

Ecological restoration: guidance from theory

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ABSTRACT

A review of the science and practice of ecosystem restoration led me to identify key ecological theories and concepts that are relevant to planning, implementing, and sustaining restoration efforts. From experience with actual restoration projects, I provide guidance for improving the restoration process. Despite an abundance of theory and guidance, restoration goals are not always achieved, and pathways toward targets are not highly predictable. This is understandable, since each restoration project has many constraints and unique challenges. To improve restoration progress, I advise that sites be designed as experiments to allow learning while doing. At least the larger projects can be restored in phases, each designed as experimental treatments to test alternative restoration approaches. Subsequent phases can then adopt one or more of the treatments that best achieved goals in earlier phases while applying new tests of other restoration measures. Both science and restoration can progress simultaneously. This phased, experimental approach (called “adaptive restoration”) is an effective tool for improving restoration when monitoring, assessment, interpretation and research are integrated into the process.

KEYWORDS

Adaptive restoration, ecological restoration, ecological theory, restoration guidance, wetlands.

INTRODUCTION

In an era in which the adverse economic and ecological consequences of environmental degradation are increasingly unacceptable, restoration ecology is emerging as one of the most important disciplines in the whole of environmental science (Ormerod 2003)

This assessment and a growing body of literature on ecosystem restoration make it timely to highlight how ecological theory might guide restoration (see also Webb 1997; Cole

1999; MacMahon 1998; Middleton 1999; Perrow and Davy 2002). Jeltsch and others (2000) consider conservation problems to be too urgent to wait for theory to solve specific problems, but they argue that “a slight shift in focus or an orientation towards general frameworks for problem-solving” are not only helpful but necessary in finding practical solutions to biodiversity loss and ecosystem degradation. Here I explore ecological theory and concepts to suggest guidance for the practice of ecological restoration. Restoration efforts could in turn test the utility of guidance to improve the science of restoration ecology.

As defined by the Society for Ecological Restoration International (SER 2004), “Ecological restoration is an intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability.” Restoration typically begins with practical questions, such as “Which sites are available?” “How have they been degraded?” and “Which targets are feasible?” Additional questions develop from cultural and socio-economic perspectives, including “Which targets are most desirable?” “Who gets to decide?” “How much effort can be expended to achieve targets?” and “How can local communities become involved?” The latter questions are extremely important, and I look to other experts to seek answers from local activists, politicians, and those with traditional ecological knowledge. From the ecological perspective, restoration is an opportunistic arena. A landowner or local entity might decide to restore a degraded site, or a developer might be required to restore a site to mitigate damages that are permitted elsewhere. Rarely is a site strategically selected by a detailed prioritization process conducted at the landscape or watershed scale (although Landers 1997 reviewed a set of papers that attempt to do so). Even where federal monies pay for wetlands to be restored on farmlands, it is the individual farmer who decides to volunteer land for restoration. Although projects are usually initiated through cultural and economic motives, restoration practice is founded in the science of ecology (SER 2004).

Restoration guidance has at least two origins: ecological understanding of natural and disturbed ecosystems and explanations of phenomena that occur in restoration sites (akin to the “top-down” and “bottom up” approaches to riparian restoration described by Landers 1997). Ecology has contributed theory on succession and interspecific interactions, while restoration prompts concepts of reversibility of degraded states and suitability of reference sites. Few restoration efforts include a research component, so new ideas from

restoration projects rarely undergo repeated testing that might elevate them to the level of theory. This is regrettable, because ecology-derived theory is not sufficient; if it were, fewer outcomes would surprise us (Box 1). In most projects, the assumption is made that some restoration action will achieve the target, i.e., if an appropriate method is used, the restoration pathway will, in a reasonable time period, lead to the desired outcome. In the 8-ha site described in Box 1, however, we expected that excavation of tidal creeks, amendment of soils, and planting of seedlings would suffice to achieve high vegetative cover in a year or two, resulting in a species-rich salt marsh. In actuality, most plantings died, necessitating multiple replanting efforts. The surviving transplants spread slowly, and voluntary establishment was limited to *Salicornia virginica*. At five years (spring 2005), the site was still mostly bare and the vegetation far from diverse.

In the U.S., much of wetland restoration is undertaken in a legal context where specific criteria must be met within short time frames (NRC 2001). Missing the target can set in motion corrective measures, which in turn extend the assessment period, both of which add cost to projects. Non-mitigation projects, on the other hand, might seek more general outcomes, with no penalty for deviation from the target. In both cases, managers need to know if results are likely to match the target. Three plots of actual projects in Figure 1 help explain their different outcomes, and plotting new projects on similar web diagrams can help planners decide if goals are likely to be met at a specific site or help select projects from a range of potential sites. Since there is some debate over how exacting the restoration process should be (Mitsch 1998; Ehrenfeld 2000) and how much intervention is needed during restoration (Middleton 1999), a range of outcomes might be anticipated instead of the success-versus-failure dichotomy that pervades ecological restoration literature.

Box 1. Every Restoration Project Has Some Surprises

Although the ability to restore salt marshes in southern California is improving, several events were unanticipated during the restoration of tidal flows to parts of Tijuana Estuary (a National Estuarine Research Reserve in San Diego County, California). The Pacific Estuarine Research Lab documented many surprises in a small (~0.5-ha) site, where disturbed upland was excavated to the level of the nearby marsh plain and connected by a dredged channel to a natural salt marsh on one side and a tidal mudflat on the other:

- During excavation, the bulldozer operator encountered a hard pan at the elevation of the nearby marsh plain. Contractors had to auger holes through the hardpan to transplant *Spartina foliosa* sod blocks that were salvaged during channel dredging. We hypothesized that this substrate would impair vegetative spread of *S. foliosa*. Transplants were installed in early 1997 and many survived and appeared to spread as sediments accumulated on the marsh plain; however, by 2003 the site was dominated by *Salicornia virginica*, with less *Spartina foliosa* than can justify the \$100,000 salvage operation.
- For the experimental plots, we had contractors break up the hard pan and incorporate fine sediment dredged from the channel excavation. During 1997, a bloom of macroalgae (mostly *Enteromorpha*) covered the channel. While dredging can be expected to liberate nutrients and stimulate algal growth, the magnitude of the problem was a surprise. Thick algal mats floated onto the marsh plain and smothered many of our transplanted seedlings.
- Also in 1997, about 100 coots trampled seedlings. This was unexpected because coots are rare in salt marsh vegetation. We hypothesized that the algal mat and the open, short plantings were attractive to coots. The birds could land on water in the channel and walk onto the marsh plain. We installed a chicken-wire fence between the channel and marsh plain, and damages ceased.

In a larger (8-ha) site, where sediments were removed from the surface of a historical marsh plain, we observed the following:

- Flood events were more frequent and sedimentation much greater than expected. The steep bank at the edge of the restoration site slumped and filled much of the excavated channel; additional sediment came from river flood waters (Elwani and others 2003, unpublished report).
- Soil salinity became much higher than expected ($>100 \text{ g L}^{-1}$ in February 2000). We hypothesized that the large size of the site and dark surface color caused substantial warming of tidal waters, which enhanced evaporation and wicked salts to the surface (Zedler and others 2003). While planting in spring predictably avoids inundation stress (astronomic tide amplitudes are lowest in Mar.-Apr.), drought, river flooding, and sea-level anomalies are still risks, and none of these is predictable far enough in advance to reset schedules for growing and transplanting seedlings.
- Vegetation was especially difficult to establish (>4000 transplants died). Few seedlings recruited on their own. Cover along one 640-m-long transect was $<10\%$ at the beginning of the third growing season. We hypothesized that the combination of extreme hypersalinity and sedimentation caused transplant mortality. We correctly predicted that virtually all the volunteer seedlings would be *Salicornia virginica* but were surprised by the long period of low cover.
- Tidal creeks were incised onto the marsh plain to provide macrotopography, but sedimentation reduced these to microtopographic features. We hypothesize that this was the effect of unusually frequent storms/floods, rather than a predictable effect of chronic sediment loading. Then, in winter 2004-05, near-record rainfall and flooding caused massive sedimentation.
- Many shallow but large pools formed on the marsh plain. They impounded water after high tides, creating an additional source of horizontal heterogeneity. We hypothesize that these unintended pools provide additional habitat diversity of importance to invertebrates and fish.
- Nurse plants experienced high mortality on the marsh plain, and artificial shades had no effect on recruitment of the annual plant, *Salicornia bigelovii* (only 17 established from $>10,000$ seeds sown; Zedler and others 2003). Observation of two *Suaeda esteroa* plants that grew in (2002) and sheltered seedlings in (2003) suggest that nurse plants would have been effective, had more transplants survived.

