

Excerpt from:

Eckert, Gregory E. (ed.). 2009. *Interim Technical Guidance on Defining Meaningful Desired Conditions for Natural Resources*, version 1.0. National Park Service, Biological Resources Management Division, Fort Collins, Colorado. 145 pp.

# Appendix B

## Some Key Ecological Concepts for Natural Resource Management

Roger Latham  
continentalconservation.us

### Table of Contents

Scale and Hierarchy .....	B2
Succession.....	B7
Community Assembly Rules .....	B13
Disturbance Ecology and Patch Dynamics .....	B19
Alternative Persistent States, Thresholds and Resilience .....	B27

## Scale and Hierarchy

Ecological research and natural resource management conducted without considering what is happening at more than one scale has had a history of ill-fated outcomes. A well-known example begins this way: wildlife biologists in the 1950s and 1960s observed that game species abundance and songbird species richness tend to be highest near forest edges. This led some to recommend increasing edge areas by changing the pattern of timber cutting to scattered, relatively small clearcuts. However, in the 1980s, studies at the scale of whole landscapes revealed an unexpected consequence. Even while the diversity of certain groups of animal species increases locally around forest edges, the resulting fragmentation often decreases overall species diversity at the landscape level. Loss of forest-interior and area-sensitive species, nest parasitism by cowbirds, appropriation of habitat by invasive species, and other processes play roles in generating this outcome.

Looking at a system at one scale reveals certain information and, at the same time, conceals other information. Natural resource researchers, planners, and managers must choose the scales of their analyses carefully, recognizing what kinds of information are likely to emerge at a particular scale of observation and, just as importantly, what kinds of information are likely to be hidden at that scale. Addressing a question at only one scale often leads to the wrong conclusions. Most often, it is the larger perspective that is missing when scale-related failures crop up in this field. In response to many such episodes, natural resource researchers, planners, and managers are increasingly considering scale explicitly, early on in any course of action, as a key step toward reaching their goals. To do so effectively requires a basic understanding of a few fundamental concepts.

**Scale** in ecology and natural resource management refers either to tangible things (for example, areas of land, bodies of water, organisms, weather events) or to processes (for instance, photosynthesis, succession, nitrogen cycling, climate patterns). Scale categorizes the spatial or temporal dimensions of these things or processes, that is, how big they are or how much time they take. Scale embodies two things at once: the **extent** (the size or length of time of a thing or process), and the **resolution** or **grain** (the finest level of detail considered).

The concept of scale is useful to ecologists and natural resource managers only in the context of a **hierarchy of scale**. In other words, scale is always relative — a particular scale is defined in reference to its position in an ordered sequence of scales. Often, a manager can get useful new insights by simply going through the exercise of thinking about a resource or management challenge at scales one step upwards and one step downwards in the hierarchy, from the scale at which it is ordinarily considered.

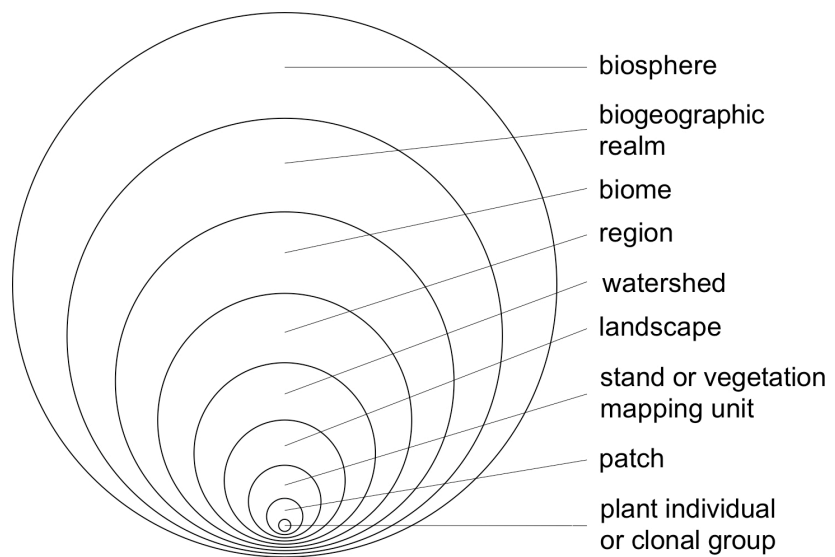


Figure 1. Example of a nested, scale-defined hierarchy.

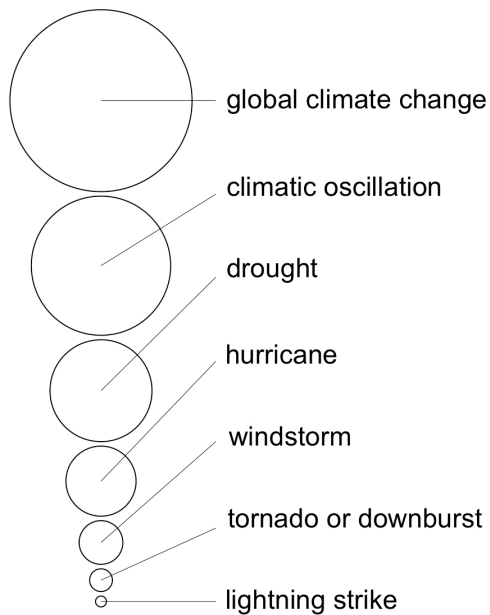


Figure 2. Example of a non-nested, scale-defined hierarchy.

A **hierarchy** is an ordered sequence of related things or processes in which the relationships are asymmetric, that is, upper levels are above lower levels and the relationship upwards is the inverse of the relationship downwards. Upper levels either (1) are the context of, (2) impose constraints upon, (3) behave more slowly or at a lower frequency than, (4) affect a larger area than, or (5) contain and are made up of — lower levels. In a given hierarchy, several or just one of these criteria may apply. Hierarchies come in two flavors; one is scale-related and the other is not, but both are important to ecologists and natural resource managers:

A **hierarchy defined by levels of scale**, sometimes called an **observational hierarchy**, is ordered by the relative sizes or durations of its parts. An example is: plant individual or clonal group → patch → stand or vegetation mapping unit → landscape → watershed → region → biome → biogeographic realm → biosphere (Figure 1). This example also happens to be a **nested hierarchy**, which means that upper levels consist of and contain lower levels. Hierarchies defined by levels of

scale may or may not be nested. A scale-related example of a **non-nested hierarchy** is: lightning strike → tornado or downburst → windstorm → hurricane → drought → climatic oscillation → global climate change (Figure 2).

A **hierarchy defined by levels of organization**, often called an **organizational hierarchy**, is ordered by a consistent type of relationship other than size or duration. An example is: genes → individual organism → population → metapopulation → subspecies → species → higher taxonomic group (for instance, all birds) or functional group (for instance, all herbivores). This example is essentially a nested hierarchy with one trivial inconsistency: an individual contains, but does not entirely consist of, its genes (Figure 3). It is not a hierarchy defined by levels of scale because there is not a consistent size relationship. An individual of one species can be larger than an entire population of another — for instance, a large mammal and a population of parasites living in or on its body. As the name suggests, organizational hierarchies also may describe human elements of natural resource management, for example, the managerial hierarchy of the National Park Service (a non-nested hierarchy).

Levels within a hierarchy of scale are distinguished based on the two facets of scale: **extent** (overall size or duration) and **resolution** (grain size). Here the terminology can sometimes be a bit confusing. The term **broad scale** or **large scale** refers to an area of analysis or management with a larger extent (more acreage or longer duration) relative to one described as **small scale**. The term **coarse scale** or **coarser resolution** refers to a level with larger pixel sizes, longer durations (lower frequencies) or broader categories, relative to one at a **fine scale** or

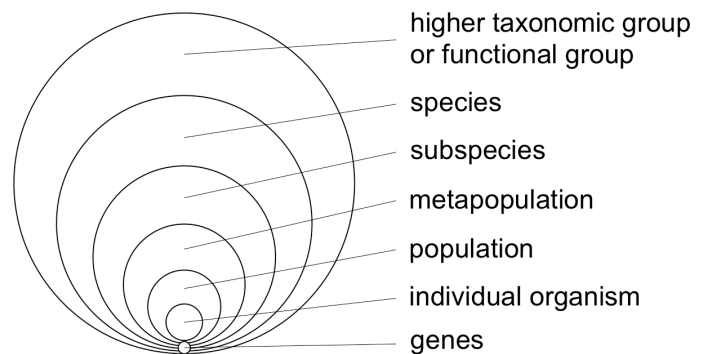


Figure 3. Example of a partly nested, organizational (not scale-defined) hierarchy.

*finer resolution*, with smaller pixels, shorter durations (higher frequencies) or more detailed categories. (Note: The latter concept is often confused with *cartographic scale*, the ratio of the distance on a map to the distance that it represents on the earth's surface, for instance, 1:24,000 or 1:25,000, typical of U.S.G.S. topographic quadrangles. The terms "large scale" and "small scale" should be avoided in referring to a level of resolution or grain size because they are inherently ambiguous. For instance, "large scale" is often used by cartographers to mean fine scale but many outside that profession may assume that it means coarse scale.)

As one moves upward through the levels in a hierarchy, new principles and new properties emerge that cannot be predicted from the properties of lower levels. For nested hierarchies, this is just another way of saying that the whole is greater than the sum of its parts. In both nested and non-nested hierarchies, such "surprises" surfacing at higher levels are called *emergent properties*. For example, the decline in species diversity with forest fragmentation at a landscape scale is an emergent property that could not be predicted by extrapolating from processes studied at a patch scale.

Changes, disturbances or management actions at a particular scale or level of hierarchy frequently have major impacts downward in the hierarchy but their effects upward are usually attenuated. Attenuation is mainly due to averaging across the aggregate of finer-scale or lower-level components and their behavior. For instance, small, scattered fires, occurring at a scale of a patch or stand, may have a catastrophic impact at the scale of an individual plant or animal, a moderate impact at the scale of a landscape or population, and a negligible impact at the scale of a region or metapopulation.

Several key decisions are involved in selecting the appropriate spatial and temporal scales for natural resource management and planning, for baseline data collection, and for long-term monitoring. The manager or planner must determine the appropriate:

- boundaries (spatial extent) of the planning landscape (study area);
- timespans (temporal extent) for a historical perspective and for the planning horizon; and
- spatial resolution (grain) to address management objectives.

In almost every case, consideration of multiple levels in a hierarchy of scale will be necessary. This is partly because emergent properties at higher scales will make it essential to take multiple scales into account. Another reason is that managing a unit of the National Park System usually requires that both a coarse-filter and a fine-filter approach be applied simultaneously. Applying a *coarse filter* — an approach to ecosystem management that involves providing for an appropriate mix of ecological communities across a planning landscape — is virtually always desirable in the context of conservation management. However, in many parks particular species are of special concern because of their endangered status, economic importance, invasive impact, or other reasons. In those cases, it is also essential to apply a *fine filter* — an approach to ecosystem management that involves a focus on the needs of individual species or groupings of species as a basis for landscape planning.

Even within the fine-filter approach, the appropriate scale of analysis, planning, implementation, and monitoring may be different for different organisms. Consider this example of a nested hierarchy of scale: plant individual or clonal group → patch → stand or vegetation mapping unit → landscape → watershed → region → biome. Large animals are often wide-ranging; a single individual's or social group's movements may span multiple landscapes or watersheds. Small animals often are short-ranging, never straying from a stand, patch or even a single plant in their lifetime. The movements of migratory animals are typically off the scale, spanning multiple biomes. Most predators have much larger ranges than most herbivores. Rare

plants and animals often are confined to small patches of specialized habitat. Many other targets of fine-filter management are wide-ranging, for instance brown bears and bison.

A first cut in selecting the appropriate spatial and temporal scales for natural resource management and planning, initial data collection, and long-term monitoring is to brainstorm among knowledgeable individuals answers to some fundamental questions:

- Concerning the target resources in the park (identified in park-establishing legislation, endangered and threatened species lists, the Clean Water Act, etc.), what are the **key ecological attributes**, that is, “factors that most clearly define or characterize the target, limit its distribution, or determine its natural variation over time”<sup>1</sup>? Typically, key ecological attributes might include particular species (considered as key because they are dominant, keystone<sup>2</sup>, imperiled, charismatic or invasive), their population structure, spatial relationships, species interactions, movement of organisms, community structure, energy flows, biomass distribution, or physical features of the landscape.
- What are the predominant ecosystems and communities?
- What are the distinct and important patch habitats?
- What are the influences of all of these at various spatial and temporal scales? Most importantly, how high in the hierarchy do their influences extend?

Each target resource and key ecological attribute may have a different range of scales where its own influence, and external influences upon it, are significant (see Figure 4). A rule of thumb for scale selection in analysis, planning, implementation, and monitoring for natural resource management is to start with the highest relevant level in the hierarchy of scale for each key ecological attribute and then subdivide downward. Sometimes it is useful to think of what whole or wholes each key

ecological attribute is a part of, and in turn, what parts each key ecological attribute is logically divided into. However, just because we can conceptualize influences at several scales doesn't mean that every such scale is relevant. Part of the knack of thinking at multiple scales without getting bogged down in potentially limitless information-gathering is recognizing which scales are useful to understanding and managing target resources and what levels of detail are least likely to be productive.

