SUCCESSION,
PHENOMENON OF

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I. Introduction
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GLOSSARY

autotrophic successions These generate energy from internal processes (photosynthesis).
climax community According to some theories of succession, the end result of succession in which successional change ends with a community that does not change and which is in equilibrium with the climate.
disturbance Major alternations of vegetation due to events such as wildfires, hurricanes, landslides, and human clearing.
heterotrophic successions Dependent on already fixed energy, such as the successional of communities associated with decomposition of dead logs.
individualistic view of succession Concept that succession is a consequence of species interacting with one another and their environment.
primary succession Succession on newly exposed substrates such as a sandbar or rubble at the foot of a receding glacier.
progressive succession Successions in which the dynamic changes are in the directions of increasing species diversity, structural complexity, greater biomass, and increased stability. Retrogressive successions are in the opposite directions.
secondary succession Succession on existing substrate (soil) following a disturbance.
succession The pattern of change expected in a community over time after a disturbance or after new substrate has been exposed.

ECOLOGICAL SUCCESSION is an ordered progression of structural and compositional changes in ecosystems toward an eventual stable condition. Descriptions of succession involve the nature of the changes and the factors that cause the changes. Ecologists have debated whether the succession is a community process or the summation of the consequences of individual species and their interactions with each other and the environment. Most ecologists doing research in this area currently favor the latter view. Investigations of the types of interactions among species have led to an increased interest in the mosaic nature of vegetation and to the application of computer models to project the expected patterns of change in vegetation over time. The biodiversity of landscapes may be highest when there is an intermediate level of disturbance. The appearance of species at different times in succession appears to be idiosyncratic to the particular vegetation; the rate of
loss of species from communities seems to decrease logarithmically.

I. INTRODUCTION

Ecological succession is an ordered progression of structural and compositional changes in ecosystems toward an eventual stable condition. Primary successions are initiated on new substrates, such as a new volcanic island, a new sandbar in a river, or rubble fields at the foot of a receding glacier. Secondary successions involve the recovery of vegetation on established soils from land abandonment and from disturbances such as wildfires, hurricanes, or human alterations to vegetation. Other significant dichotomies used to categorize succession involve whether a given successional sequence is

1. Progressive (dynamically changing in the directions of increasing species diversity, structural complexity, greater biomass, and increased stability) or regressive (in the opposite directions)
2. Autotrophic (generating energy from internal processes) or heterotrophic (dependent on already fixed energy, such as the successional of communities associated with decomposition of dead logs)
3. Autogenic (changing due to interactions from inside the system) or allocogenic (changing in response to changes in external variables)

Ecological succession is an early concept in ecology and was essential in the early definitions of ecological communities. Although the basic concepts of succession are easily understood, debates about succession (Box 1) have spawned considerable confusion and discussion. The mechanisms that drive ecological succession and its very existence as a natural phenomenon have been the subject of continual debate among ecologists. McIntosh (1985) identifies two contrasting views that typify traditional natural history and also can be found in current discussions of theoretical ecology. This dichotomy, which can be used to organize theories about ecological succession, contrasts mechanistic explanations and organic (holistic) explanations of the causes of succession. For mechanistic theories about succession, known laws explain the actions of the individual parts of a system and the whole system is the sum of these parts and their interactions. In the case of organic or holistic explanations, the whole system, its existence and design, explains the actions of the parts. Mechanistic explanations often are taken as the more modern interpretation of succession, but these “modern” views may have been the first developed and certainly developed as early as the organic views. Organic explanations of succession were most popular, at least in the United States, between the 1920s and early 1950s and have had a considerable impact on land use and conservation policies.

II. ORGANIC EXPLANATIONS OF ECOLOGICAL SUCCESSION

Organic explanations seek to understand succession in terms of principles that operate at the level of the whole system. In the 1920s and 1930s, F. E. Clements and particularly John Phillips were ascribing to ecological communities the attributes of a superorganism—a highly organized and coevolved assemblage of plants and animals interacting in a dynamic system. The ecosystem concept had its roots in debates regarding the organization and dynamics of natural systems. It was Tansley's negative view of Clements' and Phillips' interpretation of the community as a superorganism that in 1935 inspired his development of the ecosystem concept as an alternative to the organic term ‘community.’