A post mortem of the small vs. large sites documents their different pathways and outcomes; the former is fully vegetated, while the latter is mostly bare with only one species (*Salicornia virginica*) able to colonize the site without transplantation (Zedler and others 2003). These experiences show that project scale matters. Environmental stressors differ in large vs. small sites, and project scale affect outcomes. Second, timing is critical but subject to stochasticity. In a year of favorable weather and low sedimentation, the pathway and outcome could be very different.

Others have conceptualized restoration as a process of shifting an ecosystem along a trajectory from degraded to historical conditions, notably Bradshaw's (1987) structure-function model. In a previous review (Zedler and Lindig-Cisneros 2001), we found shortcomings in diagrams that equate functional change with structural change, as there are multiple measures of both function and structure, and they do not necessarily follow the same trajectory during restoration (Zedler and Callaway 1999). Since most restoration projects do not employ measures of function (e.g., productivity and nutrient cycling), practitioners are left with simple measures of structure, such as plant species lists, vegetation cover, and sometimes wildlife use. Appropriate plant species and cover can be present without providing suitable habitat for birds that require a specific canopy structure; conversely, some rare birds can thrive in woodlands dominated by invasive salt cedar (*Tamarix* spp.), which restorationists seek to eradicate (D'Antonio and Meyerson 2002). Depicting the restoration process as a reversal of simultaneous changes in structure and function does not match reality, even when partial restoration (rehabilitation) and offshoots (replacement) are included. More realistic are state-transition models showing multiple thresholds that need to be overcome for restoration to proceed (Yates and Hobbs 1997). Also appropriate is the alternative states model, which acknowledges that degradation and restoration follow different trajectories and that each state resists reversal through feedback interactions (Suding and others 2004). Restoration is a multi-dimensional process with multiple constraints (Figure 1). To become more predictive about a project's ability to achieve desired outcomes, practitioners need to acknowledge the range of constraints and work harder to avoid or overcome them.

Practitioners also need to recognize the role of chance. Suitable weather and an influx of appropriate native colonizers can speed recovery, while unusual environmental stress, such as sedimentation (Box 1), or an early invasion of an unwanted species can slow or sidetrack a project. Chance might also

accelerate progress, as in some European peat mines, where vegetation recovered more rapidly than expected (cf. Wheeler and Shaw 1995). Given multiple constraints and chance events that leave persistent legacies, practitioners should look to ecological theory for guidance, and then design tests of theory into restoration projects.

Predicting the ability to achieve restoration targets eludes us, in part because restoration is undertaken within a broad spectrum of landscape contexts (Hobbs 2002; Kimmerer and others 2005), where several factors constrain restoration outcomes. In Figure 1, I suggest that restoration targets will be more difficult to achieve where or when (A) the target is stringent, e.g., if a site has to attract an endangered bird with specific habitat needs; (B) if the quality of inflowing water is poor relative to that needed, e.g., if the watershed is mostly developed and runoff is polluted; (C) if the processes critical to sustaining the site demand a large spatial scale, e.g., the site relies on flood pulses or very hot fires; (D) if the site is large relative to reference sites, e.g., a large restoration area in a fragmented landscape with few corridors, few nearby populations of native species, and many propagules of invasive species will have less potential than a small site among intact habitats (Bradshaw 1997; Ormerod 2003); (E) if the site is highly degraded, e.g., bare rock in a former strip mine will be more difficult than re-exposed soil; or (F) if there is a high likelihood that the site can be damaged by extreme events, such as blow-downs, sedimentation, or chemical spills. More factors can be added to such diagrams, as needed, to help characterize the difficulties in achieving project goals or to explain differences in outcomes among past restoration efforts. In three examples (Figure 1), Tijuana Estuary's Tidal Linkage was rapidly revegetated, while the Friendship Marsh was not, and the greater ease at the former site relates to differences in goals (A) and catastrophic sedimentation (B, C, F), which overshadowed the effect of a more restorable substrate, where historical soil was re-exposed (Box 1). San Diego Bay's

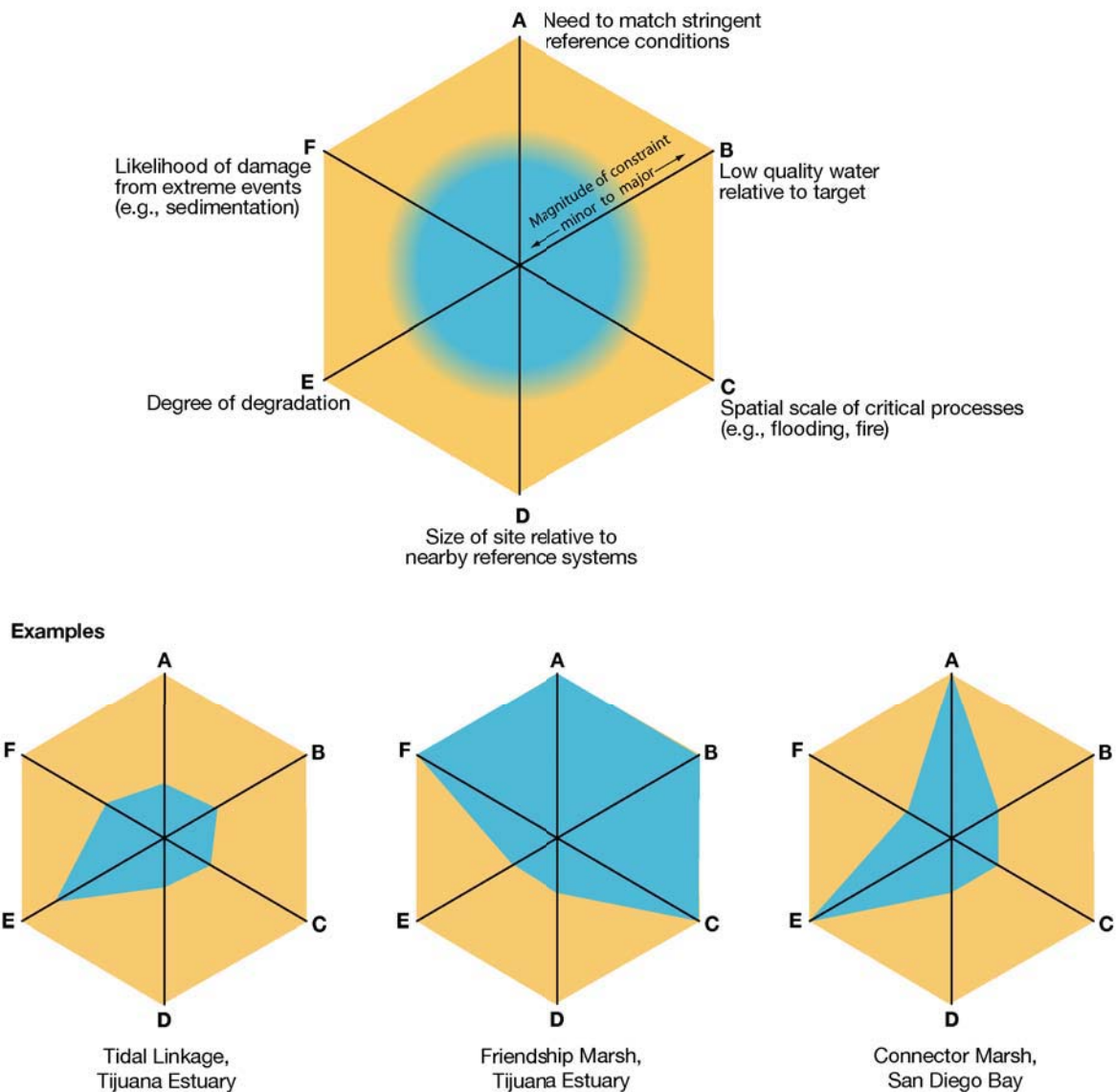


Figure 1. Individual restoration projects differ in multiple factors that help predict their potential for achieving goals. The range of each factor is depicted as a vector. Key factors are the (A) degree to which the outcome must match a natural ecosystem target, (B) degree of developed land within the landscape setting, (C) scale of processes that are essential to the site, (D) size of site relative to size of reference ecosystems, (E) degree of degradation of the site, and (F) likelihood of extreme events, such as flooding, earthquakes, wildfire, etc. Predictability is likely to differ across each spoke, with expectations more easily met for projects that fall closer to the center point. Additional factors can easily be added to describe projects. Connecting points along each vector creates polygons, with smaller areas indicating less challenging projects. Characterizing a project in this way identifies the major constraints, which is where experimentation could most help restorationists “learn while doing.” The most challenging constraints could be addressed by applying alternative restoration methods, as in “adaptive restoration.”

connector Marsh was an intermediate challenge, where the principal limitations were the stringent target (need to provide nesting habitat for an endangered bird) and the degraded site (sandy dredge spoils that could not support tall vegetation; Zedler and Callaway 1999).

