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Forests, Competition and Succession[1]

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Competition, the struggle for limited resources, and succession, the sequence of change in dominant organisms following colonization, have long been key concepts employed by ecologists to understand and organize the patterns of nature. Although competition and succession are distinct processes, they are closely related for at least two reasons. First, successional trajectories are largely driven by interactions among organisms, including (but not restricted to) competition. Second, both are intimately related to the degree of equilibrium or disequilibrium in ecosystems and landscapes. Ecologists once believed that succession led inexorably to a stable equilibrium within a given community of organisms, the composition of which was determined in large part by who won the struggle for limited resources. Although that view has not been totally discarded, most ecologists now recognize that change is the rule rather than the exception in nature, with few if any ecological communities achieving a long-lasting equilibrium in species composition. Disturbances at many spatial and temporal scales create "shifting mosaics" of communities in different stages of succession, resulting in diverse niches that allow more species to coexist than would be possible if all were competing for the same set of resources.

This article first discusses competition: why it occurs, why it does not occur, and how it shapes the structure of communities. It then turns to the patterns and mechanisms of succession, many of which turn on the nature of both competitive and cooperative interactions among species.

I. COMPETITION

> "The inhabitants of the world at each successive period in its history have beaten their predecessors in the race for life." (Charles Darwin, "The Origin of Species," 1859)

One of the oldest ideas in ecology is that individuals utilizing the same resource will compete if that resource is in short supply. For many years ecologists assumed that the sizes of all populations within a given community were ultimately limited by resources, hence competition was believed to be an inevitable consequence of making a living and the major determinant of community structure (i.e., the number of species and size of each population). Constant struggle is not necessarily implied; over many generations species may evolve ways to avoid competition through allocating resources. Nevertheless, communities are ultimately struc-

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tured by competition, be it ongoing or, as a popular phrase puts it, the "ghost of competition past."

Although competition for resources undoubtedly occurs (at least in some trophic levels), the notion that it is the major organizing force in nature is overly simplistic. Most ecologists now recognize that ecological communities are complicated and variable, with their structure shaped by many interacting environmental and biotic factors in addition to resource competition. Species may not compete for resources at all or they may simultaneously compete and cooperate. For example, multispecies flocks of insectivorous birds commonly follow ant swarms in the tropics, feeding on insects flushed by the ants. In 1983, F. Bourliere listed two possible advantages to such mixed flocking: more efficient hunting in a patchy environment and more eyes and ears for protection against predators. Different species of monkeys also frequently forage together, even when they are quite similar in body size and diet. Once again, Bourliere (1983, p. 87): ". . . the main advantage for mixed groups (of monkeys) appears to be to make easier the location of patchily distributed food sources and the detection of predators. A monospecific group of similar size might well offer the same benefits to its members, but at the cost of a stringent social hierarchy which would imply a greater energy expenditure for its enforcement." A. F. Hunter and L. W. Aarssen list the following ways in which coexisting plant species have been demonstrated to help one another: ". . . improving the soil or microclimate, providing physical support, transferring nutrients, distracting or deterring predators or parasites, reducing the impact of other competitors, encouraging beneficial rhizosphere components or discouraging detrimental ones, and attracting pollinators or dispersal agents." [*See* Foraging Strategies.]

At least three things come into play to modify the importance of competition within ecological communities.

1. Species within a given trophic level may be limited by factors other than resources, hence seldom or never have to compete. It has been suggested that the importance of competition alternates up the trophic ladder: plants compete; herbivores are held down by predation, hence do not compete; and carnivores compete because they are at the top of the food chain and therefore have no predators. Evidence in support of this idea is equivocal. However, there is little doubt that predation, disturbance, or climatic fluctuations can and frequently do act to maintain populations below what their food supply would permit. This is often the case with herbivorous insects and its can also occur in plant communities when herbivores and pathogens increase the species richness of plant communities by reducing the ability of any one species to competitively dominate others. Higher order interactions other than predation may come into play to reduce competition. Such is the case with at least some types of mycorrhizal fungi, which by mediating a more equitable distribution of resources among individual plants reduce the ability of one or more species to dominate a community.

2. Species may compete for the same resources but also benefit one another in some way that tends to dilute or negate their negative effects. This undoubtedly occurs in ecosystems (as exemplified by the mixed foraging groups discussed earlier), but may not be readily apparent from casual observation or even from experiments unless conducted over many years (which seldom happens). It has been hypothesized that plant species participate in defense guilds, i.e., either directly or indirectly reduce herbivory and/or pathogenesis within the community. For example, flowering plants are common in young conifer forests, where they probably compete with the conifers for various resources. However, nectar produced by flowers of these plants is important in the diet of at least some insects that prey on defoliating insects. It has been documented that 148 species of parasitoids (important predators of defoliating insects) are associated with flowering plants in forests of northern Germany. What is the net effect of these plants on conifers? If they were not in the ecosystem would faster conifer growth eventually be negated by larger populations of defoliating insects made possible by lower populations of their predators? Questions such as these are seldom entertained in

competition studies. Potentially competing species have also been hypothesized to form cooperative guilds based on protecting and stabilizing ecological commons such as shared mutualists (e.g., pollinators, mycorrhizal fungi) and soils. "Facilitation," in which one plant species has some effect that benefits others, is commonly observed during succession. It does not follow that a "facilitator" does not also compete for resources; however, the net effect is positive rather than negative. On the other hand, there are clear instances in which one plant species has a net negative effect on others, and other cases in which the net effect of one species on another varies with time and environment. These points are followed in the section on succession.

3. Complexity at scales ranging from landscapes through individual trees to soil aggregates creates diverse niches that allow species to avoid competition through specializing.

One of the primary criticisms leveled against the idea that communities are structured primarily by competition is that few experiments have really tested this. If one wants to know the effect of species A on species B, then species A must be removed in a properly designed study, and the response of species B must be measured over a sufficiently long time to assess the fitness of B. Experiments in which one or more plant species are removed are common in forestry and frequently show that removing "competitors" improves the growth of those that remain. However, these are seldom followed long enough to tell whether long-term effects tell a different story. While competition is generally an ongoing process that is readily measured in short-term experiments, the beneficial effects of one species on another may be subtle, long term, or manifest only during certain critical periods. For example, nodulated nitrogen-fixing plants are common pioneers on disturbed sites, where they play an important ecological role by replenishing soil nitrogen and carbon. In the short term these plants compete with others for resources whereas in the longer term they benefit others by increasing soil fertility. To give another example, some hardwood species that grow intermixed with conifers are relatively resistant to fire. During much of the lifetime of a stand these may compete with conifers, but during wildfire they protect the conifers. Species-diverse grasslands are more stable during a severe drought than species-simple grasslands. [*See* FIRE ECOLOGY.]

