# 5

# ASSEMBLY

## Chapter Outline

Facilitating succession or assembly of a functional and integral eco-system after disturbances is an important task of ecological restoration. Various ecological models have been used in these restoration processes. These models can predict changes in community composition with time and therefore aid in the restoration work. Some models have background in community ecology, whereas others are derived from biogeography. These include the deterministic model of succession (sensu Clements), the individualistic model of succession (sensu Gleason), and assembly models (sensu McArthur and Wilson and Diamond).

Succession models in particular have provided the theoretical framework for restoration of plant communities, as discussed in Chapter 4. These models have mainly been applied on terrestrial ecosystems. On the other hand, restoration of aquatic ecosystems has put much more emphasis on assembly models, which consider the possibility of alternative ecosystem states instead of only one final "climax" community. Recently, assembly models have been applied successfully in the restoration of terrestrial ecosystems. Many basic aspects underlying assembly models, such as the importance of arrival time of species to a new site in determining an alternative ecosystem state, are already incorporated in various succession models. The emphasis of succession models, however, is on the trajectory leading to a climax community, or final state whereas assembly models demonstrate the possibility of various different endpoints.

Restoration ecology benefits from using assembly models to consider the possibility of multiple stable states instead of one final state. Another practical aspect of assembly models in restoration work is to consider ecological constraints and especially what actions are needed to relie degraded states to move along an assembly trajectory toward a desirable ecological end state.

## 5.1 Equilibrium Theory of Island Biogeography

The equilibrium theory of island biogeography was proposed by Robert MacArthur and Edward O. Wilson in 1967 and has since had a profound impact on ecology, biogeography, and conservation biology. The equilibrium theory also has strong implications for restoration ecology. MacArthur and Wilson used the gradual colonization of offshore islands derived from a mainland source as a model system for community assembly. In essence, their work predicts that the number of species on offshore islands is based on a balance between the rate of random dispersal of colonizing species from the mainland and the rate of random local species extinction on the islands (**Figure 5.1**). The model, therefore, describes community assembly mainly as a result of random immigration and random local extinction. An important aspect of the model is that it assumes all species have the same probability of dispersal to an offshore island as they do to facing local extinction. The main parameters of the model are

1. Distance of the islands from the mainland determining the dispersal rate of new species

2. Size of an island determining the rate of species extinction

In practice, large islands close to the mainland are more likely to experience higher numbers of immigrating species and lower extinction of species than small islands. The opposite effect increases the farther the small islands are from the mainland. The size of these islands and distance from the mainland,
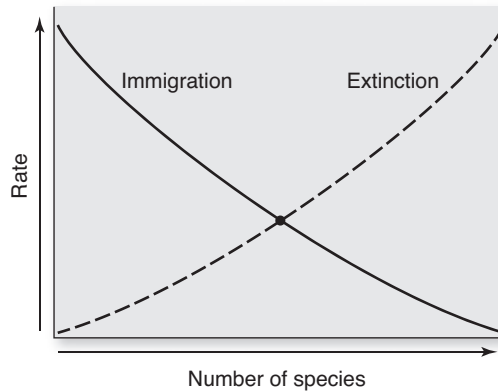
**Figure 5.1** Model of equilibrium theory. Equilibrium in community assemblages is formed by the rate of immigration and extinction.

therefore, determine the number of species that exist there in a flux. Such random community assembly does not imply that these colonizing species are necessarily coadapted or preadapted to specific niches on the new site. The equilibrium theory does provide, however, a powerful insight into community assembly by emphasizing a few factors such as random dispersal and colonization resulting in random assemblages of species derived from the mainland source. It is assumed that random dispersal processes alone play an important role in structuring communities.

The prediction of the equilibrium theory is similar to Gleason's individualistic model of succession. The "individualistic model" of succession assumes that community composition is the result of a random process influenced by the availability of vacant niches and species dispersal. The individualistic model is analogous to a carousel where seats become vacant randomly and are filled by nearby passengers (that represent different species).

Practical uses of the equilibrium theory have been extended to conservation biology, especially to predict extinction rates of species in parks or nature reserves. At the same time the model has been used to predict the necessary size of reserves and need for restoration, buffer zones, and connectivity between fragments to facilitate species dispersal into parks and reserves where the goal is to avoid species extinctions. These factors (size and connectivity) are probably more important to avoid species extinction than protection alone. In fact, most nature reserves are too small to fully support biodiversity conservation in the long run. Large nature reserves are needed to inhabit large predatory animals that roam over huge territories. Such animals are often keystone species that influence functioning of large ecosystems. Restoration sites by themselves are often small and isolated away from pristine or larger intact habitats that can act as a source of colonizing species. Such sites must be effectively connected in the local landscape

**Figure 5.2** Model showing community assembly as colonization by stepping-stone process. (Adapted from V. M. Temperton, et al. (eds.). *Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice.* Washington, DC: Island Press, 2004.)

