Foundations of Restoration Ecology

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Chapter 1

Ecological Theory and Restoration Ecology

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Ecological restoration has been practiced in some form for centuries. For instance, many indigenous peoples tended lands to sustain natural ecosystem services, such as production of basket-weaving materials, food crops, or forage for game animals, and they continue to do so (Stevens 1997). Today, the practice of ecological restoration is receiving immense attention because it offers the hope of recovery from much of the environmental damage inflicted by misuse or mismanagement of the Earth's natural resources, especially by technologically advanced societies (*Economist* 2002; Malakoff 2004).

Strictly speaking, ecological restoration is an attempt to return a system to some historical state, although the difficulty or impossibility of achieving this aim is widely recognized. A more realistic goal may be to move a damaged system to an ecological state that is within some acceptable limits relative to a less disturbed system (Figure 1.1). In this sense of the term, ecological restoration can be viewed as an attempt to recover a natural range of ecosystem composition, structure, and dynamics (Falk 1990; Allen et al. 2002; Palmer et al. 2005). Correspondingly, restoration ecology is the discipline of scientific inquiry dealing with the restoration of ecological systems.

The simplest restorations involve removing a perturbation and allowing the ecosystem to recover via natural ecological processes. For example, a small sewage spill to a large lake might correct itself, if microorganisms can decompose the organic matter and the added nutrients do not trigger algal blooms. Locally extirpated species can recolonize sites as habitat quality improves, and the physical structure of communities can begin to resemble the predisruption condition.

More often, however, restoration requires multiple efforts, because multiple perturbations have pushed ecosystems beyond their ability to recover spontaneously. For example, restoring streams affected by urbanization often requires new stormwater infrastructure to reduce peak flows, followed by channel regrading and riparian plantings (Brown 2000). For coastal marshes that have been dredged for boat traffic, restoration might involve removing fill, recontouring intertidal elevations, amending dredge spoil substrates, and introducing native plants. In some cases, "restoration" *sensu latu* is never finished, as some level of maintenance is always needed (e.g., in wetlands dominated by invasive species). Full restoration means that the ecosystem is once again resilient—it has the capacity to recover from stress (SERI 2002; Walker et al. 2002). Yet it is rarely possible to achieve the self-sustaining state

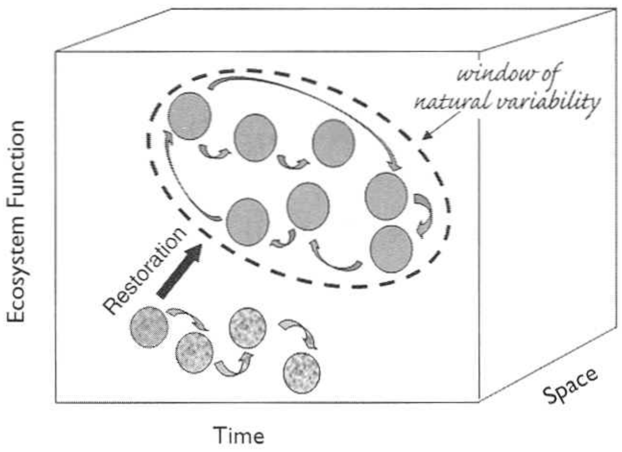


FIGURE 1.1 Ecological systems are highly dynamic entities. Thus, all attributes of natural systems, including levels of ecosystem processes (dark grey spheres), vary over time and space within a natural window of variability (dashed oval line). Restoration should be attempted when the system attribute moves outside that window of natural variability (mottled grey spheres). Once "restored," the system is unlikely to be exactly where it was predisturbance. Although this figure is drawn in three dimensions, the true assessment of both reference and degraded conditions is likely to be multivariate. Illustration motivated by Walker and Boyer (1993).

because degraded ecosystems typically lack natural levels of environmental variability (Baron et al. 2002; Pedroli et al. 2002) and their resilience is no longer recoverable (Suding et al. 2004).