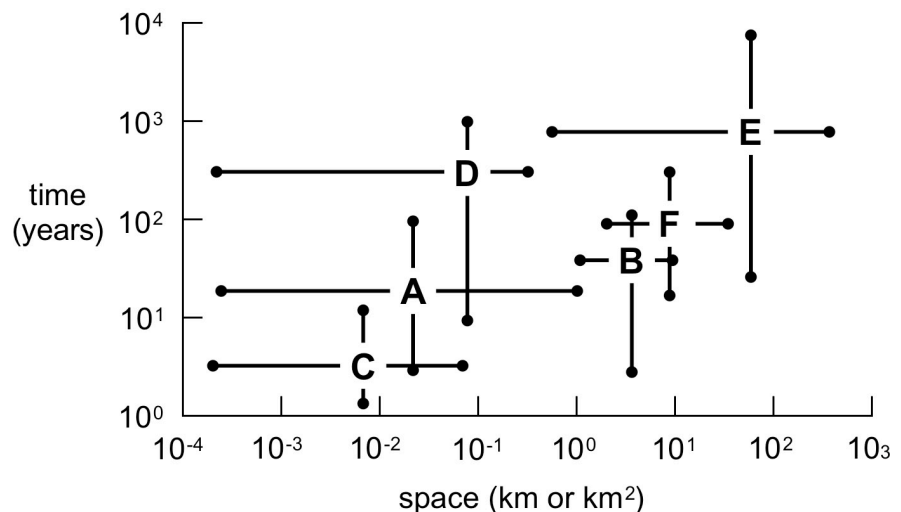


Figure 4. Illustration of the diversity of spatial and temporal scales influencing the creation and maintenance of riparian forests in the coastal temperate rain forest of North America.<sup>3</sup> (A) Colonization surfaces created by flooding, (B) colonization surfaces created by debris flow, (C) seedling germination and establishment, (D) longevity and size of species patches, (E) persistence and movement of dead wood in channel, and (F) impact of herbivores.

<sup>1</sup> Unnasch et al. 2002, p. 6.

<sup>2</sup> See definitions of dominant and keystone species on p. 16 (under Community Assembly Rules).

<sup>3</sup> Adapted from Figure 16.1 in Naiman et al. 1997.

## References Consulted for Section: Scale and Hierarchy

- Allen, T. F. Undated. A summary of the principles of hierarchy theory. International Society for the Systems Sciences. [www.iss.org/hierarchy.htm](http://www.iss.org/hierarchy.htm) (accessed 2006-07-12).
- Caraher, D. L., A. C. Zack and A. R. Stage. 1999. Scales and ecosystem analysis. Pp. 343-352 in R. C. Szaro, N. C. Johnson, W. T. Sexton and A. J. Malk (eds.), *Ecological Stewardship: a Common Reference for Ecosystem Management*, Vol. II, Elsevier Science, Oxford, U.K.
- Foreman, R. T. T. and M. Godron. 1986. *Landscape Ecology*. John Wiley & Sons, New York. 620 pp.
- Haufler, J. B., T. Crow and D. Wilcove. 1999. Scale considerations for ecosystem management. Pp. 331-342 in R. C. Szaro, N. C. Johnson, W. T. Sexton and A. J. Malk (eds.), *Ecological Stewardship: a Common Reference for Ecosystem Management*, Vol. II, Elsevier Science, Oxford, U.K.
- King, A. W. 1993. Considerations of scale and hierarchy. Pp. 19-45 in S. Woodley, J. Kay and G. Francis (eds.), *Ecological Integrity and the Management of Ecosystems*, St. Lucie Press, Boca Raton, Florida.
- Malk, A. J., D. L. Caraher, J. Haufler, J. Sendzimer and R. C. Szaro. 1999. Scale phenomena: why consideration of scale is important to ecological stewardship. Pp. 47-52 in N. C. Johnson, A. J. Malk, R. C. Szaro and W. T. Sexton (eds.), *Ecological Stewardship: a Common Reference for Ecosystem Management*, Vol. I: *Key Findings*, Elsevier Science, Oxford, U.K.
- Naiman, R., P. A. Bisson, R. G. Lee and M. G. Turner. 1997. Approaches to management at the watershed scale. Pp. 239-253 in K. A. Kohm and J. F. Franklin (eds.), *Creating a Forestry for the 21st Century: the Science of Ecosystem Management*, Island Press, Washington, D.C.
- Turner, M. G. and R. H. Gardner. 1991. Definitions and concepts of space, time, and scale. Pp. 6-8 in M. G. Turner and R. H. Gardner (eds.), *Quantitative Methods in Landscape Ecology: the Analysis and Interpretation of Landscape Heterogeneity*, Springer, New York.
- Unnasch, R., J. Parrish, D. Braun et al. 2002. Ecological integrity assessment: a framework for conservation planning and measuring success. Draft report of the Ecological Systems Viability Workgroup, The Nature Conservancy, Arlington, Virginia. 88 pp.
- White, P. S. and A. Jentsch. 2004. Disturbance, succession, and community assembly in terrestrial plant communities. Pp. 342-366 in V. M. Temperton, R. J. Hobbs, T. Nuttle and S. Halle (eds.), *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*, Island Press, Washington, D.C.

## Succession

One of the oldest concepts in ecology is succession, dating back at least to 1860, when Henry David Thoreau borrowed the term for the sequence of rulers in a monarchy to describe the changes in the trees that dominate a forest over generations. In the 1890s, the concept was formalized by Henry Cowles to describe the series of different plant community types that replace each other as bare ground gradually converts to forest vegetation. In the 1910s, Frederic Clements theorized that plant communities are “superorganisms” whose developmental stages toward full maturity — an idealized equilibrium state that he termed the “climax” — should be as predictable as those of an organism as it grows from embryo to adult. According to this theory, the composition of any climax community is determined chiefly by climate. In the 1920s, Henry Gleason countered with a highly individualistic view of vegetation. He saw the plants growing and replacing one another in a given area as a chance mixture of independent species, not a “community” in any meaningful sense. In this view, succession is merely the sum of the plants’ individual responses as they come and go. Clements’s and Gleason’s ideas were touted by opposing camps until the 1970s, but contemporary ways of thinking about succession are in some ways a synthesis of the two. Gleason’s non-equilibrium slant holds sway, but abundant and growing evidence that populations commonly evolve in response to the other species they live with evokes Clements. In other words, the prevalence of coevolution leads to the conclusion that non-individualistic processes are significant in community organization.

A current definition of *succession* is the non-seasonal, directional and continuous pattern of colonization, relative dominance and extinction on a site by populations, usually set in motion by disturbance. *Non-seasonal* means that succession refers usually to changes that take place over years, excluding differences between spring and fall or between the growing season and the dormant season. *Directional* — sometimes replaced in the definition by *progressive* — means that the process is an asymmetric sequence of changes, that is, some stages consistently occur either earlier or later than certain other stages. *Pattern* indicates that succession is a descriptive concept. The dynamic interactions that underlie successional patterns are a separate topic, community assembly.<sup>4</sup> *Population* in this case means all of the members of an individual species living in an arbitrarily defined area, such as a watershed, a park, or an enclave of a particular habitat type. *Disturbance*<sup>5</sup> in this context is any event that rapidly causes a major reduction, sometimes even local extinction, of one or more populations among the dominant species in the affected area. The spatial scale of such disturbances is highly variable, from a single fallen tree in a forest to an entire region affected by a drought or a herbivorous insect outbreak. Examples include severe windstorm, landslide, acute drought, forest fire, disease, a spike in an insect or mammalian herbivore population, timber cutting, or land clearing for agriculture. Less severe, non-lethal disturbances also may have significant effects on an ecological community, but succession is usually set in motion by disturbances that are high in severity, that is, ones that kill off a large fraction of the dominant organisms.

Succession is often sorted into two main types: primary and secondary. **Primary succession** begins on areas that are essentially unoccupied by organisms. Sand dunes, bare rock, soil recently vacated by glaciers, and thick volcanic ash are examples of substrates where primary succession takes place. **Secondary succession** begins where significant quantities of organisms or their residues are present, for instance, a forest stand flattened by a severe windstorm, a burned-over area of prairie, or an abandoned farm field. In such situations, the remaining soil organic matter, wood ash, living roots and seed bank, soil fungi and bacteria, surviving animals,

---

<sup>4</sup> See Community Assembly Rules (p. 13).

<sup>5</sup> See Disturbance Ecology and Patch Dynamics (p. 19).

and dead vegetation have strong influences on the course of succession. One of those influences is that secondary succession is generally much faster than primary succession.

Although succession is a pattern of continuous, year-by-year change, for convenience the pattern of gradual change is often broken into segments, roughly bounded by milestone events such as a shift in dominance from one species to another or from one category of species to another. The species composition within each segment is called a *seral stage* (*seral* and *successional* are synonyms; seral stage is sometimes shortened to *sere*). Within any region, some species are consistently present in early seral stages but not late seral stages, some the reverse, and some have no association with a particular stage. Whether a species is associated with early or late seral stages depends on certain properties and abilities of that species. How it competes for resources, what it needs to regenerate, its maximum lifespan, and its dispersal and colonizing abilities affect an organism's successional status. For plants, maximum height and degree of shade-tolerance are also important (Table 1).

Table 1. Examples of plant traits associated with early and late succession.

trait	early-successional species	late-successional species
photosynthesis		
• light saturation intensity (light level above which photosynthesis does not increase)	high	low
• light compensation point ("break-even" light intensity where photosynthesis rate = respiration rate)	high	low
• efficiency at low light	low	high
seeds		
• number produced by an individual	many	few
• size	small	large
• dispersal distance	large	small
• dispersal vector	wind, birds, bats (short- and long-range)	gravity, mammals, ants (mostly short-range)
• viability	long	short
root-to-shoot biomass ratio	low	high
mature height	short	tall
structural strength	low	high
growth rate	fast	slow
maximum life span	short	long

Traits such as those in either column of Table 1 have a strong tendency to co-occur in a species as a unified suite, in part because of *evolutionary trade-offs*. For instance, an increase over generations in the number of seeds a plant produces has to be accompanied by a decrease in seed size, assuming resources available for reproduction do not change. Likewise, an evolutionary increase in the size of a plant's seeds must be coupled with a decrease in the total number produced per parent plant. For another example, an increase over generations in how fast a plant species grows taller is linked to a sacrifice in structural strength, because building the apparatus

of physical support takes time; lower structural strength, in turn, imposes stricter limits on how tall a plant can grow without falling over. Conversely, an evolutionary increase in maximum height compels more investment in structural strength, which means a slower growth rate.

Succession is most often described in terms of plant species turnover, but animals, fungi, algae, bacteria and other groups of organisms all show successional trends as well (see Figure 5). In some cases plants in the narrow sense (vascular plants, bryophytes and green algae) are less important than other players in succession or even entirely absent, for instance, in boulder fields dominated by lichens or in marine systems dominated by brown algae or corals.

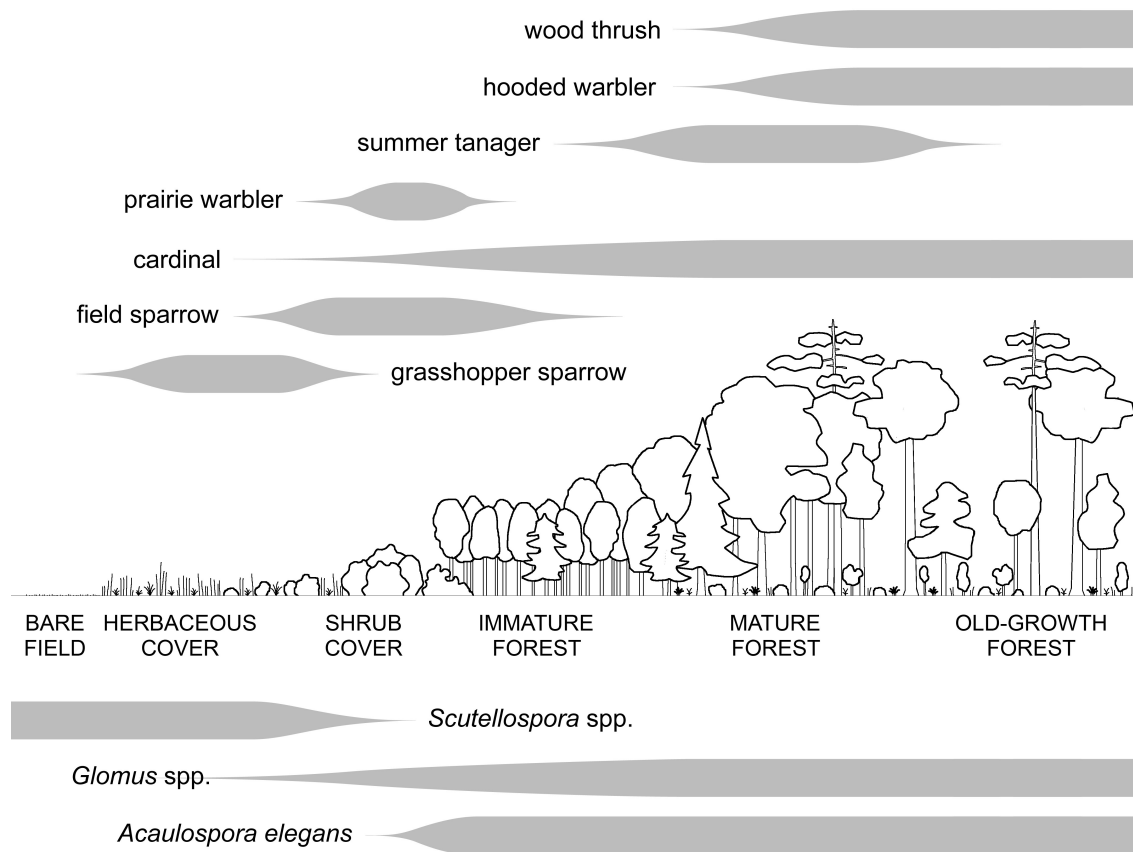


Figure 5. Examples of species distributions associated with successional stages from abandoned farm field to forest in eastern North America: birds (top) in the Piedmont region of Georgia and vesicular-arbuscular mycorrhizal fungi (bottom) in Minnesota. Time since field abandonment progresses toward the right-hand side of the diagram. Width of bars represents relative abundance across successional stages.<sup>6</sup>

A series of ecological communities that replace each other over time on a site is termed a **successional pathway** or **successional trajectory**. As long as they are not deflected in mid-course by severe disturbance, many successional pathways culminate in communities that achieve some degree of stability, that is, they persist for a long time. Simplified, textbook accounts of succession often call a persistent community at the end of a successional pathway a “climax” community. However, the original concept of a climax as the inevitable, stable endpoint of

<sup>6</sup> Adapted from Figure 17.18 in Begon et al. 1996, based on Johnston and Odum 1956, Gathreaux 1978 and Johnson et al. 1991.

succession in a given combination of climate, topography and soil is often a poor fit to what we see in the real world. Succession involves an element of chance; the endpoint can be influenced by which species arrive first after disturbance.<sup>7</sup> Some successional pathways have no persistent endpoint but are cyclic. In some cases, alternative pathways on the same site may diverge in time to endpoints with completely different sets of dominant species.<sup>8</sup> Communities may undergo severe disturbance regularly, oscillating among early successional stages and never achieving a persistent state. In other cases, chronic disturbance leads to and sustains a persistent state dominated by a small subset of the regional species pool that can survive events that are lethal to most species.<sup>4</sup> Regional species pools themselves change over time with introduced plant and animal species, local extinction, novel diseases and climate change, which can have profound effects on successional pathways and the species composition of seral stages.