A. Clementsian Concepts of Ecological Succession

Between 1905 and 1935, F. E. Clements promoted a dynamic plant ecology built around a “supraorganismic” view of the ecological community. At the time of their conception, Clements' ideas represented a significant emphasis on the dynamics of vegetation and were an important early attempt to develop a formal theory predicting the pattern and expected change in ecological communities. The underlying conviction was that evolution and internal interactions would produce a homogeneous regional “climax” vegetation or community of regular species composition. The development of this “climatic climax” community was ecological succession, which was viewed as the community analog of the embryological interactions that produce an organism. In this view, succession was typified by a progressive sequence of serial stages or seres, communities that sequentially replaced one another over time until the climax stage was reached. Successional development was the result of a set of processes:

1. Nudation—the creation of a bare area (or partially bare area) to initiate succession...
Complex Debates Arising in a Simple Definition

Is the pathway of successional change ordered because the mechanisms that cause succession need to occur in a proper sequence or can the steps in the order be skipped in some cases? Is there more than one ordered progression? How much variability can be tolerated before the apparent order in the progression becomes recognized as disordered or chaotic?

Ecological succession is an ordered progression of structural and compositional changes in ecosystems toward an eventual stable condition.

In 1935, A.G. Tansley coined the term “ecosystem” to replace “community” because he felt the trend of thinking of the community as a direct analogue to a living organism — with succession an equivalent to embryological development — was scientifically and conceptually unwarranted.

Classically, the eventual target of successional development is the climax community - a stable community associated with a given climate. Can this condition be reached before the dynamic climate changes? If so, is there more than one stable climax community?

2. Migration—the arrival of organisms at the location
3. Ecesis—the establishment of organisms at the location
4. Coaction—the interactions, particularly competition, among the organisms
5. Reaction (or facilitation)—the modification of the site by the organisms and the subsequent change in the relative abilities of the organisms to establish and survive
6. Stabilization—the development of a stable community called the climax community
Stabilization is less a process and more a consequence of the iterative reapplication of the migration, ecesis, coaction, and reaction processes until a stable community is reached. Clements' concept of the climax community was that there was only one stable vegetation type that was in equilibrium with the regional climate. Succession was the orderly, predictable, progressive, and linear development toward this climax community.

### B. Application of Clementsian Concepts

The Clementsian succession paradigm had a pronounced effect on ecology in the United States in the first half of the twentieth century (much less so in Europe), and it shaped many of the laws and policies on the use of public lands. Earlier ecologists developed some of these ideas, and others evolved over Clements' and associates' scientific careers. Important aspects in the Clementsian paradigm, many of which continue to be a part of natural land management today, are

- **Community-level management**: The idea that one could use the state of ecological communities to evaluate their past and present conditions and to predict their future is a significant contribution of Clements and associates. Although it has been established by paleoecological studies that communities are not necessarily stable over century and millennial timescales, short-term changes and disturbances are often seen as changes in communities. Conservation groups often make considerable effort to preserve unique communities (as well as unusual or important species). Wildlife and endangered species management is often based on maintaining particular communities or habitat types appropriate to the survival of focal species of animal or plants.

- **Indicator species concept**: Clements believed that the presence or absence of particular species could be used to assess the state of a community and its potential for agricultural conversion. For example, the presence of poisonous or distasteful plants on a range indicates overgrazing, the occurrence of certain species of Lupine (Lupinus platensis) in a Nebraska prairie connotes a deep soil suitable for tilling and agriculture, and land with plants such as Salticornia might be so loaded with salt as to be unreclaimable. One could use indicator species to determine the past history of a landscape and to predict its future changes and potential uses.

