

RESTORATION ECOLOGY

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example of irreversible regime shift. Costs of restoration may determine the degree to which regimes can be restored. The nature of alterations may also determine the degree to which a system can be restored. For example, restoration of anadromous fish populations may not be possible without the removal of human-constructed dams. Another consideration for managers is the issue of hysteresis, which suggests that the path to a restored regime may be very different from the one that led to the degraded state. In the overgrazed rangeland example, simply lowering grazing pressure will not restore the system once it has shifted to a woody state.

Ecological restoration in many cases involves active management that seeks to shift from an undesired regime to a desired one. Many environmental issues, such as cattail stands or the decline in the number of wading birds in the Everglades, can be described as undesired regimes. Restoration of desired regimes requires a careful assessment of ecosystem dynamics and exploration of feasible policy options. In many cases restoration policies are numerous and depend on how ecosystems are thought to respond to various actions. A growing set of experiences indicate that many large-scale restoration projects can only proceed through an adaptive management process, because of the inherent uncertainty of system responses. In an adaptive management framework, policies are acknowledged as guesses about system response, and actions are designed to help better understand how the system responds. Generally, ecosystem-scale experimentation is needed to understand how to shift regimes for restoration purposes.

5.2

Case Study

Phylogenetic Structure of Plant Communities Provides Guidelines for Restoration

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One of the fundamental goals of restoration ecology is to understand the factors that influence assembly and establishment of colonizing species after disturbance. A long tradition of research and theory in community ecology provides a useful framework for the newer, more applied discipline of restoration ecology. One of the central differences between restoration and community ecology is that in restoration ecology the endpoint of the assembly process is defined by agreed upon restoration goals rather than by ecological conditions and dynamics alone (Temperton et al., 2004).

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The linkage between ecological structure (e.g., species diversity, habitat complexity) and ecological function (e.g., biogeochemical processes, disturbance regime) has the potential to advance the practice of restoration. Theoretical and empirical work focused on this linkage is critical to advancing the science of restoration ecology and the practice of restoration (Palmer et al., 2006).

Current issues in community ecology relate directly to decisions about the restoration goals themselves. There is currently significant debate about the extent to which community assembly is influenced by deterministic processes including niche differentiation and matching of organismal traits to the environment or by stochasticity and neutral processes, in which species are essentially equivalent (Hubbell, 1979; Goldberg and Werner, 1983; Hubbell, 2001; Tilman, 2004; Hubbell, 2006; Leibold and McPeck, 2006). To use an analogy of the late Stephen J. Gould (1989), if nature's tape were replayed again and again, would the same communities result? If community structure is random and merely the result of historical contingency, perhaps attempting to restore them to specific endpoints is misguided. On the other hand, if community assembly follows specific rules leading to predictable outcomes, these may serve as guidelines for reassembling communities after disturbance. Therefore, understanding the extent to which communities are randomly or deterministically assembled influences how the goals of ecological restoration are set.

According to one deterministic perspective on community assembly, the assembly process can be understood in terms of a series of filters that includes both the physical environment and the interactions of species (Lambers et al., 1998). Together, these filters determine the composition and structure of local communities. Early on in the development of community ecology, Schimper (1898) described the physical environment as a filter that eliminates species that have arrived but lack the physiological traits to grow and survive under those conditions. Species interact with one another and can form a biotic filter that determines whether species can persist in the presence of other species. In the first half of the twentieth century, it was theoretically and empirically demonstrated that multiple species that compete for the same resources cannot coexist (Gause, 1934). The principle of competitive exclusion is considered a central component of the biotic filter. Lack (1944) was one of the first to point out that closely related species living together in nature might coexist by partitioning resources between them, and MacArthur and Levin (1967) demonstrated mathematically that competition could set a limit to the similarity of coexisting species. Hutchinson (1957, 1959), an animal ecologist, extended the idea of resource partitioning in his conceptualization of the *N*-dimensional niche, which was later applied to plant communities by Bazzaz and collaborators (Bazzaz, 1996). The axes of species occurring in multidimensional niche space were the various biotic and abiotic factors in the environment along which species could partition resources. Distributions of species, therefore, were thought to reflect their relationship with both the physical environment and other species, including predators, prey, pathogens, hosts, pollinators, dispersal agents, and other mutualists. This deterministic view of community assembly holds that niche differentiation allows for the coexistence of species, particularly those in the same trophic level.