Any description of a successional pathway or the successional status of an area is scale-dependent.<sup>9</sup> For instance, viewed at a landscape scale, an old-growth forest stand dominated by trees hundreds (or thousands) of years old is most likely at a persistent end-stage of succession. Zoom in at a finer scale and you see temporary canopy gaps formed by fallen trees, at various stages of early or mid-succession. At some scale, nearly every ecosystem is a mosaic of successional stages.<sup>10</sup> Patchy disturbance — the norm in most ecosystems — allows regeneration of certain species and increases community and species diversity at the landscape scale. Many species depend on particular successional stages. Many animal species depend on more than one successional stage within an individual's lifetime, or even within a single day's activity.

As species come and go during the course of succession, properties emerge at the ecosystem scale that are not necessarily predictable from the characteristics of the individual species. Some *emergent properties* associated with succession are remarkably similar between different ecosystems, even those that have no species in common. For example, in the early stages of most successional pathways, net community production is greater than total respiration and total biomass increases. In the later stages, net community production and total respiration are nearly equal and biomass approaches a steady state, with gains and losses roughly balancing each other.

The earliest descriptions and theoretical treatments of succession — those by Thoreau, Cowles, Clements, Gleason and others — were based on forest development in eastern North America on barren sand dunes, abandoned farmland, and clearings created by windstorm, fire and timber harvest (see Figure 1). The study of succession is still somewhat skewed towards forests worldwide. Other “classic” examples include the sequences of successional stages on bare ground vacated by glaciers, in kettle-hole bogs created by the melting of huge chunks of ice embedded in glacial drift (rubble and soil churned up and deposited by glaciers), and on land flooded and then abandoned by beavers. Some successional sequences are much faster and involve fewer species than these examples, for instance, the sequence of marine algae that colonize boulders overturned by wave action along the southern California coast. As described in the 1970s by Wayne Sousa, cleared boulders are colonized within a month by a mat of green algae in the genus *Ulva* and barnacles. In the first fall and winter an assortment of red algae colonize the surface, including species in the genera *Gelidium*, *Gigartina* and *Rhodoglossum*, and begin crowding out the green algae. Within two to three years, *Gigartina canaliculata* becomes dominant. Without further disturbance, this late-successional species quickly spreads and forms a near-monoculture that excludes virtually all other sessile (stationary) organisms.

---

<sup>7</sup> See Community Assembly Rules (p. 13).

<sup>8</sup> See Alternative Persistent States, Thresholds and Resilience (p. 27).

<sup>9</sup> See Scale and Hierarchy (p. 2).

<sup>10</sup> See Disturbance Ecology and Patch Dynamics (p. 19).

Success in meeting biodiversity conservation and ecosystem management goals often depends on the judicious use of disturbance and addition of seeds or transplants to manipulate succession. Effective management involves careful consideration of when it is appropriate to allow succession to unfold on its own and when, and by what means, it is appropriate to intervene. For examples of how succession has been manipulated to beneficial effect, read *Community Assembly Rules* (p. 13), *Disturbance Ecology and Patch Dynamics* (p. 19), and *Alternative Persistent States, Thresholds and Resilience* (p. 27).

## References Consulted for Section: Succession

- Begon, M., J. L. Harper and C. R. Townsend. 1996. *Ecology: Individuals, Populations and Communities* (3rd ed.). Blackwell Science, Oxford. 1,068 pp.
- Calaway, R. M. and Maron. 2006. What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology and Evolution* **21**: 369-374.
- Clements, F. E. 1916. *Plant Succession: an Analysis of the Development of Vegetation*. Carnegie Institution Publication No. 242. Washington, D.C. 512 pp.
- Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* **27**: 95–117, 167–202, 281–308, 361–388.
- Dighton, J. 2003. *Fungi in Ecosystem Processes*. Marcel Dekker, Inc., New York. 432 pp.
- Gauthreaux, S. A. 1978. The structure and organization of avian communities in forests. Pp. 17-37 in R. M. DeGraaf (ed.), *Proceedings of the Workshop on Management of Southern Forests for Nongame Birds*, General Technical Report SE-14, Southeastern Forest Experiment Station, Asheville, North Carolina.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**: 7-26.
- Johnson, N. C., D. R. Zak, D. Tilman and F. L. Pflieger. 1991. Dynamics of vesicular-arbuscular mycorrhizae during old field succession. *Oecologia* **86**: 349-358.
- Johnston, D. W. and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the piedmont of Georgia. *Ecology* **37**: 50-62.
- Thoreau, H. D. 1860. The succession of forest trees. (An address read to the Middlesex Agricultural Society in Concord, Massachusetts; first published 6 October 1860 in the *New-York Weekly Tribune*.) Pp. 184-204 in H. D. Thoreau, 1906, *Excursions and Poems*, Houghton Mifflin, Boston.

## Community Assembly Rules

*Community assembly* consists of the processes and interactions that produce the patterns of succession.<sup>11</sup> Successional patterns are the series of species assemblages called successional (seral) stages or communities that result from the rise and fall of species in a given place over years and decades and are roughly consistent from place to place within a region. Succession itself is often thought of as a process, but strictly speaking it is a description of the patterns in species composition that emerge from a set of processes and interactions. In verbal or written accounts of succession, the underlying processes — those of community assembly — often go unmentioned and unanalyzed, treated as the proverbial “black box.”

*Community assembly rules* are not rules in the usual sense, but are analogous to rules in much the same way that the laws of physics are analogous to laws enacted by a legislature. As plants, animals and other organisms come and go through the stages of succession, they act in some ways as if they were obeying a set of rules. Our understanding of some of those rules, gained through experimental research, can be usefully applied to ecosystem restoration and management.

Concepts of community assembly fall into three main categories: *determinism*, *stochasticism* and *alternative persistent states* (also known as alternative or multiple stable states). Frederic Clements in 1916 pioneered the deterministic viewpoint: a community’s development was seen as the inevitable consequence of the underlying combination of physical and biotic factors, always progressing along a specific successional pathway<sup>1</sup> toward a stable “climax” community. A decade later Henry Gleason put forward the stochastic perspective: species composition and structure were attributed to essentially random factors — historical events, environmental conditions, availability of space and resources, the set of species that live in the area, and the order in which they arrive — and the number of possible successional pathways was seen as essentially unlimited. Most ecologists today accept a hybrid of the two, whether or not they choose to call it alternative persistent states.<sup>12</sup> In this view, first formalized in 1974 by John Sutherland to describe a marine ecosystem, community development is constrained to certain pathways that occur repeatedly in at least roughly similar fashion at different times and places, but various pathways are possible on any given site, leading to very different persistent end states. Which one actually happens depends on chance factors or, in some cases, disturbances of human origin.

Community assembly rules are the constraints on species’ presence and relative abundance in a community. They are often described as *filters* (see Figure 1). Of the *species pool* — the sum of all species within dispersal distance of a site — only those that are adapted to a site’s physical and biological conditions can become members of the community there. *Biotic filters* are the constraints on community membership that arise because of interactions among organisms. Biotic filters arise from competition, mutualisms (such as mycorrhizae, pollination, nitrogen fixation and defense), trophic interactions (herbivory, predation and parasitism), order of species arrival, biological legacy (past composition and structure), biotic disturbances (such as trampling and wallowing by bison herds, digging by prairie dogs, tree-felling and flooding by beavers), and interactions among all of these. *Abiotic filters* are the underlying physical factors that limit community membership, including attributes of climate, soils, landscape position, hydrology, and abiotic disturbances such as fire, flood, windstorm and drought.

---

<sup>11</sup> See Succession (p. 7).

<sup>12</sup> See Alternative Persistent States, Thresholds and Resilience (p. 27).

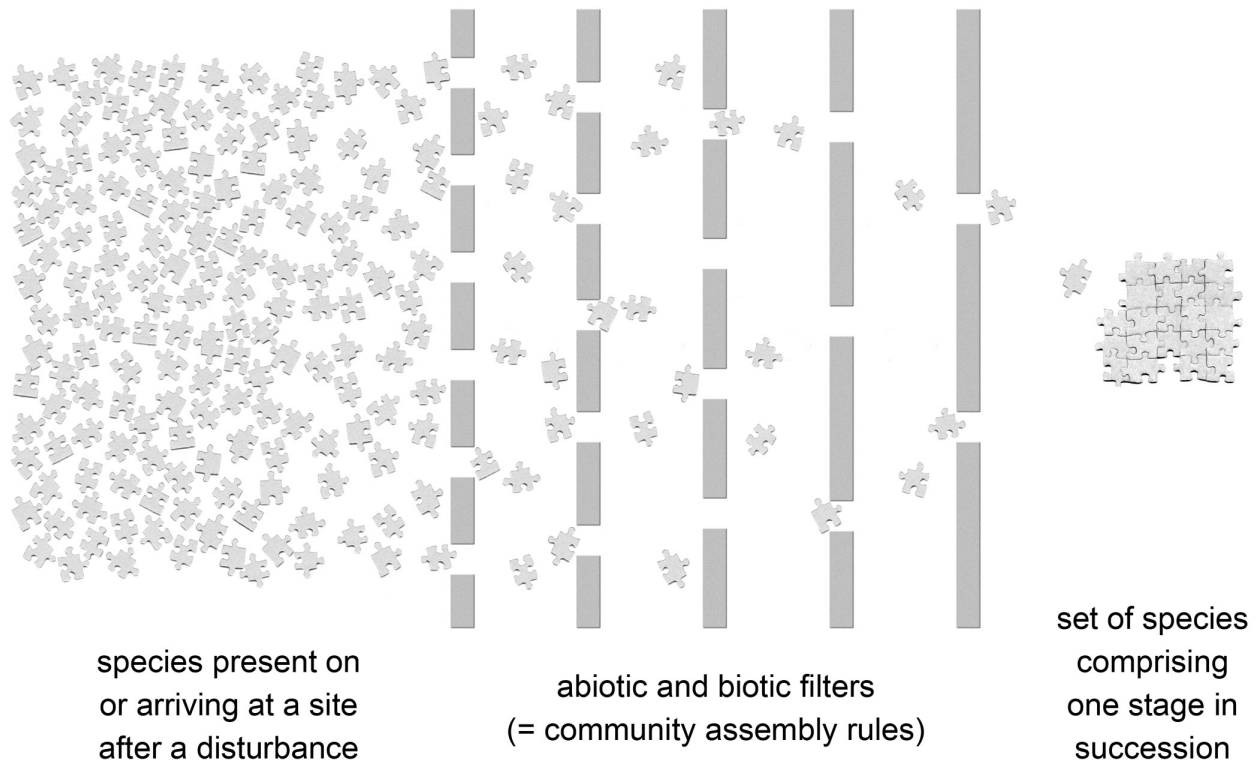


Figure 1. Conceptual model of community assembly rules. The diagram represents only a snapshot in time of a highly dynamic process. The biotic filters change with the ascendancy of new species and from one successional stage to another as organisms' populations rise and fall, modify the environment, and interact with each other.

One of the most important things to consider about community assembly rules is their dynamic nature; they change over time as a community evolves. Disturbances<sup>13</sup> change the rules suddenly and often dramatically, for instance, by killing some species but not others, or by altering the availability of essential resources. More gradually, but often just as profoundly, the organisms themselves cause filters to change over time. Each species modifies the environment and interacts with newcomers in its own way. The sum of these modifications and interactions changes as species composition changes.

Three concepts are often used as keys to understanding biotic filters, that is, how community assembly works in terms of the interactions among individual organisms: *facilitation*, *inhibition* and *tolerance* (Connell and Slatyer, 1977). They may be thought of as categories of community assembly rules. They are not mutually exclusive; one, two or all three may apply in varying degrees to different species and at different points in the same successional pathway.