(discussed in Chapter 6). In practice, fragments of pristine landscape can be viewed as islands of intact habitat surrounded by a human-dominated landscape, such as agricultural lands, industrial parks, and urban and suburban areas. Restoring connectivity to facilitate dispersal rates of species can potentially restore functioning of such fragmented landscapes.

The equilibrium theory incorporates dynamic aspects of colonization. For example, in the mainland–island scenario offshore islands are colonized as stepping stones (i.e., species jump from one island to another) (**Figure 5.2**). The island that is closest to the mainland receives the highest number of immigrants from the mainland. However, colonization of islands that are farther away from the mainland depends on the species assemblage of the first island. The island farthest away from the mainland consequently has fewer immigrating species than the first island. Similarly, restoring connectivity between isolated fragments can be restricted or limited by dispersal distance from a source site and therefore create a dispersal barrier. In practice, such dispersal barriers can be alleviated by strategically restoring habitat patches to be "stepping stones" in the landscape.

## 5.2 Ecosystem Resilience and Stability

### Resilience

Ecosystems can usually recover after mild disturbances. The time it takes an ecosystem to recover after a disturbance to its predisturbance ecological condition is termed resilience (see **Case Study 5.1** on page 116). Resilience is also defined as the amount of disturbance (frequency and duration) that an ecosystem can tolerate without causing a regime shift. Ecosystems vary in their resilience in that some recover rapidly after disturbances, while others need much longer time and may even require restoration efforts to do so.

Loss of resilience can trigger a shift to another ecological state. To avoid undesirable regime shifts in communities, the most pragmatic strategy is to restore and maintain resilience of the desired ecosystem conditions, in which various strategies can be used. Such efforts include increasing biodiversity (especially by increasing the number of species in diverse functional groups), controlling invasive species, and regulating disturbances that contribute to a shift in

ecosystem state. Disturbances that provoke a shift in ecosystem state are usually stochastic and include climate extremes (strong storms, exceptional droughts), fires, eutrophication, and disease outbreaks. It is usually difficult to predict or control such disturbances. An alternative restoration strategy, therefore, is to put the emphasis on the resilience or the ability of the ecosystem to recover rapidly after any disturbances.

It is not unusual for a degraded ecosystem to show resilience to restoration efforts. To diminish this resilience, ordinary restoration efforts such as soil nutrient management or introduction of keystone native species can be used to facilitate a **regime shift** to a more desirable state. Restoration strategies should therefore focus on factors that induce a shift from a less desirable to a more desirable ecological state along assembly trajectory.

## Resistance

Ecosystems can respond to disturbances by resisting ecological changes altogether. This is termed **ecological resistance**. In such a setting an ecosystem showing high resistance can be stable even while being frequently disturbed. An important task of restoration efforts is often to inhibit disturbances that may lead to ecosystem degradation. An alternative restoration strategy is to increase the resistance of the ecosystem instead of focusing only on inhibiting disturbances. This can be achieved, for instance, by restoring diversity of plants in diverse functional group. Doing so may increase the resistance of the ecosystem.

## Stability

Ecological stability depends on various factors that change slowly, such as biodiversity, nutrient levels, soil properties, and existence of long-lived organisms. Many of these factors may be monitored and restored if needed to maintain stability. The importance of biodiversity for ecosystem stability was demonstrated by Tilman's field experiment on a prairie community in Minnesota. In his experiment biodiversity was manipulated and plots with high biodiversity were most stable under adverse climatic conditions.

## Ecological Constraints

Disturbances and factors of degradation that are responsible for maintaining certain ecological conditions are termed **ecological constraints**. These include, for instance, invasion of non-native species, dispersal barriers, lack of available nutrients, eutrophication, habitat fragmentation, and loss of keystone species. Degraded ecosystems may have shifted to a new alternative state that cannot be easily restored to predisturbance conditions. An example of such a degraded ecosystem can be found in overgrazed semiarid grasslands that are invaded by shrubs. Here, decreasing grazing pressure of livestock may not be efficient in restoring the grass-dominated ecosystem. Restoration of such a degraded ecosystem often requires massive efforts, such as mechanical eradication of shrubs

followed by ground stabilization and introduction of native grasses. Non-native species in a degraded ecosystem can represent another example. In this case the frequency and intensity of ecosystem processes such as fire regime, nutrient cycling, and hydrology might be permanently altered.

To restore degraded ecosystems it is important to identify ecological constraints and feedbacks that maintain the degraded conditions. Restoration efforts can release degraded systems from such constraints. This work might involve reducing grazing pressure; overcoming dispersal limitations by seeding native species, introducing keystone species; manipulating soil fertility; eradicating non-native species; and implementing other necessary restoration efforts.