Interactions among species requiring the same resources are complex, varying over time and with environmental conditions. In contrast, much of the traditional ecological thinking about the role of competition in structuring communities has been shaped by mathematical models that treat two interacting species as if they were in a constant environment and isolated from other species in the system. L. Stone and A. Roberts developed a more realistic model that evaluates the interactions between any two species ". . . within the framework of the community to which they belong." Their approach, which they refer to as the "inverse method," deals strictly with interactions *within* a given trophic level. In other words, these are interactions in which the participants potentially compete for resources. The criterion they use to determine whether a species benefits or suffers in interaction with another is population growth: in essence, they ask "what happens to numbers of species A if numbers of species B increase?" If A increases, it benefits from B (at least within the range of increase of B that is modeled), if A decreases, it suffers from B. Stone and Roberts conclude:

> "Remarkably, the 'inverse' method finds that generally a high proportion (20–40%) of interactions must be beneficial, or 'advantageous,' when not lifted out of the community context in which they actually occur. The contrary case, called here 'hypercompetitive,' in which each species suffers from every other species, can occur only if the environment is nearly constant, and the species closely akin to each other, with both of these conditions holding and persisting to a degree that must be considered implausible."

Given the current evidence for major extinctions caused by meteor impacts, Darwin's "survival of the fittest" may be appropriately modified to "survival of the luckiest." Nevertheless, while various factors reduce competition for limited resources, there seems little doubt that important aspects of community structure reflect the "ghost of competition past." Evidence suggests that through evolutionary time conflicts over food have frequently been resolved through specialization; this is thought by some to have been a significant diversifying force in nature. Examples of food-related niche diversification within animals are widespread in nature. In the neotropics, fruits compose the primary diet of 405 species of birds, 33 species of primates, and 96 species of bats. But the diverse array of fruits produced by the numerous plant species of these areas permits frugivores to specialize to some degree and thus reduce competition or avoid it altogether. In the dry tropical forests around Monte Verde, Costa Rica, it has been estimated that only 13 of the 169 species of fruit eaten by birds are also eaten by bats. Similar studies throughout the tropics have found little overlap in the diets of fruit-eating bats, birds, and primates. [*See* EVOLUTION AND EXTINCTION.]

Niche diversification may take numerous forms, including type of food, timing of feeding, place of feeding, and, in some instances, the ability of a species to capitalize on food provided by periodic extraordinary events. One of the better known examples is Robert MacArthur's study of five warbler species that coexist in conifer forests of New England. All are insect eaters and are about the same size. These species feed in different positions in the canopy, move in different directions through the trees, feed in different manners, and have slightly different nesting dates.

Numerous studies of niche diversification among animals have focused on the so-called *metric traits,* readily measurable attributes such as body size or, in birds, shape and size of the bill, that are assumed to reflect differences in diet. MacArthur discusses bird species diversity on the island of Puercos off the coast of Panama.

> "(T)here are . . . four species of interior forest flycatchers on Puercos. The smallest, the beardless tyrannulet, . . . has an average weight of 8 gm; the next smallest is the scrub flycatcher . . . with an average weight of 14.6 gm; then follows the short-crested flycatcher . . . with a mean weight of 33.3 gm. Each of these is about double the weight of the previous one. Finally, the largest is the streaked flycatcher . . . that weighs an average of 44.5 gm. . . . Other families do not seem to sort by size. For instance, there are two flower-feeding 'honeycreepers,' the bananaquit . . . and the red-legged honeycreeper. They feed together among the flowers in the canopy and their mean weights are 10.7 and 12.8 gm, respectively. There is a plausible explanation for the (fact that flycatchers sort by size while honey-creepers do not). Large flycatchers do eat larger foods than small ones . . . , whereas there is no simple way that a large honeycreeper could eat . . . different food than a small one. . . . Rather the bills are of different shape, and it is very likely that these species eat nectar from different flowers or eat different insects while feeding on nectar."

In summary, long-term, diffuse interactions are the rule in ecological communities instead of the exception. Species certainly compete among themselves for resources, and it will never be known how many are now extinct because they lost a struggle to a superior competitor. However, species also depend on one another in numerous ways that are not readily apparent. Those that compete most of the time might benefit one another during certain critical periods. When one reflects on the multiplicity of indirect, diffuse, and subtle interactions that are possible in ecosystems, it is apparent that the experiments necessary to truly grasp the patterns of nature will be formidably difficult at best, and maybe even impossible (which is not to say that they should not be attempted). Like physicists (who deal with much simpler systems), ecologists may have to accept an "uncertainty principle," i.e., we may never completely capture the richness of nature within the framework of scientific hypotheses and models.

II. SUCCESSION

"No matter what forms we observe, but particularly in the organic, we shall find no-

> where anything enduring, resting, completed, but rather that everything is in continuous motion." (Goethe, 1790)

Envision a landscape of bare rocks exposed by a retreating glacier. This is an inhospitable environment for life. There is no soil, hence no water and nutrient storage capacity to support plants. Animals find little shelter and no food. Some life is adapted to such conditions, however. Lichens colonize the rocks, obtaining nitrogen directly from the air and other nutrients by releasing acids that break down the rock. They scrounge water from cracks in the rock. Lichens provide a food base for animals and, mixing their own organic matter with the products of rock weathering, slowly build a soil, which allows higher plants to establish. These, along with the set of animals and microbes that accompany them, further modify the environment, casting shade and building litter layers, resulting in yet another set of plants and animals—adapted to the new conditions—coming to occupy the site.

This sequence represents what is termed *primary succession;* the term "primary" is applied because there was no preexisting community on the site (or if there was all traces were obliterated). It is an idealized picture—some higher plants, including trees, are quite capable of colonizing fields of bare rock and do not have to wait on lichens—but nevertheless illustrates a common pattern in primary succession:

- A disturbance (glaciation in the example just given, but it could be something else, e.g., volcanic eruption, lava flows) wipes out life and most or all traces of life on a site.
- A set of organisms adapted to survive and reproduce in these "primary" conditions becomes established; the colonizing plants are often characterized by an ability to extract nitrogen (N) directly from the atmosphere and other nutrient elements directly from rock.
- Colonizing organisms modify the site, accumulating nutrients and building soil, thus creating the conditions that permit a second wave of organisms to establish.
- Over many years the site becomes increasingly modified by the biotic communities that occupy it: that combination of minerals, dead organic matter, complex biochemical molecules, and living organisms that is called soil continues to be built, litter accumulates, and, particularly in climates capable of supporting trees, the accumulation of leaf area increasingly shades and buffers the interior of the community from environmental extremes.
- As one set of organisms modifies the site, it is replaced by another set better adapted to the new conditions. Barring another disturbance, a relatively persistent community eventually comes to occupy the site, in forests often (but not always) dominated by tree species that are able to reproduce in shade. The qualifying term *relatively* must be taken seriously when applied to the persistence of late successional stages. Trees may live from hundreds to thousands of years, but they are not immortal. If fire, wind, insects, pathogens, chainsaws, or something else does not kill them, old age eventually will. Each death creates space for new individuals of the same or different species to grow, hence forests are dynamic rather than static. A given set of species virtually never persists indefinitely on a given piece of ground, although constancy in species composition does occur at regional scales (except during major changes in climate).