*Facilitation* refers to the changes early-successional organisms make to the environment that later-successional organisms can use to their own advantage, eventually supplanting the pioneers. In this process, in a sense, the later arrivals “bite the hand that feeds them,” but they do so without penalty. An example is the colonization of newly deposited glacial drift in Alaska. The extreme scarcity of nitrogen and other nutrients essential to plant growth acts as a filter, allowing establishment by only a few tolerant species such as yellow mountain-avens and Sitka alder, which host nitrogen-fixing microbes. The unavoidable byproducts of these plants' growth — increased mineral nitrogen and organic matter in the soil — eventually make it possible for

<sup>13</sup> See Disturbance Ecology and Patch Dynamics (p. 19).

Sitka spruce and other taller plants to move in. Their shade soon suppresses or eradicates the nitrogen-fixers and acts as a new filter, inhibiting further colonization by shade-intolerant plants. Facilitation is seen most clearly and unambiguously in primary succession.<sup>14</sup>

**Inhibition** is shorthand for the idea that species with a head start inhibit the establishment of later arrivals. Among the species present immediately following a disturbance, those that are long-lived tend to dominate into late succession. Inhibition applies mainly to secondary succession. For instance, when a forest is felled by wind or by timber cutting, the formerly shade-suppressed tree seedlings that are already established on the forest floor are immediately in the lead in the race to colonize newly vacated rooting space and fill out a new upper canopy. Long-lived species, which may have been present from the start, eventually outlive species with shorter lifespan and their shade keeps new potential competitors from establishing. Inhibition is one way in which invasive, nonnative species can gain dominance in a community. An example is Norway maple, a Eurasian invader of forests in much of the East and in riparian woods of the Pacific Northwest. Its seedlings persist in the shade of native forest trees and, after canopy thinning or removal by disturbance, quickly grow to form a new canopy. Few plants of any kind — tree seedlings, shrubs or herbaceous species — can live in the exceptionally dense shade of Norway maples, which are long-lived and prolific seed-producers.

**Tolerance** refers to the tendency for late-successional species to be tolerant of lower resource levels than early-successional species. It is pertinent to secondary succession where resources are relatively abundant just after a severe disturbance. In moist climates, for example, most wild plants grow well in the high light, high soil-nutrient conditions that typically follow the abandonment of a farm field. As plants grow larger and more crowded, however, those that tolerate lower light or soil nutrient levels perform relatively better, eventually crowding out less shade-tolerant and more nutrient-demanding plants. Plants that are dominant late in succession often are among those that are the most efficient in resource utilization. Their efficiency gives them an advantage in a crowded situation. As resources are spread ever more thinly among increasing numbers of individuals, those that are least debilitated by scarcity eventually will win out. Competition for resources acts as a filter, preventing resource-demanding (“high-maintenance”) species from thriving. Late in succession, numbers of individuals fall again as scarcity-tolerant trees and clonally spreading plants grow large and achieve a near-monopoly over light and nutrients.

A key strategy of ecosystem restoration is to deliberately modify filters to speed up or redirect the assembly of the desired community and to overcome thresholds of resilience against change.<sup>15</sup> An example in the eastern U.S. involves white-tailed deer. In some areas, increased food availability (croplands, old fields and landscape plantings in fragmented forest) and the lack of effective predators have allowed these large herbivores to become so abundant that forest understory vegetation and its functional values — including shrub and herbaceous species diversity, seed bank replenishment, tree reproduction, and vertical habitat structure for wildlife — have been devastated. However, massive culling to restore low deer density does not bring about understory recovery and tree regeneration, even with reseeding or planting. First the forest floor must be exposed to sunlight by the death of adult trees and, in some cases, by the reduction of rhizomatous<sup>16</sup> fern cover, which can reach 100% where deer have been abundant for so long that they have all but eradicated the more-palatable competitors of ferns. Where quick results are desired in a closed-canopy forest stand, selective canopy thinning and judicious placement of

---

<sup>14</sup> See Succession (p. 7).

<sup>15</sup> See Alternative Persistent States, Thresholds and Resilience (p. 27).

<sup>16</sup> Rhizomatous means spreading from underground runners, which in monoculture may result in a continuous, turf-like cover.

tree seedling, shrub and herbaceous transplants can speed up understory restoration. In this example, large predators, deer and rhizomatous ferns are filters — literally so, in the case of the ferns, which filter most sunlight from reaching the soil surface. The cascade of changes in those filters is a source of ecosystem degradation. Deliberate manipulation of the filters is a key to ecosystem recovery.

Restoring full species diversity, composition and resilience to a damaged ecosystem is more difficult and takes longer to achieve than restoring basic ecosystem function. For one thing, it may not be possible to know the full range of species that were present before ecosystem degradation. Moreover, various members of a particular *functional group* of organisms are somewhat interchangeable in terms of their most basic contributions to the ecosystem. For instance, restoring just a handful of native, perennial, warm-season grass species to a prairie may fully restore the gross contribution of this functional group to the ecosystem, even if historically the prairie included dozens of such species. Among plants hosting nitrogen-fixing symbionts — another functional group in prairie ecosystems — just one or two species may add as much available nitrogen to the soil in a year, if they are abundant enough, as several times that number of N-fixing species found in a “pristine” community. This phenomenon, known as functional redundancy, does not mean that a subset of a functional group acts in precisely the same way as the full complement of group members present in an intact community. In the N-fixer example, species are redundant in their ability to increase soil nitrogen availability but differ from one another in other traits — response to drought and other disturbances, the species of insects that depend on them for food, and so on — and thus have subtly different roles in ecosystem function and in shaping assembly rules. Most importantly, higher species diversity within functional groups confers greater overall ecosystem resilience in the face of various kinds of disturbance, because species differ in their specific tolerances.

Some species have no functional equivalent in certain ecosystems. Known as *keystone species* or *ecological engineers*, such species have a disproportionately powerful influence on ecosystem processes. They and *dominant species* are the most influential assembly-rule-setters. Dominant species are those that exert strong control over environmental conditions by virtue of their high population density or majority share of total ecosystem biomass. In contrast, keystone species account for a small or even negligible share of ecosystem biomass. However, if such a species is removed from an ecosystem, profound changes in community composition and structure result. One of the best-known examples is in kelp forests along the Pacific coast. Sea otters, which comprise an insignificant fraction of total ecosystem biomass, are essential to the maintenance of the entire species-rich kelp forest community. That discovery was made the hard way, only after otters were over-harvested for their pelts. Otters are the main predators of sea urchins, sea urchins are the main herbivores of kelp, and kelp is the dominant life form in terms of ecosystem productivity, biomass and structure. At a critical low density of sea otters, urchin numbers skyrocket and the kelp is nearly eradicated. The result has been the creation and spread of “urchin barrens,” with much lower productivity, biomass and species diversity than the kelp forests that they replaced. In this case, the devastating impact of the loss of a keystone species reverberates well beyond the ecosystem where it resides. Intact kelp forests provide food and specialized life-stage habitat for residents of neighboring communities and they help to dissipate the energy of waves affecting intertidal and shoreline ecosystems.

Filters sometimes change unpredictably, making the outcome of species assembly differ following the same type of disturbance, depending on the timing. One example is in Northern California serpentine grasslands. This ecosystem is called “serpentine” because it occurs on soils with a highly unusual chemistry derived from serpentinite bedrock. The community consists mainly of native annual forb (non-grass) species, many of which depend on soil disturbance by gophers to provide regeneration sites. Rainfall in the region is highly variable. How much rain

falls around the time of a particular gopher excavation strongly influences plant colonization of the bare soil, both in terms of relative success among species and total cover. Because of the strong but unpredictable effect of weather, a particular type of disturbance — in this case, gopher digging — does not always result in reassembly of the same plant species mix at different times and places within a single community.

This illustrates an important principle in community assembly that applies to many ecosystems: the results of a particular restoration or maintenance action may vary widely due to chance differences in weather or other volatile filtering factors. In some cases, this makes the success of a restoration or management action a matter of luck as much as good planning and execution. However, at times such randomness can be a benefit. Restoration of a degraded site is usually done piecemeal, which generally means that any restoration activity will be undertaken in a variety of weather conditions. Given limited resources, piecemeal restoration is generally the only practical way to proceed, and it is often necessary in any case to afford sensitive populations adequate refugia to ride out the management activity, for instance, if a rare butterfly depends on fire to maintain an area of habitat or a host plant population, some of its eggs, caterpillars, pupae or adults are likely to be killed within a patch as it is burned. Differences in weather, time of the season, seed availability or other uncontrolled filtering factors from one management event to another may result in a patchiness of community composition that more closely resembles the “pristine,” pre-degradation state than if management were more uniform. Such factors are variable by their nature and past disturbances that helped to maintain most ecosystems took place in a range of weather, seed set and other conditions.

One handicap for the restorationist is that the original assembly sequence of a community that is a target of restoration is usually unknown and often unknowable. Expert help is needed to formulate one or a small number of hypotheses for what sequence is most likely to achieve the desired result. Ideally, a working group should be assembled that includes naturalists who have broad knowledge of the particular ecosystems of interest and research scientists in ecology and other pertinent disciplines who have experience in restoration, reclamation or management of similar ecosystems. One or more hypotheses can then be put to the test in an *adaptive management* approach. Adaptive management is a system of management that embraces uncertainty and emphasizes learning by structuring management actions to test hypotheses, using experimental design and data analysis principles from field ecology. Monitoring the results of management actions and comparing them in statistically valid ways with each other and with appropriate control (untreated) areas is a vital part of the process.

In some cases, humans have inadvertently changed community assembly rules in ways that will be impossible to reverse at a time scale of decades or even centuries. Examples include massive soil losses on rangelands and croplands and ongoing climate change. At some sites of conservation concern, historical conditions may not be achieved despite managers' best efforts. In such a case it may be necessary for a desired condition analyst to choose model or reference communities of a different type from those that occupied the target site historically, for example, communities at sites elsewhere in the same region where conditions most closely resemble those present at, or predicted for, the target site. The challenges will be to predict what community or communities will succeed best at the site, recognize the key filters in those communities, and develop hypotheses on what will be the best assembly sequence and methods for establishing the desired community on new ground.

## References Consulted for Section: Community Assembly Rules

- Clements, F. E. 1916. *Plant Succession: an Analysis of the Development of Vegetation*. Carnegie Institution Publication No. 242. Washington, D.C. 512 pp.
- Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**: 1119-1144.
- Diamond, J. M. 1975. Assembly of species communities. Pp. 342-444 in M. L. Cody and J. M. Diamond (eds.), *Ecology and Evolution of Communities*, Harvard University Press, Cambridge, Massachusetts.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**: 7-26.
- Harper, J. L. 1977. *Population Biology of Plants*. Academic Press, London. 892 pp.
- Latham, R. E., J. Beyea, M. Benner, C. A. Dunn, M. A. Fajvan, R. Freed, S. B. Horsley A. F. Rhoads and B. P. Shissler. 2005. *Managing White-tailed Deer in Forest Habitat from an Ecosystem Perspective: Pennsylvania Case Study*. Audubon Pennsylvania and the Pennsylvania Habitat Alliance, Harrisburg. 340 pp. (pa.audubon.org/deer\_report.html)
- Lockwood, J. L. and S. L. Pimm. 1999. When does restoration succeed? Pp. 363-392 in E. Weiher and P. Keddy (eds.), *Ecological Assembly: Advances, Perspectives, Retreats*, Cambridge University Press, Cambridge, U.K.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* **108**: 859- 873.
- Temperton, V. M., R. J. Hobbs, T. Nuttle and S. Halle. 2004. *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*. Island Press, Washington, D.C. 439 pp.

## Disturbance Ecology and Patch Dynamics

All ecosystems are dynamic, that is, they are in constant flux due to the growth, death, immigration, and replacement of organisms. The rate of change would be glacially slow in most ecosystems, however, if it were not for disturbances, both natural and human-induced, which speed up these processes. In ecology, “a disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment<sup>17</sup>.” A forest fire, for example, can bring about a variety of changes in each category, including: *ecosystem structure*, by razing the tree canopy and shrub layers; *community structure*, by killing some species but not others; *population structure*, by skewing plant and insect age distributions toward the youngest (seed or egg) stage; *resources*, by intensifying decomposition and nitrate release by soil microbes and exposing dormant seeds to full sunlight; *substrate availability*, by opening up vacant areas of land; and the *physical environment*, by exposing the soil surface to drying wind and the heat of direct solar radiation.

Ecosystem disturbance is an integral part of the key ecological concepts of succession<sup>18</sup>, community assembly rules<sup>19</sup>, alternative persistent states and resilience<sup>20</sup>. Resilience refers to an ecosystem’s response to disturbance. Succession is the pattern of species recovery after a disturbance and community assembly rules describe the underlying processes. Viewed a different way, disturbance sets the stage for community assembly and succession. However, in some cases the path of succession leads, not to the recovery of the community that was present before the disturbance, but to an alternative persistent state.<sup>3</sup> The type and timing of disturbance can strongly affect the trajectory that succession takes, and thus helps to determine the composition of the persistent ecosystem state that often occurs late in succession.

Disturbances occur over a wide range of spatial and temporal scales<sup>21</sup>. The *area* or size of a disturbance may be expressed as the area affected by a single event or as the percentage of the total area under consideration that is affected by each type of disturbance in a given time period. Spatial *distribution* is another scale-related attribute of disturbance. Relative to an area under consideration (for instance, a section of a park, an entire park, a watershed, or a region), disturbances may fall anywhere along the continuum, from widely dispersed to randomly distributed to tightly clustered, or from rare and sparse to abundant and dense.