Ricklefs (1987) highlighted the importance of historical processes in influencing local diversity and urged incorporation of historical, systematic, and biogeographical information into community ecology. He reminded ecologists that the equilibrium theory of island biogeography (MacArthur and Wilson, 1967) was based on a balance of regional processes (those that increase colonization) and local processes (those that cause local extinction). He argued that limiting similarity was in most cases a weaker force than regional processes in community assembly and that local diversity, rather than being determined solely by local environmental factors and limiting similarity, was consistently dependent on regional species diversity (Schluter and Ricklefs, 1993). The roles of dispersal, disturbance, and stochastic processes in community assembly, which played a central role in the theory of island biogeography (MacArthur and Wilson, 1967), were given new prominence by Hubbell (2001) in his unified neutral theory of biodiversity. Hubbell challenged the perspective that deterministic niche processes influence community assembly, asserting that ecological communities are open, continuously changing, non-equilibrium assemblages of species whose presence, absence, and relative abundance are governed by random speciation and extinction, dispersal limitation, and ecological drift. According to this view, species differences do not predict outcomes of competition, species do not specialize for specific habitats, and interactions between species and with the environment are not relevant to community assembly.

More recently, niche theory has been merged to varying degrees with neutral theory (Tilman, 2004; Leibold and McPeck, 2006), acknowledging the importance of both niche-based and neutral processes in community assembly. Where any given community falls along the spectrum between these two extremes depends perhaps on community age, the extent to which current species interactions have influenced the evolutionary process, and the heterogeneity of the environment. Proponents of both perspectives generally agree that large-scale processes such as speciation, migration, and dispersal determine how many and which species form the regional species pool from which local communities are established (Ricklefs, 1987; Lambers et al., 1998; Ricklefs, 2004). In the face of human dispersal of organisms around the globe, a changing regional species pool sooner or later will alter local community composition, even if other factors remain constant.

Florida Plant Communities

Empirical evidence from oak-dominated forest communities in north central Florida, at the confluence of northern temperate and subtropical ecotones, provides support for a largely deterministic, niche-based model of community assembly. A filtering process is apparent in these plant communities because species distributions are not random with respect to the environment or with respect to each other. Most strikingly, in this system, 17 species of oaks (genus *Quercus*) occur in close proximity, begging the question of how so many closely related species can co-occur. Closely related species have much of their evolutionary history in common, and, therefore, are presumed to share many phenotypic attributes and to have similar niche preferences. There are limits

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to how similar coexisting species can be (MacArthur and Levins, 1967), making the sympatry of such a large number of congeners challenging to explain.

The oak species occur in three broadly defined communities in north central Florida: scrub, sandhill, and hammock. Hammocks themselves have been subdivided by other authors into hydric, mesic, and xeric hammocks based on the hydroperiod and hydrology of the soils. These communities differ significantly in soil moisture availability and fire regime (Cavender-Bares, et al., 2004b). The first indication that a filtering process is at work in the assembly of these communities is that the distribution of oak species across the major environmental gradients is not random. Rather, their distributions are predictable based on the functional traits they possess (Cavender-Bares and Holbrook, 2001; Cavender-Bares, et al., 2004b). A matching of trait to the environment is found both under field conditions where traits may vary plastically with environment, as well as in a common garden, where environmental variation is minimized. Furthermore, species show evolved trade-offs, indicating that they specialized for one set of environmental conditions at the expense of another. The matching of phenotypic traits to the environment has long been recognized in other systems and has been demonstrated in plants across the Earth's major biomes (Reich et al., 1999; Wright et al., 2004). Functional traits of species, therefore, can serve as guidelines for where they should be planted across environmental gradients.