There are many variations on this theme, but one feature is common to all primary successional sequences: primary succession involves a progressive "imprinting" of biological features onto a physical landscape.

Perhaps the most important biological imprint is soil. Joan Ehrenfeld discusses soil development during primary succession on sand dunes:

> "The soil microflora interacts with plants in promoting soil development in dune ecosystems. Hyphae of both saprophytic and endomycorrhizal fungi help bind sand grains into aggregates through the excretion of amorphous polysaccharides which in turn serve as substrate for colonization by bacteria,

> actinomycetes, and algae. The presence of a diverse microflora enhances the process of aggregation. The degree of soil aggregation increases (as succession proceeds) . . . soil aggregates (mg/kg soil) increase from 5 in the foredunes to 40 on the mobile dune slope, 300 on the dune crest, and 1260 on young fixed dunes. The aggregates contain a variety of fungal species, including mycorrhizal species, and various bacteria . . . thought to be nitrogen fixing. There is an interactive effect between plant root growth and aggregate formation . . . (the) total amount of aggregation, and concomitantly the abundance of all microfloral species . . . increases dramatically in the presence of roots."

Now envision the mature forest that is the "end point" of primary succession on that bare rock. In fact, it is not an end point at all, but one stage in a (more or less) cyclical alternation of communities that will dominate that site. At some future date the glaciers will probably return, but in the intervening period there will be many more disturbances such as fire or severe windstorms that will kill the trees and initiate the process called secondary succession, which occurs where disturbance has left biological imprints (or legacies) such as soil, surviving individuals, and dead wood. Virtually all ecosystems exist within a matrix of fluctuating environments punctuated by periodic disturbances ranging from mild to severe. The twin processes of disturbance and succession form the core of natural dynamics and create much of the variety that is seen in the natural world. On the other hand, disturbances that are too frequent, severe, or "foreign" (i.e., have characteristics to which the species composing the system are not adapted) can throw succession off track and lead to persistent changes that frequently include loss of diversity and productivity, a widespread phenomenon in today's world. Hence understanding the mechanisms of community response to and recovery from disturbance is more than an academic exercise, it yields insights into how humans can protect and sustainably utilize natural systems.

A. Brief Historical Notes

Among American ecologists, two names stand out in the development of successional ideas during the early years of the 20th century: Frederick Clements and H. A. Gleason.[2] Clements believed that communities were superorganisms and that succession was a maturation of the community toward its most mature state, which he called the "climax:"

> "Succession must then be regarded as the development or life history of the climax formation. It is the basic organic process of vegetation, which results in the adult or final form of this complex organism. All the stages that precede the climax are stages of growth. They have the same essential relation to the final stable structure of the organisms that seedling and growing plant have to the adult individual." (Clements, 1916)

For Clements, the composition of the climax vegetation was uniquely determined by climate:

> "Such a climax is permanent because of its entire harmony with a stable habitat. It will persist just as long as the climate remains unchanged, always providing that migration does not bring a new dominant from another region."

Like Clements, Gleason recognized the importance of environment in determining the composition of plant communities; however, he rejected Clements' idea that a given community was a repeatable entity that occurred whenever a given set of environmental conditions occurred. In his 1926 paper, Gleason argued that two factors came into play to make each community distinct from every other. The first was the independent nature of plant species:

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[2] The same contrasting viewpoints were developed in early 20th century Europe. There, the Russian Sukatchew and the Frenchman Braun-Blanquet argued that plant communities were repeatable entities, whereas the individualistic view was developed by the Russian, Ramensky, and the Frenchman, Lenoble.

> ". . . every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. . . . The behavior of the plant offers in itself no reason at all for the segregation of definite communities." (Gleason, 1926)

The second factor was randomness, by which Gleason meant that the composition of a given community was not completely predetermined by environmental factors. Instead, any number of plant species might be able to occupy a given site, but may or may not depending on whether their seeds were dispersed into disturbed areas. Gleason argued that community composition might be repeatable in regions with few species, simply because there were few alternative communities that might develop. But, as species diversity increased within a region, so did the variety of community types that might develop on a given site during the course of succession.

As with most polar issues, the "truth," at least how it is perceived today, contains some elements of both Clements and Gleason, but is adequately captured by neither. Most modern ecologists reject Clements' idea of communities as superorganisms. But, if a community is not an organism in the same sense as an oak tree or a swallowtail butterfly, neither is an individual plant, as Gleason suggests, a law unto itself. Every organism is part of and in interaction with a larger community: feeding, being fed upon, competing, cooperating, and coexisting. Moreover, although randomness is clearly a powerful force in nature, species evolve strategies to reduce the uncertainty associated with randomness and to retain a presence, or a potential presence, on a site. Biological legacies, including (but not restricted to) buried seeds, live roots from which new tops sprout, and mycorrhizal fungi, are passed from the old community to the new, shaping the new in the image of the old, as Clements suggested. Finally, despite the undeniable (and not surprising) fact that different species differ in their environmental requirements (as Gleason argued), the Clementsian view of mutual dependence among members of a community also has validity.

Through the years there has been a shift in emphasis among ecologists who study succession. Clements, Gleason, and others who followed them focused on end points—of which Clements' climax was the archetype. Today, ecologists are more concerned with the mechanisms and processes that shape community dynamics. The following two sections explore successional patterns, then consider mechanisms behind those patterns. It must be kept in mind that what follows are generalizations that may or may not hold in a given situation. As Blaise Pascal observed, "Imagination tires before nature."

B. Stages of Succession

Particularly in severe disturbances, rapidly growing, often short-lived species with widely dispersed seeds are often the most abundant early pioneers. These nomads, as Gomez-Pompa and Vasquez-Yanes call them, are frequently herbs but may also include some tree species. Nomads seldom dominate a site for long periods, generally being quickly replaced by shrubs and trees that were present in one form or another in the predisturbance community. These include plants that grow from buried seeds, sprout from roots, or that survive the disturbance unharmed. In many cases, early successional plants are intolerant of shade, hence their seedlings do not survive and grow beneath an established canopy; in the absence of disturbance the early successional community generally does not perpetuate itself.

