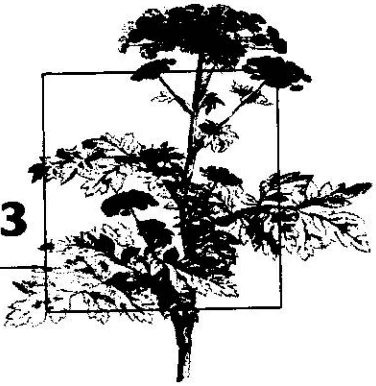
CHAPTER 13



Succession

OVERVIEW

Ecological succession is the process of temporal change in community composition. This chapter begins by reviewing the historical development of ideas about succession. Early studies inferred repeatable patterns of community change from comparisons of communities of different age, but stopped short of directly investigating the mechanisms responsible for species replacements. These early ideas differed in whether succession was seen as an integrative process operating at the community level or as simply the natural consequence of life history differences among species. Succession has been alternately viewed as a directional process that maximizes various ecosystem processes or as the simple outcome of various interspecific interactions that only coincidentally cause changes in ecosystem properties.

Three mechanisms—facilitation, tolerance, and inhibition—probably describe species-by-species replacements during succession. Recent conceptual models of succession integrate the importance of multiple factors, which operate hierarchically, in driving temporal patterns of community composition. Two quantitative models of succession (one descriptive, one mechanistic) show how temporal changes in community composition can be rigorously described. Finally, case studies of succession in different field settings provide insights into the relative merits of different models and point to the need for studies that directly test the mechanisms thought to drive successional patterns.

SUCCESSION

Succession is the nearly universal phenomenon of temporal change in species composition following natural or anthropogenic disturbances. Succession is a conspicuous feature of plant assemblages that develop on barren sites created by geological events (volcanism, glaciation) or other disturbances. Although the study of succession was pioneered by plant ecologists who traditionally focused on vegetation change, succession results in corresponding changes in the community composition of animals, fungi, bacteria, and protists.

Succession is the process of community change through time.

Early studies by plant ecologists identified striking temporal changes in plant species composition (Cowles 1899; Clements 1916; Keever 1950; Bard 1952). These studies emphasized sequences of species replacements that appeared to be typical in particular locations. For example, after agricultural fields in the North Carolina piedmont are abandoned, there is a gradual transition from horseweed (*Leptilon*) to asters (*Aster*) to broomsedge (*Andropogon*) to coniferous trees such as loblolly pine (*Pinus taeda*). Eventually a forest dominated by mixed deciduous hardwood species becomes established (Keever 1950). Analogous patterns involving different species occur at other sites. In the New Jersey piedmont, some 500 kilometers north of North Carolina, abandoned fields undergo a transition from annuals such as ragweed (*Ambrosia*) and biennials such as evening primrose (*Oenothera*) to perennial herbs such as goldenrod (*Solidago*) and then to short-lived conifers (*Juniperus*). Eventually another mixed-hardwood forest dominated by oaks and hickories occurs (Bard 1952). Although the dominant species vary between these two locations, the common theme is a transition from annuals and biennials to perennial herbs and then to a coniferous tree. And although the patterns are not as frequently studied, succession in the identity of dominant plant species is accompanied by changes in animals and fungi.

Some ecologists suggest that the phrase *plant succession* should be replaced by *vegetation dynamics* to emphasize that the population dynamics of interacting organisms are ultimately responsible for successional patterns (Pickett and McDonnell 1989). Similarly, the term *community dynamics* could describe the overall process of temporal change in community composition, thereby emphasizing that succession involves the dynamics of the entire com-

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plement of species interacting in communities, not just the vegetation. The point is that temporal changes in community composition are a natural consequence of interactions among species with different life history strategies, rather than some special process operating only at the community level.

Primary vs. secondary succession.