Perhaps more interesting is the evidence for a biotic filter that emerges when the phylogenetic structure of these communities is examined. Across a fertility gradient, the number of woody species occurring in a 0.10-hectare (ha) plot increases with soil fertility until a saturation point is reached while the number of oak species is capped at three, regardless of habitat (Cavender-Bares et al., 2004b). This indicates that there is a limit to the number of oak species that can co-occur irrespective of the physical environment, and this number may be linked to the phylogenetic diversity in the group. There are three major clades that occur in this region: red, white, and live oaks. The white oaks and live oaks together form a clade that is sister to the red oaks. Comparing observed co-occurrence patterns of species to null models, in which species distributions were randomized, we found that the oak species were phylogenetically overdispersed (Cavender-Bares et al., 2004a). Statistically, this means that closely related oak species (those within the same clade) are unlikely to co-occur within the same 0.10-ha plot while oak species from different clades are more likely to co-occur than expected by chance. In other words, only one member from each of the major clades was likely to occur in any given plot. The pattern of phylogenetic overdispersion is a result of the evolutionary history of the group in which the oaks appear to have adaptively radiated into contrasting soil moisture and fire regimes (Cavender-Bares et al., 2004a). As a result, there is considerable functional diversity among species within the same clade, and functional traits important for habitat specialization show convergence among distantly related oaks. The overdispersion of close relatives may prevent competitive exclusion or reduce density-dependent mortality because of clade-specific pathogens (Webb et al., 2006; Gilbert and Webb, 2007). It may also reduce introgression of close relatives (Cavender-Bares et al., 2009).

The so-called "phylogenetic repulsion" (Webb et al., 2002) of close relatives has important implications for community restoration. Density dependent processes, such as disease and competition, may prevent the long-term coexistence of close relatives, and highest-diversity, oak-dominated communities may be realized when communities are drawn from distantly related oaks. Maximizing phylogenetic diversity, even within a single lineage such as the oaks, may, therefore, be an important restoration goal. With the availability of tools and data for phylogenetic analysis, simple metrics to determine phylogenetic structure and diversity of communities are readily accessible (e.g., Webb et al., 2005; Webb et al., 2008, reviewed in Vamosi et al., 2009; Cavender-Bares et al., 2009).

In a subsequent study, we asked whether only the oaks were structured in this manner or whether all plant species showed non-random distributions. We found that when all plant taxa were included in the analysis, species showed phylogenetic clustering (Cavender-Bares et al., 2006). In other words, closely related species that shared many functional traits in common were more likely to occur together than expected by chance. This pattern resulted from a matching of functional traits to the environment and conservatism of traits through evolutionary history. Within communities, species' traits were more similar than expected by chance. We did not find definitive evidence that other groups of close relatives (such as pines or hollies) were overdispersed. Several other research teams, however, have found evidence for phylogenetic overdispersion among speciose clades in which the member species occur in the same region (Slingsby and Verboom, 2006). These results suggest that both environmental filtering and species interactions are important in structuring communities but at different scales. At small spatial scales and among close relatives, evidence for species interactions emerge. At large spatial scales and among diverse taxa, evidence for matching of phenotypes to the environment is apparent. These results do not preclude the importance of stochastic processes and historical contingency in influencing community assembly. They do show, however, that many plant species in Florida have specialized for particular environments and that environmental filtering plays an important role in community assembly.

Phylogenetic Diversity and Ecosystem Function

The phylogenetic structure of communities shows promise for predicting ecosystem processes and properties that may be targets of ecological restoration. There is increasing evidence that phylogenetic diversity is linked to ecosystem function in plants (Maherali and Klironomos, 2007; Cadotte et al., 2008; Cadotte et al., 2009). In both plant and plant-mycorrhizal communities, studies have demonstrated that phylogenetic diversity can predict community productivity better than species richness or functional group diversity. These studies provide support for the hypothesis that phylogenetically diverse communities can maximize resource partitioning and hence use greater total resources. This is based on evidence that the more differentiated species are the greater their resource exploitation (Finke and Snyder, 2008). If phylogenetic relatedness predicts ecological similarity, phylogenetic diversity should

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enhance complementarity and increase ecosystem productivity by maximizing total resource uptake. By the same logic, high phylogenetic diversity may be predicted to increase ecosystem stability by ensuring that sufficient ecological strategies are represented in an assemblage to ensure persistence of the ecosystem in the face of changing conditions. Similarly, phylogenetic diversity may be linked to nutrient cycling, resistance to invasion, soil carbon accumulation, and other ecosystem processes, goods, and services (Cavender-Bares et al., 2009). Such links, if they continue to be substantiated, support the argument that phylogenetic diversity has higher utility than species richness as a conservation criterion for management decisions (Faith, 1992; Gerhold et al., 2008).