Early successional stages are relatively short in both time and stature of the dominant vegetation, whereas the intermediate stages are increasingly lengthy and taller, culminating in Clements' climax community, one that, in theory, persists indefinitely, but in fact rarely does. (In fact, coniferous forests become highly susceptible to crown fires when the mid-successional trees are senescing and late successional conifers begin to grow taller.) Note that a successional sequence refers to changes in *dominance,* or the degree to which the site is occupied by canopies and roots, not to the presence or absence of a given life form. Shrubs and trees that sprout from roots or grow from buried seed, legacies of the old forest, are likely to be present during the earliest stages of secondary succession (unless the disturbance is so catastrophic that surface soils are lost). Many species that come to dominate forests in late successional stages are also able to pioneer newly disturbed sites. Western hemlock, a shade-tolerant, late seral tree of the Pacific Northwest, has light, readily dispersed seed and frequently pioneers clear-cuts in relatively moist habitats. In New England forests, both early and late-seral tree species establish soon after disturbance, with fast-growing pin cherry dominating early in succession and slower growing species emerging to dominate later. In general, throughout any given successional sequence, the community at any one point in time is likely to contain not only the dominants, but seedlings of future dominants. The period prior to complete canopy closure is a time of great species richness, containing mixtures of herbs, shrubs, and tree seedlings, which in turn create diverse habitats for animals.

Most, if not all, forest communities include species that are adapted to recover quickly from disturbances. For example, in the black spruce forests common to the interior of Alaska, burned sites are quickly occupied by sprouting grasses, shrubs, and small trees (willows, birch) and by numerous black spruce seedlings originating from seed stored in semiserotinous cones. In the Pacific Northwest, wildfires create a mosaic of species that either survive the fire through heat-resistant bark or regenerate through sprouting or from buried seed. The initial colonizers in areas where the overstory is killed are generally nomads that persist for a few months to a few years before being succeeded by former residents growing from sprouts or buried seed. [*See* FOREST STAND REGENERATION, NATURAL AND ARTIFICIAL.]

Disturbance severity acts as a filter on the available species pool, modifying the composition of the early successional community. Disturbances that preserve soil but destroy aboveground parts favor sprouters or species with seed stored in the soil. Species with serotinous cones are generally an exception, but not always. In the Rocky Mountains, very intense burns may consume the serotinous cones of lodgepole pine, favoring sprouting aspen. This may also occur in black spruce/aspen stands that occupy certain habitats in interior Alaska. On the other hand, fires that generate excessive heat in the soil either delay recovery by sprouting plants or kill the roots so no sprouting is possible. Tropical trees, many of which sprout prolifically following windthrow, are particularly vulnerable to roots being killed in fire. Without the sprouters, the composition of the early successional community depends on seeds stored in the soil or input to the site following disturbance. Disturbances severe enough to destroy soil (e.g., landslides) generally initiate primary succession, and sites must be colonized by seeds from elsewhere. However, biological legacies have a surprising ability to persist and shape early successional communities. Foreign disturbances—those for which species that comprise the system have no adaptations (e.g., herbicides, fire in some forests)—may eliminate biological legacies and open the site to colonization by nomads.

Along with disturbance severity, timing of a disturbance also filters the available species pool. Composition of the early successional community often depends on coincidences between the time at which a disturbance occurs and the natural rhythms of species within the colonizing pool. Three different time scales are important: time of year, the year itself, and the interval between disturbances. The first two time scales relate to coincidence between disturbance and the availability of propagules (seeds or sprouts) whereas the third relates to life span.

Plant species vary in their seasonal rhythms, hence a disturbance occurring at one time of the year may select for quite a different set of early successional plants than one occurring at another time of year. The ability of some species to sprout following the destruction of aboveground parts varies seasonally: destroyed at one time of year these recover vigorously, at another time of year not at all. Seeds of different species mature, hence are available for colonization, at different times of the year. For example, in interior Alaska most wildfires occur during June and July, coincident with the ripening and dispersal of aspen and balsam poplar seed, but before seeds of white spruce and paper birch ripen. In the tropics, where yearly rhythms of the biota are not constrained by low temperature for part of the year, species vary widely in phenology. Trees that produce animal-dispersed seeds tend to fruit year-round, while those producing wind-dispersed seeds fruit only during the dry season and, moreover, seeds are dispersed only on days with relatively low humidity. Other factors being equal, a disturbance coinciding with this dispersal would probably result in a relatively high proportion of wind-dispersed species in the pioneering community, whereas one that did not coincide would have more animal-dispersed species.

Many trees produce seeds at intervals of several years. In Alaska, for example, birch produces heavy seed crops at least once every 4 years, but white spruce only once every 10 to 12 years. Hence the capacity of a given species to deliver seed to a newly disturbed site depends, among other things, on whether the disturbance coincides with a good seed year. Such a coincidence is not totally random, however, because weather conditions that increase the probability of wildfire, such as hot, dry springs, also trigger seed production by white spruce.

Finally, the interval between disturbances can also influence the composition of the pioneering community. For example, an 80-year-old western hemlock forest in northern Montana was established following a fire without being preceded by lodgepole pine, which is the usual early successional tree of that area. In that case the interval between fires had been sufficiently long that shade-intolerant lodgepole pine had dropped out of the forest, leaving only hemlock to colonize. (Unlike many late-successional trees, hemlock produces light, widely dispersed seed, enabling them to play the role of the pioneer.)

The Steady-State Forest

Once the forest becomes dominated by species that reproduce successfully under their own canopy or in gaps created by the death of old trees, community composition may become relatively stable. This is Clements' climax, and is also called the *steady-state* or *equilibrium* community. The dominant trees are called *climax species*. The steady-state forest is not static, but is composed of a dynamic mosaic of patches created by old trees dying and young trees filling the gaps that are left—a condition termed "shifting-mosaic steady state." Species composition may or may not change over time at any one point on the ground, but on the larger scale of the landscape it will remain constant. The age structure of the forest changes from the relatively even-aged condition of earlier successional stages to the many-aged condition. Biomass accumulation levels out to zero and total biomass remains relatively constant. When discussing steady states, it is important to distinguish between forests and forested landscapes. In theory, all forests attain a steady state as the end point of succession. In fact, however, many do not, or if they do, they do not stay there long because disturbance is always part of the scene. On the other hand, forested landscapes may maintain a relatively stable distribution of stands in different successional stages (the shifting mosaic), even when disturbances are frequent. The landscape area within such a relative steady state depends on the average scale of the disturbance: a regime dominated by small-scale disturbances, such as minor windthrow or low intensity fire, produces a steady state within relatively small areas. This seems to be the case in moist tropical forests that are not on hurricane tracks, mixed conifer hardwood forests of eastern and central North America, dry ponderosa pine forests of interior western North America, and dry miombo woodlands of southern Africa. In each of these, the steady state is characterized by frequent minor disturbances, such as the death of old trees, minor windthrow, or ground fires, that create space within which young trees can establish and grow. The steady state of both ponderosa pine forests and miombo woodland depends on frequent ground fires, in the absence of which new species invade and the character of the forest changes. When the disturbance regime is characterized by large events (e.g., high intensity crown fires), a steady-state may be found only within very large landscapes. Because the disturbance regime of many forest types is characterized by relatively frequent small-scale events punctuated by infrequent large-scale events, the scale at which constancy is found on the landscape varies over time. F. G. Hall and colleagues used remote imagery (Landsat) to document the nature of the shifting mosaic in the 900-km^2 area of the Superior National Forest in northeastern Minnesota, a little less than one-half of which was in wilderness (no logging allowed). Using spectral characteristics (light reflected from the surface) of both visible light and near-infrared, different tree species were distinguished along with the degree of crown closure. This information was used to identify five successional stages (from early to late) from Landsat photos: clearings, areas of regeneration (cleared areas covered by low shrubs and young trees), mature stands of deciduous trees, mixed deciduous–conifer stands, and closed canopy pure conifer stands. Photographs from 1983 were then compared to 1973 photos to determine the rate of change from one type to another. The landscapes of both the wilderness and nonwilderness were very dynamic. Over the 10-year period that was studied, about one-half of the stands changed from one successional stage to another. Despite the dynamism at the stand level, however, the proportion of different successional stages across the landscape remained relatively constant.