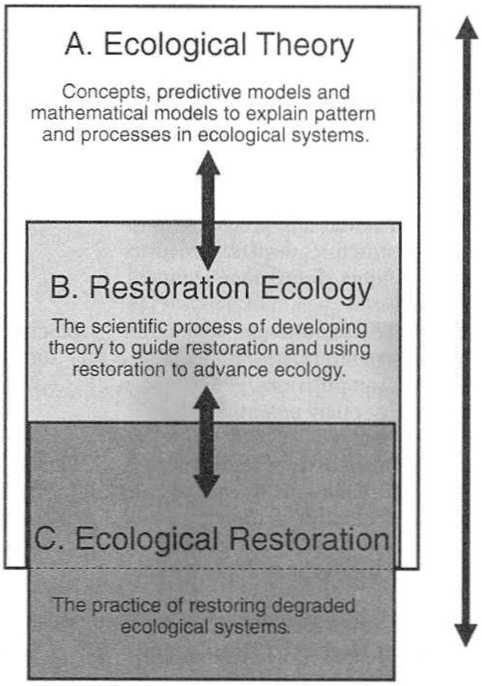
While restoration is sometimes considered an art or a skill that is honed by practice and tutelage (Van Diggelen et al. 2001), science-based restorations are those projects that benefit from the infusion of ecological theory and application of the scientific method. Science-based restorations follow (1) explicitly stated goals, (2) a restoration design informed by ecological knowledge, and (3) quantitative assessment of system responses employing pre- and postrestoration data collection. Restoration becomes adaptive when a fourth step is followed: (4) analysis and application of results to inform subsequent efforts (Zedler and Callaway 2003). Analogous to adaptive management, the corrections that are made to the restoration process should be guided by sound theory and experimentation, not just trial and error.

An unfortunate aspect of ecological restoration as it is commonly practiced today is that the results of most efforts are not easily accessible to others. Despite pleas to report long-term responses (Zedler 2000; Lake 2001), most projects are not monitored postrestoration (NRC 1992; Bernhardt et al. 2005). Informing later efforts is in many ways the most critical element—science, in its simplest form, is the sequential testing of ideas that over time leads to a better understanding of nature.

Ecological Experimentation in a Restoration Context

The focus of this book is the mutual benefit of a stronger connection between ecological theory and the science of restoration ecology. Ecological restoration provides exciting opportunities to conduct large-scale experiments and test basic ecological theory, both of which have the potential to build the science of restoration ecology (Figure 1.2). A fundamental premise of this book is that the relationship of restoration ecology to ecological theory works in both directions: restoration ecology benefits from a stronger grounding in basic theory, while ecological theory benefits from the unique opportunities for experimentation in a restoration context (Palmer et al., 1997). Many examples of this reciprocity are found throughout this book.

Although ecology overall lacks a general unified theory, the field has developed a strong and diverse body of theory addressing nearly every aspect of ecological interactions (Weiner 1995; McPherson and DeStefano 2003). As evidenced throughout the book, this body of theory is highly relevant to both the science of restoration ecology and the practice of ecological restoration (Table 1.1). While ecological restoration has scientific underpinnings, the integration of ecological theory and restoration has been uneven, despite recognition that the practice could be enhanced by such integration (Young et al. 2005).



Concepts, predictive models and mathematical models to explain pattern and processes in ecological systems.

The scientific process of developing theory to guide restoration and using restoration to advance ecology.

The practice of restoring degraded ecological systems.

- Offers opportunities to study ecosystem elements in a manipulative context
- Offers opportunities to test and expand theories that are central to ecology
- Offers opportunities for ecologists to contribute directly to vital restoration efforts worldwide
- Provides an intellectual framework for restoration
- Clarifies multiple interactions that may operate in even a simple restoration project
- Improves the quality and effectiveness of restoration efforts

FIGURE 1.2 The relationship between ecological theory, restoration ecology, and ecological restoration can be viewed in a hierarchical fashion. While there is a very large body of ecological theory (A, unfilled box), only some of it can be directly applied to restoration ecology at the present time (B, grey box). There is thus a demand to extend and develop theory, and the benefits of doing so extend in both directions. Ecological science benefits from the linkage, as does restoration ecology and ecological restoration. There is also a large part of ecological restoration that will never be guided by restoration ecology (C, black box); instead, contextual constraints and societal objectives, such as co-opting natural resources or modifying ecological systems for human use, will determine restoration objectives and potential much of the time.

TABLE 1.1

Broad areas of ecological theory that are foundational to the science of restoration ecology and are covered in the book.