Restoration of Vascular Plant Communities on Degraded Land

Restoration efforts are often directed at areas that have been severely degraded or affected by mining activity. Such is the case at The Wilds, a 3,700-hectare center for conservation research and education located on reclaimed strip-mined land in Muskingum County, Ohio. Mining for coal began on these lands in the 1940s and was completed by 1984. The process of coal extraction requires the complete removal of vegetation, topsoil, and rock, so that the coal seam can be exposed and extracted on the surface.

A majority of what is now The Wilds was coal mined by the Big Muskie, the world's largest coal mining dragline. Following coal extraction, much of the reclamation included replacement of rocky overburden and topsoil, grading, and shaping to the approximate original contour of the land followed by re-vegetation.

Although the land at The Wilds before European settlement was deciduous hardwood forest, re-vegetation efforts for reclamation included planting cool-season, non-native grasses and legumes. The area of The Wilds has now been recovering from this disturbance for more than two decades, but it remains extremely altered from its original state and has associated environmental problems. Loss of the native seed bank and microflora, severe soil compaction, low nutrients, and presence of invasive species all must be addressed while attempting restoration.

In ecosystems that have been dramatically altered and have crossed the threshold of irreversibility, it becomes important to consider the landscape context. The site, such as the one described, holds restrictions to what can actually be achieved, and it is extremely difficult to target historical references. It, therefore, becomes necessary to set ecosystem functional goals that can be achieved in a shorter time frame. Historical references can be used to set long-term goals, but more short-term goals such as increasing biodiversity, phylogenetic diversity, improving soil structure, and enhancing wildlife become more realistic targets in early restoration. Computation tools that allow analysis of phylogenetic diversity (methods reviewed in Vamosi et al., 2009 and Cavender-Bares et al., 2009) may provide a useful approach for measuring and monitoring indicators linked to functional goals.

As an example, in 2003, a large-scale restoration effort began at The Wilds with the intention of improving components of ecosystem function, habitat quality, and

Table 5.1 Changes in Species, Family, and Phylogenetic Diversity Before and After Restoration in Reclaimed Mine Land in Southern Ohio

Time Period	<i>n</i> Species	<i>n</i> Vascular Plant Families	Sum of Branchlengths (my)	Phylogenetic Diversity (Faith's PD Index)	Mean Phylogenetic Distance Between Species Pairs
Before	18	11	581	0.218	84.17
After	93	30	2,621	0.984	87.08

biodiversity. Two major goals included improving vascular plant diversity and increasing the butterfly populations. Invertebrates are essential to self-sustaining ecosystems and can be useful to measure restoration success (Webb, 1996; Majer, 1997; Wheeler and Cullen, 1997; Halle and Fattorini, 2004). Butterflies, and pollinators in general, have shown major declines in recent years, and increasing their numbers and richness was an essential goal to the project. With their dependence on a wide variety of plants for various stages of their life cycle, increasing plant diversity became an important driver for this restoration project.

Before restoration activities began, the site comprised mostly cool-season, non-native grasses with few high nectar-generating plants (**Table 5.1**). From 2003 to 2007, a variety of herbaceous plant species, mostly native to Ohio, were introduced by seed using a no-till drilling technique and hand broadcasting. Many of the herbaceous species chosen for augmentation included those adapted to tallgrass prairie ecosystems. Because prairie species develop deep and fibrous root systems, they may be better adapted to poor and compacted soils and improved soil organic matter structure (Burke et al., 1995; McLauchlan et al., 2006; Matamala et al., 2008).

A long-term monitoring transect was established simultaneously with vegetation augmentation to monitor butterfly activity. An 870-m transect was established throughout 6 hectares of habitat following the methodology used by The Ohio Lepidoptera Society's Long-term Monitoring Program (adapted from Pollard and Yates, 1993). This fixed transect was mowed regularly and divided the site into sections according to habitat changes, so that observations could be made according to location and habitat. The transect was surveyed for butterflies weekly from early spring through late summer (2004–2007), and observations were made including the presence of vascular plants.