Restoration of degraded ecological conditions to a more desirable state probably follows a different sequence than did the degradation process itself. For example, in ecosystems where eutrophication is a constraint, a perturbation program of nutrient exhaustion can be implemented. Mowing and biomass removal of alpine grasslands in Switzerland is, for instance, used effectively to exhaust nutrients to maintain high biodiversity of these grasslands.

Successional trajectories have often been unpredictable and controlled simultaneously by several different ecological constraints. Restoration efforts might, therefore, need to simultaneously manipulate multiple ecological constraints in a strategic way. Such manipulation is needed over a long period of time to direct the desirable assembly trajectory. These may include, for instance, the establishment of natural fire regime, nutrient cycling, and introduction of native plants. For example, restoration of heathlands in northern Europe involves the manipulation of abiotic and biotic constraints. In these cases the abiotic constraints were eutrophication and acidification, whereas biotic constraints were dispersal barriers and impoverished soil seed bank. Simultaneous manipulations of these constraints resulted in effective restoration of heathland ecosystems.

## 5.3 Alternative Stable States

Succession is often found to be unpredictable. Instead of ending in a single stable community, the climax, it may result in different endpoints, also termed "alternative communities." In fact, these different alternative communities have been considered as variations on successional trajectories (**Figure 5.3**). These variable outcomes of succession have been recognized and termed as arrested succession, polyclimax, metaclimax, and disclimax. **Alternative stable states** exist as a result of several ecological factors such as random species dispersal and colonization. This strong impact of early colonizing species on the community is termed "historical contingency." Once early arriving species are established, they can inhibit or delay colonization by other species and therefore maintain a characteristic ecological state. The stability of some alternative stable states can be explained by the fact that the dominating plants are clonal, form dense stands, and are long-lived. For instance, aspen (*Populus* sp.) and coastal redwoods (*Sequoia sempervirens*) can form such ecosystems.
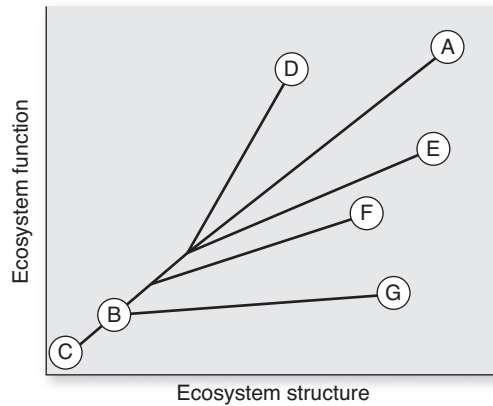
**Figure 5.3** Model of alternative stable states with various endpoints as results of different assembly trajectories. (Reproduced from *Assembly Rules and Restoration Ecology* edited by Vicky J. Temperton, Richard J. Hobbs, Tim Nuttle and Stefan Halle. Copyright © 2004 by Island Press. Reproduced by permission of Island Press, Washington, D.C.)

## Regime Shift

The existence of alternative stable states and regime shift between states is regulated by disturbances and has been identified in several ecosystems (**Figure 5.4**). Disturbances such as grazing pressure can regulate regime shift. For example, in rangelands a grass-dominated state can shift to a shrub-dominated state due to change in grazing pressure. Also, mountain birch (*Betula pubescens* sp. *czerepanovii*) forests in northern Scandinavia can exist in several states characterized by the dominance of the understory species. Even regime shifts between some of the most dominant states have been observed, for example, the shift between a lichen-dwarf, shrub-dominated forest to a more grass- and herb-dominated forest. Transition between these alternative states of the mountain birch forest was regulated by grazing and browsing of reindeer stocks. Such intensive reindeer grazing can further promote regime shift by transforming, for example, lichen–moss-rich heath tundra into grass–sedges-dominated tundra vegetation.

