecosystem service goals may benefit from increased species diversity to keep ecosystem function stable, while restoration projects with more species-specific goals may benefit from high genetic diversity of the target species to maintain desired species richness.

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21.5.1 Relationships between genetic and species diversity

The interplay between genetic and species diversity is just beginning to be explored. Initial studies are finding more complex interactions than anticipated. For instance, adaptive change, potentially facilitated by high genetic diversity, could allow species to maintain their abundance and avoid extinction under changing conditions, thus maintaining species diversity (Scoble & Lowe 2010). On the other hand, de Mazancourt *et al.* (2008) used a modelling approach and found that species diversity increased the chance that some species were pre-adapted to new conditions, which restricted the ecological opportunity for evolutionary responses in all species. Consistent with these results, the work of Silvertown *et al.* (2009) regarding the 150-year *Park Grass Experiment* in England revealed contradictory changes in species and genetic diversity in response to nutrient addition: genetic diversity of a population of *Anthoxanthum odoratum* increased, while species diversity decreased, with the number of resources added to a plot. Thus, it appears that in some cases species living in species-rich communities are less likely to be able to evolve in response to environmental change than species living in species-poor communities because competition among species may constrain genetic diversity of any one species.

21.5.2 Role of functional diversity

Evidence is accumulating that high functional response diversity might be critical to **sustainable** restoration (Elmqvist *et al.* 2003). The goal of high response diversity would be to have assemblages that contain species or genotypes that have a diversity of responses to change. For example, Steiner *et al.* (2006) found that diversity of functional groups increased community **resilience** in experimental aquatic food webs because more diverse communities had a greater likelihood of containing a particularly resilient species. Restoration projects can increase response diversity by expanding species mixes to include many seemingly 'redundant' species from a wider range of environments, increasing emphasis on genetic diversity in addition to local adaptation, and considering assisted species migration and reintroduction of species lost from the regional **species pool**. This consideration also implies that a successful restoration is not necessarily the one that attains a particular community or genetic composition, but one that has the capacity to change in order to maintain core **ecosystem functions** and **services** over time (Choi *et al.* 2008).

Even if communities targeted for restoration are initially diverse, the processes that maintain diversity also need to be considered in order keep diversity levels high over time. Maintenance of high diversity assemblages requires stabilizing processes – those that lead towards coexistence among species through niche differentiation (MacDougall *et al.* 2009). Succession often homogenizes, rather than diversifies, over time (Kuiters *et al.* 2009), posing another type of challenge for restoration; in many systems disturbances need to be incorporated to maintain diversity, yet some of the species that arrive after a disturbance are undesirable.

21.6 PERSPECTIVES

In this period of unprecedented environmental change, it will be critical to apply understanding of evolutionary and community dynamics in order to anticipate and incorporate future – and largely uncertain – change in restoration projects. To use an analogy from *Through the Looking Glass* (Carroll 1871, 135; which also forms the basis of evolutionary Red Queen Hypothesis, proposed by van Valen 1973), intervention may be needed simply to remain in the same spot along a degradation trajectory in this era of change: 'Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!' To deviate a bit from the analogy, it may also be necessary to change the nature of the intervention to incorporate expected changes and consider the increased need to maintain **ecosystem integrity** over a large potential range of variability; resetting the ecological – and evolutionary – clock to a historic range of variation may often not be feasible or sustainable (Hobbs & Cramer 2008).

In this chapter, we have focused on how to run with, rather than reset, the rapidly ticking ecological clock, emphasizing two perspectives. First, we may need to acknowledge that even maintenance of a less-than-desired system may require intervention just 'to keep in the same place.' Second, the very nature of the intervention employed in restoration may need to be changed to reflect the need to maintain system integrity over a large potential range of variability that does not necessarily match historic reference conditions.

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Many aspects of interventions that stem from these perspectives are similar regardless of whether evolutionary or ecological dynamics are forefront priorities; both should be integrated and considered integral parts of restoration projects. To take into account these perspectives, we suggest four goals:

1. Establish systems that have the capacity to change, rather than ones that are designed for a static end goal. Consider sustainability in projected future, not past, environments.

2. Acknowledge that restoration planning is largely uncertain. Use experimental trials and management iterations to better increase knowledge about mechanisms of biotic response and dynamics.

3. Monitor at multiple levels of organization over the project lifetime rather than just at the initial stages of the project.

4. Focus on ecosystem services in addition to, or rather than, biotic composition as restoration goals. Accept that particular genotypes and species may be unable to persist in future conditions.

While these goals may not seem surprising given the current prognosis of environmental change, the expectation of genetic and species reordering through time is at odds with many restoration goals and monitoring programmes, which have metrics aimed at past-oriented static approaches (Choi *et al.* 2008). In fact, while we have some guidelines from basic research, it remains largely uncertain whether restoration can successfully establish ecosystems that are sustainable in the context of future environmental change. Many fruitful avenues of research concerning variability, resilience and adaptability in restoration lie ahead.

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Chapter 22

RESTORATION ECOLOGY AND THE PATH TO SUSTAINABILITY

James Aronson and *Jelte van Andel*

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22.1 INTRODUCTION

The last two chapters dealt with the global phenomenon of biological invasions, the multifaceted concept of resilience and 'shifting baselines' in population and community dynamics, especially as these complex issues and ideas affect ecological restoration in today's rapidly changing world. In this final chapter, we come back to economics, politics and transdisciplinarity, all of which were introduced in Chapter 2, as key for the integration and mainstreaming of ecological restoration and restoration ecology. Once again, we address ourselves primarily to scientists starting their careers in the rapidly growing and evolving field of restoration ecology, who aspire to contribute towards the further development of sustainability science.

22.2 RESTORATION ECOLOGY REVISITED

In the introduction to Part 4, we asked whether restoration ecology could really help society to find a way towards sustainable use, development, conservation and restoration of terrestrial and aquatic ecosystems. The answer to that question, we think, is 'Affirmative', despite the complexity of this task. Firstly, the science of restoration ecology and the practice of ecological restoration have advanced enormously in the last 30 years, as is amply shown in the first 21 chapters of this book. We have also gained significant new insights from functional and evolutionary ecology, covering landscapes, ecosystems, communities and populations. The body of practical know-how is also growing fast. Anyone seeking to restore any of a huge range of ecosystems – including arctic, tropical, temperate, arid, montane, coastal and wetland systems – can already find considerable guidance in both conceptual and practical terms.

We now also have much keener insights into the complexity of, and obstacles to, ecological restoration, not only within a traditional ecological framework of analysis but also from a more advanced and holistic socio-ecological perspective. It's important to realize how challenging it is to promote and assist the self-regeneration of ecological systems that have been transformed, degraded or deeply impaired by human profligacy and mismanagement in the past; it's not just a matter of planting a few trees or removing a few dams. One main challenge is to make the scientific insights into the complexity of ecosystem structure and functioning, and responses to interventions and disturbances, applicable to the practice of ecological restoration on a case-by-case basis.

Another thing we now know concerns the limitations to truly restoring ecosystems, in the sense of going back to the way things were before. We now see that a large part of the Earth's soils and surface, including the ocean floors and the tops of mountains, and the very atmosphere, are so deeply transformed by human activities that biodiversity worldwide is plummeting and non-analogue biotic communities and ecosystems – sometimes referred to as 'emerging ecosystems' (as in Chapter 2) and sometimes as 'novel ecosystems' (as in Chapter 3) – are now increasingly replacing historical ones. However, as strongly emphasized by Murcia *et al.* (in press), this does not alter the fact that in many, many places, restoration is still a very good option indeed provided, of course, that we recall the lessons outlined in this book and adopt the SER paradigm of 'restoring to the future' and the principle of adaptive management (Figure 22.1). Restoration must also be integrated in the larger goal of helping move society towards a more 'sustainable and desirable future' (Costanza *et al.* 2006), with restoration of natural capital and enhancement of ecosystem services pursued in tandem with conserving biodiversity (Bullock *et al.* 2011; Figure 22.1). But that requires that we all contribute to forging a new language capable of communicating across disciplines to meet the unprecedented challenges involved in this project. In view of humankind's rapidly growing numbers and given our very deep ecological footprint, a footprint that is growing deeper and wider day by day, we need to work hard on achieving a more enlightened, just and sustainable mode of living; ecological restoration has a large role to play in that scheme. Finally, it is essential that we keep sight of the importance of historical reference systems as guides and benchmarks for restoration, without which the whole enterprise loses its ecological bearings.

So, what do restoration ecologists need to know about the best paths towards sustainability that are currently under discussion, and is there any good news out there?

22.2.1 Economics and Politics

The best roadmap we can report here is called the Economics of Ecosystems and Biodiversity (TEEB), the

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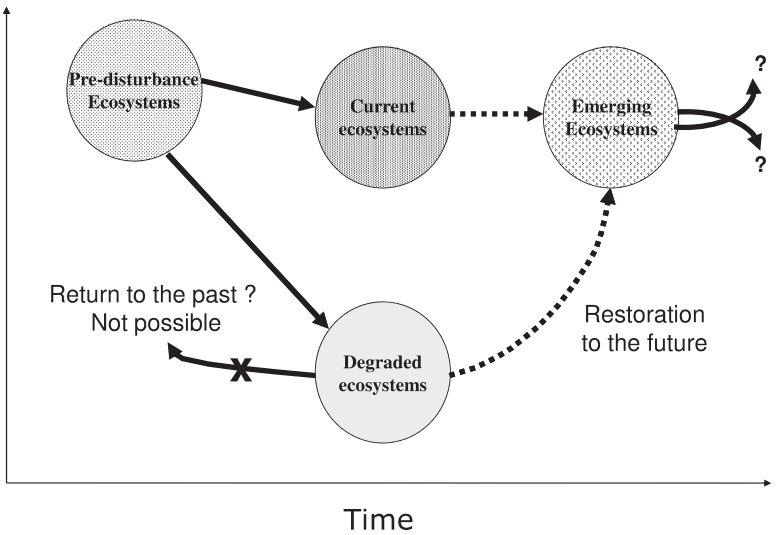


Figure 22.1 A new restoration ecology dynamics model in a world of changing ecosystems, ever-deeper human footprint and global ecological flux. Various possible trajectories exist which are not linear, nor even entirely predictable.

project we introduced back in Chapter 2. Following on from the Millennium Ecosystem Assessment (MA 2005) and the Stern Report (Stern 2006) dealing with the economic costs of anthropogenic climate change, TEEB (2010, 2011) is a high-level international study dealing with the economic costs of ecosystem degradation and the loss of biodiversity. It also addresses the cost of inaction and proposes concrete solutions that could move global society towards sustainability. TEEB adopts a much more ecologically informed approach to economic science than did the Stern report, which adhered to the currently dominant 'neoclassical' approach, which advocates an unregulated 'free' market. What TEEB spells out, in five different books aimed at different audiences, and in simple language, is that the costs of ecological degradation and biodiversity loss are enormous, and that a big part of the sane, or intelligent, answer is to invest much more heavily in the restoration of degraded ecosystems and the revitalization of fragmented landscapes.