During the initial four years of restoration, perennial vascular plants increased from 11 species to 93, and vascular plant families increased from 11 to 30. A hypothesis of the phylogenetic relationships of species was generated using Phylocom (Webb et al., 2004). Faith's phylogenetic diversity index increased from 0.218 to 0.984 demonstrating a dramatic increase in vascular plants across the tree of life, indicating that not only

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Table 5.2 Total Butterfly Species Richness and Average Individual Butterfly Counts Surveyed Over a 23-Week Period Between 2004 and 2007

Monitoring Year	2004	2005	2006	2007
Species Richness	26	23	37	33
Average # of Individuals	653	787	1,403	2,138

were more species represented in the system but also more evolutionary innovations must be represented. The phylogenetic distance between any two species in the system also increased (largely due to the colonization of a conifer, *Taxodium distichum*) although not significantly post-restoration. This indicates that species accumulated (both through management and from the regional pool) and occurred in a consistent and random manner from across the vascular plant phylogeny. Thus, while species were selected for management and are likely to have persisted in the system based on adaptive functional traits, the new species were not highly concentrated in any particular evolutionary clade. This highlights the diversity of functional strategies that persist in the same environment. In studies of the economic spectrum of plant traits (Wright et al., 2004), for example, a high proportion of the total variance in the functional attributes of plants is found at the same site.

At the beginning of the restoration project an average of 653 butterflies were recorded, a 227% increase, and butterfly species richness had increased by 42% (**Table 5.2**).

Restoration activities are ongoing at the site with goals of restoring more than 80 hectares primarily for enhancing pollinator habitat. Although the restoration project is still developing, the integration of monitoring tools such as vascular plant and butterfly diversity and phylogenetic diversity provide guidance in meeting restoration goals in both the short and long term.

Conclusion

The non-random structure of oak-dominated communities, both in terms of the phylogenetic relatedness of species within communities and in the degree to which traits match the environment, indicates that deterministic processes are at play in assembly of these communities. Understanding the filters that are operating in a community and the traits that are critical for establishment can serve the goals of restoration ecology. The matching of functional traits to the environment, particularly hydraulic architecture of plants, indicates that specific microsites should be selected for planting individual species. In north central Florida, attention should be paid particularly to the fire regime and the hydrology, a notion well understood by the Florida Park Service. Ongoing restoration efforts rely heavily on prescribed burning to maintain fire-dependent communities. Floridian plant communities also provide an example of how community structure can be understood in an evolutionary context

(Cavender-Bares and Wilczek, 2003). The repeated pattern of phylogenetic overdispersion among the oaks indicates that local coexistence among members of different clades is more likely than among members of the same clade. As a result, phylogenetic overdispersion of close relatives has specific implications for restoration of oak-dominated communities. High diversity should be expected to persist in the long term only when distantly related oak species, rather than closely related species, are planted together.

In degraded lands where novel communities must be created *de novo* to improve land and habitat quality, the emphasis is less on restoration of specific community types. Here, as well, phylogenetic structure can provide guidance in meeting ecological goals. In restoration efforts at The Wilds, a dramatic enhancement of phylogenetic diversity in vascular plants, incorporating species with a diversity of rooting depths and resource use strategies, has improved soil structure and ecosystem productivity. It has also led to a significant increase in the diversity and population sizes of other trophic levels including butterflies. Together, these case studies highlight the importance of matching functional attributes of plants to the environment and the restoration successes achieved in maximizing functional diversity in degraded land. Links between functional and phylogenetic diversity are complex (e.g., Prinzing et al., 2008; Cavender-Bares et al., 2009; Cadotte et al., 2009), but they reinforce their importance as conservation criterion. Inclusion of phylogenetic structure and diversity as an indicator for monitoring progress in ecosystem restoration is an emerging and promising approach.

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Key Terms

Alternative stable states	106	Ecological resistance	105
Ecological constraints	105	Ecosystem threshold	113
Ecological drift	114	Nexus species	112
Ecological filters	113	Perturbation	117
Ecological resilience	117	Regime shift	105

Key Questions

1. Describe the main predictions of the equilibrium theory of island biogeography.
2. Define the terms *ecological resilience* and *resistance*.
3. How can ecological constraints curtail restoration efforts?
4. Define factors that regulate regime shifts.
5. What implications do assembly rules have on restoration ecology?
6. What are the main differences between assembly rules and the UNTB?