Regime shift between alternative ecological states can also be regulated by fire; for example, forests of northeast Florida can exist in two alternative states. The first state is characterized by pyrogenic longleaf pine (*Pinus palustris*) with open savanna. The second state is characterized by mesic oak (*Quercus* sp.) forest. Longleaf pine and oak show different responses to fire. Longleaf pines are adapted to frequent low-intensity ground fires. In fact, mature longleaf pines shed pyrogenic needles that promote such ground fire. Increased cover of pines leads to an increased number of pine needles on the ground that, in turn, promotes fires. The pyrogenic pine needles accumulate on the forest floor until
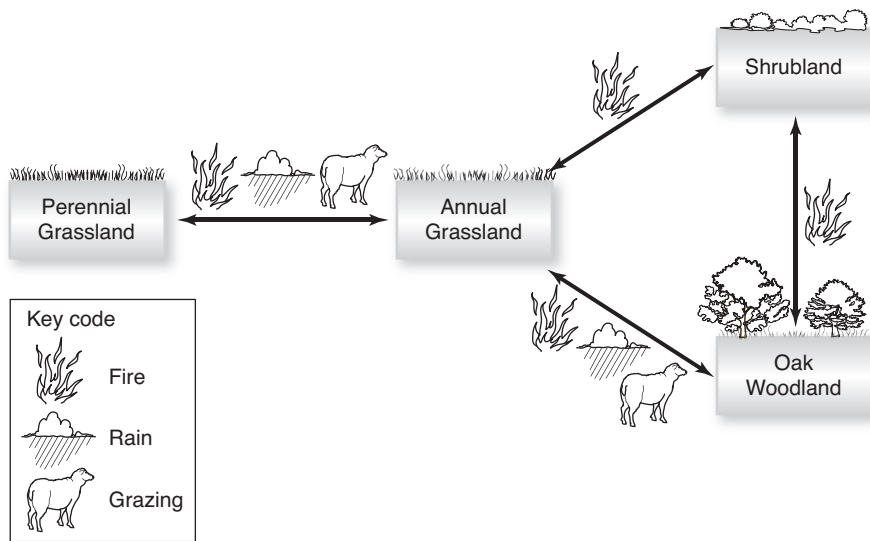
**Figure 5.4** Model of alternative states in Californian grasslands. Switches between states are shown by arrows. (Adapted from V. M. Temperton, et al. (eds.). *Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice.* Washington, DC: Island Press, 2004.)

a critical threshold is passed and a ground fire can break out (usually initiated by thunderstorm lightning). In contrast, young oaks are intolerant of fire, and mature oaks shed leaves that suppress ground fires. Both species, therefore, give positive feedback for further growth. In the absence of fire oaks eventually replace longleaf pine in the forest. However, low frequency of fire suppress oak growth or even eliminate them altogether, allowing longleaf pine to dominate the forest. In this ecosystem fire regulates the "switch" (also known as hysteresis) or regime shift between two alternative states. Here, the desired ecosystem state can be restored by using prescribed burning or fire suppression as a restoration tool. Another example of how fire can induce regime shift is the gradual conversion of heathlands in northern Europe into forests due to fire suppression. Restoration of heathland communities requires intensive fire that consumes the surface organic layer.

Eutrophication of terrestrial ecosystems has already caused regime shift in numerous places. Nitrogen deposition has done just that in wet heathlands in the Netherlands. These wet heathlands were previously dominated by bog heather (*Erica tetralix*) but have now been replaced by purple moor-grass (*Molina caerulea*). The restoration effort of these wet heathlands now focuses on removing top soil that has been overloaded with nitrogen. In addition, liming has improved the acidity of the soil.

In shallow lakes, regime shift between alternative states can be regulated by eutrophication and, especially, excess phosphorus loading. Such regime shifts are

(a)



(b)

**Figure 5.5** Alternative states of shallow lakes; clear **(a)** and murky **(b)** waters.
(Part a © Stanislav Komogorov/ShutterStock, Inc.; part b © Justforever/Dreamstime.com.)

common where clear water state dominated by aquatic plants is transferred to murky water state dominated by phytoplankton (algae) along with other ecological changes (**Figure 5.5**). Shallow lakes can rapidly shift from clear to murky states with each state being relatively stable. Curtailing eutrophication is most often not enough, however, to restore the clear water state of a lake. In the clear water state, sediments are stabilized by aquatic plants. The murky water state persists in the absence of aquatic plants due to waves that resuspend sediments. The murky waters decrease light penetration in the water column and, in turn, curtail the establishment of aquatic plants. Restoration of the clear water state involves biomanipulation. This involves implementing selective fishing that decreases

the size of populations of planktivorous fish. When this is accomplished, an increase in populations of herbivorous zooplankton follows and, in turn, leads to a reduction in phytoplankton (algae) populations and increased light penetration through the water column. Increased light penetration facilitates establishment of aquatic plants, which stabilize sediments. Conversely, shifts from a clear to a murky water state can also result from overgrazing of aquatic plants by fish or waterfowl. It is noteworthy, then, that the disturbances that induce regime shift do not necessarily have similar impacts in the opposite direction. Considerable restoration efforts are usually needed to establish a clear water state of a shallow lake. In this context the nutrient levels of the lake need to be brought to a substantially lower level than the predisturbance clear water state of the lake. This is often accomplished by mechanically dredging nutrient-rich sediment and removing it from the lake.

In any restoration effort it is important to identify factors that regulate regime shift to alternative states. For this purpose a plan that outlines restoration efforts that can shift less desirable conditions to more desirable ones should be in place. Considering the possibility of multiple stable states along an assembly trajectory, restoration efforts need to be selected carefully to obtain the most desirable ecological endpoint. Using the passive restoration approach may return the degraded ecosystem to its predisturbance condition with little effort. Alternatively, the active restoration approach may be required to ensure agreeable results.