We note that in some countries, like South Africa, Ecuador, Costa Rica, Japan and Brazil, and some states and regions in Canada, the United States, Mexico and elsewhere, ecological restoration is increasingly seen as a sustainable development strategy as well as a conservation one; indeed no dichotomy between restoration and development exists when all costs and benefits are factored into the valuation of restoration, and it is incentivized by legislation. There is resistance, of course, from both vested-interest lobbies and other sectors, but this core idea is making progress.

For more progress to happen in these areas, all stakeholders and decision makers need to have a much clearer idea of the importance to human society of ecosystems and biodiversity, which we have seen can be described metaphorically as renewable natural capital or 'ecological infrastructure' (TEEB 2010). In the very first chapter of the first of the five planned TEEB volumes, de Groot *et al.* (2010) present a very useful 'cascade' image (see Figure 22.2), starting with a 'box' on the upper left of the schema which represents 'ecosystems and biodiversity', renewable natural capital (*sensu* MA 2005; Aronson *et al.* 2007), in which biophysical structure and processes are distinguished from ecosystem functions. To wit, the biophysical structure and processes are the infrastructure that provides the matrix for the functions or 'workings' of ecosystems, hence the term 'ecological infrastructure' used metaphorically by TEEB (see Neßhöver *et al.* 2011). Note that the functions are defined here by their potential to deliver ecosystem goods and services for human interests (EGS, given in the central box of the figure). This schema presents for the first time an illustration clearly showing the difference between

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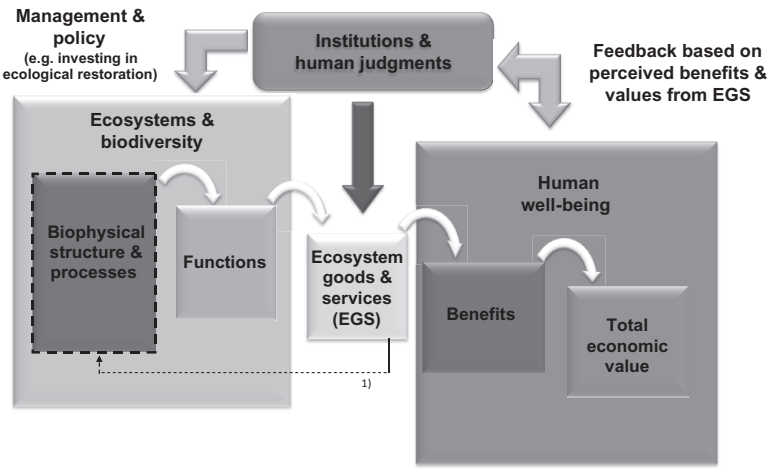


Figure 22.2 Conceptual framework for linking ecosystems and human well-being, according to TEEB (from de Groot *et al.* 2010, modified). Ecosystem functions are defined as a subset of the interactions between ecosystem structure, and the processes, that together determine the capacity of an ecosystem to provide goods and services. Ecosystem goods and services (EGS) are defined as the direct and indirect contributions of ecosystems to human well-being (MA 2005). The TEEB framework distinguishes between ecological, sociocultural and economic benefits and values. Different values can be attached to a particular benefit. NB: Each ecosystem function influences various ecosystem services. Concurrently, unsustainable exploitation of goods, or excessive use of certain services, can adversely affect ecosystem structure and processes.

ecosystem functions and ecosystem goods and services, and also showing the pivotal role of the latter. This should help dispel the very common confusion that exists between ecosystem functions on the one hand, and ecosystem services on the other. For example, the provisioning *service* 'clean water' is based on 'water purification' as a *function*, which in turn is based on underlying *structures and processes* such as food chain dynamics and nutrient cycling.

In a third box on Figure 22.2, we find human welfare and well-being (at the societal level) with 'benefits' distinguished from 'values'. The TEEB distinguishes ecological, sociocultural and economic benefits and values. Benefits are what can be measured in terms of what people receive from EGS, while Values are assigned by economists and others by various means. It is important to distinguish between the two. For example, benefits from catching fish from the ocean can be measured as food for people, as cultural identity for fishers or as income from the market, whereas the valuation of these benefits may have a subjective component, depending on who attaches values to a particular benefit. Note that both use and non-use (or active-use and passive-use) values – that is, values that can readily be assigned monetary equivalents and those that cannot – are included in the term 'Total Economic Value', which thus is an estimate of the full economic value of a good or service, and not just its direct monetary value (National Research Council (NRC) 2005). As Loomis *et al.* (2000), Robbins and Daniels (2011) and others have shown, this approach is highly valuable in promoting a closer union between restoration ecology and economics.

As mentioned in Chapter 2, the TEEB project represents an anthropocentric approach towards ecosystem functions, where they are instrumentally valued for their benefits to human society (human well-being). Instrumental valuation is defined as assessing functions for their contribution to the benefit of some particular reference, in this case human well-being. Intrinsic values of nature are by definition non-instrumental, and have thus not played an equivalent role in decision making (see the discussion in Farber *et al.* 2002). However, as proposed by Weesie and van Andel (2008), ecosystem functions can, from a biocentric point of view, similarly be valued in an instrumen-

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tal way, in this case for their importance to the ecological and evolutionary functioning of the global ecosystem. Both types of ecosystem function can thus be valued for decision making. Recently, Bullock *et al.* (2011) explored whether anthropocentric and biocentric positions – restoration of ecosystem services, and restoration of biodiversity – can be achieved simultaneously (cf. Rey Benayas *et al.* 2009). We quote from their study:

> A meta-analysis of 89 restoration assessments in a wide range of ecosystem types across the globe indicates that ecological restoration increased provision of biodiversity and ecosystem services by 44% and 25% respectively. However, values of both remained lower in restored than in intact reference ecosystems. Increases in biodiversity and ecosystem service measures following restoration were positively correlated. Results indicate that restoration actions focused on enhancing biodiversity should support increased provision of ecosystem services, particularly in tropical terrestrial biomes.

Such research vindicates public and private investment in restoration on both anthropocentric and biocentric grounds. In order to bring restoration into the economic and political mainstream, however, new economic concepts and levers are required. A key example is the still somewhat controversial concept of 'payments for ecosystem services'. This concept is already being usefully applied in the important negotiations currently underway through the REDD+ mechanism within the UNFCCC. REDD+ is an expansion, agreed at the UN climate change discussions at Cancún, Mexico, in December 2010, of a scheme for Reducing Emissions from Deforestation and (Forest) Degradation, through payments for services provided by conservation and restoration of forest biodiversity in developing countries, with ancillary benefits for people indigenous to such forests. Such initiatives are intended to improve upon the Kyoto Protocol, which comes to an end in 2012 (see Alexander *et al.* 2011).

As noted before, we must recognize that ecological restoration cannot and should not be approached in isolation. Instead, it should be approached as part of a global movement towards landscape-scale and bioregional sustainability. A growing body of evidence from the field shows that investing in the restoration of renewable natural capital makes economic sense, in terms of cost effectiveness and rates of return, once the whole range of benefits provided by maintained or augmented biodiversity and ecosystem services are taken into account (de Groot *et al.* unpubl. MS; Elmqvist *et al.* unpubl. MS). But laws and economic incentives will be required to give practical expression to these insights into the real value of natural capital and ecosystem services provided by ecological economics. For example, de Groot *et al.* (unpubl. MS) calculated benefit–cost ratios for 91 ecological restoration projects carried out in 10 different biomes. They compared the results using conservative and optimistic discount rates (see Blignaut & Aronson 2008), the latter being one that recognizes that restored ecosystems should lead to an increase in the benefits people perceive and hence the Total Economic Value, as compared to current, unrestored ecosystems at the same site. Their analysis shows that even under a 'worst-case scenario' (using a discount rate of 8% and 125% of average restoration costs), investing in restoration 'pays' well for most ecosystems, except coral reefs and some coastal and freshwater systems. With a 'best-case scenario', the results show even more compellingly that proactive investment strategies in renewable natural capital are fully justified and need to be further developed and implemented.

> Decision and policy makers on all levels, both in the private and public sector, should be made aware that money spent on ecosystem restoration should not (only) be seen as a cost, but as an investment that brings multiple benefits and can help them to achieve their policy goals. This applies to sectors such as urban development, water purification and waste water treatment, and regional development, as well as improved systems and policies for public health and adaptation to climate change. (de Groot *et al.* unpubl. MS)

From a policy maker's perspective, we note, there are several other positive features that make restoration attractive: ecological restoration programmes can contribute to the range and quantity of job opportunities and livelihoods in rural areas, and they also play a pivotal role in mitigating some of the effects of

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anthropogenic climate change. Thanks to this bundle of attractive pluses, ecological restoration is indeed taking on an increasingly central role in national and global environmental policy (Calmon *et al.* 2011, Wu *et al.* unpubl. MS). Yet things are still moving far more slowly than global environmental conditions demand.