Projects that would more likely meet their targets would have less demanding targets, appropriate water quality (clean groundwater for a sedge meadow or moderate nutrient loadings for a wetland designed to improve water quality), small scale processes that determine the site's sustainability (e.g., a vernal pool's reliance on local rainfall), and a small site in an intact landscape (with ample propagules to colonize), little degradation (intact soil), and low likelihood of an extreme event that would re-set succession. All of these factors would push the project toward the center of Figure 1. To restore historical levels of diversity and ecosystem functioning, however, vector A should not be relaxed. Instead, sites that have fewer constraints along vectors B-F would be needed to achieve high expectations.

THEORIES THAT GUIDE ECOLOGICAL RESTORATION

Virtually every ecological theory has some application in restoration practice, since all the components of ecosystems need to be in place and functioning naturally for a project to be considered ecologically complete. My aim is to highlight theories with high utility in guiding restoration. For practitioners, the stages of the restoration process suggest an order; thus, I consider theories that guide goal setting, site prioritization, manipulations of abiotic processes and biota, and maintenance of the resulting ecosystem (Table 1). Then, I offer guidance related to each theory (Table 2).

Because the lines between ecological theory, concept, hypothesis, and explanations of phenomena are blurry, the designations

herein are open to debate. For example, the rich literature on eutrophication might not be considered an area of theory, but it falls within the dictionary definition (an analysis of a set of facts that relate to one another). I emphasize theories that inform the restoration of communities and ecosystems, rather than single-species reintroductions. In examples, I emphasize herbaceous wetlands, with which I am most familiar. Much of the text concerns vegetation, which is usually the proximal target of restoration, even where efforts are catalyzed by the desire to attract animals. My purpose is not to provide exhaustive analyses of theory but to highlight theories with considerable relevance to restoration and identify guidance that derives from those theories. While any one theory could lead to a book about such applications (e.g., assembly rules; Temperton and others 2004), my aim is an overview, with entries to the literature. Following the sequence of planning and implementing restoration, I begin with theories that are relevant to goal setting, followed by those that help prioritize sites for restoration, then those that can assist site preparation, and lastly those that can provide guidance for ecosystem maintenance.

Goal setting is the first step in restoration (Table 1). Although the process combines both ecological potential and human choice (Simberloff and others 1999; Higgs 2003; Davis and Slobodkin 2004), only the ecological rationales are treated here, i.e., goals relating to ecosystem structure, function, heterogeneity and resilience (Hobbs and Norton 1996). According to Ehrenfeld (2000), specific restoration goals might be drawn from conservation biology, landscape ecology, ecosystem management, or a need to recover extremely disturbed lands. Relevant ecological theory and concepts concern the suitability of restoration models, relationships between biodiversity and ecosystem function, and eutrophication.

Table 1. Five stages of restoration can be guided by theory and concepts drawn from ecology and restoration experience

<i>Stages of Restoration</i>	<i>Questions</i>	<i>Guiding Theory/ Concept</i>	<i>Origins of Theory/ Concept</i>
1. Goal setting; developing the conceptual model	Which restoration targets are suitable for the landscape?	1. Suitability model	Restoration experience
	Can individual restoration projects aim to achieve multiple goals?	2. Biodiversity, ecosystem function	Ecology and conservation biology (predicting impacts of lost species richness)
	Are biodiversity and ecosystem services compatible goals?	3. Eutrophication	Lake ecology (limnology), landscape function
2. Prioritizing sites for restoration within the region	Of the most promising sites, which would have the fewest constraints?	4. Reversibility of degradation, alternative states	Restoration experience, rangeland ecology, landscape ecology
	Is it better to restore a few large or many small restoration sites?	5. Island biogeography	Ecology of islands that differ in faunal diversity
3. Manipulating abiotic conditions on site	What habitats will support the desired species?	6. Niche	Community and population ecology
	What physical preparations are needed?	7. Primary (and secondary) succession	Community ecology, gradients in composition, disturbance regimes
	What physical conditions would support the most species and functions?	8. Topographic heterogeneity	Ecology and conservation biology (explaining biodiversity patterns)
4. Manipulating the biota on site	Which functional groups are needed; which should be introduced and when?	9. Secondary succession and land-use legacies	Old-field ecology, extrapolations (space-time substitutions), disturbance regimes
	How should we prepare the site for desired species?	10. Assembly, interspecific interactions	Plant community ecology, animal population ecology
	How can we control unwanted invaders?	11. Invasion	Alien species ecology
	Will the system respond to bottom-up or top-down manipulations?	12. Food web dynamics	Animal ecology, population ecology; limnology
	Does genotype matter? If so, which propagules should be sought?	13. Extended phenotypes	Ecological genetics, restoration ecology, plant-animal interactions
5. Ecosystem maintenance	Will the restored system persist?	14. Resilience	Ecosystem dynamics and management, restoration experience

Table 2. Guidance that follows from ecological theory/concepts and restoration practice.

<i>Theory/Concept</i>	<i>Guidance for Restoration</i>
Model Suitability	• Suitable models are grounded in ecosystem theory. • Suitable reference data come from multiple sites and long time periods, including modal and extreme conditions.
Biodiversity-Ecosystem Function	• Establishing species-rich assemblages should speed ecosystem development and shorten restoration time. • Introducing “high-performing species” should accelerate the development of functions such as productivity.
Eutrophication	• Nutrient influxes tend to reduce plant species richness, so biodiversity and high productivity are not necessarily compatible goals. • Restoration of wetlands in strategic landscape positions can improve conditions downstream. • Topsoil removal can reverse nutrient loading.
Reversibility of Degradation / Alternative States	• Increased effort will not necessarily reverse degradation. • Recovery is severely constrained where the stress cannot be removed.
Island Biogeography	• Large restoration sites should attract and sustain more species. • Restoring many small sites has validity for some ecosystems. • Restoration sites that are near existing habitat blocks should attract and sustain more species than restoring a site that is isolated within a developed area.
Niche	• The restoration of fully functional ecosystems requires the manipulation of sites to include the variety of habitats that comprise desired species’ niches.
Primary Succession	• The more degraded sites require more site preparation.
Topographic Heterogeneity	• The addition of topographic heterogeneity to a restoration site should enhance both species richness and functional diversity.
Secondary Succession	• Potential early dominants of a restoration site should be predictable from key attributes of species in the regional pool, while actual establishment might be limited by site conditions at the time of species’ introductions. • Some early dominants can persist indefinitely. • Succession can be jump-started by introducing woody plants. • Animal activities influence restoration, especially via dispersal. • Slowing or reversing succession requires considerable effort and continual stewardship.
Assembly / Facilitation / Competition	• Conditions that support mature plants can differ substantially from the regeneration niche. • Plants benefit from facilitators in stressful restoration sites. • Tipping the competitive balance toward desired species and away from opportunists is challenging.
Invasion	• Restoration actions disturb sites in ways that invite colonization by invasive species. • Exotic invaders that rapidly form monotypes are the most significant threats to the restoration of native species.
Food Web Dynamics	• Both bottom-up and top-down controls can influence restoration progress.
Extended Phenotypes	• Locally adapted genotypes are suitable for mildly degraded sites. • Highly degraded sites might require alternative genotypes of key species or novel combinations of more tolerant species.
Resilience	• Ecosystems that are commonly disturbed (e.g., floodplains) should be resilient to similar disturbances (flooding, sedimentation, mechanical denudation), but not necessarily novel disruptions (chemical spills). • Restored vegetation gains resilience when multiple, broadly tolerant species and multiple functional groups are present.

1. The concept of model suitability occupies considerable literature that can guide stakeholders in specifying the desired outcome of restoration. For example, an entire issue of the journal, *Restoration Ecology* (vol. 3, issue 3, 1995), presents models developed for restoring Florida's Kissimmee River. In many cases, models focus on structural components—what people want to see. In others, the objective is a function, such as timber production or improved water quality. For the Ayuquila River Valley in Jalisco, Mexico, a community-based restoration effort involves treating sewage before discharge to the river and reforesting river banks by replanting trees. The multiple objectives are to please adjacent landowners, stabilize the banks to reduce erosion and slow eutrophication, shade the river to cool the water, and improve water quality for downstream communities who depend on the river for subsistence (Allen 2004). Functional goals (water quality improvement) outweigh appearances.