C. Mechanisms of Succession

In brief, successional trajectories are influenced by two primary factors: which species colonize first (the so-called priority effects) and how the initial dominants (and each succeeding wave of dominants) influence what follows. Numerous factors combine to determine which species (or set of species) initially establish, although biological legacies provide threads of continuity that facilitate the recovery of species with prior history on a site. According to J. H. Lawton and V. K. Brown, "There is growing evidence for priority effects in community assembly (either species A or species B can establish in the habitat; which one actually does depends upon which arrives first). Priority effects may then lock community development into alternative pathways, generating different end points or alternative states." Through what mechanisms do the earliest arrivals shape subsequent patterns of community development?

In an influential paper in 1977, J. H. Connell and R. O. Slatyer proposed three ways in which a plant might influence a potential successor: *facilitation, tolerance,* and *inhibition.* These terms refer to the effect of environmental modification by early colonizers on the subsequent establishment of late successional species. In the facilitation model, only early successional species are able to colonize disturbed sites, and these modify the environment in such a way that it becomes *less* suitable for their own species and *more* suitable for others. In the tolerance and inhibition models, disturbed sites are potentially colonized by both early and late successional species (i.e., there is nothing inherent in the newly disturbed environment to prevent colonization by late successional species), which then modify the environment in such a way that new individuals of early successional species are unable to become established, with late successional species either unaffected by these modifications (tolerance model) or also inhibited (inhibition model).

J. H. Connell and R. O. Slatyer provided a valuable framework for thinking about species interactions during succession. However, except in a few cases, successional dynamics rarely fit neatly into one or another of the categories they proposed. The interaction between individuals of two different plant species during succession often contains elements of both inhibition (e.g., competition for resources) and facilitation, with the net effect varying depending on factors such as soil fertility, climate, and the relative stocking density of each species. The net effect may also vary over time, a relationship dominated by competition at one stage of stand development becoming predominantly facilitative later on or vice versa. Moreover, successional dynamics can rarely be reduced to interactions between two species: the nature of the relationship between any two individuals is conditioned by numerous other plants, animals, and microbes.

With this background in mind, the mechanisms of interaction will be explored in more detail, beginning with facilitation, then moving to inhibition, and closing with higher-order interactions.

D. Facilitation

Primary successions probably always involve facilitation of one kind or another, most often related to soil building and nutrient accumulation. Soils do not develop without plants, and pioneers facilitate establishment of their successors by weathering rocks, accumulating nutrients and carbon, and providing the energy base that allows populations of soil microbes and animals to establish and grow. Facilitation commonly occurs during secondary as well as primary succession. For example, large amounts of nitrogen can be lost from ecosystems during fire, and nodulated plants are often among the earliest pioneers on burned sites. These plants are often rapid growers that initially compete with other trees and shrubs for water and nutrients, and foresters have often viewed these as undesirable competitors with crop trees. However, in the long run they facilitate the growth of other plants in the ecosystem by restoring soil fertility.

Early successional plants may create certain structures or habitats that facilitate the establishment of later successional species. Providing cover or perches for animals that disperse seeds is one way in which this happens: fruits are eaten and the seed is defecated and nuts are dispersed through the caching behavior of animals. Seeds buried by birds (particularly nutcrackers and jays) and mammals (e.g., squirrels, bears) are a primary avenue of establishment for heavy-seeded species such as oaks, beech, hickories, and some pines (whitebark, limber). It has been estimated that, in a good seed year, a single Clark's nutcracker may cache 100,000 whitebark and limber pine seeds and that jays are able to disperse 150,000 nuts from a beech woodlot. Since animals are exposed to predators when in the open, they frequently constrain their movements, including seed caching, to areas with cover. Jays, for example, avoid open fields when burying acorns. Hence the cover provided by early successional trees and shrubs facilitates the seed dispersal of late successional trees.

One of the more common examples of facilitation during early succession, at least in some environments, is the so-called "island effect," in which tree or shrub seedlings establish most readily in the vicinity of an already established tree or shrub (the *nurse plant*). (This should not be confused with facilitation by nodulated plants discussed earlier; nurse plants may or may not be nodulated.) Tree seedlings invading savannas in Belize, for instance, establish preferentially near other trees, and the same is true for tree seedlings establishing in savannas in the Philippines and in abandoned pastures in Amazonia. The island effect has been noted often in both forests and deserts of western North America. Both ponderosa and pinyon pines require nurse plants to establish on certain droughty and/or frosty sites. Live oak seedlings are strongly associated with some species of woody shrubs in central California, and Douglas fir seedlings establish preferentially beneath some species of oaks in northern California. One study of natural regeneration in Oregon found nearly five times more Douglas fir seedlings beneath Pacific madrone trees than in the open. Not all trees and shrubs necessarily act as nurse plants on a given site. For example, while abundant Douglas fir seedlings establish beneath canopies of Pacific madrone and some species of oaks, none establish beneath nearby Oregon white oak stands.

Reasons for the island effect are not always clear, but there are at least three plausible mechanisms, any or all of which could be operating in a given situation. Nurse plants might (a) shelter seedlings from environmental extremes, (b) act as foci for seed inputs, and (c) provide enriched soil microsites. Shelter can significantly improve survival in droughty sites as well as in cold environments. For example, in the droughty forests of southern Oregon and northern California, shade cast by early successional hardwood trees and shrubs may reduce the water use by conifer seedlings growing beneath them (less transpiration is needed to cool leaves). On high elevation or other frosty sites, nurse plants provide a relatively warm nighttime environment by preventing excessive loss of radiant heat. As discussed earlier, established trees and shrubs act as foci for seed inputs because they attract birds, and birds often leave behind seeds. Over one 6-month period in an abandoned pasture in Amazonia, nearly 400 times more tree seeds were dispersed beneath *Solanum crinitum* trees colonizing the pasture than fell in the open. Eighteen different tree species were represented in the seed rain beneath *Solanum*.