Our new economic and ecological thinking must contribute to a paradigm shift in our political and economic cultures, engendering laws and legally bolstered economic incentives for restoration; the 'market' alone will fail to stimulate progress at the rate so clearly needed (Aronson *et al.* 2011). Further-reaching legislation is needed to ensure that 'mitigation' and compensatory 'offset' measures involving restoration are required from public or private developers whose projects cause unavoidable environmental harm. Restoration scientists have an obligation to communicate this imperative to the general public, and assist in forming lobbies demanding such measures. Given the scale of environmental crises on our planet, some degree of political engagement is not just an option for restoration scientists, it is a necessity. To assist this shift to participation in public affairs, the overarching theme of our book has been the search for transdisciplinarity, the topic of the next section.

22.2.2 Transdisciplinarity

To be successful, ecological restoration must be approached by a team of scientists from different disciplines working in concert with engineers, managers, professionals of all sorts and of course ordinary citizens, be they farmers or city dwellers, as appropriate to the context in which the project or programme is undertaken. How can this take place?

In Chapter 13, we learned about a beautiful example of transdisciplinarity, namely, the Fire Learning Network that focuses on 400 000 ha in western North America, in a context where land ownership and management responsibilities are highly variable, and there is a very long history of political and resource use conflicts. A Collaborative Forest Landscape Restoration (CFLR) Program was set up to encourage the collaborative, science-based ecosystem restoration of priority forest landscapes. A similar programme is underway in the Atlantic Rainforest region of coastal Brazil (see Calmon *et al.* 2011). Other examples exist, but much more effort and much more synergy are needed to see them spread and multiply across the globe.

Whether you are a scientist, professional or volunteer practitioner, an effective interface that communicates between restoration science and society is vital to achieving effective and lasting restoration. In this section, we wish to stress some of the thorny problems and obstacles that can arise from the poor quality of communications among scientists, between scientists as a guild and in society at large. So we now consider a number of problems in communication and consensus building – not to mention the ideological, economic development and information divides we have already identified – that can hinder the process. These problems are of course not restricted to restoration ecology, but are encountered in all transdisciplinary projects. We perceive three main causes of problems in communication: (1) lack of transparency among ecologists about codes of conduct, (2) poor interdisciplinary cooperation (i.e. between ecologists and social scientists) and (3) lack of cooperation and feedback among scientists and the most deeply affected stakeholders. We discuss these issues in this chapter, in conjunction with a case in point from the Netherlands studied by Swart and van Andel (2008). That involved a government-initiated study intended to help solve a conflict between biodiversity conservation and restoration and biological resource exploitation in the Dutch part of the Wadden Sea (Box 22.1).

Transparency about codes of conduct

In Chapter 2, we explained the difference between curiosity-driven science and problem-solving science. Let's come back to this issue. Figure 22.3 illustrates different 'modes of science', including curiosity-driven science (what we call ABC science), applied science, contextualized science and politicized science. Not recognizing the societal context in which a research project is embedded may cause misunderstandings about the codes of conduct agreed on. People in the various fields of science are taught different codes of conduct – or none at all; they acquire different methods for examining questions, and develop differing core values, and core logic and psychology about what they are doing. This range may also occur within a specific field, such as ecology. Curiosity-driven scientists, in ecology and other disciplines, in principle learn to respect the 'ethics of science' that were nicely formulated by sociologist Robert Merton (1973), as follows:

1. Communalism, that is, the notion that scientific knowledge is a common value based on the need

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Box 22.1 The cockle controversy on the tidal flats of the Dutch part of the Wadden Sea

The Wadden Sea – an estuary along the coasts of the Netherlands, Germany and Denmark – is a wetland of international importance from many points of view. The tidal flats and the salt marshes around the sea's edges, with extensive and soft sediment bottoms, provide a huge amount of food for large populations of both migratory and resident bird species. So the region has exceptionally high biodiversity value, but this ecosystem also provides multiple goods and services to human society. Its intertidal flats and salt marshes, like shallow seas of this kind in most parts of the world, have experienced human exploitation for more than 5000 years. Initially, exploitation of shellfish from the Wadden Sea consisted of small-scale fishing and gathering by hand. With the advent of motorized power over the past century, however, and the use of large nets and dredges, human exploitation now heavily influences natural processes (Bakker & Piersma 2006). This has resulted, since the 1980s, in an ongoing conflict between fishermen, who were until then permitted to freely exploit the common cockle (*Ceratostigma edule*) and the blue mussel (*Mytilus edulis*), and various nongovernmental organizations fighting for nature conservation. The conservation lobby was supported by university-based ecologists and colleagues from the ABC science group (Figure 22.3) who had performed research in the area for many years and had assembled long-term data sets. In view of this conflict of interest, the Dutch Ministry of Agriculture, Nature and Food Quality was confronted with a dilemma, as it was legally designated to represent all stakeholders. The Ministry initiated an ecological evaluation study in the early1990s, which resulted in a final report only 15 years later. Swart and van Andel (2008) analysed the 15-year long interactions among the various parties, from which we draw the following summary.

The situation in 1980 was taken as a reference model for the evaluation of changes since then. The study group, called EVA (for evaluation), consisted of supposedly 'independent' ecology researchers from a consortium of semigovernmental institutes for applied research, but not including the aforementioned university-based researchers, as they were not considered independent, associated as they were with the anti-fishermen lobby. The latter academic group increasingly disagreed with the interpretation of results published by the EVA study group. As a result, in addition to conservation and commercial interests, ecology itself became part of the controversy. For example, the EVA study group focused its research efforts on changes in biodiversity, as measured in particular by the decline of bird populations, which conceivably could result from natural cycles and fluctuations. Other researchers, outside this group, perceived what they considered to be irreversible disturbances of the ecosystem, as reflected, they argued, in changes in the composition of soilborne fauna after dredging.

The final, still informal, reports of the ministerial study group became available in 2003. One of the hot topics was that a popular version of the final report, meant to be read and cited by the public media, implied that the steep decline of populations of bird species might have been due to environmental changes, rather than to the exploitation of their food by fishermen. At that time the ecological research centre of the University of Groningen, drawn by the scientific interest of the problem, organized a symposium and invited representatives of each group to a public discussion of their results. Next, it transpired that the ministerial study group had an internal constraint in their contract, which meant that they were not allowed to speak in public about their preliminary reports as long as an Audit Committee of three renowned and independent scientists had not agreed on the scientific quality of their reports, including the interpretation and evaluation of the results. The Steering Committee, composed of all the stakeholders, insisted on this point. As a result, even though the results from the evaluation study had already been made public, as preliminary reports, the members of the EVA group could not participate in the public discussion. There was no choice but to postpone the symposium until a few months later. By then, all the scientists participating in the symposium agreed on the conclusion that the shellfish exploitation was the cause of the damage of the soil ecosystem of the Dutch Wadden Sea. However, it remained unclear whether the damage was irreversible, depending on the time required for recovery and on the criteria for a reference system.

Lessons learned from this project, as well as from the follow-up, are given in the main text.

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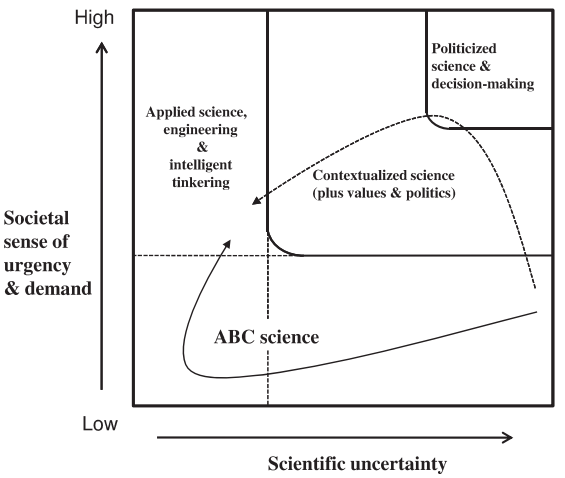


Figure 22.3 Different modes of scientific research as a function of societal interests and scientific uncertainty. The solid arrow in the figure indicates the classic route of autonomous science that is followed by applied science. The dashed arrow is a schematic representation of the route of research projects involved in the cockle fishery controversy which became strongly societally contextualized and skewed, in both directions, by political bias. ABC, autonomous, basic and curiosity driven research. (Modified from Swart & van Andel 2008.)

for openness and public exchange of results and insights;

2. Universalism: the pursuit of universal truth, which implies that scientific statements should be based on objective observations and consistency in logical discourse, thereby avoiding insofar as possible individual and subjective prejudices or preferences, be they political, racial, cultural or gender-related;

3. Independence or freedom from ideology or commercial interests imposed or suggested by a financial sponsor that might influence the conduct of research or the interpretation of results; and, finally,

4. Scepticism, implying a critical attitude towards scientific claims, results and interpretations in published papers, including those by the researcher himself or herself.

Based on their analysis of the long-term controversy on the shellfish exploitation in the Dutch Wadden Sea (Box 22.1), Swart and van Andel (2008) concluded that codes of conduct like Merton's need a number of provisos, or footnotes, in the case of sponsored scientific projects aiming at application in practice, whether they be initiated and paid for by a corporation, a governmental agency or a nongovernmental organization (NGO). We stress that these provisos are not meant to protect any exclusive rights of the sponsor, but only to make transparent to the public the context and constraints under which any given set of research findings has been reached. Not only is sound science required if we are to move forward, but also sound ways of interacting and communicating with all the actors and stakeholders in the larger context, outside of academia. This requires these amendments to the aforementioned classical scientific ethos.

In the light of the issues raised by the Wadden Sea controversy, Swart and van Andel (2008) proposed to extend Merton's code of conduct for what they call 'contextualized research' (see Figure 22.3). Their recommendations include (1) recognition of the potential context of each research project and willingness to conduct open and interactive communication, (2) consideration of requirements of confidentiality as an exception, particularly in government-funded research, (3) willingness to consider and discuss seriously competing, including politically inspired, rationales for a research project, (4) presentation of scientific results and interpretations in publicly accessible texts, with the proviso that the scientific quality of the original research should not be 'lost in translation', and (5) stipulation of a scientific evaluation of the political decisions following the presented research results in the original contract, thus contributing to a transparent relationship between science and society.

Interdisciplinary cooperation

In the case mentioned in Box 22.1, neither economists nor social scientists were involved in the EVA study group, which consisted of ecologists only. Economists calculated the budgets related to the shell fisheries, but they did not form part of EVA, and their reports remained informal. Yet this kind of case obviously calls for the high level of the kind of interdisciplinary approach we have described in earlier chapters.