- **Climax community concept**: The climax community is the community that is stable in a given climate condition and is the ultimate product of successional processes. Current vegetation maps, particularly for large regions, display the expected climax community or potential natural vegetation expected in a region rather than the actual vegetation found there. Parks and wilderness areas are managed to maintain the natural climax community that is typical of the region. As an issue in conservation of diversity, often considerable effort is made to preserve unique communities (as well as species).

- **Progressive nature of succession**: Clements viewed succession as being progressive (moving in a positive direction) toward the climax community. The succession progressed toward more diverse, more stable, and more desirable communities. This is a concept associated with eighteenth-century intellectuals and tied to other concepts such as the divine design of natural systems and ideas about the ‘balance of nature’ and the antiquity of certain ecological communities. Whether from Clements or earlier sources, these ideas have considerable influence on the aesthetics of conservation in the valuation of wilderness and the assessment of the importance of preserving certain species rather than others.

Perhaps the most enduring legacy from Clements is his pioneering attempt to synthesize quantitative observations about succession into a unified theory. Even strong detractors of the details of Clements' concepts are still involved in understanding succession as a general phenomenon.

### C. Alternative Organic Theories on Succession

Clements' theory is the most frequently presented organic succession theory, so much so that textbook writers often term Clementian theory to be "classic" succession theory. However, all American and British ecologists did not accept these ideas. This rejection was certainly the case for ecologists from continental Europe. Some of these ecologists emphasized a more individual species-oriented mechanistic description of succession. Others shared an interest in the holistic causes of successional change but differed from Clements in significant details. H. C. Cowles, who in 1899 was one of the first American ecologists to study ecological succession, characterized succession as "a variable approaching a variable": Succession was considered the change of a system perturbed away from—but moving toward—an equilibrium that is itself changing. Cowles believed that the climax community was never reached. In 1935, A. G. Tansley contrasted Clements' climatic
climax or monochimax theory with a polyclimax theory that had the climax vegetation of a region as a mosaic of local vegetation climaxes related to local conditions and disturbance history. In 1913, W. S. Cooper studied the forest succession on Isle Royale (Michigan) and found that the mature forest was a mosaic of patches of different ages and not the uniform climax community expected in Clementsian succession. He also believed that succession took multiple pathways and was not a linear progression of changes in seral stages. Similarly, in 1901, Cowles noted, “Succession is not a straight-line process. Its stages may be slow or rapid, direct or tortuous and often they are retrogressive” (Bot. Gazette 31, 73–108, 145–182). Recognizing that there is and has been considerable difference in opinion among ecologists who use organic explanations of ecological succession, there is an even stronger contrasting of concepts between Clementsian succession and mechanistic explanations of ecological succession emphasized by some ecologists.

III. MECHANISTIC EXPLANATIONS OF ECOLOGICAL SUCCESSION

Some of the debate about the nature of succession concerns the degree to which the vegetation can be arranged into communities that are natural units of biological organization. Introductions of modern biology or ecology texts often have diagrams of biological organization that illustrate an organizational hierarchy from cells to tissues to individuals to populations to communities, etc. Such progressions convey the idea that the community is a unit of organization as demonstrable at a level such as the existence of the liver or spleen as an organizational unit is at some other level.

The American H. A. Gleason (in 1926) and the Russian L. G. Ramensky (in 1924) emphasized that vegetation was mostly the consequence of the chance arrival of species at a location and the subsequent interactions among the available species to produce the observed pattern of relative species abundance. These interactions did not produce distinct unit communities. The vegetation was believed to vary continuously with changes in the underlying environmental conditions. Under this “individualistic” view of ecological succession, the process of succession was a consequence of species interacting with one another in the context of the environment to produce vegetation dynamics or successional change. Today, most ecologists subscribe to this individualistic view of ecological succession.