Plant islands may also facilitate the establishment of later-arriving species during secondary succession through soil chemistry, biology, or structure.

This is in some ways similar to, but in other ways quite different than, the facilitation that occurs through soil building during primary succession. Pioneers during secondary successions may restore soil carbon, nutrients, and organisms lost during disturbance; however, what is probably more common following natural disturbances is that the most resiliant members of the former community, species that are able to sprout from roots or grow from buried seeds, prevent soil degradation in the first place by preventing excessive nutrient loss and by maintaining critical elements of soil biology and structure.

Ecologists have known for some time that early successional plants prevent excessive nutrient loss after disturbance. A growing body of evidence suggests that islands of pioneering shrubs and trees, especially those that are legacies of the previous forest, also stabilize soil microbes that facilitate the reestablishment of later-arriving plants. The survival and growth of tree seedlings establishing in disturbed areas may depend on their ability to quickly reestablish links with their belowground microbial partners, especially on infertile soils or in climatically stressful environments. That would seem not to be a problem for plants that can sprout from roots because they presumably never lose contact with belowground partners. However, it could be a problem for trees that reestablish slowly because their seeds must be dispersed to disturbed sites from elsewhere. What happens to their microbial partners during the period the host plant is absent? One possibility is that the microbe simply goes dormant until its host plant reestablishes. Another possibility is that the microbe is flexible enough to utilize other food sources, perhaps by soil organic matter or a pioneering plant. The latter seems to be the case in tropical and at least some temperate forests. The most common mycorrhiza-forming fungal species in tropical forests are widely shared among different tree species, as are some of the fungi that form mycorrhizas with temperate trees and shrubs. An early successional plant that supports microbes needed by later-arriving plants effectively facilitates the reestablishment of the latter, although it may also compete with the late arrival for light, water, and nutrients. In southwest Oregon and northwest California, Douglas-fir and various hardwood trees and shrubs share some of the same mycorrhizal fungi. The hardwoods sprout from roots following disturbances whereas Douglas-fir must reestablish from seeds. Douglas-fir seedlings tend to survive and grow better in the proximity of at least some hardwood species than in the open; controlled studies indicate that the phenomenon is related to soil biology. The Douglas-fir are believed to "plug into" the network of hyphae extending from the hardwood mycorrhizae, which allows seedlings to rapidly develop their own water- and nutrient-gathering capacity. But the phenomenon is complex and appears to involve other factors as well, including nitrogen-fixing bacteria and perhaps bacteria that stimulate root tip production by seedlings. Nutrients also cycle faster in soils near hardwoods than in the open, a reflection of greater biological activity. The evidence amassed so far suggests that hardwoods of this area act as selective filters of soil biology, retaining beneficial soil microbes and inhibiting detrimental ones. Studies of unreforested clear-cuts have found that the inability of seedlings to establish may be related to the buildup of certain types of microbes that inhibit seedlings and their mycorrhizal fungi. In at least one instance, soils near sprouting hardwood islands within a clear-cut were relatively free of deleterious microbes. At present, ecologists have only a rudimentary understanding of the complex relationships among plants and soil organisms, and how these influence successional dynamics.

I. Inhibition

Succession always implies a change in the availability of resources. The deepening canopy shades and alters the microclimate within a stand, favoring shade-tolerant species over those that need high light levels to establish. Nutrients become increasingly tied up in biomass. In what has been called the resource ratio hypothesis, David Tilman argues that relative change in the availability of different resources is generally an important mechanism for species change during both primary and secondary successions. In many cases early successional species create the conditions that inhibit their own progeny from succeeding them. For instance, many sites that had been clear-cut in the Oregon Cascades during the 1960s and early 1970s became dominated by nitrogen-fixing shrubs in the genus *Ceanothus*. Foresters and some scientists were concerned that ceanothus might exclude trees for many decades. Eventually, however, intermixed conifers began to grow above the shrub canopy, and most of those sites are now dominated by Douglas-fir. Inhibition was not permanent in these cases because of the inherently different growth rhythms of the species: ceanothus and alder grow fast and reach maximum heights at a relatively young age, whereas Douglas-fir grows more slowly but maintains growth, eventually becoming taller than the others.

On the other hand, inhibition of one species by another can be relatively long lasting when circumstances permit an aggressive early successional plant to form a dense, monospecific cover that effectively excludes other species. The pioneer could exclude other species by preempting site resources so fully and quickly that no other species can establish, or it might allelopathically inhibit other plants and/or their mycorrhizal fungi. In eastern North America, for example, the failure of trees to reestablish in old clear-cuts, abandoned agricultural fields, and areas burned by wildfire has been related to the allelopathic inhibition of tree seedlings by herbs, ferns, and grasses. In the Sierra Nevada of California, the herbaceous perennial *Wyethia mollis* has spread widely in old burns and allelopathically inhibits tree regeneration. Excluding wildfires from Swedish forests resulted in the spread of a dwarf shrub (*Empetrum hermaphroditum*) that allelopathically inhibits tree regeneration. The inhibitory plants in these examples are often natives that once had been present in relatively low numbers and that were apparently triggered into a more aggressive mode by some foreign disturbance; in other words, a balance was disrupted. In Pennsylvania, tree seedlings were originally eliminated from recovering clear-cuts by forest fires and exceptionally high populations of deer. In California, overgrazing allowed the unpalatable *Wyethia* to spread at the expense of more tasty plants. In Sweden and elsewhere, excluding wildfire has shifted a balance so as to favor the spread of plants previously limited by fire.

Woody plants can have particular difficulty getting a foothold within established grass communities. In western North America, annual grasses are often deliberately sown in recently burned forests to stabilize soils. However, the grasses can completely inhibit the recovery of native shrubs, at least for several years. In Central and South America, areas cleared of forest are frequently seeded to grasses to provide cattle pasture, then abandoned after a few years because they decline in productivity. Trees have great difficulty in reinvading abandoned pastures. According to D. Nepstad *et al.* (1990):

> "Directly or indirectly, grasses present barriers to tree seedlings at every step of establishment in abandoned pastures with histories of intensive use. Seed dispersal into grass-dominated vegetation is low because grasses do not attract birds and bats that eat fleshy fruits of forest trees. Grasses provide food and shelter for large populations of rodents that consume tree seeds and seedlings . . . . The dense root systems of grasses produce severe soil moisture deficits in the dry season and compete for available soil nutrients. Finally, grasses favor fire so that tree seedlings that do surmount the numerous obstacles to establishment are periodically burned."