As mentioned, in Chapter 2 and in section 22.2.1, the interdisciplinary field of 'ecological economics' has finally emerged, after a long period of tentative communication and miscommunication between ecologists and economists. Both disciplines have much in common, including a quantitative orientation in methodology, and an interest in scarce resources and in holistic approaches to cost-benefit analyses. Furthermore, as Hardin (1991) noted, economics is quite

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mature among the social sciences and has a common conceptual origin with ecology, something that is less clear for the other social sciences. Quite recently, the *Journal of Applied Ecology* devoted a special feature to problems related to cross-disciplinary research between ecologists and social scientists. From the review article by Lowe *et al*. (2009), we learn that one of the causes of limited cooperation is that many ecologists, along with many colleagues from the other natural sciences, consider the social sciences as focusing on 'human values and societal interests' and 'understanding human behavior and impacts'. It is increasingly recognized by some ecologists, however, and restoration ecologists in particular, that they have no choice but to recognize, and incorporate the 'human–social dimensions' of their own areas of study much more explicitly. This, they have understood, leads to benefits including 'communication and policy translation' and 'facilitation of environmental management' issues, both of which are vital for achieving real improvements in the ecological status of almost any target area or ecosystem. Apart from the challenge in finding a common methodology, and carefully exploring to what extent methods and concepts from the natural sciences can be extended to the social sciences and vice versa, there is a fundamental, underlying issue to be considered, namely the place of humans in nature. Lowe *et al*. (2009) distinguish three views among ecologists on the subject of people: (1) as 'ecological audience', (2) as 'ecological agents' and (3) as 'ecological subjects/objects'. The first relates to studying pristine ecosystems and does not make specific claims on the social sciences, and the second one recognizes human impact on ecosystems. However, with the third perspective ecology crosses into and joins hands, so to speak, with the social sciences. The very notion of 'socio-ecological systems', frequently used in this book, contains an implicit challenge for those engaged in interdisciplinarity.

Communication among stakeholders

Transdisciplinarity, in our view, goes beyond interdisciplinarity between professionals, and extends to interaction with stakeholders. In the case described in Box 22.1, the Steering Committee set up by the Ministry brought together all the stakeholders, whereas the EVA study group, as well as the Audit Committee, consisted of only ecologists. This internal structuring of the project might have been one of the causes of the problems in communication between the EVA study group and the Steering Committee, and with independent ecologists and interested NGOs. Nevertheless, the scientific results published by the EVA study group, and the ongoing scientific debate around those results, led to a number of political decisions that reached far beyond the focus of the study project. First, in 2004 the Minister of Agriculture, Nature, and Food Quality, with the support of the House of Representatives, decided to ban shellfish exploitation from the Dutch part of the Wadden Sea. At the same time, the minister unexpectedly lifted the long-standing moratorium on the exploitation of natural gas deposits lying at the bottom of the Wadden Sea; the sole condition imposed for this was that new, supposedly safe and environmentally friendly techniques would be employed. Through a levy on such exploitation, the government creates a fund to compensate the fishers and to initiate integrated research for nature protection in the region.

A 'Dutch Wadden Academy' was established in 2008, under the auspices of the Netherlands Royal Academy of Arts and Sciences, in which all stakeholders participate, including administrators, policy makers, and scientists, covering expertise in ecology, geology, economics and cultural history, and on the impact of climate change. To set the research priorities, an initial document was produced entitled 'Knowledge for a Sustainable Future of the Wadden: Integrated Research Agenda of the Wadden Academy' (http://www.waddenacademie.knaw.nl). After having formulated its guiding principle, 'to preserve the natural values of the Wadden Sea Area while allowing sustainable human use', it is immediately recognized that 'there is a debate as to which natural values are the most important and as to the nature and extent of the restrictions of human use'. Therefore, research into conceivable future scenarios for environmental and socio-economic development options is called for. An integrated systems approach, with emphasis on interactions between the natural and social sciences and humanities, and international cooperation are now considered as indispensable attributes of both scientific research and sustainable development in the region.

Innumerable examples show that science cannot in most cases be directly translated into political measures, nor should politics be allowed to dictate the direction of science. In this case, the contentious relationship between scientists and politicians over a 15-year period has resulted in a positive outcome: science contributing knowledge used for political decision making,

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which in turn included the facilitation of interdisciplinary science, but also initiated another potential environmental problem (gas exploitation). Perhaps the only way forward in such a situation is for some of the profits to be devoted to ecological restoration, in addition to nature protection and research in the region. We expect to see numerous cases like this in the future, all over the world. For that reason, we argue, once again, that restoration ecology will play an increasingly important role in moving societies towards a more 'sustainable and desirable future'. But that requires mutually respectful communication among all scientists and other stakeholders and indeed a new, transdisciplinary language appropriate to the huge, and partly unprecedented, needs and challenges we face today. Such a language is indispensible to the coherent development of the new transdisciplinary field called 'sustainability science' (Aronson 2011). As noted back in the 1770s by Antoine Lavoisier, breakthroughs in science must overcome blockages of communication: 'We cannot improve the language of any science without at the same time improving the science itself; neither can we . . . improve a science without improving the language or nomenclature which belongs to it' (translation cited in Goldenfeld & Woese 2007). In the next section, we explore this challenge a bit further.

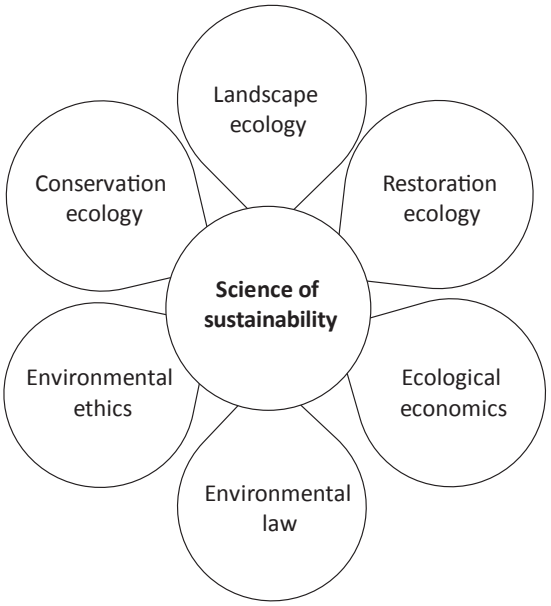


Figure 22.4 Six-petal flower for the science of (and search for) sustainability. The upper three petals are about science and engineering, while the lower petals are about where we as a society want to be, and the social means to get there. Ethics, economics and laws ideally combine to inform and refine the policies and jurisprudence governing our collective behaviour. Science and engineering will be required in areas of management, conservation, sustainable use of resources and restoration of degraded ecosystems. (From Aronson 2011. Reproduced with permission of Springer Verlag.)

22.3 SUSTAINABILITY SCIENCE

Aronson *et al.* (2010) have argued that the road to sustainability must cross three divides, namely, the ideological divide between deep ecologists and fundamentalist neoclassical economists, the economic divide between the rich and the poor and the information divide between 'the environment' and 'the market'. For this to happen, clearly we need new language, as noted here, with clear enunciation of concepts, definitions and methods. But sustainability science will not be possible just by improving the language of any one science, as per Lavoisier's comment noted in section 22.2.2, but rather on the forging of a new, transdisciplinary language, and way of thinking. In other words, we need new paradigms to understand the fundamental character of interactions between nature and society, and thereby help advance the new science of sustainability.

But what is the science of sustainability really about? At the simplest level, sustainability science comprises the fields of scientific endeavor that contribute to the goals set for sustainability by the Brundtland Commission of the UN in 1987: 'Sustainable development is development that meets the needs of the present without compromising the ability of future generations to meet their own needs' (WCED 1987). However, additional characteristics may be highlighted for our purposes here: (1) it is problem-driven, and transdisciplinary (as illustrated in Figure 22.4), and (2) the scientific process in the interplay between science and society is highly dynamic, as depicted in Figure 22.5. Of course, the scientific disciplines to be included in any project of ecological restoration will differ according to the problems to be analysed and solved. But in all cases it is important to recognize the importance of transdisciplinarity, given the seriousness of the challenges at hand and the fact that we lack models to follow. As we noted in the preface, humanity needs not only new paradigms but also a new *modus operandi* if

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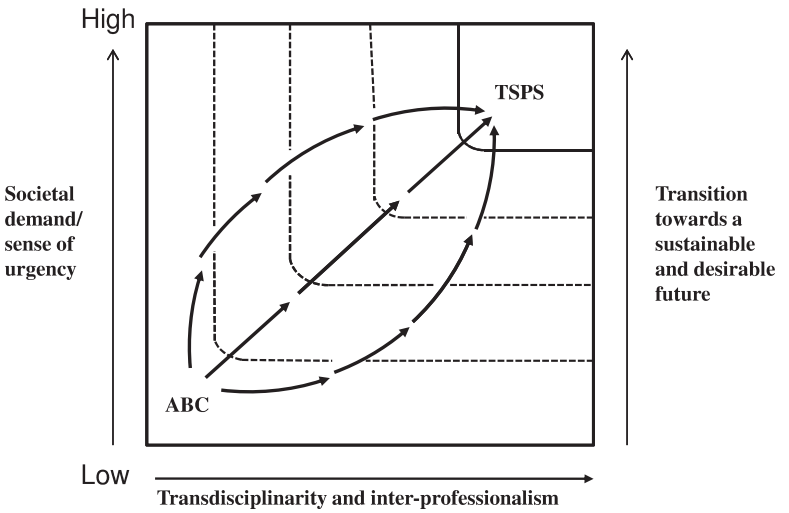


Figure 22.5 The path toward sustainability in an increasingly non-analogue future. ABC, autonomous, basic and curiosity-driven research; and TSPS, transdisciplinary science and problem solving.

we wish to move away from the precipice of ecological and environmental crisis we have come to. As the inventor Buckminster Fuller put it, several decades ago, we need a 'new operating manual for Spaceship Earth'.