Models of alternative ecosystem states can be used to guide restoration of degraded conditions of an ecosystem. This is especially important where switches that regulate regime shifts have been identified and can be manipulated. The fact that a degraded ecosystem can possibly regenerate along an assembly trajectory to several different multiple stable states, any one of which has desired end points, has strong implications for restoration. The possibility of alternative stable states puts emphasis on tight monitoring and continuous active restoration efforts. This involves an initial restoration effort such as planting a variety of native species and should then be followed by intensive restoration activities as the ecosystem moves along the assembly trajectory.

## Restoring Alternative Stable States

In planning restoration work the existence of multiple stable states requires the use of well-defined reference sites (see Chapter 14). Considering the possibility of multiple ecological states, the definition of reference sites may involve several choices, therefore, becoming a moving target along assembly trajectory.

Restoration efforts can be used to shift a degraded ecosystem to another more desirable one, for instance, by alleviating dispersal barriers of species into restoration sites. As outlined earlier, the tight control of species' arrival on site is important because it can be a determining factor in the community assembly. Additionally, dispersal barriers can result in a lack of native species that are critical for succession on restoration sites. In this regard dispersal barriers often serve only to maintain a certain ecological state. To overcome such dispersal

barriers of keystone species, ordinary restoration efforts can be put into place, such as transplanting or direct seeding of these species on restoration sites. This is often followed by restoration efforts that aim at enhancing the establishment of these species on sites (i.e., nutrient additions or elimination of non-native species). Building perches on restoration sites for birds or bats, for example, increases seed dispersal. In practice, the restoration of prairie communities has been accomplished successfully by interseeding a mixture of native species (without any soil preparation) that are missing from the restoration sites. This step relieves dispersal barriers and also allows rare prairie species to establish themselves in the community. An alternative strategy might include the management of surrounding landscapes (i.e., building stepping stones or corridors) to alter seed pools and dispersal vectors, thus facilitating the establishment of desired species and therefore reducing dispersal barriers. Such efforts help in overcoming dispersal barriers of species that otherwise would not be able to colonize by natural means on isolated restoration sites.

## 5.4 Assembly Rules

Assembly rules were pioneered by Jared Diamond in 1975 in his study on bird communities of New Guinea, where characteristic assemblages of birds were observed in different habitats. Assembly rules are an alternative to the commonly used succession model in restoration (see Chapter 4). They predict that active restoration involving intensive control over species establishment within a restoration site is critical for attaining the final ecosystem state. On the other hand, restoration efforts that rely on succession models have traditionally focused on the final ecosystem state, determined by a selected reference site. Assembly rules are analogous to jigsaw puzzles and their intricately shaped, interlocking pieces; predicting that only certain species combinations are possible in each habitat. These species assemblages represent alternative stable states, as discussed previously.

Assembly rules make several important assumptions. First, they assume that communities are niche assembled. Second, unlike the deterministic model of succession with emphasis on the climax community, assembly rules assume that degraded ecosystems will not necessarily return to the original ecological state because the order of species colonization affects the final ecosystem state. Third, assembly rules predict that communities are relatively stable and not easily invaded by other species (native or non-native) (**Figure 5.6**)

### Sequence Introduction

Assembly rules predict that appropriate species combinations must be introduced sequentially to a restoration site. Introducing many species simultaneously to a restoration site might lead to competitive exclusion and should be carefully examined. Because the order of species colonization affects the final ecosystem state, assembly rules can be used to predict the sequence of species
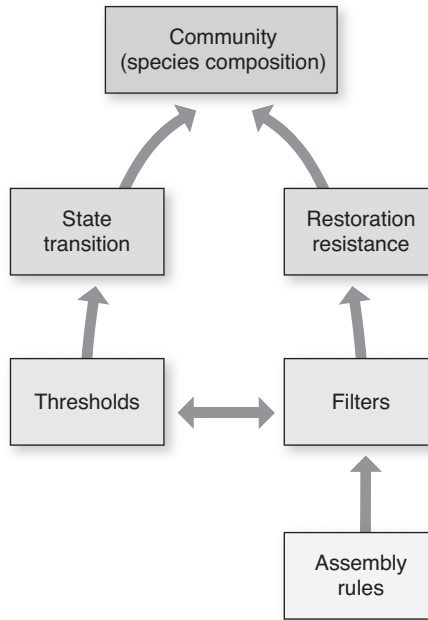
**Figure 5.6** Interrelationships among the concepts of assembly rules. (Reproduced from *Assembly Rules and Restoration Ecology* edited by Vicky J. Temperton, Richard J. Hobbs, Tim Nuttle and Stefan Halle. Copyright © 2004 by Island Press. Reproduced by permission of Island Press, Washington, D.C.)

colonization on a restoration site toward the final ecosystem state. For instance, on a derelict mine site, tolerant species can be introduced to ameliorate the microenvironment. These are followed by introducing mid- and late-successional species, but only after appropriate microenvironmental conditions are reached. Similarly, on deflated coastal sand dunes plants are introduced strategically in a sequence to restore the dune ecosystem (see Chapter 9). Because of the emphasis of assembly rules on species arrival time for the final ecosystem state, intensive management of the critical sequence of species introduction is needed for restoration to be successful.