Perhaps the most basic hypothesis in restoration is that a degraded site can be designed and modified to mimic some model. Suitable models can be based on historical information (Egan and Howell 2001), including land-use legacies (Foster and others 2003) and on data from remnants of naturally occurring ecosystems, also known as reference sites (White and Walker 1997). For purposes of mitigation, the U.S. Army Corps of Engineers has promoted the use of a hydrogeomorphic approach (Brinson 1993, 1995; Brinson and others 1995; Smith and others 1995) for identifying suitable reference sites, with suitable models being the “best” examples of each wetland type within a region, including sites that are somewhat degraded when pristine examples are not available. A suitable reference site (model) typically has little evidence of perturbation plus attributes that are desirable, such as high species richness, an abundance of rare species, and values, such as shellfish production.

Restoration expectations are moving from the idea that a specific outcome can be achieved to the reality that some outcomes will not be feasible within the scope of a given project (Ehrenfeld 2000). Models are now based on the new paradigm, that ecosystems are potentially open systems, regulated by external processes, have multiple endpoints, follow multiple pathways (trajectories) and undergo both natural disturbances and human effects (Pickett and Parker 1994; Parker and Pickett 1997; Wissmar and Bisson 2003). Ecosystems are dynamic and nondeterministic (Hobbs and Norton 1996; Hobbs and Harris 2001). Projects can thus be evaluated in relation to a range of potential outcomes. The larger the project, the more flexible the goal will need to be. The Wildlands Project, for example, aims to restore the full range of native species (including large predators) across North America. Their model recognizes and embraces environmental variability across space and time (Simberloff and others 1999). Thus, suitable models are grounded in ecosystem theory.

Even suitable reference sites might not provide suitable models if data on their spatial and temporal variability are not available. In our early salt marsh research (e.g., Zedler and Callaway 1999), we measured restoration progress in relation to a single reference site, which had been partially destroyed and for which replacement was required. Analyses of mitigation compliance focused on detailed, simultaneous comparisons of the restored and reference sites (Zedler 1993). Both experienced high interannual variability, and only by comparing attributes at the restored site as a percentage of those at the reference site in the same year could we plot the trajectory of ecosystem development and predict long-term outcomes (Zedler and Callaway 1999). Hence, simultaneous sampling of mimics and models has high utility. In San Diego Bay, it became clear that the target grass, *Spartina foliosa*, could not grow tall or provide nesting habitat for an endangered bird when planted into sandy soil, because nitrogen was limiting. Furthermore,

nitrogen limitation could not be alleviated, even with annual additions (Lindig-Cisneros and others 2003). Ideally, reference data would come from multiple sites and long time periods, including modal and extreme conditions.

In some cases, the model is a sophisticated simulation of how species composition and productivity will change once restoration is underway. Simulation models can predict specific targets and pathways by which they will be achieved (e.g., mangrove productivity by species in relation to salinity and hydroperiod; Twilley and others 1998). Where reality differs from prediction, mid-course corrections can attempt to redirect the ecosystem. Alternatively, if the trajectory cannot be corrected, the model can be adjusted to depict a greater range of potential outcomes.

2. Biodiversity-ecosystem function theory can help planners identify models that might serve multiple stakeholders. This theory predicts that ecosystem processes, such as productivity, increase with species richness (Kinzig and others 2002; Hooper and others 2005), although there is considerable debate about the extent to which effects are due to species richness (the number of species) vs. the inclusion of one or more productive species in the assemblage (Loreau and others 2002). If diversity and function are correlated, then a project that simultaneously provides high biodiversity and multiple ecosystem services could attract broad support. Those interested in plants and birds, for example, would champion a project aimed at maximizing species richness, while those interested in recreational fishing and drinking water supplies would welcome a project that produced cleaner water.

We recently tested biodiversity-ecosystem function theory in a salt marsh restoration site and found that planting species-rich assemblages (six native halophytes) increased canopy complexity and invasion resistance, as well as biomass above and below ground and nitrogen retention (in root and shoot biomass),

relative to one-species plots (Keer and Zedler 2002; Lindig-Cisneros and Zedler 2002a; Callaway and others 2003). Subsequent restoration efforts in southern California salt marshes used these results to design species-rich plantings. A caution is that many species-rich plant communities persist only where nutrient limitations prevent any one species from dominating a site; in such situations, species richness can persist but overall productivity is reduced. Hence, eutrophication theory needs to be considered as well (cf. #3, to follow). Determining if biodiversity-ecosystem function theory is generalizable to other regions or other ecosystems will require well-planned research (Naeem and Wright 2003). Wardle (2002) holds that the positive effects of diversity are limited to assemblages with low species richness, an attribute of many restoration plantings.

Advocates of biodiversity-ecosystem function theory (Kinzig and others 2002) acknowledge that individual species can be differentially important to ecosystem function, and establishing species-rich vegetation will likely include such influential species (Wardle 2002). Hence, it is not always easy to determine if a function is the result of high species richness or adding a specific plant. Indeed, our salt marsh experiment indicated the importance of the regional dominant, *Salicornia virginica*, to biomass, although an analysis of the effect of species richness persisted in plots where *S. virginica* was not included in the randomly-drawn assemblages. Two compatible guidelines are relevant for restoration sites: Establishing species-rich assemblages should speed ecosystem development and shorten restoration time. Introducing “high-performing species” should accelerate the development of functions, such as productivity.

3. Eutrophication is the process of excessive nutrient enrichment, and this well-tested theory predicts undesirable algal growth in lakes with inflows of phosphorus. Similarly, influxes of nutrients to grasslands and wetlands also have negative impacts on

restoration sites. Nutrients are not always delivered in surface water; e.g., airborne delivery from automobile exhaust and decomposing dairy-manure is a huge problem in The Netherlands (cf. Wheeler and Shaw 1995). Either nitrogen or phosphorus in excess can stimulate increased dominance by a few productive species, at the expense of species richness. Although freshwater wetlands are often characterized as limited by phosphorus, and coastal wetlands by nitrogen, these stereotypes are far from absolute (Bedford and others 1999; Sundareshwar and others 2003).

Nutrient influxes tend to reduce plant species richness, so biodiversity and high productivity are not necessarily compatible goals. In fens, low-nutrient conditions allow many species to coexist (Bedford and others 1999). When nitrate loads exceed some threshold, wetland plant communities lose species (Bakker and Berendse 1999; Green and Galatowitsch 2002). The result is often a monotype of either an alien species or a native, such as *Molinia caerulea* in European wet heaths. The loss of species-rich vegetation can then mean a loss of animal species richness (Jacquemart and others 2003).

Eutrophication problems can be reduced by restoring wetlands to remove nutrients from runoff. The wetlands slow the flow of water, trap sediments and phosphorus, and create anoxic soils where nitrate is denitrified to harmless N_2 gas. Landscape function models can predict optimal locations based on nitrate concentrations in the water, loading rates, and retention times (cf. Crumpton 2001). In the U.S., the Natural Resources Conservation Service can fund wetland restoration efforts to reduce runoff from agricultural fields, but not necessarily in strategic locations. Iowa's new Conservation Reserve Enhancement Program is an exception; sites are enrolled on the basis of their predicted ability to remove nitrates. The restored wetland must drain at least 200 ha of agricultural land that is tiled or ditched and the restoration site must be large (0.5% to 2% of the drainage area) and shallow (Crumpton 2001). *Guidance:* Restoration of wetlands in

strategic landscape positions can improve conditions downstream.

At individual sites, a wetland or upland that is already eutrophic might require drastic action, such as removal of nutrient-rich topsoil (Jacquemart and others 2003). This costly approach is being used in the Florida Everglades to restore species-rich native vegetation in place of exotic Brazilian pepper (*Schinus terebinthifolius*), which forms a monotypic, impenetrable thicket. Historically, nutrients were liberated when porous limestone substrates were "rock plowed" for agriculture; once abandoned, the soils remained nutrient rich and the pepper trees invaded en masse. Topsoil removal allows native plants to revegetate the bulldozed sites without planting and with little threat of pepper tree re-invasion. Less costly techniques involve burning to volatilize nitrogen and export ash (Brye and others 2002) or mowing and harvesting above ground plant material. Mowing, however, favors grasses over forbs and might be undesirable for some restorations. Topsoil removal can reverse nutrient loading.

Prioritizing sites for restoration follows goal setting and relies on at least two areas of theory, namely, reversibility and island biogeography. While planners cannot always choose from a large range of potential restoration sites, wetland projects under U.S. Farm Bill restoration programs could become more strategic in locating projects in key watershed positions.