In Figure 22.5, we illustrate a blueprint for sustainability-science-in-action. Problem solving requires, first of all, a fundamental scientific analysis, using available tools from all the appropriate sciences in the group we call ABC (autonomous, basic and curiosity-driven), while at the same time evaluating these tools according to their applicability to the problem. Depending on the disciplines, stakeholders and urgency factor involved, the way towards problem solving is straightforward or roundabout. Intermediate solutions and/or reports may be useful as well. Of course, we recognize that there is feedback from problem solving back towards the ABC sciences, as many of the scientific problems taken into account are inspired by societal problems. The ultimate test of success in this dynamic field is whether the world is getting more – or less – sustainable. Not only our well-being but also our survival depends on it.

22.4 EPILOGUE

In closing, let us recall the discussion of natural capital, ecosystem services and transdisciplinarity in Chapter 2, and the idea that ecological restoration can provide the link or the bridge between sustainable economic development objectives and nature conservation ones. Many communities, NGOs, individual nations and multinational corporations are now actively investing in, or encouraging investment and legislation for, ecological restoration; several international organizations and treaties (CBD, UNFCCC and UNCCD) and the European Commission, are going further still, by embracing the paradigms that describe natural capital as the vital factor required to guarantee the flow of ecosystem services (see also Comín 2010).

We hope we have shown that restoration is vital to maintaining biological diversity, to adaptation and mitigation in the face of climate change and desertification, and to improving the quality of ecosystem services to the benefit of human welfare across the globe. We would like to conclude with an account of an exemplary project that illustrates the capacity and potential of restoration to achieve these goals when a collaborative approach is taken by a transdisciplinary team of scientists, professionals and volunteers, working in conjunction with local communities and landowners. In Box 22.2, we introduce an excellent example of this kind of interaction, within a large-scale restoration programme addressing the subtropical thicket biome in South Africa. We think this project represents an example of a *modus operandi* that should be applied, adapted and tested in many countries in coming years.

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Box 22.2 Investing in sustainability: a long-term, large-scale restoration project in South Africa (based on Mills & Cowling 2006; Mills *et al*. 2007, 2010)

Subtropical succulent thicket, comprising a very diverse and forest-like formation with the characteristic tree or shrub spekboom (*Portulacaria afra*) as a key species, is a type of vegetation unique to the south-western part of the Eastern Cape province of South Africa. This vegetation is rich in trees, shrubs, vines and many other forms of plants, with a rich fauna as well. It formerly covered an area of close to 1.4 million hectares (Lechmere-Oertel *et al*. 2005), but after a century of over-exploitation, mainly through injudicious farming with angora goats, only about 200 000 hectares of healthy intact bush remains. Apart from its biodiversity value, the ecosystem services provided are immense. The spekboom thicket protects the soil from erosion and sustains water supply and quality to large human populations. It supports a burgeoning wildlife industry (including elephant and rhino) linked to nature-based tourism, as well as numerous plant and animal species of medicinal and cultural heritage value. It is also a source of many plant species and varieties grown worldwide as ornamentals. Moreover, it is capable of capturing and storing considerable amounts of carbon. These are reasons enough to restore the desertified areas and, happily, the degraded thicket is remarkably amenable to restoration.

Due to the fact that planted cuttings of spekboom readily take root and grow relatively rapidly, a healthy stand of spekboom can be established within several years, at least in areas where it formerly occurred. As the re-established spekboom plants grow and begin to establish the natural vegetation structure of the thicket, other native shrubs, trees and herbaceous plants are able to re-establish and the ecosystem gradually recovers, even without irrigation. There is evidence that some 50 years after the start of restoration, the full complement of thickets shrub and tree species is able to re-establish (van der Vyver *et al*. unpubl. MS).

Restored sites have high potential for earning biodiversity credits. Even more significantly, it is estimated that, on average over a 30-year period, restored sites can capture some 15.4 tons of carbon dioxide per hectare per year. This could be traded for a similar amount of credits on the international carbon market, which should make the restoration entirely self-financing. This is a key condition for sustainability, especially in a developing country like South Africa (Mills *et al*. 2007).

To achieve all these remarkable sustainability targets, deeper involvement by both the public and private sectors is required. They will need to collaborate in order to create the new institutions to convert environmental and climate change challenges into opportunities for development, and to implement the large-scale projects required for sustainable restoration and job creation. The potential is clear, and the principles behind subtropical succulent thicket restoration are a model for other restoration projects around the world, as long as the right case-specific adjustments are made.

Finally, we would like to cite Pavan Sukhdev, Special Advisor and Head of UNEP's Green Economy Initiative, and study leader of the TEEB project (2010, 2011; Chapter 2): 'The greening of economies, including the restoration of degraded ecosystems, is not and should not be considered as a burden on economic growth; instead it is a new engine for growth, employment, and the reduction of persistent poverty.' In that same vein, we here affirm that the ecological restoration of degraded ecosystems is a core element in society's progress along the path away from profligacy, and towards prudence, justice and sustainability. We invite our readers to join the effort to bring this vision a little bit closer to reality in the coming years.

ACKNOWLEDGEMENTS

We are very grateful indeed to Paddy Woodworth for his edits, comments and tough questions on three previous versions of this chapter. We also thank Richard Cowling for checking and improving Box 22.2.

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GLOSSARY

> Nomina si nescis, perit et cognition rerum.
> (If you do not know the names of things, the very knowledge of them disappears.)
> Carl Linnaeus, *Philosophia Botanica* (1751)

> The first step to wisdom . . . is getting things by their right names.
> E.O. Wilson (1998, p. 4)

The following definitions pertain to their usage in this book. Some terms may have broader or additional definitions that are not listed. Terms in italics in a glossary definition are also defined elsewhere in the glossary. References to chapters can be found via the subject index.

Abandonment Temporary or permanent interruption of previous management regime of a natural, seminatural or, more often, an agricultural or other production system; generally induces a *succession* of the vegetation.

Acidification A process that results in a lowering of pH values of a volume of soil or body of water, which may be caused by natural decalcification due to rainfall or by human-induced 'acid rain'.

Adaptation Processes by which an organism or human society adjusts to its biophysical environment so as to reproduce more or live longer and better. Adaptations of populations are genetic responses to natural selection.

Adaptive management An approach to management that encourages periodic changes in management objectives and protocols as needed, in response to monitoring data and other new information.

Afforestation The planting of open land (land that has been non-*forest* or *woodland* for 25 years or more) with trees, whether *native* or non-native. See also *reforestation*.

Alien species – See *exotic species.*

Alternative stable states Alternative combinations of *ecosystem* steady states and environmental conditions that may persist at particular spatial and temporal scales. A principle thesis of alternative state models is that the system can shift abruptly between two or more states, due to positive feedback mechanisms that operate when a system crosses a *threshold*. See Suding *et al*. (2004) for discussion of the consequences for restoration ecology.

Anthropocene Era A term coined by Paul Crutzen (2002) to characterize the massive human impact on the environment since the beginning of the Industrial Revolution, circa 1784, that also accelerated the global process of urbanization.

Arcadian landscape – See *seminatural landscape.*

Assembly rules A set of principles or laws that predict the development of specific biological *communities*, in contrast to development that is attributable to random processes. Assembly rules identify environmental filters for the dispersal and establishment of species, followed by local species interactions, thus restricting the realm of permissible species combinations that are likely to assemble from a larger regional pool of potential contributor species (Weiher & Keddy 1999; Temperton *et al*. 2004). See also *species pool*.

Assisted migration (synonyms: managed relocation, assisted colonization) A new – and highly controversial – conservation tool or strategy to move species or ecotypes upslope or 'poleward' (i.e. northward in the northern hemisphere, and southward in the southern hemisphere) to conserve and protect *biodiversity* in the face of anthropogenic *climate change* in general, and global warming in

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particular (see Hunter 2007; McLachlan *et al.* 2007; Hoegh-Guldberg *et al.* 2008; Ricciardi & Simberloff 2008).

Assisted natural regeneration A more precise term for *passive restoration*. A set of *interventions* that aim to promote natural regeneration or recovery of an *ecosystem*, such as the *reintroduction* of native fauna that will disperse seeds, or controlling grazing by domestic herbivores, and/or the control of *exotic invasives*.

Biodiversity The diversity of life at all levels of organization (genetic, individual, population and community) and all taxonomic ranks (e.g. species, genus and family) at a specified location or in general, in the biosphere. Note that this differs slightly from the widely cited CBD definition, 'the variability among living organisms from all sources including (. . .) terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems' (http://www.cbd.int/convention/articles.shtml?a=cbd-02). Following both the MA and the TEEB initiative (MA 2005; TEEB 2010), it is useful to distinguish clearly between *biodiversity* and *ecosystem*, and then combine them under the term (renewable) *natural capital*.

Biomanipulation The restoration of a food chain or of the main elements of a food web. For example, lakes and reservoirs can be treated to reduce nutrients following *eutrophication* (Kasprzak *et al.* 2002). This is also widely used in fisheries and *invasive species* management where the goals may or may not be consistent with restoration to some 'former' or more 'pristine' condition but instead may be targeting desired species.

Biome A broad-scale grouping of areas of similar climate and associated vegetation, generally within a given geographic region. Examples are tropical rain forest, savanna, desert and tundra.

Biotic community The assemblage of all the species (biota) living together in an *ecosystem*. See also *community*.

Capital A stock variable with five principal forms (Rees 1995; MA 2005), namely, (1) financial capital (i.e. money or substitutes), (2) manufactured capital (i.e. buildings, roads and other human-produced fixed assets), (3) human capital (i.e. individual or collective efforts and intellectual skills), (4) social capital (i.e. institutions, relationships, social networks, and shared cultural beliefs and traditions that promote mutual trust) and (5) *natural capital*, which is an economic metaphor for the stock of physical and biological natural elements some but not all of which serve as resources for society.

Carbon sequestration The capture and storage of carbon in sinks such as *forests*, soils, ocean sediments and wood products. In some contexts, long-term carbon storage is a preferable term.

