Integrating restoration ecology and ecological theory: A synthesis.

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Restoration ecology would be easier in a world of linear, deterministic, ordered, predictable change tending toward stable equilibria. In such a world, many restoration projects would require only that the restorationist give a degraded or damaged ecosystem an initial push, and then stand back and watch the system heal itself.

But this is not the world that most ecologists believe we inhabit (Botkin 1990; Wu and Loucks 1995). Contemporary ecology describes a world characterized largely by non-linear, stochastic, imperfectly predictable processes where historical contingencies, spatial context, and initial conditions are strong determinants of change following perturbation, and in which equilibria, if they exist at all, are likely to be unstable (Maurer, Menninger and Palmer, Suding and Gross, *this volume*). Contemporary ecology sees constant interactions between intrinsic or endogenous dynamics (for example, population cycles) and a non-stationary physical environment with multiple frequencies and amplitudes of change. What we now understand about climate variability suggests that the physical environment is nowhere near as stable – even on "ecological" time scales – as was once supposed (Cayan et al. 1998, Millar and Brubaker, this volume; McCabe et al. 2004). Indeed, ecological and evolutionary adaptation to spatial and temporal variability is a powerful new line of ecological inquiry (Chesson 2000; Clauss and Venable 2000; Reed et al. 2003).

These emerging views of how the world works pose a fundamental challenge for restoration ecology (Pickett and Parker 1994; Hobbs and Norton 1996; Anand and

Desrosiers 2004): Given that ecosystems are in a constant state of dynamic flux, what state should be restored?

The contributors to this volume offer some novel and important answers, if only as working hypotheses. On the whole they emphasize *ecological processes* that underlie the visible composition and structure of ecological communities. Although “saving the parts” (*sensu* Leopold) is often used as shorthand for restoration, restoration ecology shows that *how* the pieces are assembled, and how they work together, are at least as critical (Naeem, *this volume*).

Retaining all the individual components (species) of communities and ecosystems remains important, however. Thus, restoration is becoming more attuned to under-appreciated keystone functional groups such as soil microflora and microfauna, cryptobiotic crusts, and dispersal agents. Uncommon and rare species may also play unknown ecological roles at small spatial scales. Nonetheless, there is a world of difference between having all the parts of an automobile laid out neatly on the garage floor, and an assembled machine that can take you down the highway. Restoration requires having all the right pieces, even if the real interest is how they will function once reassembled.

Perhaps the most important lesson from these fifteen chapters is the reciprocal, mutually beneficial relationship between ecological theory *sensu latu* and restoration ecology (Hobbs, Palmer *et al.*, *this volume*). We see many compelling reasons for closer connections between restoration ecology and ecological theory, two of which emerge as central themes in this book:

Ecological theory can help to inform and improve the science and practice of restoration. The idea that ecological theory can be of significant value to restoration science and practice runs through every chapter in this book. The science of restoration was motivated initially by practical applications rather than theoretical inquiry (Jordan et al. 1987). Increasingly, however, restoration ecology is defining itself as a scientific discipline, in the sense that it strives not only to observe, but to explain (Palmer et al. 1997; Ginzburg and Jensen 2004). This is reflected in the growth of journals such as *Restoration Ecology*, as well as academic and research programs in restoration ecology around the world (www.ser.org).

In principle, there are important differences between restoration science and restoration practice. Science is a means of inquiry, which progresses by asking questions, collecting data, and forming interpretations that help us to understand the world around us. The aim of research is ultimately understanding, and the ability not only to quantify but more importantly to offer coherent explanations for how the world works (Weiner 1995). In science, to learn is to succeed.

Restoration practice typically begins with a different goal, which is to accomplish specific objectives. Clients might want to re-establish a species in a particular place, reduce rates of soil erosion, bring the pH of a lake within its natural range, re-establish a natural disturbance regime such as fire, eliminate an aggressive invading species, or create vegetation structure that will provide nesting habitat for a species of interest.

In reality, the line between restoration science and practice is often fuzzy, and both can advance simultaneously if each capitalizes upon the other. Even when a restoration project has only a limited objective, the practitioner usually tries out a few alternative treatments to evaluate “what works”. We assert throughout this book that even applied restoration practice offers many opportunities for learning and testing of scientific ideas. For example, Callaway *et al.* (2003) accomplished restoration of the species-rich canopy in a degraded salt marsh plain while simultaneously testing predictions of biodiversity-ecosystem function theory.

Of course, not all important insights begin with a theoretical question; ecologists sometimes have to begin by being good natural historians, observing and processing what they see in a synthetic, holistic mode of thinking. In complex systems, the best questions – and the most challenging problems – may not be amenable to a simple reductionist paradigm (Pickett et al. 1994). Depending on ones training and research focus, testable hypotheses can emerge from good natural history at least as often as the reverse (Weiner 1995).