A. Descriptive Mechanistic Models of Succession

When one compares modern descriptive models of succession with the Clementsian model, it is apparent that there is a substantial difference in the spatial scale considered by the two schools. Clements’ climax community was considered by him to be a phenomenon that occurred over large areas. This is evident by the fact that Clementsian succession proceeded toward a regional-scale climax. Also, the union of the climax community (vegetation) and associated animals was a “biome” of which there were thought to be only 13 in nontropical North America. Clements believed that when the community in a given location was too small to have all of the species represented, succession might take different courses. However, he also believed that the succession processes he had described (nudation, ecesis, coaction, and reaction) are also represented by a mechanistic explanation of succession, albeit with different names and differing emphases. The differences are most pronounced with regard to the importance of the reaction (facilitation). Certainly in many primary successions, the changes produced by one set of species appear necessary for the success of the next. For example, the rapidly growing willows (Salix sp.) that stabilize sandbars in rivers seem to be a necessary preamble to the success of subsequent species; the ability of alder (Alnus sp.) to symbiotically fix nitrogen increases the fertility of sites uncovered by receding glaciers; and the organic acids produced by blue-green algae, lichens, and mosses speed the breakdown of granite and the development of a thin soil. The importance of the reaction (facilitation) is demonstrated by the fact that many primary successions, the changes produced by one set of species appear necessary for the success of the next. For example, the rapidly growing willows (Salix sp.) that stabilize sandbars in rivers seem to be a necessary preamble to the success of subsequent species; the ability of alder (Alnus sp.) to symbiotically fix nitrogen increases the fertility of sites uncovered by receding glaciers; and the organic acids produced by blue-green algae, lichens, and mosses speed the breakdown of granite and the development of a thin soil to support grasses, herbs, and even trees in primary successions on granite outcrops.

However, some species appear to block the success of others and hold sites against species that might otherwise succeed them. In some secondary successions, all the species involved in the succession are present as seeds or other propagules from the initiation. In these cases, the familiar successional sequence of grasses and herbs yielding to shrubs and then to trees may reflect a difference in rate of growth of individuals present from the start. Evolutionarily, it is difficult to explain why a species would evolve to help another take over a site it could otherwise occupy.
TABLE I

<table>
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<tr>
<th>General causes of succession</th>
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<th>Clementsian succession analog processes</th>
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<td>Coarse-scale disturbance</td>
<td>Site, severity and timing of disturbance, dispersion of species</td>
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<td>Differential species availability</td>
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<td>Availability of resources</td>
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<tr>
<td>Ecosystem availability</td>
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<td>Life history</td>
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<td>Competition</td>
<td>Hierarchy of competitive interactions, the presence of competitors, identity of competitors, with-in community disturbances, predators, herbivores, resource base</td>
<td>Climate cycles, predator cycles, plant vigor, plant defenses, community composition, patchiness</td>
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<td>Herbivory, predation, disease</td>
<td></td>
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<td>Environmental stress</td>
<td>Climate cycles, site history, prior occupants</td>
<td>Soil chemistry, soil structure, microbes, neighboring species</td>
<td>?</td>
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</table>

*The first three columns are from a review by Pickett et al. (1987).

Connel and Slatyer (1977) developed a descriptive model of the succession processes based on a mechanistic understanding of succession (Fig. 1). They used the reaction/facilitation issue to frame three models of succession based on mechanisms of interaction (the facilitation model, tolerance model, and inhibition model). In Fig. 1, the facilitation model is most like Clementsian succession as typically interpreted. The three models are different and have different implications for land management and particularly land reclamation. If one had the objective of restoring degraded landscapes, then one might speed the restoration by eliminating established species in the case of the inhibition model, but this would be ill advised in the facilitation model (Fig. 1).