4. Theory on the reversibility of degradation can help restoration planners capitalize on the most promising opportunities for restoration (Suding and others 2004). The concept of irreversibility derives from alternative state theory, which depicts natural and degraded states as coexisting under similar environments, but with both states resistant to change due to strong internal feedbacks. For example, grassland persists in dynamic equilibrium with dry environments, but can shift to shrubland under heavy grazing

pressure and then fail to revert to grassland upon removal of grazers. When resilience thresholds (McDonald 2000) are exceeded or ecological buffering mechanisms (*sensu* Jeltsch and others 2000) are overwhelmed, the soil organic matter, nutrient status, plant, animal and microbial components of pastures might not recover to their prior state (Hobbs and Norton 1996). Likewise, in long-unburned forests, the renewal of burning will not necessarily remove the legacy of fire suppression left on plant composition and soil characteristics (Foster and others 2003). Simply removing the stress that caused degradation might not suffice to recover the ecosystem. Restoration sites usually require introduction of desired species, control of invasive species, and continual vigilance (Davy 2002).

As we learn which types and degrees of degradation are not reversible when the disturbance is removed, an alternative, less restored state might need to be accepted, as in rehabilitation (SER 2004). In some cases, restoration to a pre-disturbance state will be incomplete, i.e., some legacy of the system's disturbance history will remain (Ludwig and others 1997). For example, in a five-year experiment to increase cordgrass height in a salt marsh restoration site, recovery from dredge spoil deposition was incomplete (Lindig-Cisneros and others 2003). We added urea to compensate for low nitrogen supplies in the sandy substrate, but even after four years of urea addition, cordgrass could not sustain tall growth in the next growing season; the sandy dredge spoils and the cordgrass rhizomes had inadequate nitrogen-retention capability. The fine sediments of natural marshes sustain the tall cordgrass state. The desired species was restored, but functional capacity was incomplete, even with intensive effort (Lindig-Cisneros and others 2003). *Guidance:* Increased effort will not necessarily reverse degradation.

In other cases, the constraint on reversibility is that the disturbance cannot be removed. Fens in the Netherlands have been

degraded by nutrient-rich inflows and aerial deposition of both nitrogen and sulfur. These impacts cannot be removed in the near term, so the changes that fens undergo with eutrophication and acidification are not likely to be reversible. Van Duren and others (1998) were unable to reestablish calciphiles to such fens, despite actions to reduce nitrogen inflows and raise pH. Likewise, heathlands that have become acidified have lost diversity (Roem and others 2002), and there is little prospect for reversing low soil pH across affected landscapes. We experience the same problems in wetlands receiving stormwater runoff from urban watersheds; where excess water, nutrients, and sediments cannot be diverted away from wetlands, invasive species dominate as monotypes (Maurer and others 2003; Bernthal and Willis 2004). *Guidance:* Recovery is severely constrained where the stress cannot be removed.

5. Island biogeography theory predicts that large islands have higher colonization and lower extinction rates and sustain more species than small islands (Simberloff and others (1999). This "bigger is better" concept is commonly applied to restoration and can be useful in selecting suitable sites (Webb 1997). Mark Carr (pers. comm.; Carr and others 2003) recently analyzed species' dispersal distances for terrestrial vs. ocean propagules and found a strong tendency for terrestrial dispersal distances to be shorter than via ocean currents. The single large reserve is thus more appropriate on land than for a marine reserve system, where the fish and invertebrate adults of one habitat patch supply the larvae that sustain the next patch down-current. Nevertheless, the goal of restoring many small sites has validity for some terrestrial ecosystems. Some target ecosystems are naturally small and isolated (e.g., wetlands in Pennsylvania; Cole 1998); some species, such as amphibians, require multiple small habitats, and overall diversity is sometimes greater for multiple habitat patches than single large sites.

Island biogeography theory also predicts levels of diversity from connectivity via the

processes of dispersal and extinction. The absence of sedge-meadow species in restored prairie potholes is attributed to depauperate seed banks and limited seed dispersal (Galatowitsch and others 1999). Prairie potholes are isolated wetlands that are typically surrounded by agricultural fields. Measures that improve dispersal of desirable species or reduce their extinction rates are thus warranted (cf. Webb 1997). Likewise, Middleton (1999) identified seed dispersal as a constraint on floodplain forest restoration, where flood pulses were not restored. Hence, restoration sites that are near existing habitat blocks could attract and sustain more species than isolated sites.

Dispersal of some species can be facilitated by attracting birds, using tall woody plants or structures that offer perches. Handel and others (1997) demonstrated the feasibility and value of planting trees on land fills. The trees attract birds, which import seeds of a wide variety of plant species, and many germinate and vegetate the bare land. While Handel (pers. comm.; Robinson and Handel 1993) was surprised that a few tiny woodland remnants near the land fills could play such an important role in supplying propagules, his findings will encourage others to facilitate bird dispersal.

Site preparation follows the setting of goals and selection of sites. Manipulations of abiotic conditions are guided by at least three areas of theory concerning niches, primary succession, and topographic heterogeneity.

6. Niche theory concerns the “n-dimensional hypervolume” that characterizes where a species lives and how it functions (Hutchinson 1957). Understanding niches has proven to be essential for restoring southern California salt marshes for desired animals. The light-footed clapper rail (*Rallus longirostris levipes*) relies on at least four habitat types over the course of a year. It feeds along the edges of tidal creeks; it nests in the tallest, most robust cordgrass marsh; it includes a much larger area of the marsh plain

within its home range; and it seeks cover in the high marsh and adjacent upland (high-tide refuges) during the highest tides of the year. Hence, restoration of the biota requires configuring sites to include creeks with adjacent low-intertidal elevations, which are next to a broad marsh plain, which is fringed by elevations suitable for high marsh. Restoration of a 7-ha site in San Diego Bay from a dredge spoil upland provided only two of the three essential habitats (Zedler 2001). At the same site, the excavation of a single large channel, without the connecting medium and small streams that make up a natural tidal creek network, provided habitat for deeper water fish but not those that make greatest use of the salt marsh (West and Zedler 2000). Assemblages of fish that use small creeks are intimately linked to marsh plain habitats, and the importance of excavating entire creek networks is now being tested (Madon and others 2002). The restoration of fully functional ecosystems requires the manipulation of sites to include the variety of habitats that comprise desired species’ niches.

7. The manipulation of abiotic site conditions is informed by the concept of primary succession, especially in sites that lack soil, as in gravel pits and strip mines. In this concept, soils are depicted as developing slowly from raw beginnings. Restoration ecologists have learned to amend raw substrates with organic matter (OM) and nutrients. The material can be a waste product, such as orange peels that are used to mulch exposed tropical soils (D. Janzen, pers. comm.), or a commercial product, such as kelp compost (a mixture of kelp-harvest byproducts and perlite), which enhances the restoration of salt marsh vegetation (Callaway 2001).

It is also possible to use specific plants to improve the soil, for example, rapidly-growing cover crops. In southern Mexico, Lindig-Cisneros and others (2002) are testing how planting legumes on near-sterile volcanic ash improve nitrogen and OM for transplantation of pine tree seedlings. Other practices include planting vegetation in clusters to enhance

revegetation rates (MacMahon 1998), adding a diversity of mycorrhizae to facilitate vascular plant diversity (van der Heidjen 1998), and creating depressions to accelerate soil development and revegetation (Shachak and Pickett 1997). From natural and restored ecosystems, guidance emerges that the more degraded sites will require greater site preparation.

8. Theory on topographic heterogeneity is useful in suggesting ways to configure sites so they will accelerate succession (by creating depressions that trap soil-building materials) and so they will provide more niches to support a wider variety of species. Increased topographic variability should increase in habitat diversity and species richness, as well as many other structural and functional attributes (Vivian-Smith 2001; Larkin and others, in press).

In arid regions, restoration efforts deliberately include shallow depressions, and various researchers have documented moisture trapping, OM trapping, high plant growth and survival and seed trapping, and variability in microbial processing of nutrients, and even genetic variability across relatively minor topographic variations. Depressions that act as microcatchments are critical to restoring vegetation in the Negev Desert in Israel (Shachak and Pickett 1997), in Niger (Whisenant 1999, 2002), and in Texas (Whisenant and others 1995). In California, a land form known as mima mounds, juxtaposes vernal pools and coastal sage scrub communities at the $\sim 10 \text{ m}^2$ scale. Knowledge of the topography that produces appropriate hydroperiods has aided the design of artificial pools that effectively sustain rare and endangered vernal pool plants (Zedler and others 1993).

Smaller scale topographic variability is also proving useful in restoration. Mounds on a capped landfill in Washington increased survival and growth of some prairie (Ewing 2002), and mounds designed to mimic those created by rabbits and harvester ants in

western Texas produced litter and microbe components that enhanced tree seedling growth (Dhillon 1999). And in Wisconsin, where native sedges grow tussocks that support increased species richness (Werner and Zedler 2002), Peach (2004) recently showed that plots with artificial mounds supported twice as many plant species as flat terrain, although the target species were not well represented in the outcome.