The disturbance *frequency*, which may be interpreted as disturbance *probability*, is the mean number of events per time period for a particular area of land. The disturbance *return interval* — also called the disturbance cycle or turnover time — is the inverse of frequency, that is, the mean time between disturbances for a particular area of land. The disturbance *rotation period* is the mean time it would take for the sum of the areas affected by disturbances to equal the total area under consideration. Disturbance *predictability* is inversely related to the variance in the return interval (recall that the return interval itself is a mean, which does not reflect how much the intervals between disturbances vary). Predictability is low if the variability in intervals between successive disturbances is high, and vice-versa. For instance, if the record shows that a tree-defoliating caterpillar outbreak has recurred in a given area once every fifth year without fail, then its return interval in that area is 0.2 per year and its predictability for a given year is very high, whether it is an “on” year or an “off” year. If such an outbreak has been recorded 20 times

---

<sup>17</sup> White and Pickett 1985, p. 7.

<sup>18</sup> See Succession (p. 7).

<sup>19</sup> See Community Assembly Rules (p. 13).

<sup>20</sup> See Alternative Persistent States, Thresholds and Resilience (p. 27).

<sup>21</sup> See Scale and Hierarchy (p. 2).

in the last 100 years but the between-event interval varied erratically from 1 to 15 years, then its return interval is also 0.2 per year but its predictability is quite low.

Disturbance **intensity** is the cumulative force of an event, for instance, heat released by a wildfire, wind force and duration in a storm, or depth of inundation, flow speed and duration of a flood. Because the actual forces are seldom possible to measure, they are usually estimated qualitatively, sometimes based on first-hand observations of a disturbance but usually by inference based on an appraisal of its aftermath. Disturbance intensity is usually expressed on a relative, categorical scale such as low → intermediate → high. Intensity most often varies from one part of the area affected by a disturbance to another, at various scales. For instance, a hurricane's intensity is highest along the center of its track (the temporary calm during the passage of the eye notwithstanding) and drops off steadily with distance on either side. Within those zones topography and vegetation cause further variation; wind intensity is higher on windward slopes and crests and lower on leeward slopes, in depressions, and in the understory of intact forest stands. The intensity of flooding in a river's floodplain shows similar variation across a range of scales. Spatial variation in a wildfire's intensity stems from unevenness across the affected area in several factors, including topography, wind speed and direction, fuel structure, fuel moisture, and fuel mass per unit of area.

Disturbance **severity** is the impact on an ecosystem and its constituents, including organisms, resources and the physical environment. Severity often roughly corresponds with intensity within a given disturbance, but in some situations severity and intensity can be very different. For instance, both a crown fire in chaparral in southern California and a crown fire in coniferous forest in the northern Rocky Mountains are high in intensity but they differ sharply in severity. Crown fires are typically lethal to lodgepole pine and other dominant species of northern Rocky Mountain conifer forests and therefore are high-severity. However, high-intensity chaparral fires are often low-severity because the dominant shrubs are fire-tolerant, with most individuals surviving by drawing on abundant root stores and resprouting quickly and prolifically post-fire.

Disturbances are often synergistic, that is, a disturbance of one type can reinforce the effects of a disturbance of a different type. Drought increases the frequency, size and intensity of wildfires. Damage to trees by an insect outbreak increases susceptibility to toppling by wind and may increase susceptibility to, and intensity of, fires. Fungal infection of trees can increase susceptibility to insect herbivory, and vice-versa.

Paradoxically, the ecological concept of disturbance sometimes is stretched to include instances of relatively abrupt, human-imposed *exclusion* of a long-standing disturbance regime — a category of disturbance that is actually a lack of disturbance. The best-known examples have to do with fire exclusion in ecosystems that have been shaped for thousands of years by frequent fire. Tallgrass prairies, oak savannas, pine savannas, chaparral and eastern oak forests are examples of major ecosystems in the U.S. that underwent disruptions of ecosystem, community, and population structure and changes in resources, substrate availability, and the physical environment in the mid-twentieth century by fire exclusion.

**Patch** is a useful concept but it is inherently not well defined. Its meaning is entirely relative to the system under consideration. A patch is a relatively distinct area, often defined by the particular group of species or the general category of species that are dominant, but the term can be applied to a distinct area of any size, degree of internal uniformity, or amount of contrast with its surroundings. A landscape may consist of scattered patches embedded in a relatively uniform **matrix** (predominant cover type) or a mosaic made up entirely of patches. Referring to an area as a patch implies a spatial relationship to other patches or to the surrounding matrix. **Patch dynamics** is the study or description of the changes that a set of patches undergoes, typically driven by disturbance and community assembly.

A particular kind of patch dynamics that appears often in the ecological literature is the phenomenon of a *shifting mosaic*. A shifting mosaic implies near-equilibrium in patch abundance and age structure across a landscape over a long period. The concept applies best where patches are small relative to the landscape under consideration and where the disturbance regime that governs patch establishment is consistent. An often-cited example is the northern hardwood forest in eastern North America, a forest type that is unusually resistant to fire. With no human interference, patch-creating disturbances in a mature northern hardwood stand consist mainly of windstorms and the death of large, old trees. The patches are gaps in the tree canopy of various sizes. An individual patch changes gradually with the growth of tree seedlings and saplings into adult trees, made possible by the increased light and soil resources in the gap; it eventually disappears by developing a closed canopy. In any one year, a mature northern hardwoods stand is a mosaic of patches of various ages and sizes within a matrix of mature trees. Across many years, the locations and ages of the patches change, but the overall number of patches or acres in each patch age class across the stand may vary within a relatively narrow range. Patch dynamics are crucial to northern hardwood forests and many other ecosystems. Even the most shade-tolerant tree species rarely, if ever, reach full size in a forest setting without the repeated formation of gaps in the canopy above them.

Another aspect of patch dynamics concerns *habitat fragmentation* and *connectivity*. A common example again focuses on forests, where they are reduced to fragments in an agricultural or suburban landscape. Ecosystem attrition and resulting habitat fragmentation is very different from a shifting mosaic in several ways. In a highly fragmented forest landscape, the matrix is the most highly disturbed area, dominated by crops, ornamental plantings, and mowed turf. The disturbance is artificial and occurs yearly or more often throughout the matrix, rather than being sporadic and scattered more or less randomly. Because the remnant forest patches are long-lived, populations inhabiting them behave in some ways like populations on islands. In particular, they are exceptionally vulnerable to extirpation (local extinction), with the net result that forest fragments typically have lower native species richness than large, unfragmented forest stands.

The smaller the area of a fragment (or island) is, the smaller the populations are of the native plant and animal species that depend on the habitat conditions found within it. Wild plants and animals don't have the option of responding to decreasing living space by crowding together. The amount of territory, food and other land-based resources each individual needs is a characteristic of its species, although it can vary from place to place depending on habitat quality. Displaced animals sometimes squeeze into habitat remnants temporarily, but if crowded they typically face increased competition with other members of their own species, lower reproductive rates, and higher mortality, which eventually restore normal population density. The smaller any species' local population is, the more vulnerable it is to extirpation. Wild populations fluctuate as a matter of course with year-to-year differences in weather, predator or herbivore abundance, disease outbreaks, and other factors. The smaller a population is, the higher the odds are that in an ordinary fluctuation it will fall to zero. Furthermore, the more isolated patches are from each other, the smaller the likelihood is that a species will be "rescued" from extirpation in one patch by immigration from another patch.

Unlike actual islands, forest fragments in much of the U.S. are remnants of formerly much larger, contiguous tracts of forest, which typically had higher native species richness than the sum of the remaining fragments. Species extirpations following habitat fragmentation do not happen all at once. After a habitat has been cut into pieces, native species richness declines gradually over a long period. The lag time between a habitat-fragmenting event and an ensuing extirpation is highly variable among species and dependent on a complex interplay of site-specific circumstances and chance events. This means that many remnant habitat patches are still

losing native species and will continue to do so for a long time to come, even where fragment sizes and between-fragment distances have not changed in many years.

Species extirpations in fragmented landscapes are due partly to other factors besides a decrease in living space. One is the tendency of small, isolated populations to become inbred, losing much of their genetic diversity and with it their adaptability to changing conditions. Another is the heightened risk to small populations occupying small areas of being wiped out in a single catastrophic event. There are also adverse consequences from the growth of *edge habitat* and the decline of *interior habitat*. Edge habitat is a zone along the outer edge of a patch where influences from the surrounding area degrade that part of the habitat's value for species that survive and reproduce best in the interior. Its width varies with habitat type, the species under consideration, and local conditions. The smaller the patch of a given shape is, the greater its edge-to-interior ratio. It is a fact of plane geometry: shrink any two-dimensional shape and its area will decline faster than the total length of its perimeter. The *patch shape* — its map “footprint” — also determines the edge-to-interior ratio. Of all possible patches of a given total area, a circular patch has the least edge and the most interior. At the other extreme, a very long and narrow patch or an irregularly shaped one with many lobes and indentations may be all edge and no interior for some species.

Some animal species thrive in edge habitat and others are habitat-interior specialists. Opportunistic species that have increased in numbers in agricultural and suburban landscapes tend to be edge species. Those whose populations have decreased with human land-use conversion tend to be interior species. Habitat-interior species such as those native to forests and grasslands suffer higher mortality or have higher rates of reproductive failure along the outer edge of their preferred habitat where that habitat has been fragmented. For instance, many forest birds undergo higher nest predation by mammals and other birds and higher brood parasitism by brown-headed cowbirds near the forest edge. Ground-nesting grassland birds similarly are prone to higher predation rates by mammals and snakes near the grassland edge. The forest edge can expose forest understory plants to drier and windier conditions and displacement by spreading non-forest plants and introduced invasive species, which tend to be superior competitors under high-light conditions. The grassland edge, if next to a forest, can be a hostile environment for herbaceous grassland plants, with too much shade and a thick buildup of tree leaf litter.

Habitat-interior species are sensitive to the size of contiguous habitat interior in a patch. The best-known examples are forest-interior and grassland-interior birds. There are no precise rules about how big an area of contiguous habitat needs to be to support successful breeding and fledging of offspring for these species; this has been shown to vary from one part of a species' range to another and among patches that are near each other but differ in quality. Habitat usage relative to patch size is instead expressed as a probability function — the chances of encountering a breeding pair across a range of habitat fragment sizes (see Figure 6).

A movement swept the conservation community in the 1980s advocating the preservation or establishment of habitat *corridors* between habitat fragments, an approach that had been a part of the wildlife management toolkit since the 1940s. The concept was based on the assumption that fostering *patch connectivity* should lessen the risk of species extirpation in fragmented landscapes. This assumption made intuitive sense but was challenged in the early 1990s as flawed on theoretical grounds or untested in real-world situations using scientifically rigorous methods. Research since then has hinted that habitat corridors do benefit some species in fragmented landscapes, but there are many caveats. For one thing, it is crucial to consider the difference between corridors and the larger category of *linkages*. Not all linkages are corridors. Many species disperse as well or better across the matrix surrounding fragmented habitat; for them the matrix is an effective linkage between patches. Corridors can be beneficial or

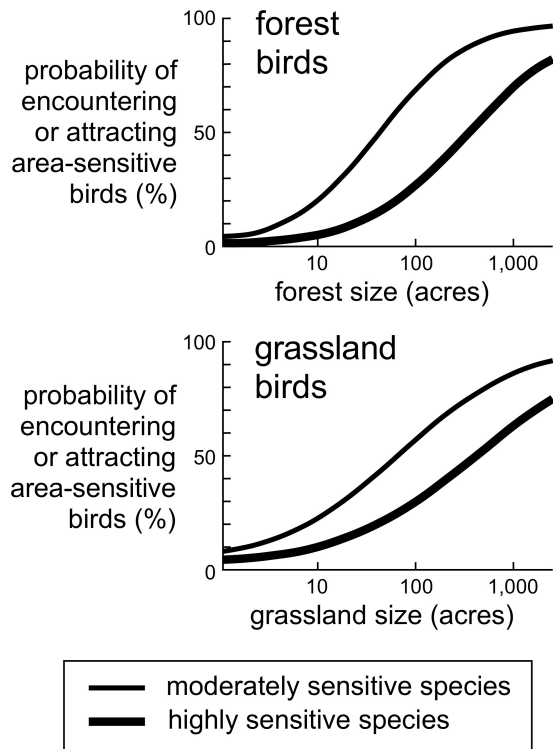


Figure 6. Likelihood of encountering or attracting breeding forest and grassland bird species that are sensitive to habitat fragmentation in patches of various sizes in the Midwest.<sup>22</sup> For example, in a forest fragment of 100 acres there is roughly a 70% likelihood of encountering a wood thrush or a red-eyed vireo (moderately sensitive forest species) and a 40% probability of encountering an ovenbird (a highly sensitive forest species). Graphs were developed from data on breeding bird distribution patterns in forest fragments in Illinois, Missouri, and Wisconsin, and grassland fragments in Illinois and Missouri.

to ecosystem management. It is vital to pay attention to native, historical patch diversity when formulating desired condition analyses and management plans. Native diversity is of great consequence at all scales — not just at the species level — including diversity of genomes and locally adapted populations within species, diversity of habitat structure and patch types within communities, and diversity of community types within landscapes and regions. In current approaches to biodiversity conservation, the most neglected level may be the patch. Based on fossil data and what is known about how ecosystem dynamics vary at different levels of human influence, it is probably correct to assume that most species in the U.S. evolved in highly patchy

detrimental, or both at once, to a particular species. For instance, a corridor may facilitate movement of a species among habitat patches and at the same time provide routes for the transmission of a debilitating or lethal pathogen of that species.