Successional patterns are conspicuous, site-specific, and influenced by many factors (Pickett and McDonnell 1989). Historically, ecologists have distinguished between **primary succession** on sites without existing vegetation and **secondary succession** on sites with established vegetation. Primary succession occurs on the sterile inorganic substrates generated by volcanism or glaciation. During primary succession species arrive from other, sometimes distant, locations. The process may proceed slowly because early colonists often must transform the environment before other species can become established. For example, soil formation requires the breakdown of rocks, accumulation of dead organic material, and the gradual establishment of soil microorganisms. Secondary succession occurs after disturbances disrupt established communities without completely eliminating all life. Storms, fires, clear cuts, mining, and agricultural clearings all provide the kinds of disturbances that set the stage for secondary succession. Ecologists also sometimes distinguish between **autogenic succession**, which is driven by processes operating within a particular location, and **allogenic succession**, which is driven by factors outside a particular site.

Autogenic vs. allogenic succession.

By understanding succession, it is possible to predict and perhaps accelerate rates of community change after natural disturbances such as fires or storms. Optimal ecological restoration of sites disturbed by human activity clearly depends on knowledge of the factors that promote rapid or otherwise desirable successional changes. Succession provides a conceptual framework for integrating the many diverse processes that affect natural community patterns and can also inform the application of sound ecological principles when restoring degraded ecosystems.

Seasonal succession.

Other kinds of temporal change in community composition are sometimes referred to as different kinds of succession, although they differ from primary and secondary succession in that they are not initiated by disturbance. **Seasonal succession** refers to a regular annual phenology of abundance or activity that occurs without the permanent loss or addition of species from the community. Examples could include the sequence of flowering by woodland plants (Poole and Rathcke 1979), seasonal variation in insect reproduction

(Morin 1984b), or seasonal variation in the activity and abundance of aquatic microorganisms (Finlay et al. 1997). **Cyclic succession** occurs in special circumstances in which a small number of species tends to replace each other over time. A classic example of cyclic succession involves the heather, *Calluna*, and the bracken fern, *Pteridium* (Watt 1947, 1955). *Calluna* can invade stands of *Pteridium* under some situations. However, as the *Calluna* plants age and senesce, they can in turn be replaced by *Pteridium*. The cycle may take over 25 years to complete.

Cyclic succession.

A BRIEF HISTORY OF SUCCESSION

Henry Chandler Cowles (1899) was one of the first individuals to recognize succession as an ecological phenomenon. Cowles used differences in the vegetation occurring on sand dunes of different age to infer successional patterns along the southern coast of Lake Michigan. Moving inland from the lake margin, dunes increase in age and differ in the species composition of the dominant plants. Observations of communities of known age in different locations is a common approach, sometimes called **space for time substitution** (see Pickett 1989) or **chronoseries**, used to infer successional patterns. The approach has the advantage that community changes can be inferred without long-term observations of a single site, which might take decades to describe. However, because differences in "comparable" sites are used to infer successional patterns, sites must be similar with respect to their species pool, environmental conditions, and any other factors that might influence succession. In practice, it is often difficult to know how much of the difference in species composition among different-aged sites is caused by conditions unique to each site, such as disturbance history, the species pool of available colonists, and so on.

Indirect ways of reconstructing successional patterns.

Early controversies about the process of succession involved some of the more bitter debates in community ecology (see Kingsland 1985; McIntosh 1985). The controversy was driven largely by the very different views of Frederick Clements (1916) and Henry Gleason (1917). Clements promoted the idea that ecological communities were analogous to superorganisms, with different species interacting in mutually supportive and often altruistic ways to promote a directed pattern of community development. Clements went so far as to compare primary succession with embryonic development, and sec-

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ondary succession with wound healing in individual organisms. For example, Clements (1916) wrote about the plant community, which he called a formation, in the following way:

> The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant. (p. 16)

Clements developed a complex and cumbersome terminology to describe succession through a series of intermediate stages, called **seres**, until a stable endpoint, called the **climax**, was reached. Clements argued that different climax communities, or **formations**, were the product of different environmental regimes and that failure to reach these typical climax communities was the consequence of various disturbances, such as fire, which maintained communities in a state of disclimax. For many years, Clements' terminology for various successional seres was used by ecologists as a standard way to describe the particular communities that they studied.