Emerging guidance is that the addition of topographic heterogeneity to a restoration site should enhance both species richness and functional diversity. It thus makes sense to mimic the natural scales of topographic heterogeneity in restoration sites and to test further the effect of varying topography.

Manipulations of the biota are broadly informed by the succession concept and its close relative, assembly theory. If natural processes can be relied on for dispersal and establishment of native species, less transplantation will be needed. Because a specific stage of succession is typically desired, predictions of temporal community sequences will be useful (van der Valk 1998). Invasive species complicate many restoration sites, so invasibility theory can guide protection and control measures. Additional assistance comes from theory on food web dynamics and extended phenotypes.

9. Secondary succession is especially relevant to restoration of vegetation where soils are still intact (Bradshaw 1997). Many land-use legacies persist for decades (e.g., fire suppression; Foster and others 2003), and in some cases, long-term changes have been monitored and cause-effect mechanisms studied. Early on, Keever (1950) suggested that dispersal capability, germination rates, allelopathy, longevity, and maximum size can all affect the sequence of species that dominate old fields abandoned from agriculture. Recently, Campbell and others (2003) developed an index to predict which plants will immigrate onto milled peatlands (sites exposed by harvesting peat). The

attributes included in the index were the species importance along the edges of the restoration site, their maximum fecundity, and their dispersal ability via wind, water, or animals. Some attributes, such as dispersal capability, are obvious predictors of early arrival, but restoration experience suggests that widely dispersed species might be prevented from establishing (Box 1). *General guidance is that:* The potential early dominants of a restoration site should be predictable from key attributes of species in the regional pool, while actual establishment might be limited by site conditions at the time of species' introductions.

The biota themselves can change the course and speed of restoration. For example, adding arbuscular mycorrhizal fungi increased growth of tree plantings aimed at restoring seasonal tropical forest (Allen and others 2003). Allen and others (2002) recommend maintaining microbial diversity by keeping topsoil intact, retaining source populations, and reintroducing micro-organisms along with plantings. *Guidance:* Microorganisms can accelerate regrowth of desired species.

Species that establish early can have lasting effects. Forbes (1999) found that adding moss cover to bare vehicle tracks on the Arctic tundra favored seedling establishment by *Eriophorum scheuchzeri* instead of the target species of *Carex*. The *E. scheuchzeri* monotype persisted for at least 18 years. Forbes (1999) related this outcome to Egler's (1954) initial floristics hypothesis, which adds the guidance that early dominants might persist indefinitely. In many wetland restorations across the temperate U.S., the first dominants will be unwanted exotic plants, such as *Phalaris arundinacea*.

Restorationists can attempt to direct succession (cf. Luken 1990) by establishing cover crops that resist invasion. In some cases, these are mid- to late-succession trees intended to shade the sun-sensitive seedlings of longer-lived trees (Parrotta and Knowles 1999), thus skipping the early succession

stages and avoiding some of the problems of invasive grasses and forbs. *Guidance:* Succession can be jump-started by introducing woody plants.

Animals affect the direction and rate of compositional change in restoration sites, since their impacts include selective or general herbivory on transplants (Zedler 2001), modification of substrates by burrowing, mound building, and predation. Restoring animal populations to a site requires that their foods and cover be established first. Southern California's light-footed clapper rail will not use restored salt marshes that lack the desired canopy architecture (Zedler 1993). Theory about sequential shifts in animal dominance includes predator-prey interactions and trophic cascades, which are not treated here. The ability of birds to disperse seeds can be harnessed to accelerate or diversify revegetation (Handel 1997). Animal activities influence restoration, just as site attributes influence animal use (cf. six chapters on animals in Perrow and Davy 2002).

In the U.S. Midwest, a common restoration goal is to slow or reverse succession, e.g., to keep mixed oak forests from succeeding to sugar maple dominance (by removing *Acer saccharum* saplings) or to return mixed oak forests to their savanna stage (by retaining open-grown bur oaks (*Quercus macrocarpa*) and removing younger, forest-grown trees, understory samplings and shrubs (especially invasive *Rhamnus* and *Lonicera* spp.). Oak forests and oak savannas must then be maintained through frequent burning, because the climate allows woody species to recruit in the absence of fire. In wetlands, the gradual succession of herbaceous vegetation to shrub carr is slowed by controlled burning (staff of the Wisconsin Dept. of Natural Resources and Wisconsin Chapter of The Nature Conservancy, pers. comm.). In nutrient-rich sites, sawdust is sometimes added to tie up nitrogen (Wilson and Gerry 1995), although evidence is lacking that this is a long-term solution (Morghan and Seastedt 1999). *Guidance:* Slowing or reversing succession

requires considerable effort and continual stewardship. Indigenous peoples have much to teach restorationists in this regard. An example from riparian ecosystems is white root (*Carex barbarae*), which American Indian basket makers tended for generations by weeding and perhaps also by planting (Stevens 2004). It is unclear how much of the distribution and character of riparian understory vegetation is due to human influence, but there is no doubt that continual weeding would shift a community toward the desired dominant.

10. Assembly theory (Lockwood 1997; Keddy 1999; Wieher and Keddy 1999; Temperton and others 2004) is closely tied to succession. If we had rules about what constrains species from entering or persisting in natural communities, we could test their efficacy in restoration sites. Experience in southern California tidal mudflats (Box 1) suggests different processes for natural vs. restored salt marsh development, and hence different rules. There, natural mudflats accrete sediments slowly and the salt marsh advances as a fringe along the edge of the lower marsh. Older plants shade the new substrate reducing salinity and transpiration stress on seedlings and rhizome sprouts (as in nurse plants). A variety of species can establish under these relatively benign conditions. In restoration, the sudden exposure of a large flat restoration site imposes novel constraints, including warmer tidewater and substrate, greater hypersalinity, more compacted substrate, and more potential for sedimentation (Zedler and others 2003). When a large site becomes tidal during a time of low-amplitude tides (March–April and August–September in southern California), a salt crust can form between high tides and create persistent conditions that are inhospitable to even the most salt tolerant halophytes. Recruitment is restricted to broadly tolerant species, in this case, mostly *Salicornia virginica*.

Acidification is another stress that constrains community assembly. Restoration of salt marshes inevitably disturbs soils, as

when water levels are dropped, channels are dredged or elevations are adjusted by bulldozers. The exposure of sulfur-rich soils to the air leads to cat-clay formation (sulfuric acid formation and toxic pH levels). Acids can be neutralized with lime, but acidified fens in The Netherlands have proven difficult to restore, even with liming (van Duren and others 1998).

Where conditions are too stressful for germination or transplant establishment, the regeneration niche (Grubb 1977) encompasses more than elevation and water level, and it often differs from the “persistence” niche. In southern California, most of the salt marsh halophytes have broad tolerance as adults, but at least five do not recruit seedlings, even where bare space is available near healthy adults (Lindig-Cisneros and Zedler 2002a, Box 1). Unusual conditions, such as lowered soil salinity following El Niño storms, stimulate rare germination events (pers. obs.). *Guidance:* Conditions that support mature plants can differ substantially from those of the regeneration niche.

Succession and assembly rules have further contributed the concepts of interspecific interactions, of which facilitation and competition (cf. Connell and Slatyer 1977) are especially useful in restoration. Facilitation is what much of restoration is about—finding species that assist the establishment or survival of other species. No restoration project can reintroduce all the native species or ensure their survival after planting. Hence, nurse plants are introduced to facilitate growth of plants that are sensitive to sunlight and transpiration stress; nitrogen fixers are added to enhance soil nutrients; and mycorrhizae are added to increase nutrient uptake (van der Heijden and others 1998). Introducing plants in clusters can facilitate recruitment and growth, and clustered shrubs grow well in arid restoration sites (MacMahon 1998). Clusters of plants not only improve trapping of organic matter and seeds, they also provide perches for birds to increase seed deposition (Handel 1997). *Guidance:* In stressful restoration sites, plantings can benefit from facilitators.

Competition imposes constraints on plants desired in restoration sites. Competition from invasive plants is a major constraint on the establishment of diverse plant assemblages (Budelsky and Galatowitsch 2000; Green and Galatowitsch 2002). A few highly aggressive species (*Phalaris arundinacea*, *Typha x glauca*, *Phragmites australis*) are noted for their ability to colonize and dominate wetland restoration sites. Some native species are also blamed for being too competitive. *Andropogon gerardi*, a tall caespitose grass, tends to dominate tallgrass restoration sites in the U.S. Midwest. A compensating mechanism is to introduce fewer seeds of this species in the planting mix or add it after other species have established. Tipping the competitive balance toward desired species and away from opportunists is challenging. This is especially true where soils are rich in nutrients (Bedford and others 1999; Green and Galatowitsch 2002).