What constitutes an effective linkage between habitat fragments is highly species-specific. Plant and animal species rarely act as though they perceive the landscape as divided into just two categories of patches: habitat and non-habitat. Instead, they utilize a range of patch types, which vary in the availability and quality of essential resources and in the risks associated with being in them or moving through them. A corridor plan therefore has to focus on a particular species or set of species, whose actual habitat selection and movement behavior must be investigated (for instance, by telemetry experiments) and used as the primary basis for planning. Corridor plans also need to consider potentially adverse effects on the target species and on other species and weigh them against the benefits.

Strong scientific evidence for the effect of corridors on genetic diversity within fragmented populations and on species diversity in patchy landscapes is in short supply. Evidence is mostly anecdotal because it is usually too expensive and logistically impractical for investigators to conduct true experiments with adequate controls (for instance, dead-end corridors) and replication. The few full-scale experiments on the effects of corridors in patchy landscapes have shown no effect on salamanders, grassland arthropods, or most rodents, but clear positive effects on arthropods living in moss on boulders, meadow butterflies, and meadow plants whose pollinators are butterflies, wasps and bees.

Patch dynamics are a matter of key importance

<sup>22</sup> Adapted from Figure 2 in Herkert et al. 1993, based on data in Blake and Karr 1984, Hayden 1985, Temple 1986 and Herkert 1991.

environments. This is partly because now-extinct megaherbivores for millions of years had strong impacts on community structure, creating patchiness in the course of their everyday feeding, sleeping, wallowing, and traveling behavior, until their mass extinction in North America just 13,000 years ago. Where megaherbivores persist today in southern and eastern Africa, their disproportionate impact on ecosystems make them keystone species.<sup>23</sup> Just as importantly, recent human activity has increasingly tended to homogenize ecosystems at several scales, but particularly at the scale of patches. For example, even-aged forests grow in the wake of large timber clearcuts, or after wildfires made catastrophic by previous fire exclusion and fuel buildup, or following farmland abandonment. Such forests take a long time to regain the patchiness (and associated higher diversity at other scales) characteristic of old growth, in some cases hundreds of years.

Even our efforts at recreating native communities have sometimes fostered homogeneity. For instance, native grassland reclamation has traditionally begun by planting large areas of land degraded by mining or industrial use or former farm fields with a uniform seed mix. However, typically a few highly competitive, perennial, warm-season (C<sub>4</sub>) grasses soon overwhelm most other species unless reclamation sites are planted in patches with different species mixes, some of which do not include any warm-season grasses at all. Over the long term, in order to sustain patch diversity it is necessary to mimic patchy disturbances. In the grassland example, this may consist of rotating fires among relatively small areas at intervals of varying duration and at different times of year, scarifying the soil or removing part of the soil organic matter in patches within areas where plant cover has become homogeneous, or rotating herds of grazers among confined areas.

Ongoing attrition and fragmentation of many ecosystems has changed the significance of large-scale natural and human-induced disturbances. Scattered fragments are all that is left of many ecosystem types that once covered large areas. Before fragmentation, the occasional large-scale disturbance that devastated an unusually large area would have little impact on a widespread ecosystem type at the scale of its total range. At the largest relevant scale, non-fragmented ecosystems had high resilience in the face of disturbance.<sup>24</sup> The same ecosystem type after fragmentation covers a much smaller total area and typically only a fraction of its remaining fragments are in conservation areas. Once it is fragmented, an ecosystem's regional or global resilience when challenged by large disturbances is severely compromised. Now, instead of having little impact on an ecosystem's global conservation status, large disturbances have the potential to do irreparable damage.

Fragmentation has also changed the significance of small-scale disturbances, especially for animal species that depend on early-successional stages of now-fragmented ecosystems for their habitat needs. For instance, certain butterflies breed only in highly specific mixtures of plants — providers of food for larvae, nectar for adults, oviposition sites, resting sites, and cover for eggs, larvae, pupae and adults — that are found only in short-lived, early successional stages after specific kinds of disturbances in particular matrix ecosystems. During the evolutionary history of such a species, when the required matrix type was widespread, suitable habitat existed as a shifting mosaic of widely scattered, disturbed patches. Dispersal behavior insured that at least a few adults would colonize newly formed habitat patches as old patches matured into the next stage. With attrition and fragmentation of the matrix, patches in the right successional stage become fewer and farther apart, and eventually may be more widely spaced in parts of the butterfly's range than its maximum dispersal distance. Where this happens, the species becomes imperiled. A conservation area is likely to contain too little of the required ecosystem type for

---

<sup>23</sup> See definition of keystone species on p. 16 (under Community Assembly Rules).

<sup>24</sup> See Alternative Persistent States, Thresholds and Resilience (p. 27).

natural disturbance to reliably sustain a large enough supply of early successional habitat patches. If the species is to recover and persist indefinitely, conservation area managers have to increase the habitat supply by mimicking the natural disturbance regime. In some cases, the most expedient recourse may be to keep fixed areas in a state of arrested succession permanently by intensive management, testing how — or whether — an imperiled nomadic species might be turned into a stationary but secure one.

All across the U.S. there is increasing use of prescribed burning for ecosystem restoration and management. It is probably now the most frequently applied simulation of pre-European-settlement disturbance regimes for conservation purposes. In much of the western U.S. and in Florida, lightning fires have had profound effects on ecosystems for millennia. In many parts of the central and eastern U.S., where lightning-ignited fires seldom occur, evidence is growing that humans have been managing the landscape using fire for a large part of the Holocene, or current interglacial interval, which is now going on 10,000 years old. In most of the U.S. (except Hawaii), a key disturbance for millions of years was the activity of several dozen megaherbivore species, which fortuitously — but probably not coincidentally — ended not long before humans began managing some of the same land by burning. The ecosystems we care most about restoring and maintaining, and their component species, evolved over millions of years with megaherbivore populations and for thousands of years with human populations. In all likelihood, both were sources of disturbances that had key roles in shaping many ecosystems as they appeared at the time of European contact and as we know them from surviving remnants.

Contemporary prescribed burning and herbivore grazing differ significantly in their effects on ecosystems from fire regimes and megaherbivore activity in the past. Consider fire as an example. In the eastern U.S., where abundant precipitation falls year-round, periodic severe fires during severe droughts were critical in the origin and maintenance of some ecosystems, but they cannot be duplicated by deliberate burning today because of safety considerations. In some locations where fire is a key ecological attribute in a community of conservation concern, prescribed burning is infeasible. Furthermore, simply restoring fire to a landscape once shaped by fire is often not enough to restore the former ecosystem; changes in species composition and other attributes due to decades of fire exclusion can alter an ecosystem to one that no longer responds in the same way to fire or is no longer capable of even sustaining a fire under prescription burning conditions.<sup>25</sup>

Ecosystem disturbances of human origin in the deep past played a vital role in shaping some of the ecosystems we place a high value on, and must be considered in any analysis of desired condition.<sup>1</sup> It is just as crucial for conservation planners and managers to consider human disturbances in the more recent past and those projected for the future, including the good (those applied intentionally in ecosystem restoration and conservation management), the bad (pollution and other forms of degradation), and those we appear to have no choice but to live with (some degree of global climate change).

---

<sup>25</sup> See *Alternative Persistent States, Thresholds and Resilience* (p. 27).

## References Consulted for Section: Disturbance Ecology and Patch Dynamics

- Blake, J. G. and J. R. Karr. 1984. Species compositions of bird communities and the conservation benefit of large versus small forests. *Biological Conservation* **30**: 173-187.
- Brittingham, M. C. and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* **33**: 31-35.
- Chetkiewicz, C.-L. B., C. C. St. Clair and M. S. Boyce. 2006. Corridors for conservation: integrating pattern and process. *Annual Review of Ecology Evolution and Systematics* **37**: 317-342.
- DeLuca, T. H. and G. H. Apler. 2008. Charcoal and carbon storage in forest soils of the Rocky Mountain West. *Frontiers in Ecology and the Environment* **6**: 18-24.
- Dublin, H. T., A. R. E. Sinclair and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* **59**: 1147-1164.
- Hayden, T. J. 1985. Minimum area requirements of some breeding bird species in fragmented habitats in Missouri. M.A. thesis, University of Missouri, Columbia. 148 pp.
- Herkert, J. R. 1991. An ecological study of the breeding birds of grassland habitats within Illinois. Ph.D. thesis, University of Illinois, Urbana. 115 pp.
- Herkert, J. R., R. E. Szafoni, V. M. Kleen and J. E. Schwegman. 1993. Habitat establishment, enhancement and management for forest and grassland birds in Illinois. Natural Heritage Technical Publication #1. Division of Natural Heritage, Illinois Department of Conservation, Springfield. 20 pp. [www.npwrc.usgs.gov/resource/birds/manbook/index.htm](http://www.npwrc.usgs.gov/resource/birds/manbook/index.htm) (accessed 2008-03-01).
- MacDougall, A. S. and R. Turkington. 2007. Does the type of disturbance matter when restoring disturbance-dependent grasslands? *Restoration Ecology* **15**: 263-272.
- Pickett, S. T. A. and P. S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida. 472 pp.
- Schowalter, T. D. 1985. Adaptations of insects to disturbance. Pp. 235-252 in S. T. A. Pickett and P. S. White, 1985, *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press, Orlando, Florida.
- Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. Pp. 301-304 in J. Verner, M. L. Morrison and C. J. Ralph (eds.), *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*, University of Wisconsin Press, Madison.
- Thompson, F. R. III and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. *Auk* **67**: 408-416.
- Townsend, P. A. and D. J. Levey. 2005. An experimental test of whether habitat corridors affect pollen transfer. *Ecology* **86**: 466-475.
- White, P. S. and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pp. 3-13 in S. T. A. Pickett and P. S. White, 1985, *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press, Orlando, Florida.
- Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin III, J. F. Reynolds and M. C. Chapin. 1995. Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist* **146**: 765-794.

## Alternative Persistent States, Thresholds and Resilience

The traditional view of succession<sup>26</sup> following an ecosystem disturbance leading to a predictable, stable endpoint is often a poor fit to what actually happens. In some cases multiple successional pathways are possible on a given site after a disturbance. Chance events and particular sets of species can change the rules as species assemble into communities<sup>27</sup> following disturbance or during a gradual change in some key ecological factor, making it possible for two or more dissimilar, long-lasting endpoints with completely different sets of dominant species to arise on a given site. *Alternative persistent states* have at least three major consequences for ecological restoration, reclamation and management:

1. Unexpected major changes can occur, sometimes rapidly. Such surprises can happen with or without management, and sometimes as a result of management. Knowledge about alternative persistent states — even though our understanding of the phenomenon is still rudimentary for many ecosystems — can help managers and biologists to anticipate and head off such changes.
2. Once an ecosystem has crossed a threshold into a degraded alternative state, it can be very difficult and expensive, or even infeasible, to bring it back to the desired state.
3. Applying a model of how alternative persistent states may operate can be crucial to restoration or reclamation success in certain situations. Because ecosystems “self-organize” along alternative successional pathways, in some cases nature can be enlisted to do most of the work in converting to a desired state, needing only a fairly small management push to nudge succession onto the desired track. In other cases, brute force may be required to switch an ecosystem already in midcourse on an unwanted successional pathway onto a favored one.

*Alternative persistent states* are defined here as different species assemblages that occur at different times or side by side in the same initial environment, persist with little change over long time periods, and resist invasion by each other’s dominant species. Although two alternative persistent states begin their development in the same initial environment following a disturbance, species-environment feedbacks (more about this later) lead to a divergence in environmental conditions. Alternative persistent states appear in various writings under an assortment of other names, including alternative community states, alternative stable states, multiple stable states, and state-and-transition models. The change on a given site from one alternative persistent state to another is called a *regime shift* or positive-feedback switch.

*State* in this context refers to the ecosystem state, which is a combination of species, their relative abundances, and environmental conditions in a given area, including those produced by the resident species themselves. Ecologists and managers can quantify ecosystem states by selecting and sampling appropriate indicators of *ecosystem state variables*, that is, characteristics that help to define a particular set of species and environmental conditions and to distinguish it from others. Examples of state variables include:

- abundances of particular dominant or keystone species;
- diversity of native species;
- standing biomass;
- species abundance in particular functional groups (examples of functional groups are forest-canopy trees, plants that host nitrogen-fixing symbionts, mycorrhizal fungi, ground-nesting birds, large predators);

---

<sup>26</sup> See Succession (p. 7).

<sup>27</sup> See Community Assembly Rules (p. 13).

- components of vegetation structure (for instance, the densities of the tree canopy, shrub, and herbaceous layers in a forest);
- fire regime (average and variability of fire size, frequency, intensity and severity over time);
- abundances of nonnative, invasive or destructive species; or
- chemical and physical characteristics of the soil, water or air (for example, seasonal variability in nitrate and ammonium levels, total nitrogen or phosphorus content, pH, buffering capacity, temperature and humidity fluctuation).