B. The Landscape as a Mosaic

In addition to an expansion of the facilitation concept associated with Clementsian succession, there has also been an emphasis on understanding the mosaic nature of vegetation. Historically, this emphasis derives from earlier concepts of "cyclical succession" (exemplified by the cyclical replacement series involving a forest canopy gap) and the "polyclimax" (the mature forest as a mosaic trees, gaps, and recovering gaps). Theories about the dynamics of landscape mosaics have been developed in forests to a significant extent, probably because, regardless of other sources of spatial heterogeneity, a forest canopy is a mosaic of tree crowns (Fig. 2). Starting with a small plot of land in a mature forest dominated by a single large tree, the large tree shades the ground and reduces the survival of smaller trees and seedlings below. There may be a few smaller shade-tolerating trees that survive under the large tree, but these are strongly suppressed in their rate of growth. The large tree dominates the resources (light, water, and nutrients) that are available at the site and blocks other trees from growing at the location. When this tree dies, the forest floor (where there had previously been little chance of a young tree's survival) becomes a nursery for small seedlings and saplings. There is adequate light and other resources, and hundreds of small trees survive and begin to grow toward the canopy. As these trees grow, they begin to compete with one another. Some of the trees lose to more vigorously growing competitors. Eventually one tree manages to win the race to be the local canopy tree and begins to
eliminate the others. This represents the closure of the cycle with a large tree again dominating the site. Over the course of time this cycle is reinitiated by the death of the new dominant replacement tree. The implications of the cyclical nature of small-scale forest dynamics were clearly elucidated by Cooper in 1913 and by A. S. Watt in a classic paper in 1947.

The expected changes in the amount of living material (biomass) over multiple iterations of a gap generation and filling should create a "saw-toothed"-shaped curve. This curve drops abruptly with the death of a canopy dominant and then builds biomass as the regenerating trees grow, compete, and occupy the site (Fig. 3, top). The distances between the "teeth" in the saw-toothed, small-scale biomass curve are determined by how long a particular tree lives and how much time is required for a new tree to grow to dominate a canopy gap.
The larger scale biomass dynamics (Fig. 3, bottom) is a simple statistical consequence of summing the dynamics of the parts of the landscape mosaic. If there has been a synchronizing event, such as a clear-cutting or other disturbance, one would expect the landscape mosaic biomass curve to increase as all of its parts are simultaneously covered with growing trees (Fig. 3,a). If the trees over the area have relatively similar longevities, there is also a subsequent period when the deaths (and biomass) on plots where a canopy tree happens to die are balanced by those on plots where large trees are still growing. During this period, the loss balances gain in biomass and the curve levels (Fig. 3,b). If there is sufficient synchronization in the sawtooth curves of the component plots, this is followed by a period during which many of the pieces that comprise the forest mosaic all have deaths of the canopy-dominant trees (Fig. 3,c) and landscape biomass decreases. Over time, the local biomass dynamics become desynchronized and the biomass curve varies about some level (Fig. 3,d). This mosaic of repairing gaps with all different stages of recovery represented on the landscape can be taken as the mature forest.

The mature forest should have patches with all stages of gap phase dynamics and the proportions of each should reflect the proportional duration of the different gap replacement stages. T. C. Whitmore believed that this was the expected pattern and process for all forests and asserted in 1982 that forests of the world are fundamentally similar, despite great differences in structural complexity and floristic richness, because processes of forest succession and many of the autecological properties of tree species, worked out long ago in the north temperate region, are cosmopolitan. There is a basic similarity of patterns in space and time because the same processes are at work.
Whitmore is referring to mosaic forest canopies as a consequence of gap replacement processes. The occurrence of such patterns has been documented for several different kinds of forests. The presence of shade-intolerant trees occurring in patches in mature undisturbed forest is another observation consistent with the mosaic dynamics view of mature forests. The scale of the mosaics in many natural forests is somewhat larger than one would expect from gap filling of single tree gaps, indicating an importance of phenomena that cause multiple tree replacements. Also, relatively long records (approximately 40 years in most cases) of forest structure and composition indicate a tendency for the forest composition to fluctuate with species showing periods of relatively weak recruitment of individuals to replace large trees and strong recruitment in other periods.