The main dispute between Clements and Gleason concerned whether communities developed as tightly integrated sets of species, with some species selflessly paving the way for others, or whether communities simply developed as a consequence of the individualistic responses of each species to the particular set of physiological constraints imposed by a particular location. Gleason argued that species tended to increase or decrease independent of one another through successional time, rather than occurring in mutually beneficial associations. This individualistic view of community development sees the community as nothing more than the collection of species whose individual physiological requirements allow them to exploit a particular location. In Gleason's (1926) own words:

. . . or collections of loosely interacting individuals?

> In conclusion, it may be said that 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. Its disseminules migrate everywhere, and grow wherever they find favorable conditions. The species disappears from areas where the environment is no longer endurable. It grows in company with any other species of similar environmental require-

> ments, irrespective of their normal associational affiliations. The behavior of the plant offers in itself no reason at all for the segregation of definite communities. Plant associations, the most conspicuous illustration of the space relation of plants, depend solely on the coincidence of environmental selection and migration over an area of recognizable extent and usually for a time of considerable duration. A rigid definition of the scope or extent of the association is impossible, and a logical classification of associations into larger groups, or into successional series, has not yet been achieved. (p. 26)

In other words, the community is simply the sum of the species living in a particular place, and species do not cooperate to generate special community attributes.

In the short run, Clements' views were widely accepted and promoted, and Gleason left ecology. In retrospect, Gleason's ideas have proven to be a better description of the process of plant succession. The disagreement between Clements and Gleason over the nature of plant succession has resurfaced in slightly different guises during the subsequent development of community ecology. For example, Whittaker's (1956, 1975) conclusions about patterns of changing community composition along environmental gradients clearly had much in common with Gleason's individualistic view of plant assemblages. Subsequent controversies about whether communities consist of arbitrary assemblages of organisms or groups of species that are highly structured by deterministic interspecific interactions (Strong et al. 1984) echoed the contentious exchange between Clements and Gleason.

Frank Egler (1952) provided the next important conceptual development in succession to follow the prolonged debate between Clements and Gleason. Egler promoted an idea that became known as the **initial floristic composition hypothesis**. This idea specifically concerns patterns of secondary succession and holds that succession at a site is determined largely by the species composition of plant propagules already present when the site is disturbed. Subsequent changes in community composition can be attributed to the fact that some species live longer than others, but grow slowly and take time to become dominant features of the community. Short-lived species are gradually replaced by longer-lived ones to create a gradual transition in the identity of dominant species.

Successional patterns may be strongly affected by the initial composition of species.

Eugene Odum (1969) viewed succession as an orderly (i.e., predictable) pattern of community development that produced significant changes in a variety of ecosystem attributes (Table 13-1). The orderly nature of the process was thought to result from modifications of the environment driven by the developing community. In Odum's view, succession culminated in a stabilized

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TABLE 13-1. Suggested changes in a variety of ecosystem properties during ecological succession.

Variable	Early Succession	Late Succession
GPP/Respiration	> or <1	~1
GPP/Biomass	High	Low
Biomass/Energy	Low	High
Yield = NPP	High	Low
Food chains	Linear	Web-like
Total organic matter	Small	Large
Nutrients	Extrabiotic	Intrabiotic
Species richness	Low	High
Species evenness	Low	High
Biochemical diversity	Low	High
Stratification and pattern	Poorly organized	Well organized
Niche specialization	Broad	Narrow
Size	Small	Large
Life cycles	Short, simple	Long, complex
Mineral cycles	Open	Closed
Nutrient exchange	Rapid	Slow
Role of detritus	Unimportant	Important
Selection on growth form	*r*-Selection	*k*-Selection
Selection on production	Quantity	Quality
Symbiosis	Undeveloped	Developed
Nutrient conservation	Poor	Good
Stability	Low	High
Entropy	High	Low
Information content	Low	High

GPP = gross primary production = total photosynthesis.
NPP = net primary production = total photosynthesis-respiration.
Modified and reprinted with permission from Odum, 1969. © 1969 American Association for the Advancement of Science.

ecosystem in which biomass and levels of symbioses were maximized per unit of energy flow into the system. Odum outlined a large list of ecosystem properties and attributes that might change during succession (see Table 13-1). Although many of these observations are accurate, others have dismissed the trends as little more than truisms. Many of the patterns are simple consequences of the fact that communities gradually acquire species over time, and as those species grow, biomass tends to accumulate in long-lived species (Connell and Slatyer 1977). Recent models also suggest that some properties, such as increased productivity, biomass, and nutrient cycling over successional time, are a simple and predictable consequence of competition for resources (Loreau 1998).