Where alternative persistent states are a concern in ecosystem restoration, reclamation or management, often there is just one desired state and one or more degraded states triggered by direct or indirect human interference. However, in some cases two alternative persistent states in a single environment may both be considered as indigenous and valued as components of native biodiversity. Such “natural” alternative persistent states can alternate with each other in the same location over long periods and coexist within a landscape as a mosaic. Conservation concerns arise where human activity has disrupted processes critical to the maintenance of one of the states, causing its degradation or widespread conversion to the other state and putting its viability at risk. For example, longleaf pine-wiregrass savanna and oak-scrub forest both occur on dry sandy soils in northern Florida and mesic oak-heath shrubland and northern hardwood forest both occur on moist glacial till plains in northeastern Pennsylvania. Moderately frequent fires maintain the longleaf pine-wiregrass and mesic oak-heath, both of which are highly flammable species assemblages. Oak-scrub forest and northern hardwood forest are fire-retardant; the latter has been dubbed the “asbestos” forest. From a conservation perspective, in each case, the fire-maintained ecosystem state provides habitat for many rare species but forest has been slowly supplanting it since fire exclusion became widespread in the twentieth century. Simply restoring fire can sustain the remnants but it does not reverse the losses.

Persistent states, by definition, are stable for long periods. An ecosystem switching from one persistent state to another is an extraordinary event. Such an event must be triggered by a major disturbance, but disturbance is not a sufficient explanation because ecosystems respond to most disturbances by gradually returning to a persistent state that closely resembles what was there before.<sup>28</sup> The other key ingredient of a regime shift is *positive feedback*. In general terms, a positive feedback is any self-reinforcing process.<sup>29</sup> Common synonyms include positive feedback loop, snowball effect, momentum, or runaway process. Cascade effects and ratchet effects<sup>30</sup> often (but not always) involve positive feedbacks. All of these terms are value-neutral. When the change is perceived as harmful, the terms vicious cycle or downward spiral may be used; when it is seen as beneficial, the analogous terms virtuous cycle or upward spiral are sometimes applied. In ecosystems, positive feedbacks have two essential components:

- A set of environmental changes brought about by abundant organisms, often fostered by influences from keystone species<sup>31</sup> or humans.
- Greater tolerance of the changes by those same increasingly abundant organisms than by the dominant species of the alternative state.

---

<sup>28</sup> See Succession (p. 7).

<sup>29</sup> *Positive* in this context is not a value judgment on the outcome. It refers only to the process’s self-reinforcing nature. (A *negative* feedback is a self-attenuating process. Two opposing negative feedbacks often are involved in equilibrium regulation, for instance, “warm-blooded” animals’ heating and cooling mechanisms are a set of opposing negative feedbacks that together keep body temperature within a narrow range.)

<sup>30</sup> Cascade effects are large changes to the state of a system resulting from a chain of events triggered by a relatively small initial event. Ratchet effect refers to a process that cannot go backwards once certain things have happened.

<sup>31</sup> See definition of keystone species on p. 16 (under Community Assembly Rules).

In an example (see Figure 7), some heathlands — areas dominated by shrubs, including one or more species in the Ericaceae or heath family — persist in regions overwhelmingly dominated by forests and on the same types of terrain and soil. Research has shown strong resilience by mesic (moist-soil) heathlands against forest invasion. U.S. examples are found on Appalachian plateaus, where a regime shift to forest cover often threatens heathland conservation; in other regions, heathland establishment and resilience against forest regrowth after timber harvest is a concern to foresters. Several positive feedbacks are apparently in play. The dominant plants of mesic heathlands acidify the soil, and they are highly tolerant of soil acidity. They produce decomposition-resistant litter, which slows nitrogen and phosphorus mineralization by soil microbes, but they also join with specialized mycorrhizal fungi that decompose and take up organic forms of nitrogen and phosphorus before soil microbes make them available to more common types of mycorrhizae or to non-mycorrhizal plants. Some heathland plants are allelopathic — effectively poisoning competing plants or soil microbes — but tolerate their own toxicity and any induced effects on nutrient cycling. Heathland shrubs tend to be highly combustible due to high surface-to-volume and dead-to-live tissue ratios, fine branches close to the ground, leaf litter with high resistance to decomposition and low water-absorbing and water-holding capacity, and abundant flammable compounds in leaves and stems, but most have the means to survive, recover quickly and even spread after fires, including abundant root reserves, prolific root-sprouting, and the predominance of vegetative reproduction. Other feedbacks involve radiative cooling on clear nights in treeless areas causing “frost pockets” lethal to tree seedlings, and formation of iron or manganese-cemented soil hardpans in the presence of soil-acidifying plants, which are often tolerant of the resulting perched water table. Such feedbacks foster heathland establishment and maintenance under certain conditions. The opposite set of feedbacks may foster forest establishment and maintenance under the same underlying or initial conditions (see Figure 7).

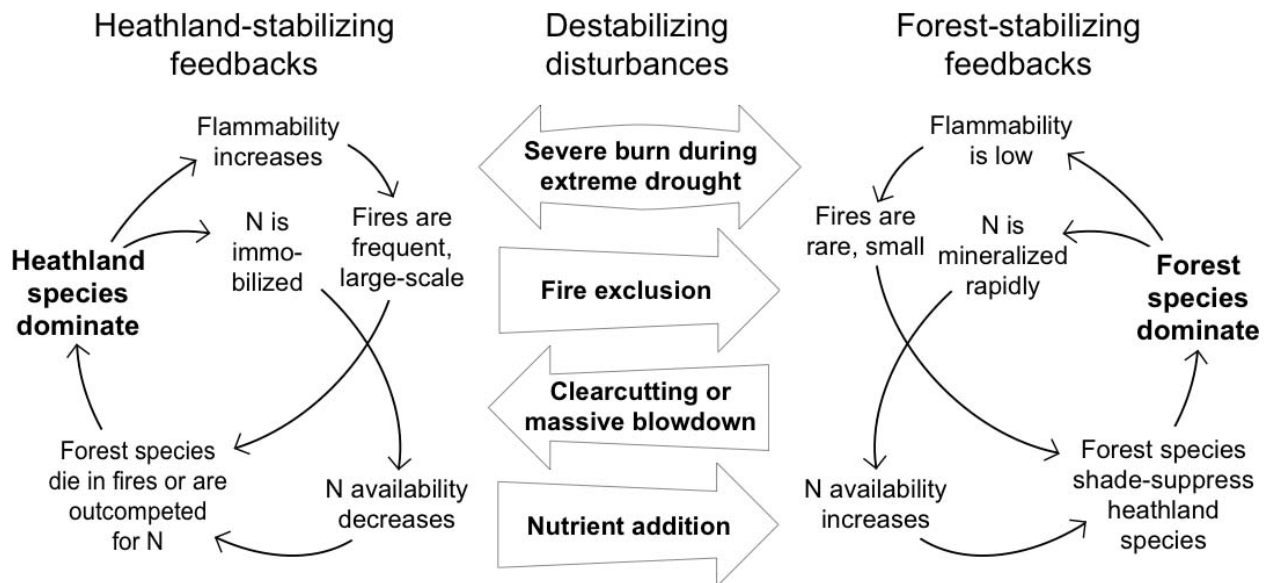


Figure 7. Example of two positive feedback-driven alternative persistent states that can arise in the same underlying environment or switch from one to the other (that is, undergo a regime shift) following certain types of disturbance.<sup>32</sup>

<sup>32</sup> Adapted from Figure 5B in Petraitis and Latham 1999.

Any of the destabilizing disturbances in the example (Figure 7) may have occurred before human influence on the landscape began — at least 13,000 years ago in North America — but today they arise mainly from human activity. Anthropogenic disturbances powerful enough to lead to regime shifts may be destructive or benign. Destructive disturbances include native species extirpation, invasive species introduction, pollution, and habitat fragmentation. Benign disturbances include ecosystem restoration actions such as species reintroduction, augmenting native plants' seed supply, invasive species control, reducing herbivore populations, and prescribed burning.

Typical ecological “drivers” fostering feedbacks that can alter ecosystem states include:

- altered historical disturbance regime, for instance, changes in intensity or frequency of fires, floods, windstorms, etc.;
- local extinction of native species or declining availability of native plant seed sources;
- presence of nonnative species with strong biogeochemical or physical effects;
- altered mutualistic relationships, such as mycorrhizae, pollination, nitrogen fixation and defense;
- changes in trophic interactions, mainly herbivory and predation; or
- environmental changes, such as regional climate change or change in soil or water nutrient status due to atmospheric deposition, runoff or septic inflow.

A major disturbance either sets an ecosystem back to some stage in succession from which it gradually recovers toward its original persistent state, or it initiates positive feedbacks that push the system onto a different successional pathway leading to an alternative state. “The ability of a system to absorb disturbance and still retain its basic function and structure<sup>33</sup>” is a general definition of *resilience*. Ecologists for several decades have defined two separate but related meanings for resilience. One is the speed at which a system returns to its former state after it has been displaced from that state by a disturbance. The other is the amount of disturbance required to push a system over a threshold onto a successional pathway leading to different persistent state, which is close to the general meaning of resilience. The jargon terms used as shortcuts to distinguish these important concepts in the scientific literature are confusing<sup>34</sup>; in this document, resilience is used in the sense related to thresholds and alternative persistent states.

Regime shifts between alternative persistent states are often marked by a *threshold*, the point where even small changes in environmental conditions can initiate a positive feedback that will lead to large, ecosystem-wide changes. The existence of a threshold reflects a *non-linear response* of ecosystem state variables to a change in environmental conditions. The difference can be envisioned by comparing graphs of hypothetical state variables as they respond over time to changing environmental conditions (Figure 8). In the two graphs on the left, a gradual increase in an environmental condition variable (for instance, nutrient concentration in soil or water, average temperature, or population size of an invasive species) is associated with a nearly constant, gradual decrease in an ecosystem state variable (such as plant or macroinvertebrate species richness, percent cover of a dominant plant species, or density of a forest shrub layer). In the two graphs at right, the same gradual increase in the environmental condition variable is associated with a large, abrupt decrease in an ecosystem state variable, which may be an indicator of a regime shift to a new persistent state.

---

<sup>33</sup> Walker and Salt 2006, p. 1.

<sup>34</sup> Some authors call the former *engineering* resilience and the latter *ecological* resilience, but some switch the term ecological resilience to the first meaning and call the latter ecological *resistance*.

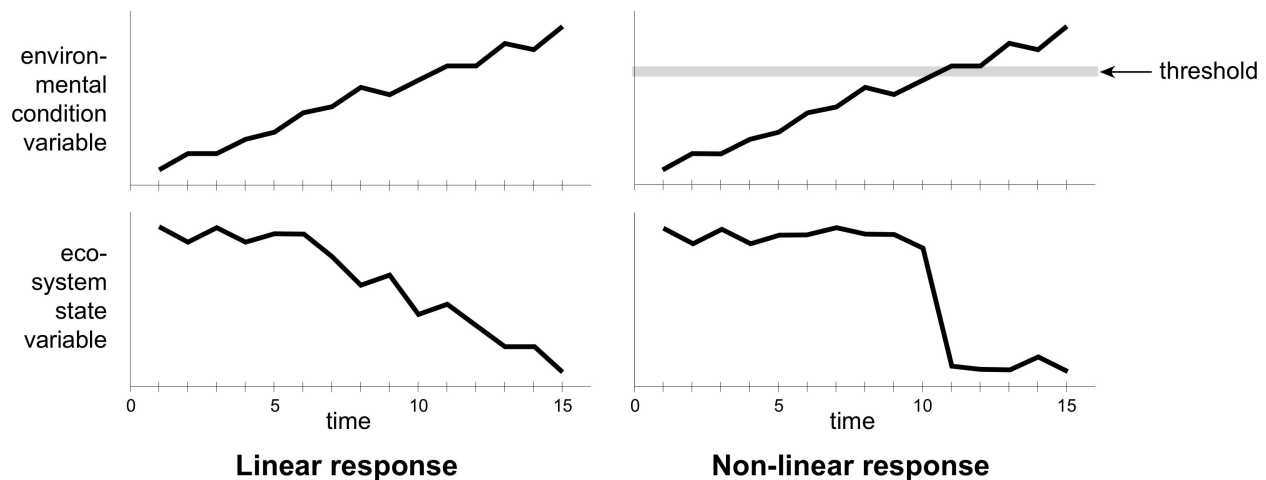


Figure 8. Linear and non-linear (threshold) responses of a hypothetical state variable to a linear change in environmental conditions over time.

An example of a threshold effect commonly occurs in ponds and shallow lakes with clear water where the dominant primary producers are submerged vascular plants. A gradual addition of nutrients from agricultural runoff or sewage effluent causes no visible change in water clarity but steadily reduces the resilience of the clear-water state. As nutrient concentration keeps increasing, the system nears the tipping point, and a small change in some other environmental variable — temperature, for instance — triggers a sudden shift to an alternative state dominated by suspended algae, in which the water resembles a green “soup.” The turbidity reduces light levels for submerged vascular plants and many die. Reducing the nutrient input may trigger a switch in the opposite direction, but often at a much lower threshold of nutrient concentration than the one associated with the switch from the clear-water state to the algae-dominated state.

A similar process has been observed in many Caribbean coral reefs. Accumulated nutrients from human sources promoted increases in growth rates of macroalgae (seaweeds). Algae-grazing fish populations quickly responded by growing and the larger populations kept the algae in check. Intensive fishing later depleted the fish populations, but sea urchins quickly filled the vacuum and their grazing continued to limit algae biomass. However, the high density of the urchin populations facilitated an epidemic spread of a lethal disease. With mass die-offs of urchins, the macroalgae were released from grazer control and abruptly overgrew the reefs.

On the graphs (Figure 8), the tick-marks on the time axis can be thought of as monitoring times, regular intervals when data on ecosystem state indicators are collected. Note that fluctuation in all variables is shown as occurring at two scales. There is a short-term, *normal range of variation* — the effects of weather and other “random” variability — and a longer-term *trend* of consistent, directional change. The graphs suggest the difficulty (in some cases, the impossibility) of distinguishing a trend from normal range-of-variation “noise” without long-term monitoring data. For instance, monitoring only at times 4, 5 and 6 or at times 2, 4 and 6 in either the left or right graph would have led to the misleading diagnosis of a slight upward trend in the ecosystem state variable. Managers can minimize this risk by monitoring indicators as often as is feasible and sustaining monitoring over the long term.