Chaos theory A term used in mathematics to describe the behaviour of certain systems that are highly sensitive to initial conditions (popularly referred to as the 'butterfly effect'). The behaviour of chaotic systems may seem random, but as soon as the initial conditions are known, it can often be explained deterministically. Chaotic behaviour of this sort is also observed in natural and in social systems.

Climate change (or anthropogenic climate change) Changes in global temperature and precipitation patterns that are largely attributable to increasing atmospheric concentrations of carbon dioxide and other so-called greenhouse gases since the mid-nineteenth century.

Community Specific parts of a *biotic community* are – according to the group of organisms under investigation – indicated as, for example, plant community, insect community and community of microorganisms. The term community is also used in studies on, for example, plant–insect or plant–herbivore–predator interactions between species that do not necessarily belong to one *biotic community*.

Connectivity The degree to which a *landscape* facilitates or impedes movement or organisms among *habitat* patches. This also depends on the dispersal abilities of a species.

Cultural landscape A *landscape* that has developed under the joint influence of natural processes and human-imposed organization and resource use. Generally, the human *ecological footprint* is much more readily apparent than in other kinds of landscapes. Typically *seminatural ecosystems* juxtapose *production systems* in a static or moving mosaic.

Degradation The simplification and loss of *biodiversity* in an *ecosystem* caused by *disturbance factors*. Different 'degrees of ecosystem degradation' can be distinguished, depending on whether or not one or more *thresholds of irreversibility* have been crossed. In cases of severe and prolonged ecosystem *disturbance*, natural ecosystem recovery is sometimes no

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longer possible in a relevant or 'reasonable' period of time. Degradation, resulting from various factors, including *climate change* and extreme events, as well as human activities, generally reduces flows of *ecosystem goods and services*.

Desertification *Degradation* of land in arid, semi-arid and dry subhumid zones resulting from the impact of various *disturbance factors*, including climate disruptions and human activities. This degradation is expressed in the deterioration of plant cover, impaired soils and reduced availability of water. At the scale of a human life, it causes diminution or destruction of the biological potential of lands and their capacity to support resident populations of people and other living organisms.

Designer ecosystem An *ecosystem* without analogues that is intentionally created to achieve *mitigation*, conservation of an *endangered species* or other management goals (MacMahon & Holl 2001). Differs from *emerging ecosystems* and *novel ecosystems*, which are not planned but instead arise spontaneously.

Disturbance A significant and often irreversible change in environmental conditions, population size, community composition and/or the magnitude and direction of some ecosystem-level process – typically by reducing numbers of individuals, species or *habitat*. Can be caused by natural or human-induced *disturbance factors*. Some authors use 'perturbation' but we avoid the term in this book.

Disturbance factor Natural or human-mediated event or activity that changes the structure, content and/or function of an *ecosystem*. The ecosystem may either return to the previous steady state (*resistance* or *resilience*) or not (*disturbance*).

Ecohydrology The science that studies hydrodynamics, and more specifically the study of gains, retention, losses and recycling of water is called '*hydrology*'. The term 'ecohydrology' is commonly used to indicate the study of the relations between plant communities and landscape-scale hydrodynamics, an aspect of *landscape* ecology.

Ecological economics 'The union of economics and ecology, with the economy conceived as a subsystem of the Earth ecosystem that is sustained by a metabolic flow or throughput from and back to the larger system' (Daly & Farley 2010). Not to be confused with *environmental economics*.

Ecological footprint A concept and calculation method developed and launched by Wackernagel and Rees (1996) to analyse and compare human impact on nature with respect to the biosphere's ability to regenerate resources and provide services. The total 'footprint' for a designated entity is measured in terms of 'global hectares' of biologically productive space with an annual productivity equal to the world average. Can be used to evaluate a corporation, an installation (e.g. a mine or an airport) or a human individual or population's impact on ecosystems of the global environment, but should not be used too liberally. Often 'environmental impact' or 'ecological impact' is a better term to use for scientific discussions. However, ecological footprint is a metaphor that has captured the attention of the entire world and thus has great value for communication.

Ecological function – See *ecosystem function*.

Ecological indicator – See *indicator*.

Ecological rehabilitation – See *rehabilitation*.

Ecological restoration 'The process of assisting the recovery of an *ecosystem* that has been degraded, damaged, or destroyed' (SER 2004). Note that the term is often used, in a very broad and rather vague way, to mean returning a site or a system to 'pre-disturbance conditions'.

Ecological structure – See *ecosystem structure*.

Ecology The study of the interactions between organisms and their environment, which includes the physical environment (temperature regime, water availability, etc.) and any influences on an organism exerted by other organisms – the biotic environment. The science of ecology covers a wide range of spatial scales, organizational levels and phenomena, moving from an individual molecule to the entire global ecosystem.

Ecosystem The system of relationships and interactions among living organisms (plants, animals and microorganisms), and the abiotic (nonliving) environment, such as soil, water and air, at a specified location. Ecosystems occur at different spatial scales, from a small pond, for example, to a whole *landscape*. In principle, or metaphorically, one can even speak of the Earth or the biosphere as a single ecosystem.

Ecosystem engineers Organisms other than humans – beavers, for example, and elephants and earthworms – that cause physical and/or chemical state changes in their environments and affect availability of resources to other species (Jones *et al.* 1994; Lavelle 1997). Rosemond and Anderson (2003) urge greater use of nonhuman 'ecological

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engineers' as helpers and even as role models in ecological design, *adaptive ecosystem management* and *restoration* and *rehabilitation* of degraded ecosystems. (See also the work of H.T. Odum and his students, many of whom have made great contributions to *ecological economics*, restoration and engineering.)

Ecosystem function (Ecosystem functioning) The rate of *ecosystem processes* such as primary production, decomposition, nutrient cycling and transpiration and emergent properties resulting from species interactions such as competition, seed dispersal carried out by animals, and mutualistic relationships. Not to be confused with ecosystem services. Functions, or functionality, depend on underlying *ecosystem structure* and *ecosystem processes* and represent the potential that ecosystems deliver *ecosystem goods and services* to humans.

Ecosystem goods and services (EGS) The Economics of Ecosystems and Biodiversity (TEEB) initiative defines ecosystem services as 'the direct and indirect contributions of ecosystems to *human well-being*' (de Groot *et al.* 2010). Often the term ecosystem services (ES) is used as shorthand for EGS. They are made possible thanks to *ecosystem functions* and the still deeper *ecosystem processes* and *structure*. An alternative, and simpler, definition is that ecosystem services are the transformation of a set of natural assets (soil, plants and animals, air and water) into things that people value (http://www.ecosystemservicesproject.org). However, the use of the word 'assets' here is problematic as it can lead readers to conclude that using the term EGS automatically leads to a commodification of nature. The Millennium Ecosystem Assessment (MA 2005) recognized four categories of EGS, namely, supporting (e.g. *carbon sequestration*), regulating (e.g. *erosion* control), provisioning (e.g. of clean water) and cultural (e.g. spiritual and recreational needs).

Ecosystem health The state or condition of an *ecosystem* in which its dynamic attributes are expressed within normal ranges of activity relative to its ecological stage of development (SER 2004). This metaphor may also include socio-economic values, such as the function of a river system as a source of clean water for human consumption (see Costanza *et al.* 1992).

Ecosystem integrity The state or condition of an *ecosystem* that displays the *biodiversity* characteristics of a *reference system*, expressed in terms of species composition and community structure (SER 2004), or an historical range of variability. Basically a metaphor, or umbrella term, like *ecosystem health*, and not to be confused with an attribute that can be easily measured or monitored individually. Cf. *ecosystem stability*.

Ecosystem processes The underlying processes of an *ecosystem*, such as energy transfer, primary production, food chain dynamics, hydrological pathways and nutrient cycling. Inextricably linked with *ecosystem structure*, but not synonymous with *ecosystem functioning*. See also de Groot *et al.* (2010).

Ecosystem restoration – See *ecological restoration*.

Ecosystem stability The ability of an *ecosystem* to maintain its given state or *trajectory* in spite of stress; it denotes dynamic equilibrium rather than stasis. Stability is achieved in part on the basis of an *ecosystem*'s capacity for *resistance* and *resilience* (SER 2004). Cf. *ecosystem health*, *ecosystem integrity*.

Ecosystem structure The individuals and communities of plants, animals and microorganisms of which an *ecosystem* is composed, their age and spatial distribution and the abiotic resources present at a certain point in time. The elements of ecosystem structure and fundamental *ecosystem processes* interact to create *ecosystem functions* as emergent properties which in turn create the potential for the flow of *ecosystem goods and services* to human society.

Emerging ecosystem An *ecosystem* that is on the way to becoming significantly different from what it was before due to ongoing and often unpredictable environmental changes, caused by natural, social, economic and cultural drivers and impacts. See Milton *et al.* (2003) and van Andel and Aronson (2006, chapter 16). Cf. *designer ecosystem, novel ecosystem.*

Endangered species Biological species considered to be in danger of extinction.

Environmental economics Branch of neoclassical economics that addresses environment issues such as pollution as externalities and seeks to value *ecosystem goods and services* with market values. In general, focuses on the efficient allocation of resources and often fails to recognize the market as a subsystem of 'the containing and sustaining global ecosystem' (Daly & Farley 2010). Cf. *ecological economics*.

Environmental gradient A local or regional change in environmental conditions, for example moisture, elevation, altitude or soil type. The gradient can be narrow or diffuse, and is often expressed in the *zonation* of a *community*.

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Environmental services – See *ecosystem goods and services*.

Eradication Removal of *invasive exotic species* with the intent of *extirpating* their populations completely from a certain locality.

Erosion Removal of soil by action of wind, water, and gravity. See also *runoff*.

Eutrophication Nutrient enrichment of a volume of soil or body of water, commonly by human activity.

Exotic species (synonyms: non-native, non-indigenous, foreign, *alien species*) A species that originates in another region than the one in which it now occurs. Antonym of *native species*. Can refer to cultivated ornamental or crop species, naturalized weeds or *invasive aliens*. Often the determination of what is native versus non-native is highly subjective and not scientific.

Extirpation Removal of *invasive species* with the intention of completely eliminating the populations of that species from a given area or locality.