Drury and Nisbet (1973) presented a somewhat more complex multifactor conceptual framework that presented succession as a consequence of the differential growth, survival, and colonizing ability of species along various environmental gradients. The basic idea is that all communities fall along gradients in soil conditions, stress, and other abiotic factors. Different species have different life history characteristics that make them specialized to exploit different sets of conditions along these environmental gradients. Once established at particular sites, individual plants have a competitive advantage over seedlings and immigrants of other species that attempt to become established. This notion clearly is at odds with Clements' earlier ideas, in that early arrivals do not pave the way for later colonists. Other life history characteristics, such as stress tolerance, are thought to be correlated with high dispersal ability, which creates a situation in which the first species to arrive at stressful early-successional sites are the ones that can also best handle stress. The final trade-off is that colonizing ability and somatic growth rates are inversely correlated with longevity and size at maturity. This life history trade-off potentially explains the transition from rapidly growing, weedy early colonists to slow-growing, large, dominant species like trees.

Connell and Slatyer (1977) viewed succession from a different perspective than Drury and Nisbet (1973) and emphasized the different mechanisms that might be involved in species-by-species replacements as communities develop over time. They were concerned that the absence of direct experimental studies of succession probably led to an overemphasis of the role of competition among plant species in generating successional patterns. A second concern was that many of the correlates of succession suggested by Odum (1969) were a tautological consequence of the simple growth of organisms or other gradual community changes through time. They pointed out that any transition involving species that arrive in the community at different times could be the result of three basic kinds of interactions between species that arrive early and later in succession:

Mechanisms of species-by-species replacements.

1. Facilitation, in which early species enhance establishment of later species.
2. Tolerance (equals no interaction), in which early species have no effect on later ones.
3. Inhibition, in which early species actively inhibit establishment of later ones.

These ideas were already discussed in relation to priority effects, but they clearly play a role in community processes operating on long successional timescales.

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In all these interactions, it is assumed that early species cannot invade and grow once the site is fully occupied, that conditions favoring establishment of later species depend on the particular mechanism, and that early species are eliminated either by competition with later ones (under facilitation and tolerance) or by some local disturbance (inhibition). How often do these different mechanisms operate? There is some evidence for facilitation, particularly among autotrophs during primary succession, and for the succession of groups of heterotrophs in various kinds of decomposing organisms. Connell and Slatyer noted little evidence for tolerance, whereas there are many examples of inhibition (e.g., Sousa 1979a).

Walker and Chapin (1987) expanded the notion of succession as a temporal gradient in the importance of various interspecific interactions and other events. They describe the relative importance of various processes in driving changes in species composition during three stages of succession that they call colonization, maturation, and senescence. They also consider how these processes might differ in importance between severe and favorable environments and in their contribution to primary and secondary succession. The factors that they consider include seed dispersal, availability of propagules on site, the importance of stochastic events, facilitation, competition, maximum growth rates, longevity, mycorrhizae, and herbivory by insects, pathogens, and mammals (Figure 13.1). Their suggestions emphasize that most successional sequences will defy simple generalizations about temporal variation in the importance of particular factors and will require qualifications concerning the harshness of the environment or whether primary or secondary succession is happening.

Pickett and McDonnell (1989) expanded on the multifactor approach of Walker and Chapin (1987) by pointing out that the whole process of vegetation dynamics is the end result of a hierarchy of interacting factors (Figure 13.2). They emphasize that temporal patterns depend first on the availability of sites, the species pool of potential colonists, and factors affecting species performance. Site availability depends on the size, severity, and spatial dispersion of the disturbance that initiates succession. Species availability depends on dispersal and the presence of a propagule pool. To understand resulting successional patterns, one needs to know about the initial disturbance, the composition of the species pool, and the ways in which species interact.