Being able to anticipate undesirable outcomes and correct restoration pathways requires understanding of interspecific interactions. Midcourse corrections will likely be needed where the restoration target is highly specific. The invasion of an exotic clonal plant can be controlled early on (by hand pulling or applying herbicide), but probably not once it has dominated and suppressed other plantings. Initial planting mixes can include native species that are clonal, tall, robust, and large-leaved, so that more light is intercepted by the plant canopy and less is available for germination of invasives (Lindig-Cisneros and Zedler 2001, 2002b, 2002c).

11. Invasion theory concerns the vulnerability of sites (invasibility) and the establishment and persistence of species (invasiveness) that have been introduced from a distant area and that produce reproductive offspring. Richardson and others (2000) recently defined invasives as species that advance >100 m in <50 yr (for species dependent on propagule spread) or >6 m per three-year period (for taxa spreading vegetatively). The challenge in restoration is to

provide appropriate conditions for desired species to establish while preventing establishment by invasives. The most unwanted invasives are those that form monotypes, suppressing virtually all native plants. *Phalaris arundinacea* readily suppresses native species richness, and the effect is augmented by nitrate in runoff (Green and Galatowitsch 2002). Similarly, the hybrid *Typha x glauca*, is increasingly dominant in Great Lakes coastal wetlands (C. Frieswyk, UW-Madison, pers. comm.).

Theory states that invasive species are able to colonize when the natural community is vulnerable and/or the invader is adept at becoming established (Lonsdale 1999). Davis and others (2000) generalized this by saying that a species can invade when resource availability exceeds uptake, which occurs intermittently in dynamic systems. A wetland that experiences flooding will have some plant mortality, opening the canopy and freeing up light for use by an invasive plant. Nutrients brought into the system in pulses would also facilitate invasion. Lindig-Cisneros and Zedler (2002b) found that a canopy disturbance that increases light allows *Phalaris arundinacea* to invade from seed, while species-rich canopies (especially those with broad-leaved forbs in the assemblage) reduced its invasion. The same holds for this species' vegetative propagules (Maurer and Zedler 2002).

We hypothesized that a disturbance that simultaneously makes a site more invulnerable while making the invader more aggressive would allow the invasion to proceed to a monotype (Maurer and others 2003). Kercher and Zedler (2004a) tested this hypothesis in an experiment employing 150 wet prairie mesocosms (a three-factor experiment varying flooding, nutrient additions, and sediment additions; and a separate experiment comparing mesocosms with and without *Phalaris arundinacea*). Flooding opened the canopy, released light, and allowed *Phalaris arundinacea* to expand vegetatively; furthermore, invasions were most aggressive where nutrients were supplied. Interactions

among two factors (e.g., flooding and addition of nutrient-rich sediment) exceeded the additive effects of each factor on its own (Zedler 2004a). In the second year, flooding plus high nutrient addition pushed the system closer to a monotype (Suzanne Kercher and Andrea Herr-Turoff, UW, pers. comm.). Invasive species are a significant threat to the restoration of native vegetation.

In contrast, some native dominants, such as *Carex stricta*, have the opposite effect; where they are present, more species co-exist (Werner and Zedler 2002; C. Friewsyk, UW, pers. comm. on Great Lakes wetlands). Restoration can aim to establish and sustain native species that facilitate richness while managing the reduction of invasives. Providing low-nutrient water and soil at the time of site preparation could help control invasives, but only vigilance, early detection and early treatment will prevent expansion.

12. While much of the above discussion on manipulating restoration sites implies that bottom-up controls are dominant in restored ecosystems, theories on food web dynamics are also relevant, especially top-down controls, trophic cascades, and size-selective predation. The presence of certain animal species within the food web can keep the restoration project on target or derail it. In restoring vegetation, bottom-up controls (e.g., substrate conditions) can usually be manipulated more readily than grazers and predators.

Our difficulties in restoring tall cordgrass (for clapper rail nesting) on dredge spoil led us to test both bottom-up and top-down controls (cf. Zedler 2001). Tests of nitrogen limitation verified that urea addition could increase plant height to levels needed by clapper rails. Observations of scale insect outbreaks on cordgrass led us to test the importance of this herbivore with and without urea addition, since nutrient-enriched plants often support more herbivores. In our case, however, nitrogen enrichment did not enhance herbivory. Bottom-up controls on vegetation appeared to be stronger than top-down controls in southern

California salt marshes. Hence, the site's substrate needs to be capable of sustaining adequate nitrogen supplies for the desired vegetation. At the same time, we were surprised to find that coots could kill large numbers of seedling transplants while feeding on algae. Thus, restorationists need to consider how grazers will affect transplants, how predators will affect the grazers, and how top carnivores will affect the entire food web. *Guidance:* Both bottom-up and top-down controls can influence restoration progress.

13. Further biotic manipulations concern genotypic variability. Locally-adapted genotypes of plants or animals are commonly preferred for introduction to restoration sites, assuming that some phase of the life history will be better adapted to local growing conditions than propagules produced some distance away (Lesica and Allendorf 1999; Hufford and Mazer 2003). For example, Gordon and Rice (1998) compared attributes of seven populations of wiregrass (*Aristida beyrichiana*) in a common garden and found differences in several attributes, leading them to recommend using local seed sources from sites with soil and hydrological conditions similar to those of the restoration site.

Extended phenotypes (Whitham and others 2003) is a new term that describes how the heritable phenotype of dominant plants can influence community composition and ecosystem function. Seliskar and others (2002) began testing this idea in 1989 in a Delaware restoration site planted with three genotypes of *Spartina alterniflora*. In addition to the local Delaware genets, they transplanted genets from Georgia and Massachusetts (a 10° latitude range). Their work is especially elegant, because it followed a common-garden experiment, in which differential growth forms persisted among the three genotypes for an 11-year period. In the restoration site, they showed that phenotype (related to genotype) alters above- and below-ground biomass, root and rhizome distribution, canopy height, stem density and carbohydrate reserves of *Spartina*, as well as microbial respiration rates,

chlorophyll in algal mats, and larval fish use (Seliskar and others 2002).

In riparian woodlands dominated by cottonwood, other members of the community, such as fungi, arthropods, and even birds are affected by the chemical and structural elements of tree phenotype (Whitham and others 2003). Litter decomposition and nitrogen mineralization rates are also affected (Whitham and others 2003). The chemistry and architecture of matrix species can set limits on other species.

Different genotypes of dominant plantings can steer restoration along divergent pathways. Locally adapted genotypes might best support fauna of local reference ecosystems, but local genotypes might not be appropriate for restoring sites that have constraints unlike those of reference systems, such as no soil (strip mines, gravel pits; Gray 2002). *Guidance:* Locally adapted genotypes are suitable for mildly degraded sites, while highly degraded sites might require alternative genotypes of key species—or novel combinations of more tolerant species (Hobbs and Harris 2001).

Ecosystem maintenance will likely be needed beyond the usual five- to ten-year monitoring period. Once restoration actions have been implemented, and the ecosystem is developing toward the model, there are still hurdles (Davy 2002). A disturbance or stress that is either natural or imposed by humans can move a system off course. Resilience theory is thus relevant.

14. Resilience is the process whereby a system recovers from disturbance. Ecosystems gain resilience from *in situ* mechanisms (e.g., resprouting capability, seed banks) and external properties (e.g., dispersal, migration). For example, prairie potholes that have been drained and farmed for decades can regenerate many native species upon reflooding (Galatowitsch and others 1999).

Some natural systems recover readily from frequent disturbances. Cattail (*Typha* spp.) marshes are dominated by widely dispersed, opportunistic plants, and they are subject to frequent drawdowns, eat-outs by muskrat, or excess flooding. Their resilience derives from both rhizome resprouting and seedling establishment on exposed mudflats. Cypress (*Taxodium distichum*) forests in southern Illinois gain resilience by recruiting seedlings after flooding. Middleton (1999) emphasizes the importance of restoring occasional river flood pulses, since this tree needs a high-water period to disperse seeds and a low-water period to germinate. Obviously, flood pulses are needed to restore persistent cypress forests (Middleton 1999). Vernal pools recover from droughts when winter rains fill these shallow basins; many of the native plants are annual species that persist as seed banks; many of the animals are invertebrates with diaspores that regenerate once rainwater accumulates. Vernal pools are readily restored by excavating depressions in appropriate substrates (with a clay pan near the surface) and introducing plant and animal diaspores from natural pools (P. Zedler, UW, pers. comm.). Lastly, the California chaparral recovers from periodic fire. It has several dominant shrubs that resprout soon after fire. The shrubs accumulate reserves below ground in their root crowns, and branches regrow robustly after fire removes the above ground material (Canadell and Zedler 1994). *Guidance:* Ecosystems that naturally experience frequent disturbance will have high resilience. Such ecosystems should require less intervention in restoration. A caution, however, is that novel anthropogenic disturbances might cause novel outcomes. An ecosystem that is resilient to crashing waves might tolerate some harvesting (since mechanical removal is common to both), but not necessarily a chemical spill that introduces new toxins to the biota.