Restoration ecology can also benefit from closer integration with ecological theory in the area of research design and statistical analysis (Michener 1997). Restoration experiments are often constrained by practical considerations that limit replication, balanced factorial designs, and the range of experimental conditions, especially at large spatial scales. New research designs and statistical methods can help restorationists deal with these contingencies, and in so doing help solidify restoration ecology as an empirical science (Osenberg *et al.*, *this volume*). Likewise, mathematical and simulation models are becoming more widely recognized in restoration ecology as valuable tools for anticipating, and in many cases simulating, the responses of complex systems to a variety of perturbations (Anand and Desrosiers 2004, Urban, this volume). Broader application of ecological modeling could help restoration ecology grow beyond trial-and-error experimentation.

Restoration ecology can help test basic elements of ecological theory. While we contend that restoration will benefit from closer integration with ecological theory, a parallel tenet of this book is that restoration ecology has a great deal of reciprocal value to offer (Jordan et al. 1987; Hobbs 1998). The contributing authors of this book highlight many interesting opportunities for restoration ecology to contribute to the development of ecological theory. It is hardly an exaggeration to suggest that restoration ecology offers some of the most promising prospects for advancements in our understanding of how ecosystems work.

We find examples of such potential at all levels of biological hierarchy. The simple act of augmenting or reintroducing a population of a single species provides opportunities for controlled, empirical tests of concepts in population and ecological genetics such as founder events, effective population size, inbreeding and outbreeding depression, metapopulation genetics, and temporal changes in gene frequencies (Falk *et al.*, *this volume*). At the population level, restoration ecology offers the opportunity to test predictions about dispersal and establishment limitation, demographic variability, intra- and inter-specific competition, and the contribution of metapopulation dynamics to persistence and resilience in changing environments (Maschinski, *this volume*).

Restorationists have already learned a great deal about the influence of spatial variability of resources such as water and limiting nutrients, and how fine-scale heterogeneity influences species interactions and community structure (Larkin *et al.*, *this* *volume*). Similarly, it is the large scale of manipulation needed to restore land (and water) that allows community and ecosystem ecologists to test ideas at the large scale. Restoration of whole communities gives ecologists unparalleled opportunities for detailed and controlled experimentation with higher-order processes such as community assembly, food web organization, diversity-stability relationships, and successional pathways under controlled, repeatable circumstances (Menninger and Palmer, van der Zanden, Naeem, Suding and Gross, *this volume*).

Disturbed or altered communities and ecosystems, including those that have been invaded by exotic species, are a central domain of ecological restoration (D'Antonio and Chambers, *this volume*). Restoration ecology overlaps substantially with disturbance ecology and invasive species control efforts, partly because species invasions are often a critical factor triggering the call for restoration. Degraded and restored settings offer a chance to examine the properties of invasive species, invaded communities, and the effects of removal at large scales under controlled conditions.

By its very nature, restoration exposes species to novel environmental conditions. In the short term, controlled *in situ* experimentation in a restoration context can reveal the ecophysiological responses of organisms to stress, and phenotypic tolerance of extreme conditions (Ehleringer and Sandquist, *this volume*). In the longer term, restoration creates empirical tests of the ability of species to adapt to novel evolutionary environments (Stockwell *et al.*, *this volume*). The evolutionary response to changing climate, biogeochemical cycles, and landscape configuration may be the most pervasive outcome not only of our globally altered environments, but also of our efforts to restore them.

Good restoration practice and science both require continual observation and data collection. To realize their full scientific potential, restoration projects need to acquire adequate baseline (pre-treatment) data, establish treatments as replicated experiments, and monitor outcomes systematically (Zedler and Callaway 2003; Zedler 2005). Unfortunately, this is still not practiced consistently; for example, Bernhardt and colleagues (2005) found that only 10% of more than 37,000 river restoration projects in the United States had documentation and monitoring protocols in place. Although some responses to restoration actions are visible immediately after treatments, others may take years to unfold. If we do not monitor consistently to decadal scales, we run the risk of basing adaptive management decisions only on the short-term component of ecological response. We would then miss important slow changes in species composition, competitive and coexistence interactions, soil properties, hydrologic regimes, and community structure (e.g. Friederici 2003; Temperton et al. 2004; Packard and Mutel 2005). If we want to learn how best to restore the dynamics of ecological systems, even in an applied context, we need to follow the outcomes of representative projects over decades, with preference given to efforts undertaken as well-documented, replicated experiments (Larkin et al., *this volume*).

Ecology *sensu latu* embodies a wide domain of subjects and subdisciplines, and in this first attempt at integration, we have not covered them all. Belowground ecology, species interactions, social organization, quantitative spatial ecology, ecosystem ecology, biosphere-atmosphere couplings, and ecological time series analysis are among the areas within ecology that merit further exploration from a restoration perspective. Ecology's allied peer disciplines – such as soil science, hydrology, geomorphology, and biogeochemistry – are equally deserving of a careful treatment of links to restoration theory and practice. We find ample room for fuller exploration of the potential to join restoration ecology to all of these fields.

In the meantime, we hope this book will lead more restoration ecologists to look to ecological theory for a unifying framework for their work, and more ecologists to look to restoration as an opportunity to test their most basic ideas.

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