Succession results from a hierarchy of interacting factors.

Current views hold that succession is not a single simple process. Rather, succession is a consequence of complex interactions initiated by disturbances that create opportunities for establishment. Life history characteristics and interspecific interactions combine to create repeatable changes in community composition over time. The next section shows how succession can be

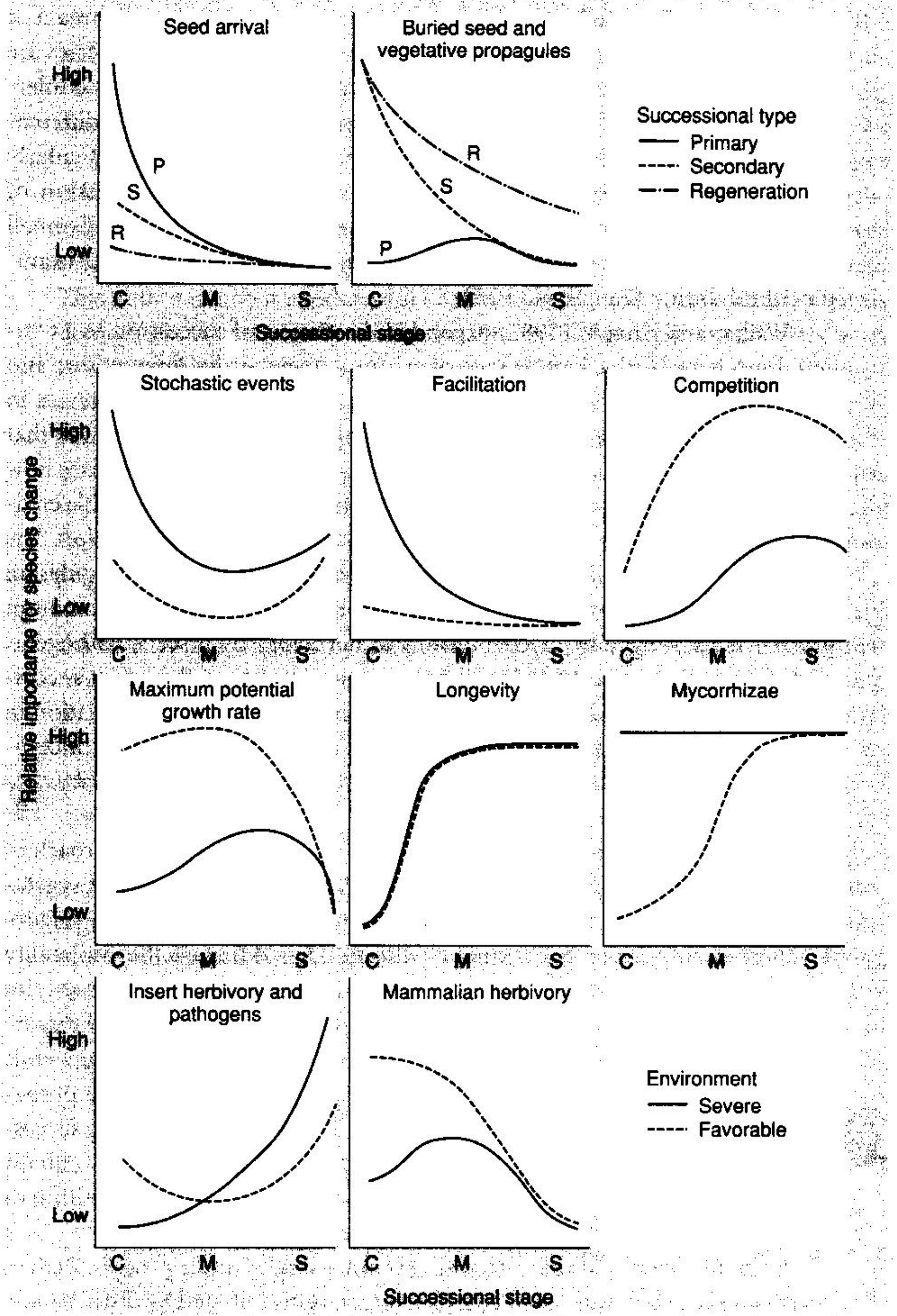
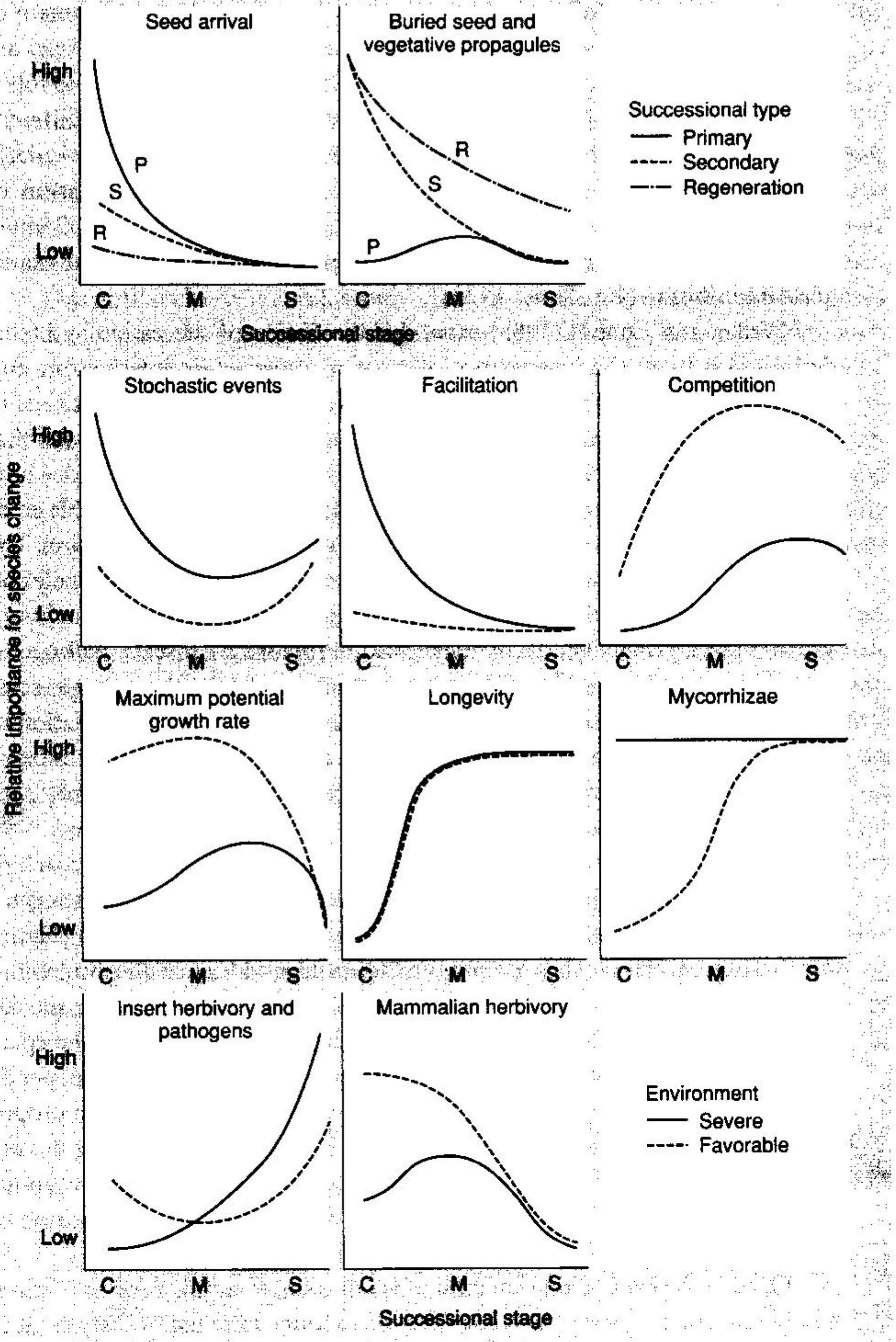


FIGURE 13.1. *Suggested changes in the importance of different factors operating early (C), midway (M), and late (S) in primary and secondary succession. (Adapted from Walker and Chapin, 1987, with permission of Oikos.)*