Forest A *vegetation type* (and the associated *biotic community*) characterized by a dense growth of trees, plants and underbrush covering a large area. NB: There are more than 250 definitions for this term, and misunderstandings about it are common. 'Primary forests' consist of *native species* that developed without clearly visible indications of human influence. 'Secondary forests' regenerate largely through natural processes following significant *degradation* or damage and display obvious differences in forest structure and/or composition with respect to primary forest on similar sites.

Foundation species (synonym: *framework species*) A single species that contributes substantially to *community* structure on account of its life form and abundance, promotes locally stable conditions for other species and modulates and stabilizes fundamental *ecosystem processes* (Ellison *et al*. 2005). Cf. *keystone species.*

Fragmentation The separation of a formerly continuous natural area into smaller natural units that are isolated from each other by lands or *wetlands* that were converted for economic production or the development of infrastructure such as road building. In the restoration ecology literature, one can find the term 'landscape fragmentation' (see Hobbs & Saunders 1992; Aronson & Le Floc'h 1996; Hobbs 2002) and the notion of reintegration, applied to efforts to rehabilitate and revitalize whole *landscapes* that have become fragmented, both ecologically and socio-economically. In this book, we use the term in the sense of *habitat fragmentation*, with a focus on species.

Framework species – See *foundation species.*

Functional group Those species that have a common set of attributes and play a particular role in *ecosystem processes*. Examples are nitrogen-fixing plant species or microbe-feeding nematodes. When the species rely on a similar set of resources, functional groups are also called guilds. See for example Wardle *et al*. (2003).

Geomorphology The study of the physical features of the surface of the Earth and their relation to its geological structures.

Grassland *A vegetation type* (and the associated *biotic community*) dominated by grass or grass-like vegetation. Found in tropical, subtropical, temperate and alpine regions and, apart from deforested areas, typically occupy regions between forests and deserts (e.g. savanna grasslands) or glaciers (e.g. tundra). A grassland can be natural, seminatural or managed for production.

Habitat The physical or potential living space of an organism or a population of a species, characterized by its particular environmental properties.

Habitat fragmentation The breaking up of a formerly continuous living space (*habitat*) or geographical range of a species population into smaller units, resulting in a *metapopulation* or in reproductively separated local populations.

Heathland A *vegetation type* (and the associated *biotic community*) found on poor, acid, sandy soils, and dominated by low shrubs, often of the heather family (Ericaceae), but also gorse, bracken fern, and other plants. May also contain scattered trees and tall shrubs as well as occasional bogs, *grasslands* or open patches.

Helophyte filter A vegetation of productive reed species, such as *Phragmites australis* or *Typha latifolia*, that can efficiently remove nutrients from surface water that traverses the site.

Heterogeneity Used to describe habitat complexity (technically the spatial arrangement of patches), habitat diversity (the number of types of habitats in an area) or even environmental variability within a *habitat* over time. It is believed to be a major driver of restoration success in many *ecosystem* types, as it potentially increases *biodiversity*.

Human well-being A condition in which members of a human society are able to determine and meet their needs and reach their potentials.

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Hydrology – See *ecohydrology*.

Hysteresis Due to myriad internal and external factors, the route to recovery or restoration of an ecosystem often takes much longer than, and differs from, the initial route of *degradation*. This discrepancy is called hysteresis.

Indicator (ecological indicator) Variables that can be readily identified, and are relatively easy to measure or monitor and that serve as synthetic representatives or signals of changes in ecological or environmental conditions (Dale & Beyeler 2001). For example, characteristic species or species combinations can be used as a sign of *ecosystem health* or *degradation*, and are also applicable to evaluate the success of *ecological restoration*.

Indigenous species – See *native species*.

Intervention A specific action or intentional strategy that will bring about an action, such as site preparation, *invasive species* removal, desirable species *reintroductions*, *biomanipulation*, altering canopy structure or reintroducing fire.

Invasive species A non-native or *alien species* that has become naturalized in an area, and whose distribution, reproduction and spread are no longer restrained by soil parameters, natural predators and so on and thus rapidly expand its distribution and abundance regardless of *habitat* (Pyšek 1995; Richardson *et al*. 2000). If this process threatens *ecosystems*, *habitats* or humans, domesticated species or wild species with health-related, economic or environmental harm, the species can be called noxious, as noted under Article 8(h) of the Convention on Biological Diversity (http://www.cbd.int/convention). In contrast, a *native species* whose distribution and/or abundance in the wild is increasing should be described simply as increasing, colonizing or spreading, not as invading.

Keystone species A species that has a substantially greater influence on other species in the food web of an ecosystem than would be predicted by its abundance or size (Paine 1966). Cf. *foundation species.*

Lake biomanipulation – See *biomanipulation*.

Landscape Many acceptable definitions exist for this concept. Here we use the ecological definition, namely an assemblage of *ecosystems* that are arranged in recognizable patterns and that exchange organisms and materials such as nutrients and water (Forman & Godron 1986). Today, most landscapes are mosaics of interacting systems that may be natural or *seminatural ecosystems*, *production systems* and spaces or landscape units managed for social and economic use without any specific systems thinking. The size of the landscape in a given restoration project is determined mostly by the scale of the restoration initiative, and the likely or hoped-for geographic extent of its impacts (see Rietbergen-McCracken *et al*. 2008). See also *cultural landscape*.

Livelihood The capabilities, assets (stores, resources, claims and access) and activities required for a means of earning a living. A livelihood is sustainable when it can cope with and recover from stress and shocks, maintain and enhance its capabilities and assets, provide sustainable livelihood opportunities for the next generation, and contribute net benefits to other livelihoods at the local and global levels in the long and short terms.

Local adaptation Process by which populations differentiate genetically in response to selective pressure acting on their respective *habitats*.

Local Ecological Knowledge (LEK) (synonym: local environmental knowledge) Useful knowledge about species and *ecosystems* gathered by people who live in rural *landscapes* and manage their land to minimize detrimental impacts. See also *Traditional Ecological Knowledge*.

Metapopulation A set of interacting local populations of a plant or animal species within a larger area of space, with long-term survival of the species depending on a shifting balance between local extinctions and recolonizations in the patchwork of an heterogeneous *landscape* or *habitat* (cf. Hanski 1999). More simply, they are assemblages of local populations connected by mutually dispersing individuals in a network of *habitat* patches.

Mires Peatlands where peat is currently being formed (Joosten & Clarke 2002).

Mitigation Compensation in terms of enhancement of an *ecosystem function*, *rehabilitation*, *ecological restoration* and so on that is required by government agencies, or international treaties and agreements, for permission to undertake or continue development projects, or other economic activities (e.g. fossil fuel extraction or refinement, the manufacture of cement or high-speed travel) that cause significant environmental harm.

Native species (synonym: *indigenous species*) Biological species that evolved in a specified region, or that arrived there before the beginning of the Neolithic period (Pyšek 1995), or that arrived there

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since that time by a method entirely independent of human activity (Cowling *et al*. 1997). In practice, these terms are often used arbitrarily or subjectively, as are the terms *alien species* and *invasive species*. Further complexity arises when subspecific variation is considered.

Natural capital An economic metaphor for the limited stocks of physical and biological natural elements found on Earth, some of which are of direct use to society (then called resources) and some of which are not. According to Rees (1995) and MA (2005), there are four, partially overlapping types: renewable (living species and ecosystems), non-renewable (subsoil assets, e.g. petroleum, coal and diamonds), replenishable (e.g. the atmosphere, potable water and fertile soils) and cultivated (e.g. crops and forest plantations). Natural capital provides the basis for all life. Following on with the metaphor, if natural capital is a stock or an asset, then the 'dividend' is the flow in *ecosystem goods and services* derived from the assets, for example from renewable natural capital, called *ecosystems* and *biodiversity*, and from cultivated natural capital, such as that found in agroecosystems and other types of *production systems*. But the concept of renewable natural capital as an asset does include all elements of ecosystems, not just the obviously marketable bits and pieces.

Natural goods and services – See *ecosystem goods and services*.

Novel ecosystem (synonym: no-analogue ecosystem) An *ecosystem* without analogues that has developed in response to radically altered environmental and biotic conditions resulting from human activities in the past century or two (after Hobbs *et al*. 2006); cf. Seastedt *et al*. (2008) and Hobbs *et al.* (2009). Cf. *emerging ecosystem*, *designer ecosystem*.

Passive restoration A term used by many authors to indicate the autonomous or autogenic recovery of a degraded ecosystem by means of the unassisted processes of *resilience*, *succession* or natural regeneration. A more precise and evocative term is *assisted natural regeneration* (cf. Clewell & McDonald 2009).

Potential natural vegetation (PNV) An image or notion of the vegetation type that would theoretically arise in an area if all direct human influences were removed. This is not necessarily the 'original' or 'pre-disturbance' vegetation, since the biophysical environment and climate may have been altered. PNV is useful as an expression of the environmental site conditions *per se* at a certain point in time (cf. Tüxen 1956).

Primary forest – See *forest.*

Production system Land or *landscape* unit, or seascape unit, allocated to the production of food, fiber, pasturage, aquaculture and other marketable commodities or subsistence items, and which is usually maintained with external inputs of energy (e.g. fossil fuels) and materials (e.g. lime and agrichemicals). Notable exceptions are agroforestry systems found in some *woodlands* of the Mediterranean region, and in some parts of Indonesia and other tropical *forest* regions.

Propagule Seed, fruit, egg or detachable part of a plant that serves as the source of new individuals.

Provenance The geographic place of origin of plants or animals, or source of seeds or other *propagules*, used for experiments or for *reintroductions*.

Reclamation Conversion of portions of land, *wetland* or shallow seas, which are perceived as being unutilizable, to a productive condition, commonly for agriculture, aquaculture or silviculture. Is sometimes erroneously used as a synonym for *rehabilitation*, particularly with respect to mine sites (NRC 1974; Whisenant 1999).

Reference ecosystem (or reference model) One or more natural or seminatural *ecosystems*, ecological descriptions thereof, or, if these are unavailable, assemblages of characteristics of presumed natural or historic seminatural ecosystems which are chosen to serve as models, benchmarks or targets for planning in *ecological restoration* and *rehabilitation* projects (White & Walker 1997; Egan & Howell 2001; SER 2004). .