Assembly rules also assume that species characterizing the final (climax) community should not necessarily be introduced in the beginning of the restoration process. There may also be species essential in the initial restoration process other than those found in the desired final community. In fact, keystone species that are the driving force in determining the assembly trajectory often disappear from the community before the final state is reached; these species are termed **nexus species**. Nexus species are important in determining which alternative state the community will reach. Such species play a very important role in the ecosystem. For instance, they can stabilize soil conditions, fix nitrogen (legumes),

or provide habitat for birds that increase seed dispersal on sites. An important task of restoration efforts should therefore be to strategically introduce nexus species into degraded ecosystems along the assembly trajectory.

## Species Compatibility

The assembly process requires "adaptive management" (see Chapter 14) where the compatibility of different species combinations is carefully examined. Assembly rules assume that only certain combinations of species can coexist in a particular community (the jigsaw puzzle analogy). The use of assembly rules in restoration efforts should help in predicting which combination of species coexist in a given habitat on restoration site. Species combinations should therefore be selected from a regional pool for certain environmental conditions, habitats, or successional phases (i.e., early, mid, or late). Assembly rules also suggest that large prey and predators be introduced together, as should symbiotic mycorrhizal fungi and mycorrhizal-dependent species, appropriate nitrogen-fixing symbiotic bacteria and legumes, and so on.

## Ecosystem Thresholds

Important components of assembly rules are **ecosystem thresholds**. These represent certain conditions that prevent regime shift from degraded to less degraded ecological conditions. A restoration effort is therefore needed to manipulate thresholds and transform the ecosystem to a more desirable state. This usually includes both ordinary restoration efforts and long-term aftercare. Biotic and abiotic factors can be responsible for the ecosystem thresholds. Biotic thresholds include heavy grazing pressure and lack of native species in the local seed pool. Abiotic thresholds include soil degradation and changed hydrology. In the restoration process itself, it is important to identify thresholds and methods to manipulate their effects. Of course, ordinary restoration methods can still be used to overcome restoration thresholds. For instance, if overgrazed and degraded rangelands cannot shift to less degraded ecological conditions due to soil compaction, massive restoration efforts, such as effective soil ripping to increase water infiltration, are needed. This example demonstrates how manipulation of ecological thresholds can be used effectively to restore ecosystem functioning.

## Ecosystem Filters

The environmental conditions of a restoration site dictate which species can occupy a particular habitat; these are termed **ecological filters**. Only species preadapted to the environmental conditions of a site can establish successfully (see **Case Study 5.2** on page 119). Ecosystem filters are responsible for selecting species out of a regional pool that are appropriate to occupy a site. For instance, a landslide within a forest creates a barren site and will only provide a niche for a limited number of forest species that are preadapted to disturbed sites. This

landslide therefore acts as a filter. Restoration efforts should focus on manipulating filters to facilitate and fasten a desirable species combination toward the final state. This work should ideally come at the same time as thresholds are being manipulated. Both abiotic and biotic filters are critical in this process.

Abiotic filters might include climate, soil type, and landscape structure (patch size and isolation). Biotic filters might include competition, predation, trophic interactions, propagule availability, mutualisms, and order of species colonization. Restoration efforts should include modification of abiotic filters such as remediation of toxic soil and improving nutrient status of soil. Concurrently, modification of biotic filters might include introducing native species on restoration sites or controlling invasive species (weeds and non-native species). Such modifications should enhance a regime shift from a degraded to a more agreeable ecological state.

## 5.5 Unified Neutral Theory of Biodiversity and Biogeography

The unified neutral theory of biodiversity and biogeography (UNTB) was recently proposed by Stephen Hubbell. In essence, the UNTB is an extension on the equilibrium theory of MacArthur and Wilson. According to the UNTB, community composition is determined by regional biogeographic processes such as random species dispersal, ecological drift, random speciation, and extinction without any role of special niche assembly. **Ecological drift** refers to random fluctuations in species abundances. The UNTB predicts that species are equal in their ability to colonize sites, and random processes structure communities that exist in a flux. Stochastic processes affecting communities are therefore at central importance in the UNTB.

The UNTB is based on a zero-sum game that is neutral and played by individuals that are identical in their functioning in the community (**Figure 5.7**). In a zero-sum game species can only increase in abundance if other species in the community decrease in abundance. The UNTB assumes that as vacant niches become available in the community they are filled up randomly without any special pre-adaptation or niche requirement. This is in contrast to the conventional view of community assembly where species are assumed to be preadapted to a specific niche.

One of the best ways to test the predictability of UNTP is to use the mainland and nearby island model system in community assembly. It is assumed that species in such a scenario would experience ecological drift, random colonization, local extinction, and adaptive radiation where new species arise.