Some resilience of plant cover and ecosystem function derives from the presence of a diversity of functional groups, each with some redundant species (Kinzig and others

2002). Species that are good gap colonizers, strong competitors, vegetative reproducers and generalists that grow well in fertile soils are most likely to perform well in restoration sites, according to Pywell and others (2003). The gap colonizers perform well early on, and the vegetatively reproducing, competitive and generalist species perform well over time. Comparing 13 grass and 45 forb species, Pywell and others (2003) found that grasses performed better than forbs overall. In our freshwater wetland research, graminoids that tolerate variable hydroperiods show promise for use in wetland restoration sites that have unnaturally flashy hydroperiods (Miller and Zedler 2003; Kercher and Zedler 2004b). Because restored vegetation gains resilience when multiple, broadly tolerant species and multiple functional groups are present, plantings should be designed accordingly.

Not all restoration targets are species-rich communities. For the salt marsh dominant, *Spartina alterniflora*, Travis and others (2002) have shown that clones in Sabine National Wildlife Refuge, Louisiana, are genetically diverse and resilient, both in natural stands and in areas where natural recruitment has restored vegetation on dredge-spoil flats. More recently, Travis (pers. comm.) has followed these populations' rapid recovery from a large-scale dieback, which opened canopies, enhanced seedling recruitment and maintained genetic diversity. Resilience was a function of both vegetative and seedling reproduction. *Guidance:* Restored monotypes gain resilience when multiple genotypes are present.

ADVANCING RESTORATION ECOLOGY WHILE IMPROVING ECOLOGICAL RESTORATION

This review highlights ecological theory and concepts that have utility in restoration. Across a multi-dimensional array of goals, landscape condition, and site conditions (Figure 1), it should be expected that restoration will follow multiple pathways with

multiple outcomes. Our ability to achieve restoration targets could improve if more restoration sites were designed to address challenges (Box 2) and test further the guidance that follows from theory (Table 2). At the same time, our understanding of nature would be greatly enhanced (Jordan and others 1987). At best, predictions of restoration pathways and outcomes are very general. Actual pathways are specific to the site, the target, the species employed, and the resources invested (time, money). Outcomes are rarely, if ever, exact matches with the reference systems that serve as targets.

Adaptive approaches can help projects achieve targets at the scale of individual restoration sites (Zedler and Callaway 2003). At the landscape scale, large-scale adaptive modeling and design can suggest ways to achieve targets (Holling 1978; Landers 1997; Huxel and Hastings 1999; Hobbs 2002). In an adaptive framework, management actions are tested with monitoring of key variables and frequent review of findings. Researchers are integrated into the process to interpret results and suggest mid-course corrections. In restoration, uncertainty about pathways and outcomes and the propensity for restoration sites to surprise us make it prudent to learn as much as possible from every restoration project. In restoration, researchers can play especially strong roles by suggesting ways to maximize knowledge gain. Restoration ecology can be advanced by designing and implementing restoration projects as experiments (Simberloff and others 1999). Large projects offer the opportunity to design work to occur in sequential modules, so that the results of early experiments can inform later modules. In this "adaptive restoration" approach, each phase is designed as a series of experimental plots that test alternative restoration methods (Zedler and Callaway 2003). The most effective method is then applied to the next phase, which in turn tests alternative methods, some of which are likely to be suggested by problems that develop in

Box 2. Challenges That Fall Within a Broad Spectrum of Degradation Conditions at Restoration Sites

1. Hydrological challenges. How can naturally-functioning communities and ecosystems be restored where wetlands have been dammed or drained, where dams have been removed, where surface water flows have been augmented, where groundwater has been depleted, where water diversions have depleted river flows, or where substrates are continually acidified? Most of these hydrological conditions cannot be restored in their entirety, and it is unclear how much of the natural condition must be present to restore ecosystem structure or function (Ken Potter, UW, pers. comm.).

2. Substrate and microbial challenges. Where should restoration begin when the site is bare due to mining, volcanic ash, or dredge spoil deposition? What can be done where the topography has been flattened or otherwise smoothed, or where sediments cover sedge tussocks and tidal creeks? How can soils be restored where cultivation has removed vegetation and collapsed soil structure? How can nutrient regimes be restored where soils have accumulated excess nitrogen and phosphorus or where nutrients are in short supply?

3. Challenges to plants and animals. How can native plant and animal communities be restored where invasive species have become dominant or where browsing or grazing has permanently altered the vegetation?

4. Challenged landscapes. How can biodiversity be sustained where the habitats have been depleted and remnants are fragmented or where the fire regime has been severely modified by providing too little or too much burning.

earlier phases. Adaptive restoration differs from the addition of small-scale experiments to restoration sites by the scale of the treatments; experimental plots fill the area being restored, so that experiments accomplish both science and restoration simultaneously. Note, however, that Cummings and others (2005) recently used the term more simply as sequential experiments in restoration sites.

Which experiments are most compelling for each project? Characterizing the constraints as in Figure 1 can help restorationists identify experimental approaches that are most appropriate to a specific site within its landscape setting. The site dictates the landscape position and the potential for phased experiments, each with a specific spatial scale. Thus, considerable creativity is required to match an experimental approach with the need for information and the scale and attributes of the module being restored. Unfortunately, scientists are not always invited to participate in the planning of specific

restoration projects. The adaptive restoration framework for restoring tidal flows to 200 ha of Tijuana Estuary (Box 3) is an exception, not the rule. Thus, the opportunities afforded by entities such as the U.S. National Estuarine Research Reserve System need to be capitalized upon, and the rewards of experimentation publicized so that adaptive restoration becomes the rule. Given that ecosystem restoration efforts are urgently needed, that efforts are often publicly funded, and that pathways and outcomes are not yet predictable, the case for learning while doing is compelling.

What restorationists need to improve restoration extends beyond the guidance presented here. Socio-political climates are ever changing, and a restoration program that begins with a strong science base will not necessarily sustain its scientific strength. Projects can succumb to change at every step. During planning, designs for diverse and costly plantings can shift to a small suite of cheap

Box 3. Adaptive Restoration at Tijuana Estuary

Tijuana Estuary's first tidal restoration module was completed in 1997 and the second in 2000; the third is being planned. In module 1, which was small in size, we learned that 7 of the 8 marsh plain halophytes needed to be planted and that species-rich assemblages would accelerate ecosystem development [Keer and Zedler (2002), Lindig-Cisneros and Zedler (2002a), Callaway and others (2003)]. Hence, module 2 was planted in accordance with those guidelines. In addition, module 2, which was large (8 ha), was able to accommodate experimental tests of the importance of vertical and horizontal heterogeneity (tidal creeks, soil amendments, and cluster plantings). These preliminary findings suggest that module 3 should include tidal creeks, kelp compost as a soil amendment, relatively tight spacing of transplants in clusters on elevated islands within a mudflat that is too low for salt accumulation. Vegetation could then advance along with accretion as in natural marshes.

Other hypotheses to test follow:

- Marshes excavated as "cul de sacs" create conditions of greater stress (hypersalinity, sedimentation, as in Module 2) than flow-through systems;
- Large bare sites experience greater warming of tidal water, which causes hypersalinity;
- Higher rates of kelp compost application can substantially increase transplant survival and growth;
- Planting "nodes of diversity" will reduce costs of planting marsh-plain halophytes;
- Clonal species planted as nodes of diversity will spread into areas with soil amendments more rapidly than unamended areas;
- Establishing nurse plants will enhance recruitment of short-lived halophytes; and
- Establishing *Triglochin concinna* will reduce growth of *Salicornia virginica* and allow more diverse assemblages to develop.

species as soon as budget limitations are recognized. During implementation, sites that are being restored to support rare species become compromised when visitors demand more access and recreational activities threaten the very species that people want to view. Over the long term, monitoring programs become vulnerable to cuts in funding, and scientists lose their ability to keep students funded where promises to manage site

conditions and control vandalism go unfulfilled. Adaptive restoration requires long-term commitments beginning with the planning stage and building in a surcharge for monitoring and research. Long-term commitments to science-based restoration would ensure that pathways of ecosystem development and intended outcomes become better understood and more predictable.

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