Relevant ecological theory	Examples of ecological restoration questions	Examples of current themes, issues, and models	Contributors
Population and ecological genetics	Which propagule sources and numbers should be introduced?	Bottlenecks and founder events, drift in small populations, locally adapted genotypes, within- and among-population genetic diversity, inbreeding and outbreeding effects, genetic neighborhoods and spatial genetics, effective population size, gene flow	Falk, Richards, Montalvo, and Knapp (*Chapter* 2)
Ecophysiological and functional ecology	What are the potential physiological challenges in the restored environment?	Stress tolerance, physiological limits of survival and reproduction, adaptation to novel environments, phenotypes tolerant of unusual conditions	Ehleringer and Sandquist (*Chapter* 3)
Demography, population dynamics, metapopulation ecology	How can we tell if populations will persist?	Population dynamics, demographic transition matrices, seed dormancy and germination, population persistence and resilience, population spatial structure, age structure and density dependence, dispersal among subpopulations, metapopulation dynamics	Maschinski (*Chapter* 4)
Community ecology	What assemblages will persist in each part of the restored site? In what order should they be introduced?	Community composition, coexistence of species, assembly theory, alternative successional pathways, sensitivity to initial conditions, predation, trophic structure, dispersal, environmental filters, disturbance regimes, mutualism	Menninger and Palmer (*Chapter* 5)
Evolutionary ecology	How will organisms adapt to novel restored environments?	Evolutionary environment, adaptation to novel environments, trait selection, metapopulations, genetic diversity, evolutionary potential, landscape genetics	Stockwell, Kinnison, and Hendry (*Chapter* 6)
Fine-scale heterogeneity	How can sites be modified to enhance diversity?	Spatial heterogeneity of resources and ecosystem functionality, spatial and temporal variation at individual or community level, coexistence of multiple species at multiple spatial scales	Larkin, Vivian-Smith, and Zedler (*Chapter* 7)
Food webs	Do interacting species need to be introduced?	Trophic cascades, bottom-up/top-down dynamics, food-web networks, productivity and food-web structure, plant-herbivore interactions, predator-prey theory, indirect interactions	Vander Zanden, Olden, and Gratton (*Chapter* 8)
Ecological dynamics and trajectories	How will the restored system develop?	Trajectories of ecosystem degradation and recovery, natural variability, linear and nonlinear dynamics, multiple stable states vs. ordered succession, resilience, multiple equilibria, ecological thresholds	Suding and Gross (*Chapter* 9)

TABLE 1.1 *(continued)*

Broad areas of ecological theory that are foundational to the science of restoration ecology and are covered in the book.

Relevant ecological theory	Examples of ecological restoration questions	Examples of current themes, issues, and models	Contributors
Biodiversity and ecosystem functioning	Can a single restoration site maximize species richness and ecosystem functions?	Diversity-stability relationships, functional diversity, functional equivalence, redundancy, interface between community and ecosystem ecology, ecological insurance and ecosystem reliability	Naeem (*Chapter 10*)
Modeling and simulations	How predictable are restoration outcomes?	Stochastic influences on deterministic processes, uncertainty, natural range of variability, spatial interactions, heuristic and simulation models, multivariate statistics	Urban (*Chapter 11*)
Invasive species and community invasibility	How should sites be managed to exclude undesired species?	Properties of invasive species, community invasibility, alteration of ecosystem processes, plant community responses, resistance and resilience, competition, top-down and bottom-up control, disturbance theory	D'Antonio and Chambers (*Chapter 12*)
Research design and statistical analysis	How can we design restoration experiments and analyze the resulting data?	Replication, power analysis, sample size, general statistical framework, time series and repeated measures, chronosequence analysis, multivariate characterization, estimating effect size, BACI designs	Osenberg, Bolker, White, St. Mary, and Shima (*Chapter 13*)
Macroecology	How does the larger spatial context influence an individual restored site?	Large-scale ecological processes, species and population migrations over time and space, ecosystem size and community diversity/structure, cross-system fluxes	Maurer (*Chapter14*)
Paleoecology, climate change	Can restoration be planned within the context of expected global change?	Climatic cycles, climate-vegetation relationships and migration of vegetation, vegetation-climate (dis)equilibrium, natural variability, temporal variation	Millar and Brubaker (*Chapter 15*)

There is also great potential to enhance understanding of the basic structure and function of ecological systems by using restoration settings to develop and test theory (Bradshaw 1987; Jordan et al. 1987; Palmer et al. 1997; Hobbs and Harris 2001; Perrow and Davy 2002). Indeed, restored sites, or those that are soon to be restored, represent virtual playgrounds for asking how well ecological theories can predict the responses of natural systems.