C. Quantitative Mechanistic Models of Succession

A consequence of recognition of the mosaic nature of vegetation and an emphasis on more mechanistic representation of the succession process has been the development of quantitative models that can predict changes in vegetation structure (Shugart, 1998). Several of these models simulate the successional dynamics by accounting for the birth, growth, death, and interactions with the environment for the hundreds of individual plants living on a small plot of land. The predictions of hundreds of these plots are then combined to obtain a prediction of the change in ecological landscapes. Because they simulate the fates of each of the millions of plants involved in a landscape succession, these models are called “individual-based” model. These models require considerable computation to solve but they can be solved relatively easily as a consequence of the increased computational power of modern computers.

An advantage of individual-based models is that the following implicit simplifying assumptions associated with other modeling approaches (e.g., the Markov process or differential equation-based models) are not necessary: (i) The unique features of individuals are sufficiently unimportant to the degree that individuals are assumed to be identical, and (ii) the population is “perfectly mixed” so that there are no local spatial interactions of any important magnitude. Most ecologists are interested in variation in individuals (a basis for the theory of evolution and a frequently measured aspect of plants and animals) and appreciate spatial variation as being quite important. These assumptions seem particularly inappropriate for trees which are sessile and which vary greatly in size over their life span. This may be one of the reasons that tree-based forest models are among the earliest and most widely elaborated of this genre of models.

One group of individual-based models simulates the establishment, diameter growth, and mortality of each tree in an area the size of a gap left by the death of a canopy tree and is called gap models. Gap models can be used as an example of the more general individual-based modeling approach. In most gap models, calculations are on a weekly to annual time step. Early gap models were developed for a size unit (approximately 0.1 ha) approximately that of a forest canopy gap. Gap models feature relatively simple protocols for estimating the model parameters. For many of the more common temperate and boreal forest trees, there is a considerable amount of information on the performance of individual trees (growth rates, establishment requirements, and height/diameter relations) that can be used in estimating the parameters of such models. Gap models have simple, general rules for interactions among individuals (e.g., shading and competition for limiting resources) and equally simple rules for birth, death, and growth of individual trees (based on the natural history of each species).

Gap models differ in their inclusion of processes that may be important in the dynamics of particular sites being simulated (e.g., hurricane disturbance, flooding, and formation of permafrost) but share a common set of characteristics. These latter characteristics involve an emphasis on the demography and natural history of plant species, relatively general rules for physiological tradeoffs among species, and an emphasis on the understanding of successional processes at the whole plant level. Each individual plant is simulated as an independent entity with respect to the processes of establishment, growth, and mortality. This feature is common to most individual tree-based forest models and provides sufficient information to allow computation of species- and size-specific demographic effects. Gap model structure emphasizes two features important to a dynamic description of vegetation pattern: (i) the responses of the individual plant to the prevailing environmental conditions and (ii) how the individual modifies these environmental conditions. The models are hierarchical in that the higher level patterns observed (e.g., population, community, and ecosystem) are the integration of plant responses to the environmental constraints defined at the level of the individuals.
IV. SUCCESSION AND BIODIVERSITY

Since the initial formulation of a progressive, holistic concept of ecological succession, there has been a tendency to associate positive attributes to mature communities. Hence, there is an expectation for increasing successional age to be associated with increased biotic diversity. There are certainly ecological systems (notably many forest systems) that demonstrate this pattern, but there are other examples of ecological successions that show highest levels of species diversity (measured as the number of species or by standard indices of diversity) at intermediate successional ages (e.g., shortgrass prairie in Colorado) or even at initial successional stages (e.g., boreal forests in areas of Canada). Succession on sand dunes on the coast of Queensland, Australia, has the highest species richness in shrub-dominated communities at the beginning and end. The pattern of diversity in different successions seems to be an idiosyncratic consequence of the attributes of the participating species and the environmental conditions at a given location.