If a pioneer successfully excludes other plants and is also capable of reproducing under its own canopy, it can, in theory at least, hold a site indefinitely. Such is the case with the Pacific coast shrub salmonberry *Rubus spectabilis,* which produces pure stands of 30,000 or more stems per ha following disturbance. By sprouting from basal buds and rhizomes, salmonberry quickly replaces old stems with new ones, thereby creating unevened periods. Once a pure stand (i.e., without intermixed tree seedlings) attains a sufficiently high density, plants such as salmonberry are likely to persist until weakened by pathogens or insects or until confronted with a disturbance to which they are not adapted. Because of their relative simplicity, species monocultures may be especially vulnerable to pests and pathogens; however, this remains to be seen.

2. Higher-Order Interactions: Those Involving More Than Two Species

In the past, ecologists thought of succession as a process driven primarily by plant–plant interactions. Studies have now shown that many other elements of the ecosystem can either directly or indirectly influence successional trajectories, including particular microbes, animals, and abiotic environmental factors. Community interactions invariably involve several species, not just two, hence complex relationships may develop during succession. In the North Carolina Piedmont, for example, early successional pines inhibit the establishment of fast-growing hardwoods such as Liquidambar, which, in the long term, facilitates the entry of slower-growing oaks and hickories. Animals often modulate plant–plant interactions during succession. In the Pacific Northwest, browsing elk and deer prefer hardwood shrubs over conifer seedlings, accelerating succession from shrubs to trees. This was demonstrated by a study that excluded elk and deer from a portion of a clear-cut in western Washington. In areas accessible to elk and deer there were 8.7 woody stems per m^2, one-half of which were Douglas-fir, whereas the area with no animals present had 19 woody stems per m^2, 11 of which were salmonberry, a particularly aggressive competitor with conifer seedlings. In eastern Oregon, early successional communities in which deer, elk, and cattle are excluded are dominated by *Ceanothus* sp. Where those animals are present, however, browsing limits the height growth of the shrub, and sites are dominated relatively quickly by conifers. On the other hand, where trees are favored food or, as is more often the case, when excessively high animal numbers result in a shortage of preferred food, animals will definitely retard succession and even jeopardize the existence of trees on a site.

Soil organisms play an important but poorly understood role in shaping the composition of successional plant communities. The belowground foodweb is critically important to the nutrient cycle, especially invertebrates and protists that graze microbes. Soils contain microbes such as mycorrhizal fungi and some types of bacteria that directly benefit plants, and microbes that are pathogenic or otherwise inhibitory toward plants. Particular microbial species within those broad groups seldom affect all plant species equally, e.g., a given species of mycorrhizal fungus may benefit some plants and not others; the same is true for the detrimental effect of pathogens. In some instances, a microbe that stimulates one plant species is pathogenic toward another. Because of the selectivity of their action, the composition of the microbial community on a site feeds back to affect the relative success of different plant species. The relationship is reciprocal because a microbe that depends on living plants for food—whether it is a mycorrhizal fungus or a pathogen—presumably cannot persist indefinitely in the absence of a host plant. As a result, feedback relationships develop between composition of the plant community and composition of the soil microbial community.

The availability of beneficial microbes in some instances determines whether their host plants can establish on a site or how well they grow once established. Mycorrhiza formation by plants may be reduced where host plants have been absent too long, on highly disturbed areas (e.g., where erosion is severe), and in some instances even with rather mild soil disturbance. Inoculating seedlings either with mycorrhizal fungi or with forest soils or litter has significantly improved the survival of trees planted in mine spoils, abandoned fields, old clear-cuts, and natural grasslands. Research in Canada indicates that inoculating with certain types of rhizosphere bacteria significantly improves the growth of outplanted tree seedlings. In one case, forest soil transfers enhanced tree seedling establishment in clear-cuts through reintroducing invertebrates and protists that are keystones in the nutrient cycle.

Inhibitory soil microbes include well-known pathogens, such as root rots and the so-called "damping-off" fungi, and less well-known groups, sometimes called "exopathogens," that can have sublethal inhibitory effects on plants and/or mycorrhizal fungi. Actinomycetes, a form of filamentous bacteria, have been implicated in reforestation failures in the Pacific Northwest. *Streptomyces,* from which the antibiotic streptomycin is derived, is a genetically diverse soil actinomycete that has complex effects on other organisms. Depending on the isolate, *Streptomyces* allelopathically inhibit plants, bacteria, and/or plant pathogens, and may either inhibit or stimulate mycorrhizal fungi. *Streptomyces* have been found to be higher in soils of unreforested clear-cuts than in forest soils and, within clear-cuts, higher in soils between islands of sprouting trees and shrubs than in soils beneath the islands.

Some of the more interesting research questions relating to successional dynamics relate to the role of the belowground community. What triggers the buildup of inhibitory microbes in some disturbed areas and how widespread is that phenomenon? How long can mycorrhizal fungi or beneficial rhizosphere bacteria persist in the absence of host plants? How does the composition of the early successional community influence the composition of the soil microbial community and how does that in turn influence the successional trajectory?

E. Threads of Continuity: Legacies and Guilds

Scientists studying the recovery of plants and animals following the eruption of Mt. St. Helens in May 1980, found some surprises. Quoting from J. F. Franklin *et al:*

> "Successional theory traditionally emphasizes invading organisms or immigrants . . . but this script for ecosystem recovery could be played out at only a few sites (at Mt. St. Helens), as surviving organisms over most of the landscape provided a strong and widespread biological legacy from the preeruption ecosystem. In fact, essentially no posteruption environment outside the crater was completely free of preeruption biological influences, although there were substantial differences in the amounts of living and dead organic material that persisted."

Within 3 years after the eruption, 230 plant species—90% of those in preeruption communities—had been found within the area affected by the blast deposit and mudflows.

> "Plant and animal species that live belowground or that have reproductive structures belowground were the most likely survivors . . . Fossorial mammals, such as the pocket gopher (*Thomomys talpoides*), and subterranean and log-dwelling invertebrates, such as ants, survived in the areas of deepest deposits. The most obvious of surviving plants were 'weedy' species such as common firewood (*Epilobium angustifolium*), thistle (*Cirsium* sp.), pearly everlasting (*Anaphalis margaritacea*), various species of blackberry (*Rubus* sp.), and bracken fern (*Pteridium aquilinum*). These plants typically have perennating structures belowground and display vigorous shoot growth which can penetrate overlying deposits." (Franklin *et al.,* 1985)

Webster defines legacy as "anything handed down from . . . an ancestor." In an ecological context, legacies are anything handed down from a predisturbance ecosystem, including:

- surviving propagules and organisms, such as buried seeds, seeds stored in serotinous cones, surviving roots and basal buds, mycorrhizal fungi and other soil microbes, invertebrates, and mammals;
- dead wood; and
- certain aspects of soil chemistry and structure, such as soil organic matter, large soil aggregates, pH, and nutrient balances.