The opportunity to test ecological theory in restoration sites is exciting; at the same time, ecologists and evolutionary biologists are challenged to use theory to devise experiments that can be conducted in restoration settings. We do not think this limits our inquiry to a reductionist paradigm: as with ecology itself, understanding can progress even when formal hypotheses cannot be framed (Pickett et al. 1994). Even more difficult is the challenge of designing experiments that are workable within a project's spatial extent, timing constraints, and resources. Finding suitable sites, receptive managers, interested researchers, appropriate ideas to test, and funding to test them—all at the same time and place—is challenging, but feasible and worth the effort. The payoff for the practice of ecological restoration comes in learning how to improve approaches, how to correct errors, how to accomplish desired outcomes, and how to plan future projects.

Can basic ecological abstractions of nature and mathematical models be used to inform restoration practice, given that ecological responses are often context-dependent? We think so. Every step in the restoration process can be informed by existing ecological theory (Table 1.1); however, every attempt to state predictions from theory also indicates the need to expand theory itself. Thus, we ask: Under what circumstances can we grow the science of restoration ecology using existing ecological theory? What issues or settings require an extension of our theories and models or even the development of theories de novo?

The Imperative to Advance Theory

Experience indicates that restoration follows multiple pathways, which means that outcomes are difficult to predict. Part of the difficulty is that restoration takes place across a multidimensional spectrum of specific sites within various kinds of landscapes, and where goals range from highly specific (e.g., enhance the population of one rare animal species) to general (e.g., encourage vegetation to cover bare substrate). The task of developing theory that offers a high level of predictability is akin to figuring out how to grow myriad crops across a heterogeneous continent. If we consider the centuries it has taken agriculturalists to optimize the crops that farmers should grow in one field in one region (e.g., alternate corn and beans or alfalfa within the cornbelt using specified soil amendments, planting, and harvesting protocols), the difficulty of reproducing entire ecosystems on demand becomes understandable. It could take much longer for the science of restoration to achieve predictable results, because there are more ecosystem types and a wider variety of tools. We assert that these conditions create a great need for guidance from ecological theory. For some ecosystems, ecological theory needs to be melded with physical science theory; for example, river restoration must be informed by geomorphic, hydrological, and ecological theory (Wohl et al. 2005; Palmer et al. 2006).

The need to develop a sound theoretical base for ecological restoration is imperative for at least three reasons. First, restoration is a booming business that requires the support of a knowledge base and research innovations (*Economist* 2002). Billions of dollars are spent annually to restore polluted and sediment-clogged streams (Bernhardt et al. 2005; Hassett et al. 2005) and to reforest lands that have been degraded and fragmented (Lamb and Gilmore 2003). Yet many restoration efforts are still trial-and-error improvisations. For example, every new biological invasion prompts a series of attempts to reduce or eradicate populations that increasingly damage native communities. Systematic evaluations of multiple tools in a common site come only after long delays in recognizing the magnitude of the problem and obtaining the resources to fund appropriate research.

Second, the stakes are far too high *not* to develop a stronger theory for restoration ecology. As the global human population continues to expand, vital resources, such as fresh water and arable soils, are threatened and depleted (Gleick 2003; McMichael et al. 2003; Stocking 2003). Obviously, conservation of resources prior to their degradation is desirable, but our crowded planet's current rate of resource consumption suggests that we must do more than hold the line (Sugden et al. 2003; Palmer et al. 2004). Where conservation has failed to sustain crucial ecological services, ecological restoration should be the option of choice (Dobson et al. 1997; Young 2000; Ormerod 2003). Given the state of our environment, restoration must use ecologically designed solutions (Pimm 1996; Palmer et al. 2004); our only other recourse is technological fixes to maintain ecosystem processes, an expensive and often ineffective option. Admittedly, some ecological technology (e.g., waste treatment) can improve people's lives, but many problems (e.g., spatially distributed water shortages) cannot be solved by technology, at least not affordably (Gleick 2003). Furthermore, technological fixes lack the aesthetic appeal of restored ecosystems and the species they support.

A third reason to enhance the linkage between ecological theory and restoration is to grow the field of ecology. Regardless of their specialty, ecologists can benefit greatly by testing theory in a restoration context (Palmer et al. 1997; Young et al. 2001). As Bradshaw (1987) noted, restoration is the "acid-test of ecological theory." If we cannot predict the development of a community at a restored or managed site based on knowledge of species and their interactions, then perhaps we can make use of what we observe to refine our theories and predictions and improve their predictive power (Zedler 2000; Hobbs and Harris 2001).

