Upstart Views of Restoration Icons

As ecological restoration efforts become better known and better studied, and as more ecologists choose to conduct research in restoration sites, the gap between applied science and theory becomes narrower. Such was the case when Margaret Palmer catalyzed a symposium for the 2002 ESA meeting in Tucson, where ecologists indicated how theory could inform restoration practice. Several speakers then expanded their remarks in a book (Falk et al. 2006) that further merged ecological theory and practice. Still, gaps will remain if the icons relied upon by restorationists are inconsistent with the latest advances in theory and understanding of how ecosystems develop. Accordingly, this symposium set out to deconstruct some icons of restoration ecology, by applying contemporary ecological theory to restoration ecology. The combined result represents a paradigm shift, away from equilibrial, predictable models and toward a world of restored ecosystems that is at least partly stochastic, time-varying, and context dependent.

One pervasive icon is a simple illustration of how ecosystem structure and function develop following some restoration effort (Fig. 1). A. D. Bradshaw (1984) depicted restoration as having a single target that is hit after substrates are modified, with ecosystem structure and function developing along the same linear pathway. His diagram continues to appear in books, papers, and even the journal Science (Dobson et al. 1997), although evidence supporting this model has never been included in those publications (Zedler and Lindig-Cisneros 2000). Our concern is not with Tony Bradshaw, who is himself an important icon of restoration ecology, for he was among the earliest ecologists to address actual restoration problems (how to vegetate mine tailings) and to urge others to recognize the value of studying restoration sites as a test of ecological understanding (e.g., Bradshaw 1987). Instead, the issue concerns those who expect restoration efforts to follow overly simple models, or who promise unrealistic pathways and outcomes.
Because there is no complete guide to the theoretical foundations of restoration ecology, and because ecologists have much to offer in helping restoration ecology mature as a science (Zedler 2005), we convened a symposium on “Upstart Views of Restoration Icons” to highlight some of the contributions of the new book (Falk et al. 2006), while asking authors and other speakers to stretch beyond previous writings to close further the gap between theory and practice. Dan Larkin solicited the speakers and organized the session; Joy Zedler moderated the symposium; and Don Falk provided the wrap-up. As a disclaimer, we did not ask speakers to critique the icon in Fig. 1; rather, we selected results from their talks that address this widely published model of how restoration works; thus, our descriptions of each presentation are not fully representative (in keeping with instructions for symposium commentaries in the *ESA Bulletin*).

Ten speakers (names in boldface type) provided evidence that dispels key elements of a key restoration icon (Fig. 1). Their presentations failed to support (1) a single obvious target for restoration, (2) a straight path to the target, and (3) a linear relationship between structure and function.

---

**Upstart view No. 1.** There is no single, obvious target for restoration; that is, reference conditions represent dynamic, multivariate, and nonequilibrial processes.

**Bob Peet** (University of North Carolina) presented a model of relationships between environmental conditions and plant communities that suggests appropriate species lists, proportions of plants/species, and sequences for introducing plants to individual restoration sites. Science-based “designer plantings” should reduce restoration efforts and costs. North Carolina’s Department of Transportation is using this approach to restore lands in January 2007.

---

**Community structure**

Fig. 1. Simplification of Bradshaw’s (1984) model of restoration, showing a single target, a straight path, and a linear correlation between community structure and ecosystem function.
Symposia

anticipation of the need to mitigate impacts of future highway construction projects.

Roberto Lindig-Cisneros (University of Michoacana) added human needs to the list of constraints on the restoration target. In southern Mexico, managers agreed to allow experimental restoration of tephra (unvegetated ash that persisted 60 years following eruption of Mt. Paracutín), but only if the target could be the two native pine species that provide livelihoods (Fig. 2). In exchange, local people helped establish experimental plantings (with and without bark mulch). As expected, mulching lowered soil temperature and enhanced pine establishment, but, unexpectedly, the effect was strong only in dry years.

![Forest-restoration experiment](image)

Fig. 2. Forest-restoration experiment in Comunidad Indígena de Neuvo San Juan (Michoacán), where two species of native Pinus were planted with and without mulch (pine bark) in tephra (ash from the 1943–1952 eruption of Paricutín volcano), and with and without fencing to exclude herbivores. Photo by R. Lindig-Cisneros.

