

Ecological Theory and Restoration Ecology**Margaret A. Palmer, Donald A. Falk, and Joy B. Zedler**

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). 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 pre-disruption 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 re-grading and riparian plantings (Brown 2000). For coastal marshes

that have been dredged for boat traffic, restoration might involve the removal of fill, recontouring of intertidal elevations, amending dredge spoil substrates, and introducing native plants. In some cases, “restoration” *sensu lato* 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 (SER 2002; Walker et al. 2002). Yet it is rarely possible to achieve the self-sustaining state 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 post-restoration 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 post-restoration (National Research Council 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 benefits 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 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 (Falk, Palmer, and Zedler, *this volume*). 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). 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).

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 (Jordan et al. 1987, Bradshaw 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 a suitable site, 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); 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 multi-dimensional 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 the bare substrate). The task of developing theory that offers a high level of predictability is akin to figuring out how best to grow a myriad of crops across a heterogeneous continent. If we consider the decades 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 producing 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 (e.g., river restoration must be informed by geomorphic, hydrological and ecological theory; Palmer et al. 2005; Wohl et al 2005).

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 freshwater and arable soils, are threatened and depleted (Gleick 2003; Stocking 2003; McMichael 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 will likely benefit 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 restoration research, 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 two 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 Society for Ecological Restoration (SER). 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 & Synthesis (NCEAS) to discuss the conceptual basis of restoration ecology (Allen 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 the present work.

Selecting the topics to include in this book was not easy. We have used the word 'theory' very 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 the first 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 are not as well covered in this book as we would have liked, 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-in’ 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 sections reflecting three general areas of ecological theory (levels of biological hierarchy, restoring ecological functions and processes, and the macroecological context). Each section is introduced briefly by the Editors. The chapters follow a common structure designed to assist the reader, and 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 (a) further tests of ecological theory research that could help build and strengthen restoration ecology, and (b) 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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