Reforestation The re-establishment of forest on recently forested or wooded land that was recently cleared, using *native* or non-native *species* by means of artificial, natural or assisted natural regeneration techniques. See also *afforestation* and *revegetation*.

Rehabilitation The improvement of functionality of an ecosystem, especially a seminatural one, without necessarily achieving a return to 'pre-disturbance' conditions. Commonly undertaken in *cultural landscape* settings. Emphasis is generally on restoring *ecosystem processes* and *functions* so as to increase the flow of services and benefits to people (SER 2004; Clewell & Aronson 2007). Care must be paid not to so heavily favour one process or function with the result of rendering the *ecosystem* more fragile or vulnerable than it was before. However,

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when returning an ecosystem to a former 'pre-disturbance' state or *trajectory* is not possible, or desirable, rehabilitation is often the best option.

Reinforcement The process of strengthening a small and vulnerable population of a plant or animal species in situ. Cf. *reintroduction.*

Reintroduction The intentional introduction of a plant or animal species in an *ecosystem* from which it has been extirpated or in areas where it is considered threatened or vulnerable. Cf. *reinforcement.*

Resilience There are many different definitions of 'resilience' (see e.g. Gunderson 2000). In this book, we follow Hollings (1973): resilience is the capacity of an ecosystem to tolerate a *disturbance factor* and recover autonomously by natural regeneration without collapsing or shifting into a qualitatively different state controlled by a different set of processes. Westman (1978) offered a simpler definition which is also relevant to restoration: the ability of an ecosystem to recover from *disturbance* (or better: *degradation*) without human intervention. This is sometimes called '*ecological resilience*'. Other authors (e.g. Pimm 1991) have put emphasis on another aspect of resilience, that is, the return time to the previous steady state, currently called 'engineering resilience'. According to an alternative definition (see Brand & Jax 2007) that more or less subsumes the notion of *resistance* (*sensu* Westman 1978), a resilient ecosystem can withstand shocks and rebuild itself, or persist on a given developmental trajectory or within a given configuration of states (sometimes called a regime) in systems where multiple regimes are possible (Walker & Salt 2006). Resilience in social or *socio-ecological systems* depends in large part on the capacity of humans to anticipate and plan intelligently for the future.

Resistance The capacity of an *ecosystem* to maintain its steady state in response to one or more *disturbance factors*.

Restoration – See *ecological restoration.*

Restoration ecology The study of ecological restoration, for which practice it attempts to provide concepts, theories, models, methodologies and technical, biological and ecological information for use by practitioners. Concurrently, the science that advances the frontiers of theoretical ecology through studies of restored *ecosystems* and those that are undergoing restoration.

Restoration of Natural Capital (RNC) Investment in *natural capital* stocks to improve the *sustainability* of both natural and human-managed ecosystems, while contributing to the socio-economic well-being of people (see *human well-being*). Renewable, replenishable and cultivated natural capital delivers *ecosystems goods and services*; RNC is required when delivery is interrupted or impeded. RNC includes the *ecological restoration* or *rehabilitation* of *ecosystems*, ecologically sound improvements to *production systems*, ecologically sound improvements in the extraction, transport, processing and utilization of biological resources, or nonrenewable natural capital, and efforts to increase public awareness and appreciation of the importance of *natural capital*.

Revegetation Establishment of plant cover on open land, often with one or few species, irrespective of their origin or *provenance*. See also *reforestation*.

Runoff Rainfall or other water that moves towards lower elevations by spreading across the land surface, rather than flowing within a defined channel, or percolating into the soil. See also *erosion*.

Run-on Rainfall or other water that flows unchannelized over the land surface from *runoff* elsewhere. Usually run-on sites are much smaller than runoff areas.

Secondary forest – See *forest*.

Seed bank The stock of viable seeds, spores and other plant *propagules* in the soil. The longevity of a seed bank may be between one or a few years to several decades or more depending on the *vegetation type* and its composition.

Seminatural ecosystem An ecosystem, often part of a *seminatural landscape*, that is extensively managed with the aim to assure the conservation of the biotic community (and the associated environmental conditions) characteristic of the *cultural landscapes* of the early twentieth century in Europe, before the introduction of artificial fertilizers.

Seminatural landscape (synonymous with *Arcadian landscape*) Seminatural managed or protected natural areas, and extensively used *cultural landscapes*, wherein, when well-managed, *biodiversity* is enhanced while also assuring maintenance of *production systems* providing goods and services to people (cf. Swart *et al.* 2001). See also *seminatural ecosystem*.

Shrubland A *vegetation type* (and the associated *biotic community*), that is limited in stature to roughly (1–)2–4(–8) m in height. Examples include the mallee of southern Australia, matorral of central

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Chile, fynbos of South Africa and chaparral of California. In the mediterranean basin, numerous shrublands occur (garrigue, machia, phyrgana, tomillares etc.), but there is much debate as to the differences among them, and concerning the possible anthropogenic origins thereof. Some shrublands are clearly derived from *woodlands*.

Socio-ecological system An ecological system largely dominated by humans, or in which cultural activities are thoroughly integrated. It typically consists of a mixture of natural ecosystems, *seminatural ecosystems* as well as *production systems*, and land or *wetlands* allocated to residences, other buildings, transport networks and so on all of which are functionally interrelated at least in socio-economic terms. More succinctly, an *ecosystem*, the management of this ecosystem by actors and organizations, and the rules, social norms, and conventions underlying this management (MA 2005).

Species pool The overall number of biological species in a biogeographic or climatic region (regional species pool), a *landscape* (local species pool) or a specific *ecosystem* (community species pool). See also *assembly rules*.

Stakeholder Any individual or group directly or indirectly affected by, or interested in, actions pertaining to a given resource.

Succession Sequence of stages in an *ecosystem*'s structure, species composition and functionality as the system develops over time, or recovers from the impact of a *disturbance factor*.

Sustainability In an economic context, the capacity of a system to remain productive indefinitely for the benefit of future generations (cf. *sustainable development*). Principles or 'rules' of sustainability are (1) stocks of renewable resources must not be used faster than they are renewed, (2) waste emissions must not exceed waste absorption capacity and (3) essential nonrenewable resources cannot be depleted any faster than technology develops renewable substitutes (Daly 1990). It is increasingly recognized that sustainability includes economic, social, ecological and environmental components (see *sustainability science*). From an individual or citizen perspective, it depends on all people in a community living responsibly, ethically and in an environmentally conscious fashion.

Sustainability science An integrated scientific approach to investigate economic sustainability (see *sustainable development*), social sustainability (*resilience* and shared awareness of responsibility of social networks and cultural systems towards future generations) and environmental sustainability (*resilience* of *ecosystems*) (Kates *et al.* 2001; Clark & Dickson 2003).

Sustainable development Economic development that meets the needs of the present generation without compromising the ability of future generations to meet their own needs (Brundtland Commission 1987).

Threshold A point in a *trajectory* beyond which a system changes dramatically (sometimes referred to as a state change). Increasingly, managers, and management communities, are seeking to identify critical thresholds (e.g. in water quality) beyond which it is difficult to restore an ecological system without major *interventions*. *Ecological economics* teaches not to allow systems upon which society depends to even approach critical thresholds of this kind. Restorationists need to identify thresholds beyond which *ecosystems* undergoing restoration can self-restore without further intervention.

Threshold of irreversibility A degree of impairment to an *ecosystem* which, when it is surpassed, is too severe to allow recovery of that ecosystem to its former, intact state by unassisted *succession*. The ecosystem is *disturbed* and *ecological restoration* will be required.

Traditional Ecological Knowledge (TEK) Ecological knowledge derived through societal experiences and perceptions accumulated within traditional societies during their interaction with nature and natural resources. See also *Local Ecological Knowledge*.

Trajectory The sequence of biotic expressions along a developmental pathway of an individual *ecosystem* over time. In restoration ecology, the trajectory begins with the unrestored ecosystem and progresses towards the desired state of recovery that is expressed in the goals of a restoration project and embodied in the ecological *reference system*. The trajectory embraces all ecological attributes – biotic and abiotic – of an ecosystem, and in theory can be monitored by the sequential measurement of coherent suites of ecological *indicators* (SER 2004).

Transdisciplinarity refers to science and problem-solving activities wherein scientists and professionals from various backgrounds work together to transcend their disciplinary habits and preconceptions. They may also engage actively with nonscientists

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and indeed with all relevant *stakeholders* and actors on a site or a project. Examples include *ecological economics*, *restoration ecology* and *sustainability science*. Similar concepts are expressed by the academic terms 'post-normal science', 'mode 2 knowledge', 'integration and implementation sciences' or 'interdisciplinary problem solving' (Kueffer *et al.* 2010).

Transhumance Transfer of domestic livestock from one grazing ground to another, as from lowlands to highlands, with the changing of seasons.

Translocation The process of collecting genotypes offsite for planting or release at a project site within the natural range of the target species (Morrison 2009). See also *reintroduction*.

Vegetation type A broad classification of vegetation based mainly on appearance, predominance of certain growth forms, characteristic plant species composition and/or functional or dynamic characteristics. Examples are *shrubland*, *woodland* or *grassland*, which can also be studied as entire *ecosystems*

Wetland Land which is transitional between terrestrial and aquatic systems where the water table is usually at or near the surface; lands that are sometimes or always covered by shallow water, or have saturated soils long enough to support plants adapted for life in wet conditions.

Wilderness Self-regulating nature with little or no human influence (Swart *et al.* 2001).

Woodland A *vegetation type* (and the associated *biotic community*) dominated by broad-leaved trees but with a lower tree density (or canopy projection) than *forests*. Typically, the open areas between trees bear grasses, forbs, and shrubs unless they are removed by plowing, burning, or overgrazing. 'Dehesas', in Spanish, also called 'montados' in Portuguese, are a type of anthropogenic woodland or savanna whose origin is tied to human use and activities. Savannas are a particular type of interface between *grassland* and open *woodland*.

Zonation On the local and regional scale, biological communities vary as the individual species respond to *environmental gradients*. Examples are gradients in moisture, altitude and soil type. The associated type of *community* variation is known as zonation.

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