A study on the forest assemblages of three small islands with similar environmental conditions found in the Bay of Panama, Central America, has collaborated predictions of the UNTB. These islands were once connected to the mainland when sea levels were much lower than what they are today. It is assumed that these islands harbored similar communities when they were connected. As the islands became isolated, ecological drift, local extinction, and
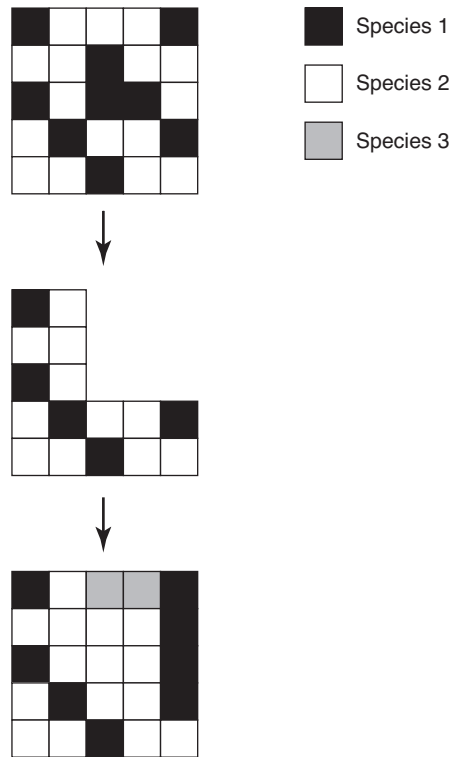
**Figure 5.7** Model of a zero-sum ecological drift. New species can only enter in the community if abundance of existing species decreases.

random colonization would probably have affected the community composition of each island. Interestingly, each island now has different assemblages of dominant tree species despite similar environmental conditions. These findings are consistent with prediction of the UNTB.

Additional support for the UNTB comes from a transplant experiment within Canadian forests. Transplanted trees that were not preadapted to local conditions did as well as local ones, therefore, supporting the prediction of the UNTB.

Another practical aspect of the UNTB relates to the prediction that most communities are open and easily invaded by non-native species. This prediction has strong implications for restoration ecology. Most communities appear to be easily invaded by non-native species. Considering the widespread occurrence of non-native species, it is questionable if restoration efforts should particularly focus on controlling or eradicating non-native invasive plants. Further considering the usual lack of funding, more passive restoration approaches could be adapted for any large-scale restoration programs.

Although there is a strong need for restoring historical communities that have been nearly decimated, it is not known how these communities will respond to the ongoing global climate change. One approach toward the assembly of future communities, which will probably be affected by global climate change and tremendous pressure from non-native species, could be to allow the assembly of species to randomly establish on restoration sites. This is not, however, to say that some aggressive invasive species that form monopopulations or alter ecosystem functioning should not be eradicated. These are all important issues that restoration practitioners will have to deal with in the near future.

## Summary

Models in community ecology and biogeography have been used successfully in ecological restoration. Traditionally, succession models have been used on terrestrial ecosystems, whereas assembly models have been used on aquatic ecosystems. The equilibrium theory of island biogeography puts emphasis on random immigration and random extinction in community assembly. Ecosystems can resist changes from disturbances and remain stable. Ecosystem resilience is determined by the time it takes to recover from a disturbance back to the predisturbance state. Restoration strategies using assembly models focus on increasing the resilience of a desirable ecosystem state and reducing resilience of a degraded state of an ecosystem. Ecosystems can exist in alternative stable states where regime shift (between states) is regulated by disturbances. Assembly rules predict that only certain species combinations can exist in a community and puts strong emphasis on niche-assembly. Assembly rules also assume that appropriate species combinations must be introduced on restoration sites. The unified neutral theory of biodiversity and biogeography describes community assembly through ecological drift, random dispersal, and random speciation. It does not assume any role for niche assembly in this process.

| 5.1 | Case Study |
| --- | --- |

### Resilience and Ecosystem Restoration

*Lance Gunderson, Department of Environmental Studies,*
*Emory University, Atlanta, GA*

The idea of resilience was originally proposed as a way of explaining unexpected and dramatic change in ecosystems. The concept describes how ecosystems change in ways that are not just linear and predictable, but ones that are sudden and unpredictable. This model of change involves a transformation, whereby systems change structure and processes into qualitatively different regimes.

Ecosystems can be described as self-organized systems that are defined within a given spatial and temporal domain. Yet many, if not all, of these systems are affected to some degree by external events or processes that occur at broader or larger scales. For example, storms such as cyclones influence structure and function of coastal ecosystems, or fires occur in many forest and grassland terrestrial ecosystems. Biotic interventions occur in the form of invasion of non-native organisms, land use transformations, and harvests of renewable resources, among others. These broader scale interventions can be described as disturbances or **perturbations** to ecosystems.