Thresholds can be classified in three categories, as viewed from a conservation perspective:

- thresholds between or among indigenous ecosystems in a historically shifting mosaic;
- degradation thresholds; and
- recovery thresholds.

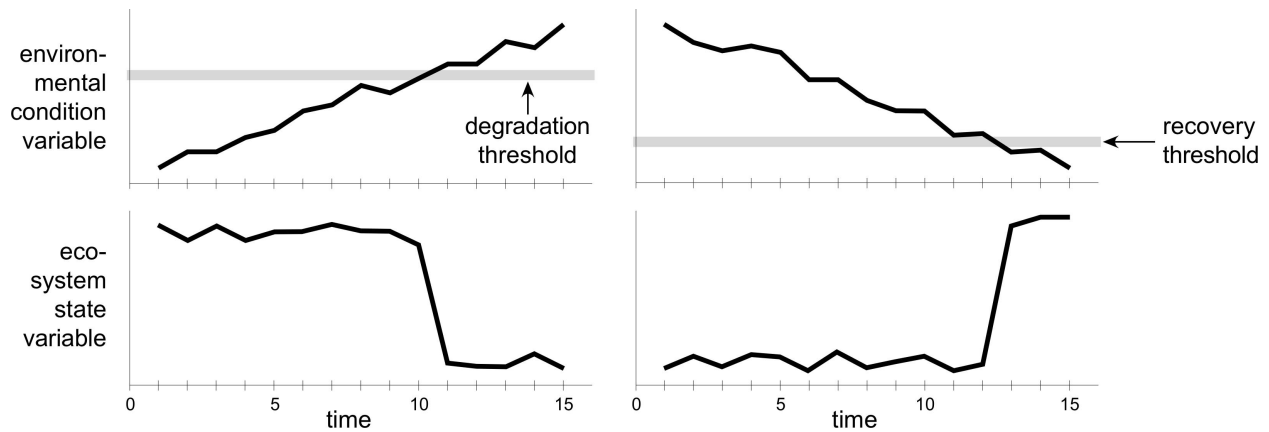


Figure 9. Non-linear (threshold) responses of a hypothetical state variable to a linear increase and a linear decrease in a harmful environmental condition. The graphs illustrate a situation where achieving recovery of a degraded ecosystem depends on reducing the causal environmental condition, for instance, nutrient pollution, to well below the level that originally triggered the shift to a degraded state.

Feedbacks can make a desired state resilient against degradation, but they can also make a degraded system resilient against restorative change. The trajectory of recovery is often different from that of degradation (Figure 9). In other words, recovery is not simply degradation in reverse. Still another way of saying this is that the recovery threshold may be very different from the degradation threshold. In such a situation, a desired ecosystem state may have lower resilience than its degraded counterpart.

Alternative persistent states, non-linear dynamics, and threshold effects are pertinent to managing some, but not all, ecosystems. Can we make educated guesses about whether a particular ecosystem of interest is likely to exhibit such behavior? One way is by analogy to similar ecosystems where such behavior has been well documented. If an ecosystem is similar in key ways to any of the examples discussed here, then the odds are high that alternative persistent states will be relevant to its restoration, reclamation or management. Moreover, ecologists have suggested that non-linear dynamics may be expected where there is:

- a capacity within a system for resource accumulation followed by release;
- a mix of fast and slow-acting variables strongly influencing system dynamics; or
- a potential for shifts of control between different drivers.

Examples of the first situation (and to some degree, the second) are spruce budworm cycles in spruce and fir-dominated forests of North America, including the northern tier states all across the U.S. The larvae of various moth species in the genus *Choristoneura* defoliate and kill large areas of mature forests in outbreaks separated by 30 to 100 years. Between outbreaks budworms are rare, their numbers kept in check by insectivorous birds and parasites. Budworm outbreaks occur only in forests that have reached a threshold level of maturity and appear to be triggered by a period of warm, dry weather. Exponential growth of the budworm population outstrips the capacity of predators and parasites in a relatively small area and then spreads rapidly over thousands of square kilometers. Outbreaks typically last 7 to 16 years, cause high mortality among the host tree species, and end with a crash when the budworms begin to run out of food. Aspen and birch species often dominate the regenerating forest following an outbreak. In a few decades, selective browsing by moose can convert this forest to one again dominated by spruce or fir. The next budworm population explosion occurs only after the slow accumulation of the budworms' resource — the foliage of mature, healthy conifers — has once again reached a critical threshold.

An example of the second situation is nutrient enrichment in the Everglades, specifically rising phosphorus levels from agricultural runoff in water and soil. Florida's famed "river of grass" is actually a patchwork of many communities, but the one that covers the largest area is marshland dominated by sawgrass, actually a sedge, *Cladium jamaicense*. Historically, the Everglades consisted mainly of oligotrophic (low-nutrient) wetlands, where the native plant life is adapted especially to low phosphorus availability, as well as to frequent fires and occasional droughts and frost. Animals concentrated nutrients in scattered small areas, giving rise to forested hammocks sustained in part by bird droppings and cattail-dominated marshes around alligator holes. In the late 1940s, the Everglades were divided into three designated land uses: agriculture, urban development and conservation. Areas receiving runoff from the agricultural and urban sectors were gradually enriched in phosphorus and other nutrients. A threshold level of enrichment was reached in the 1970s and 1980s over large areas. Patches of sawgrass plants killed by fire, drought or frost no longer succeeded back into sawgrass marsh. Sawgrass marshes persist when soil water has less than 300 ppm phosphorus but cattails and other nutrient-demanding plants easily outcompete sawgrass above that threshold. The result has been a large-scale shift to cattail-dominated marshes. A slow increase in soil phosphorus changed the ecosystem's response to short-lived disturbances such as fire, drought or frost, resulting in rapid shifts in vegetation type.

An example of the third situation arose from the long-term effects of groundwater pumping in the Owens Valley on the eastern side of the Sierra Nevada in California. The Los Angeles Aqueduct, built in 1913, diverted the valley's surface water, turning Owens Lake, formerly 16 by 24 km in size, into a dry salt flat by the mid-1920s. The city began withdrawing groundwater in the late twentieth century, eventually lowering the water table in some parts of the valley by more than 5 m. Most of the valley's plant life no longer has access to the water table when it drops to a depth of around 2.5 m. Below this threshold, the main driver of community species composition switches from groundwater to precipitation, which in the Owens Valley is generally low, seasonal, and highly variable among years. In time, many species died out almost completely and the relative abundances of the remaining species underwent major changes.

Carefully selected "disturbances" — manipulations performed for the purpose of ecosystem restoration — can release degraded systems from strong internal feedbacks. One example is the reintroduction of wolves in Yellowstone in 1996 after being absent since the 1920s. The vegetation along streams was heavily browsed by elk, whose population rose sharply after the extirpation of wolves and again after a culling program was halted in 1969. Woody plants, mainly cottonwoods, aspens and willows, were completely suppressed and replaced by an open, short-statured, mainly herbaceous community. Following wolf reintroduction, trees and shrubs have again assumed dominance in some areas, with a cascade of recoveries by beavers, birds and other wildlife that depend on riparian thickets and forests. The effect of wolves has been twofold — predation (lethal) effects, and behavioral (non-lethal) effects, the latter sometimes called "the ecology of fear." The behavioral effect has been strong in areas of high predation risk, for instance, where terrain features reduce long-range visibility of approaching wolves or would impede escape, and it is in these areas that the regime shift to a shrub and tree-dominated community has occurred. There appears to be a positive feedback at work, hastening the recovery of riparian thickets and forests — where woody plants begin to recover, elk increasingly avoid them, presumably because the reduced visibility evokes the fear of wolves appearing suddenly at close range. The increase in the lethal effect on its own has not been enough to reduce browsing lower than the threshold level below which woody plants can escape and grow. It is only in high-predation-risk areas where the elk have moved out that the browsing level has dropped below the threshold.

If ecosystem restoration or management is considered likely to involve alternative persistent states, non-linear dynamics, and threshold effects, expert help should be recruited. A panel of experts should include naturalists who have broad knowledge of the particular ecosystems of interest and research scientists in ecology and other pertinent disciplines (hydrology, limnology, etc.) who have experience in restoration, reclamation or management of similar ecosystems. Such a team can work together to formulate scenarios based on the best available information and judgment. It is unlikely that thresholds for regime shifts can be predicted with any accuracy; the feedbacks are complex and idiosyncratic, varying with the quirks of historical legacy and present and future events. However, experts can reach consensus on *assessment points*, that is, “preselected points along a continuum of resource-indicator values where scientists and managers have together agreed that they want to stop and assess the status or trend of a resource relative to program goals, natural variation, or potential concerns.<sup>35</sup>” *Assessment* in this context is not monitoring, it is a group of experts getting together to consider what to do in response to some warning sign that has been detected by monitoring. The warning sign is a previously agreed-upon level(s) of one or more indicator variables; that level is the assessment point, and its detection triggers the assessment. The indicator variables must relate directly to restoration and management objectives, which in turn are based on the long-term vision of desired condition.

Consider the example of white-tailed deer in some areas of the eastern U.S. where their abundance has become so great that forest ecosystems have shifted to a persistent degraded state, depauperate in diversity and lacking tree regeneration or a functional understory<sup>36</sup>. It might seem logical to monitor deer population density and negotiate assessment points along that continuum. However, the goal of forest restoration involves recovery of species diversity, tree regeneration, understory structure and wildlife habitat, and not any particular target density of deer. Furthermore, the threshold of deer browsing intensity associated with fundamental changes to a forest ecosystem depends on plant species composition, climate, soil chemistry, degree of forest fragmentation, proximity and quality of other food sources, and other factors that vary widely among regions where white-tailed deer live, and even from one patch to another within a forest stand. A herd size that is devastating to one forest ecosystem might do little or no damage in another. Appropriate assessment points would include agreed-upon levels of ecosystem integrity indicators; examples might include the densities of tree seedlings and herbaceous understory plants of sensitive species, overall shrub-layer density, or total cover of rhizomatous ferns, invasive nonnative understory plants, and other species that are the least palatable to deer and therefore expand to fill the space left after most species are consumed.

The core task of a panel of experts deciding on assessment points is to conduct an ecological threshold analysis. Such an analysis should include, but is not necessarily limited to, the following basic steps:

- (1) Recognize or suspect a potential non-linear response in ecosystem state to environmental change, based on known historical changes at the site or on similarities with other ecosystems that have exhibited threshold behavior.
- (2) List multiple causes potentially linked to the shift:
  - (a) natural causes;
  - (b) anthropogenic causes subject to modification or control by managers; and
  - (c) anthropogenic causes not subject to modification or control (such as climate change).

---

<sup>35</sup> Bennetts et al. 2007, p. 59.

<sup>36</sup> See more details about this example on p. 15 (under Community Assembly Rules).

(3) Identify:

(a) key response variables; and

(b) key drivers (perturbations or changing conditions) that influence these variables.

For each response variable and driver, identify the time scale(s) at which it operates (using, for instance, relative categories of rapid, intermediate or slow).

(4) Establish quantitative thresholds for variables that are under human control, as assessment points. Keep in mind the goal of ensuring resilience in the face of variables that cannot be controlled.

## References Consulted for Section: Alternative Persistent States, Thresholds and Resilience

- Beisner, B. E., D. T. Haydon and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* **1**: 376-382.
- Bennett, E. M., G. S. Cumming and G. D. Peterson. 2005. A systems model approach to determining resilience surrogates for case studies. *Ecosystems* **8**: 945–957.
- Bennetts, R. E., J. E. Gross, K. Cahill, C. McIntyre, B. B. Bingham, A. Hubbard, L. Cameron and S. L. Carter. 2007. Linking monitoring to management and planning: assessment points as a generalized approach. *The George Wright Forum* **24**: 59-77.
- Carter, S. L. and R. E. Bennetts. 2007. The road to integrating science and management: planning your next trip using hierarchical objectives and assessment points. *The George Wright Forum* **24**: 78-93.
- Didham, R. K., C. H. Watts and D. A. Norton. 2005. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? *Oikos* **110**: 409-416.
- Groffman, P. M., J. S. Baron, T. Blett, A. J. Gold, I. Goodman, L. H. Gunderson, B. M. Levinson, M. A. Palmer, H. W. Paerl, G. D. Peterson, N. L. Poff, D. W. Rejeski, J. F. Reynolds, M. G. Turner, K. C. Weathers and J. Wiens. 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* **9**: 1-13.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* **4**: 1-24.
- Petraitis, P. S. and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states in ecosystems. *Ecology* **80**: 429-442.
- Resilience Alliance and Santa Fe Institute. 2004. Thresholds and alternate states in ecological and social-ecological systems. [www.resalliance.org/183.php](http://www.resalliance.org/183.php) (accessed 2008-03-12).
- Ripple, W. J. and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* **54**: 755-766.
- Scheffer, M. and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* **18**: 648-656.
- Schröder, A., L. Persson and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review *Oikos* **110**: 3-19.
- Suding, K. N., K. L. Gross and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* **19**: 46-53.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* **108**: 859- 873.
- Walker, B. and D. Salt. 2006. *Resilience Thinking: Sustaining Ecosystems and People in a Changing World*. Island Press, Washington, D.C. 174 pp.