Denise Seliskar (University of Delaware-Lewis) demonstrated that tailoring could extend below the species level. After planting a salt marsh restoration site in Delaware (Fig. 3, photo) as an experiment to test the effects of three genotypes of Spartina alterniflora (from Maine, Delaware, and Georgia), she and others documented numerous impacts on everything from canopy height and stem density (Fig. 3, graphs), to root and rhizome distributions, edaphic chlorophyll concentration, and decomposition rates. Even the numbers of larval fish caught in pit traps differed by a factor of 2. She and Jack Gallagher then extended their research by selecting genotypes of many halophytes via tissue culture. Some genotypes are broadly tolerant of stressful field conditions, while others perform best in specific sites. “Designer genotypes” could increase survival and growth.

Stuart Findlay (Institute for Ecosystem Studies, New York) gave compelling evidence that multiple-function ecosystems are unrealistic targets for wetlands. While we might aim for clean water, high productivity, high biodiversity, flood reduction, and other functions, he argued that restoration sites are context dependent and
Symposia

typically do not provide all the ecosystem services expected of them, and that some combinations of functions are mutually exclusive (Fig. 4). If multiple driving factors are not correlated in space or time, individual sites cannot excel in several functions simultaneously. This leads to high interannual variability in site performance and argues for a relaxation of the restoration target. Thus, plans to restore multiple functions in a watershed will require multiple restoration sites and efforts.

As Don Falk concluded, the paradigm of the “single target” should shift to that of “reference dynamics” (Falk, in press), where interactions, temporal and spatial variability, and stochastic processes are emphasized. This makes defining the ecological reference more complex, difficult, and uncertain—but also more realistic.

**Upstart view No. 2. Restoration does not always follow a straight path to the target; more realistically, restoration is never finished.**

**Katie Suding** (University of California-Irvine) offered evidence that California grasslands resist

Fig. 3. Photo: Construction of a tidal wetland with creeks and a pool created near Lewes, Delaware, by excavating soil from abandoned agricultural upland. Three genotypes of *Spartina alterniflora* (from Massachusetts, Delaware, and Georgia) were planted on the marsh plain in order to study their effect on marsh function. Graphs: Among the responses were differences in canopy height and stem density of *Spartina alterniflora* at the site (pink bars); values at their site of origin are in yellow. See Seliskar et al. (2000).

Fig. 4. Functions may also have complex controlling factors, as in this example, which illustrates that the capacity of a patch of submerged aquatic vegetation to ameliorate high turbidity conditions is spatially contingent. Patches within ~100 m of the 5-m depth contour have a much lower likelihood of maintaining turbidity below 40 NTU (neothelometric turbidity units). Using this water clarity criterion as a performance measure would require relaxing the criterion for sites closer to deep waters. Graph by S. Findlay.
restoration and follow an alternative states model (Fig. 5), with internal feedbacks that help sustain each of the dominance states, namely, the native bunch grass (which competes more strongly for N) and exotic annual grasses (which compete more strongly for light). Through innovative experimentation, she showed that soils formed under the native tended to favor the native, and that soils formed under exotics favored exotics. These and other results collectively support the alternative state model. Thus, if restorationists plant the “right” species in the “wrong” soil, the site will not necessarily favor the native vegetation.

Fig. 5. Predictions of alternative states that have direct applicability to restoration ecology: threshold patterns (at $X_1$ and $X_2$), regional coexistence (dominance of one state or dynamic regime below $X_1$ and one state above $X_2$), multiple attractors where either state could exist (solid lines between $X_1$ and $X_2$; the dotted line is a repellor), the presence of positive feedbacks (to drive the system to one or the other state), and hysteresis (recovery trajectory is different from collapse trajectory). All these predictions can be tested in a restoration context; several lines of evidence are needed. A system that demonstrates these dynamics requires a shift from single-equilibrium steady-state management to an adaptive approach that incorporates regional refugia, legacy and priority effects, and resilience into its tool set. Graph courtesy of Suding.

Dan Larkin (University of Wisconsin) tested the importance of intertidal pools and tidal creeks to salt marsh food webs in a large experimental salt marsh (Fig. 6) and found increased feeding opportunities at high tide (more algal biomass, more invertebrates in pools) than where pools were lacking. Also, killifish fed more in areas with pools than without. Furthermore, tidal creeks enhanced use by mudsuckers. Thus, feeding opportunities were best restored where topography mimicked natural heterogeneity (creeks plus pools), but the relationships between species and microhabitat were complex.