Origins and Structure of This Book

The fields of *ecological restoration* and *restoration ecology* have been well served by two journals of those same names for many years. Since their inception, these journals have published hundreds of articles on topics ranging from tools, techniques, research ideas, results, and philosophy. Today, articles on restoration also appear in mainstream ecological journals (e.g., *Ecological Applications*, *Journal of Applied Ecology*, *Science*). Yet, despite years of intellectual development, restoration ecology remains to be defined as a field of scientific endeavor and its conceptual foundations articulated. This realization ultimately is what led us to create this book.

Initially, we organized a symposium (Palmer et al. 2002) for the 2002 joint meeting of the Ecological Society of America (ESA) and the Society for Ecological Restoration International (SERI). In some respects, the 2002 symposium was a follow-up to a previous (1996) meeting of ecologists and land managers at the National Center for Ecological Analysis and Synthesis (NCEAS) to discuss the conceptual basis of restoration ecology (Allen et al. 1997). This culminated in a series of journal articles (Allen et al. 1997; Ehrenfeld and Toth 1997; Michener 1997; Montalvo et al. 1997; Palmer et al. 1997; Parker 1997; White and Walker 1997) devoted to identifying the conceptual framework for restoration ecology and outlining critical research questions that offer unique opportunities to couple basic research with the practical needs of restorationists. Our hope was to move both ecology and the field of restoration ecology forward.

For the 2002 symposium, we asked scientists well versed in ecological theory—but not necessarily active in restoration work—to present their most creative ideas on the linkage (real or potential) between ecological theory and restoration ecology. We also asked scientists actively involved in restoration research to illustrate how ecological theory has been coupled with restoration efforts and/or how they have tested ecological theory in a restoration context. This emphasis on two-way communication of ideas between ecological theorists and restoration ecologists is carried forward in this volume.

Selecting the topics to include in this book was not easy. We have used the word *theory* broadly to include ecological and evolutionary concepts, predictive models, and mathematical models. We organized the book around the ecological concepts and principles that are fundamental to restoration. Our goals were to provide comprehensive overview of the theoretical foundations of restoration ecology, and to identify critical areas in which new theory is needed, existing theory needs to be tested, and new and exciting cross-disciplinary questions need to be addressed.

Each chapter in this book addresses a particular area of ecological theory. Some of these (e.g. population genetics, demography, community ecology) are traditional levels of biological hierarchy, while others (species interactions, fine-scale heterogeneity, successional trajectories, invasive species ecology, ecophysiology, and functional ecology) explore specific topics of central relevance to the challenges of restoration ecology. Several chapters focus on research tools (research design, statistical analysis, modeling, and simulations), or place restoration ecology research in a larger context (macroecology, paleoecology and climate change, evolutionary ecology). Some areas merit more specific coverage, including ecosystem processes (e.g., restoration of biogeochemical processes) and landscape-level spatial ecology, both of which are highly relevant to restoration and merit further work. Other important areas fell outside the scope of this book, and we urge readers to consult other sources for information on the economics of ecological restoration; on sociological issues, such as stakeholder "buy-ins" that often determine the success of a project; and on engineering principles and technical issues that are required for some types of restoration.

We have organized the book into parts reflecting three general areas of ecological theory (levels of biological hierarchy, restoring ecological functions and processes, and the macroecological context). Each part is introduced briefly by the Editors. The chapters follow a common structure designed to assist the reader, particularly the student new to the field. After a brief introduction to the general area and its significance within ecological research, each chapter summarizes the body of theory most relevant to restoration ecology, including its central concepts and models, current issues, and front lines of research. The authors then discuss the application of this body of theory to restoration ecology as specifically as possible, with references to the restoration literature, where possible. The chapters end with perspectives on (1) tests of ecological theory research that could help build and strengthen restoration ecology, and (2) how restoration offers opportunities to test ideas in basic ecology.

This book is meant to provide a scientific framework for restoration ecology that can be used to inform ecological restoration as well as stimulate advances in our understanding of nature. As you read, bear in mind that the implementation of ecological restoration is not only escalating at an astounding rate, but also that it remains the most ecologically viable and aesthetically appealing remedy for mending Earth's ever-increasing number and scale of degraded ecosystems.

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