A. Biodiversity on Disturbed Landscapes

At the landscape level, the overall biodiversity can be related to the frequency and intensity of disturbance and there is evidence from both theoretical work and observations that an intermediate level of ecological disturbance can produce the most diverse landscapes (Huston and Smith, 1987). This occurs in part because disturbed landscapes have a mixture of species able to successfully occupy the differently aged patches created by the disturbance history of a given landscape. One would generally expect highly heterogeneous landscapes to be more diverse. Disturbances also prevent particularly well-adapted species from occupying the entire landscape.

In 1979, J. P. Grime developed a "triangle" based on three primary plant response strategies that can be used to develop rules that can be used to predict the proportions of each strategy (and associated life-forms) expected under a particular environmental regime. Grime recognized two types of external factors limiting the biomass of plants. The first was stress, involving the conditions that restrict plant productivity (shortage of light, H2O, mineral nutrients, etc.). The second was disturbance, involving partial or total destruction of plant biomass (activities of herbivores, diseases, fire, frosts, etc.). These two external factors can operate independently so that there are four possible combinations of high or low stress and high or low disturbance.

Grime reasoned that the combined action of high stress and high disturbance created a condition from which the vegetation could not regenerate. Low-stress and low-disturbance environments would ultimately favor species that were able to compete effectively against other species (competitor strategy), high-stress and low-disturbance environments should be dominated by plants of species able to tolerate the particular stress (stress-tolerator strategy), whereas low-stress and high-disturbance environments should favor short-lived, fast-growing species (ruderal strategy). The general problem exemplified by Grime's work in development of these primary plant strategies is the identification of plant functional types. An essential basis of this as well as other functional classifications of plants is that of "tradeoffs"—the idea that, due to underlying rules that derive from the species physiology and natural history, a single species cannot simultaneously be the best at a stress toleration, a competitor, and a ruderal species.

B. The Gain and Loss of Species

One can view the richness of species on a parcel of land with the same disturbance history as a consequence of the gain and loss of species. The gain of species involves factors such as migration and establishment of species (or the species gaining sufficient abundance or size so it can be sampled). There has been debate as to whether the gain of species at a site over succession is a consequence of the different species present at the site growing and developing at different rates or is actually due to species establishing themselves in an ordered sequence. The succession is a consequence of different growth rates of an initial inoculum of seeds of all the species involved germinating and growing at different rates and is sometimes called the initial composition model (Egler, 1994). The idea that one set of species is added to the community after a previous set has modified the site and lost the site has been termed the relay floristics model (Egler, 1994). To separate these two "models," a particular succession study has to be sampled intensively enough to actually detect all the species at a location, which rarely occurs. Considering a wide range of successions of plant communities, animals associated with succession, and heterotrophic successions (such as the progression of changes in a decaying log), one finds that the appearance of species with abundances sufficient to be counted varies with the particular collection of species and with the changes in the physical environment associated with the succession.
The loss of species from successional communities tends to be somewhat more regular in its pattern of variation. Considering a wide range of communities (both autotrophic and heterotrophic successions), one finds that the rate of species local extinction through succession tends to decrease logarithmically over successional time. Successional sequences are often sampled and reported using a more or less logarithmic sampling regime (e.g., communities in a successional study might be sampled at 1, 2, 5, 10, 17, 33, 60, and 100 years). This reflects the pattern that one tends to sample successional sequences using designs where a proportion of the species in a site of a given age were found in the younger sites. Figure 4 illustrates this pattern for five different successional sequences in different locations. The initial loss rates of species are on the order of approximately 10% of the species found on a plot disappearing each year. In the later successional stages, this decreases to less that 0.1% species lost per year (Fig. 4). Because this pattern occurs across a wide range of successional sequences, this does not appear to be a consequence of the later successional species living longer (as is often the case in forest successions).

See Also the Following Articles

DISTURBANCE, MECHANISMS OF • ECOSYSTEM, CONCEPT OF • ECOSYSTEM FUNCTION, PRINCIPLES OF • INDICATOR SPECIES • LANDSCAPE DIVERSITY

Bibliography