Holly Menninger (University of Maryland) culled the literature for examples of real evidence that substrate heterogeneity increases the diversity of taxa. In contrast to the above speakers, she found none for a dozen ex-
experiments in streams, including the work of her co-author, Margaret Palmer (Fig. 7). While the experiments being done in streams have not enhanced diversity of the taxa being explored, a focus on restoring processes in streams might help researchers figure out how to enrich diversity.

As Don Falk summed it up, the emerging view of the postrestoration state is one of complex, and at least partly stochastic, spatially contingent systems, with nonlinear response functions to treatments, nondeterministic outcomes, and nonequilibrial properties.

Fig. 6. An 8-ha experimental marsh in the southwesternmost corner of California allowed comparison of areas with and without tidal creeks and with and without tidal pools. At high tide, killifishes preferentially occurred and fed in pools, where algal and invertebrate foods were most abundant. Fig. 6a shows a 1-ha “cell” with a creek branching off the tidal channel at the base of the photo; Fig. 6b shows tidal pools at the opposite side of the marsh and the dominant plant, *Salicornia virginica*. July 2005 photos by J. Zedler.

Fig. 7. Invertebrate taxa richness did not differ among heterogeneity treatments imposed by Brooks et al. (2002) in a Virginia stream. Treatments differed in the variability of streambed particle sizes in entire riffles. Redrawn from Brooks et al. (2002).
Upstart view No. 3. Structure and function are not linearly related.

Shahid Naeem (Columbia University) indicated that many plant species combinations might be viable restoration targets, based on biodiversity–ecosystem function (BEF) theory, and that the relationship to species richness will differ by function. He unveiled a new 5-year experiment (Fig. 8) that is underway in Mongolia, involving >700 plots (each 6 × 6 m) that will have controlled composition and species richness for the first years, before opening plots to grazing and assessing their functional capacity (including livestock production). “Combinatorial forecasting” could lead to recommendations for specific richness levels and/or assemblages for use in restoring specific ecosystem functions.

Fig. 8. Ambitious new 5-year experiment to test Biodiversity Ecosystem Function (BEF) theory in grasslands of Inner Mongolia. Plots are 6 × 6 m; weeded by hand to control species richness. Photo by S. Naeem.

Greg Bruland (University of Hawaii) tested the ability to restore both species and functions to a former forested wetland that was farmed (and flattened in the process), and then regraded to create a large experiment in topographic heterogeneity (1.3-m vertical range). Aboveground biomass accumulated least on hummocks and most in hollows, while species richness increased from hummocks to hollows to flats (Fig. 9)—not a linear correlation between these measures of function and structure. Overall, the specialization of species to microhabitats led to high diversity at the site scale.

Joy Zedler (University of Wisconsin) filled a gap in the program with Suzanne Kercher and Andrea Herr-Turoff’s data from wet prairie mesocosms. As an invasive grass expanded, biomass increased and species richness decreased. Then, despite killing the grass with herbicide, biomass remained high where few species remained. Productivity and species richness were negatively related, contradicting the notion of a positive linear
correlation; furthermore, restorability was lower where stormwater treatments (flooding and nutrients) were continued than where they ceased.

Clever theorists and talented experimentalists continue to amass impressive data sets that challenge traditional views that restoration outcomes are predictable (we achieve a specific target), defined (variation is around a predetermined mean condition), and stable (we can keep the system that way). We summarize with:

*Upstart view No. 4: Restoration outcomes are unpredictable, stochastic, and nonequilibrial, and the work is never finished.*

While the “Bradshaw icon” might characterize some components of some restoration projects at some times, a more dynamic paradigm for restored ecosystems would accommodate variability and even unpredictability as positive signs of healthy, functioning systems.

**Fig. 9.** Mean species richness (i) and aboveground biomass (ii) in three microtopographic treatments in a restored wetland. Data are means ± 1 SE; a,b,c differed using ANOVA. Redrawn from Bruland and Richardson (2005).
Symposia

Literature cited


Joy B. Zedler, Botany Department and Arboretum, University of Wisconsin-Madison, Madison, WI 53706, E-mail: jbzeder@wisc.edu
Donald A. Falk, Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ 85721
Daniel J. Larkin, Botany Department, University of Wisconsin-Madison, Madison, WI 53706