Most, if not all, legacies probably influence the successional trajectory of the recovering system to one degree or another. That is clearly the case with surviving plant propagules, which directly affect composition of the early successional community. Other legacies may shape successional patterns in more subtle ways or perhaps not at all—this is a relatively new area of ecology that needs much more research. Despite the uncertainties, however, a variety of plausible mechanisms exist through which legacies might influence succession.

1. Soil Biology

As already discussed, the composition of the soil biological community following disturbance is a legacy that potentially influences the relative success of different plant species during succession.

2. Dead Wood

Dead wood has the potential to influence system recovery in several ways. Standing dead snags mitigate environmental extremes within disturbed areas by shading and preventing excessive heat loss at night. Down logs within forests are centers of biological activity, including not only organisms of decay, but also roots, mycorrhizal hyphae, nitrogen-fixing bacteria, amphibians, and small mammals. As Franklin *et al.* noted at Mt. St. Helens, logs provide protective cover for their inhabitants during catastrophic disturbances. After disturbance, down logs reduce erosion by acting as physical barriers to soil movement and provide cover for small mammals that disseminate mycorrhizal spores from intact forest into the disturbed area. The sponge-like water-holding capacity of old decaying logs helps seedlings that are rooted in them survive drought.

3. Soil Aggregates and Soil Organic Matter

Plants and associated microbes literally glue minerals together to form soil aggregates, which are intimate mixtures of minerals, organisms, and nutrients. These aggregates are essentially little packages of mycorrhizal propagules, other microbes, and nutrients that are passed from the old forest to the new. Soil organic matter in general, whether contained in aggregates or not (most is), provides a legacy of nutrients for the new stand. Depending on its origin and stage of decay, soil organic matter can either stimulate or inhibit plant pathogens.

4. Soil Chemistry

Different plant species may affect soil chemistry quite differently: by the particular array of nutrients they accumulate, their effect on soil acidity, or allelochemicals they release. To the degree these chemical imprints persist after the plant is gone constitute legacies which, in theory at least, could influence the composition of the early successional community.

Legacies interact with one another, creating chains of direct and indirect influence. At Mt. St. Helens, for example, pocket gophers, which survived below ground, facilitated the establishment of some plant species by digging up soil buried beneath the ash. The exposed soil provided establishing plants with nutrients and mycorrhizal spores, and its organic matter retained water during drought. As discussed previously, sprouting plants, and those growing from buried seeds, often become foci for the recovery of other plants. Whatever the reason, whether providing shelter, perchs for birds that disseminate seeds, or food for mycorrhizal fungi, pioneers that sprout from roots or buried seed constitute legacies that influence the recovery of other species within the system. The legacies provided by pioneers do not necessarily affect other species uniformly, hence can shape successional trajectories by favoring the establishment of some species over others.

One hypothesis holds that species within a given community form into guilds based on common interests in mycorrhizal fungi and perhaps other beneficial soil organisms. According to this view, early colonizers during secondary succession facilitate subsequent colonization by members of the same guild by providing a legacy of mycorrhizal fungi (and perhaps other beneficial soil organisms) and inhibit colonization by members of other guilds because they provide no such legacy. The guild concept may be extended to include animals that are tied into a relational network with plants and their mycorrhizal fungi. For example, truffles, the belowground fruiting bodies of some species of mycorrhizal fungi, are the primary food source for some small mammals, and the small mammals spread spores of the fungi. In forests of the Pacific Northwest, the primary diet of the endangered northern spotted owl is the northern flying squirrel, whose primary diet is truffles. Hence the long-term welfare of both flying squirrels and spotted owls depends on successional trajectories that lead back to trees that support truffle-producing mycorrhizal fungi.

G. Summary of Successional Mechanisms

To summarize this section, patterns of species establishment and changing dominance during succession are likely to result from a mixture of random factors and complex interactions among plants, animals, and microbes. To a certain degree, composition of a pioneer community is determined by which species arrive first, which is, in turn, a function of interactions between the nature and timing of disturbance on the one hand and the early successional environment, which filters colonizers according to their adaptations, on the other. Biological legacies facilitate recovery of the system and act to shape the new community in the image of the old. Dominance changes over time in part because developmental patterns differ among species—some are fast growing and short-lived, others are slow growing and long lived, and yet others are somewhere in between—and in part because, for various reasons, some species establish more successfully in a preexisting community than in a newly disturbed site. Interactions among plant species during succession often include elements of both facilitation and inhibition, and are influenced by complex interactions among climate, resource availability, and many nonplant species such as animals, pathogens, mycorrhizal fungi, and other soil microbes. Moreover, the nature of interaction may change with time: inhibition becoming facilitation or facilitation becoming inhibition. As a result, one must proceed cautiously when judging interactions among plants during succession.

Glossary

Competition Interaction between individuals of the same species (intraspecific competition) or between different species (interspecific competition) at the same trophic level, in which the growth and survival of one or all species or individuals are affected adversely. The competitive mechanism may be direct (active), as in allelopathy and mutual inhibition, or indirect, as when a common resource is scarce. Competition leads either to the replacement of one species by another that has a competitive advantage or to the modification of the interacting species by selective adaptation (whereby competition is minimized by small behavioral differences, e.g., in feeding patterns). Competition thus favors the separation of closely related or otherwise similar species. Separation may be achieved spatially, temporally, or ecologically (i.e., by adaptations in behavior, morphology, etc.). The tendency of species to separate in this way is known as the competitive exclusion or Gause principle.

Niche (ecological) Functional position of an organism in its environment, comprising the habitat in which the organism lives, the periods of time during which it occurs and is active there, and the resources it obtains there.

Seral stage A phase in the sequential development of a climax community.

Sere Characteristic sequence of developmental stages occurring in plant succession.

Succession Sequential change in vegetation and the animals associated with it, either in response to an environmental change or induced by the intrinsic properties of the organisms themselves. Classically, the term refers to the colonization of a new physical environment by a series of vegetation communities until a final equilibrium state, the climax, is achieved. The presence of the colonizers, the pioneer plant species, modifies the environment so that new species can join or replace the initial colonizers. Changes are rapid at first but slow to a more or less imperceptible rate at the climax stage, composed of climax plant species. The term applies to animals (especially to sessile animals in aquatic ecosystems) as well as to plants. The characteristic sequence of developmental stages (i.e., nudation, migration, ecesis, competition, reaction, and stabilization) is termed a sere.

Trophic level A step in the transfer of food or energy within a chain. There may be several trophic levels within a system, for example, producers (autotrophs), primary consumers (herbivores), and secondary consumers (carnivores); further carnivores may form fourth and fifth levels. There are rarely more than five levels since usually by this stage the amount of food or energy is greatly reduced.

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