In ecology, the term resilience has at least two different meanings and contexts. Both meanings apply to the interaction between internal system structures and processes and external perturbations. The word resilience is derived from Latin roots meaning "to jump or leap back." Hence, the general meaning of resilience is the ability to recover from external disturbances or adjust easily to change. Resilience is used by many ecologists to describe how quickly a system returns to its previous state after a perturbation. In 1973, however, the theoretical ecologist C. S. Holling argued that many systems, population systems to ecological systems, change into fundamentally different systems and resilience is the property that mediates the transitions among different system configurations, rather than just postdisturbance recovery. Each of these two definitions is elaborated in the next paragraphs.

Some ecologists (and engineers) define resilience as the time required for a system to return to an equilibrium or steady-state after a perturbation. Implicit in this definition is that the system exists near a single or global equilibrium condition. Hence, the measure of resilience is how far the system has moved from that equilibrium (in time) and how quickly it returns to that state. There is an implicit assumption of global stability; that is, there is only one equilibrium or steady state and hence resilience is the ability of the system to return to that prior state. This type of resilience has been called engineering resilience.

The second definition of resilience characterizes the systems with multiple equilibria, pathways, or configurations. **Ecological resilience** in this case examines the dynamics that can transform a system into another regime of behavior (i.e., to another stability domain). In this case resilience is measured by the magnitude of disturbance that can be absorbed before the system changes into another system or regime, as a result of shifting controls in key variables and processes.

### *Regime Shifts*

An ecological regime shift occurs when characteristic or defining features of an ecosystem change. The change fundamentally alters the way the system looks (its structure) and functions (processes), thus creating a new regime. The ecological components of coupled systems undergo dramatic transformations, or regime shifts, as a result of human interventions.

Case Study (*continued*)

All over the planet humans directly and indirectly modify ecosystems to secure a supply of goods and services. In many systems this can result in ecological regime shifts, for example,

- Forests change and habitat is lost as humans remove trees for fuel, timber, and pulp.
- Lakes, rivers, and estuaries become eutrophic from nonpoint pollutants.
- Overgrazed rangelands become woodlands.
- Excessive water use leads to soil salinization.
- Over-fished coral reefs become covered with algae.

Each example describes an ecological regime shift, whereby the structure and processes that characterize one regime are replaced by others. Some of the changes are brought about by direct manipulation, such as agriculture and forestry practices. Others, such as water pollution and algae-covered reefs, are the indirect result of other activities. In rangeland ecosystems a shift in state can occur because of a loss in biodiversity due to overgrazing. If grazing pressure is high, grazers remove many drought-tolerant plant species. When the system is subjected to a drought, few (if any) tolerant species survive, leaving the system vulnerable to colonization by shrubs and other woody species. Overgrazed rangeland systems often shift from a grass-dominated system to one dominated by woody plants. In other systems nutrient enrichment leads to regime shifts. Many freshwater systems, such as lakes or wetlands, receive inputs of nitrogen or phosphorus (or both) from surrounding areas of intensive agriculture or urbanization. The Everglades wetland is one example where small increases in soil phosphorus concentrations make the system vulnerable to a regime shift. Historically, much of the Everglades wetland was covered by monotypic stands of the sedge *Cladium jamaicensis*. In areas of elevated soil phosphorus concentrations, perturbations such as fire, frost, or drought can lead to a marsh system dominated by *Typha* sp. Other mechanisms that lead to a loss of resilience include the removal of keystone species (top predators, key grazers) or the modification of the physical environment. In many cases the alternative regimes are less productive, less desirable, and become the focus of ecosystem restoration.

### Ecosystem Restoration and Resilience

Around the United States and the world, managers and governments are attempting restoration of resource systems. Much effort is placed to actively manipulate systems to reach a desired or restored condition. In many cases restoration can be considered as regime management, that is, restoration involves changing the system from a degraded or undesirable state to a restored state.

In attempting to restore degraded regimes to more desired ones, managers are faced with issues of reversibility and hysteresis. In some systems it may be physically impossible to restore the system to a desired state. In these cases regime shifts are unidirectional and cannot be recovered. The extinction of a keystone species is one

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

*Jeannine Cavender-Bares, University of Minnesota, Saint Paul, MN;*
*Nicole Cavender, Chief Programmatic Officer/Director of Restoration Ecology,*
*The Wilds, Cumberland, OH*

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).

*(continued)*

Case Study (*continued*)

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 McPeek, 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-equilibrial 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 McPeek, 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

Case Study (*continued*)

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

Case Study (*continued*)

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 Sommunities 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 | *n* Species | *n* 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; Wheater 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

Case Study (*continued*)

**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 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 lead 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 constraints   105
Ecological drift   114
Ecological filters   113
Ecological resilience   117

Ecological resistance   105
Ecosystem threshold   113
Nexus species   112
Perturbation   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?

# Further Reading

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