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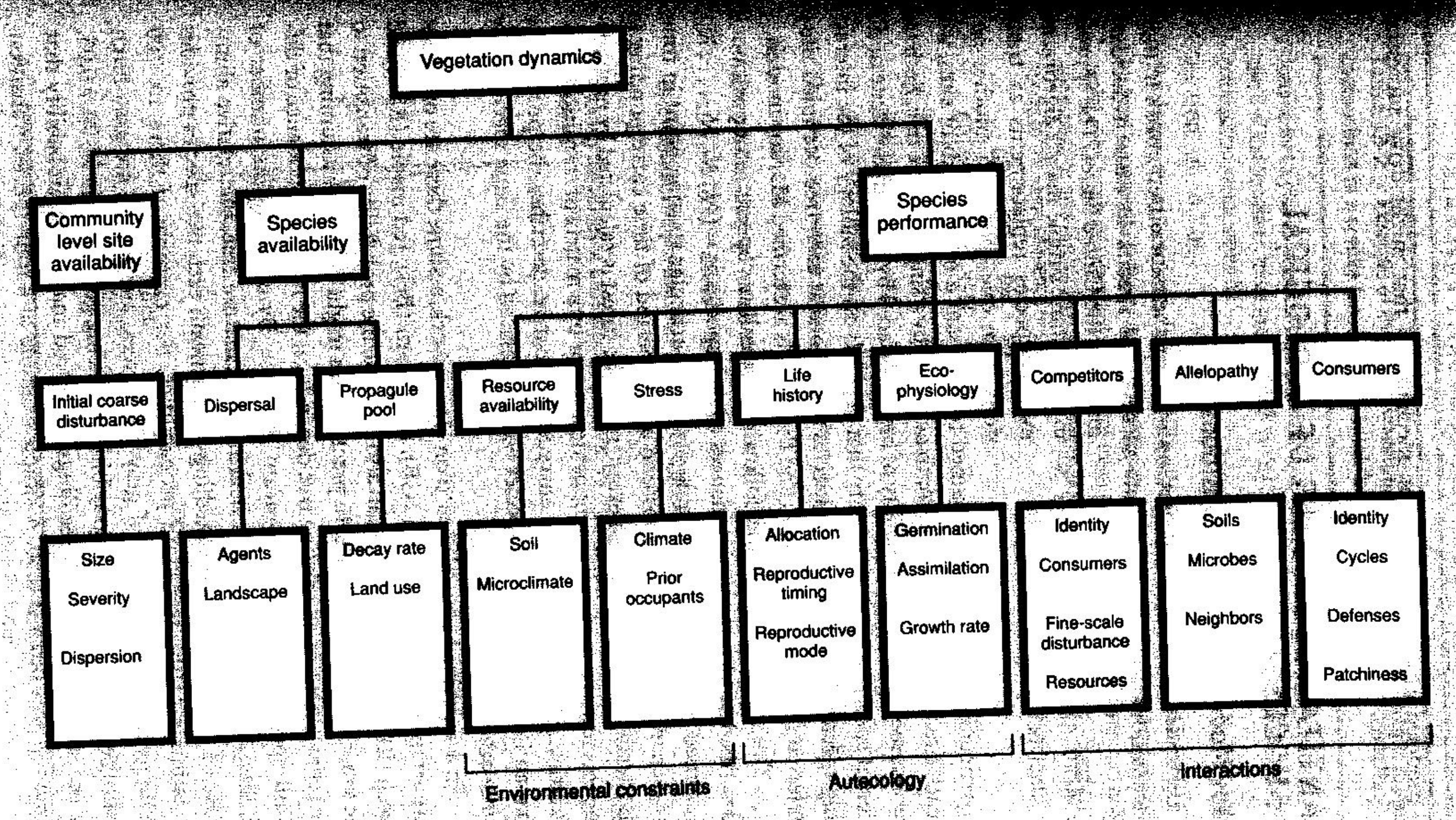

FIGURE 13.2. *Factors affecting the pattern of succession within a given site occur in a hierarchy of interacting events, properties, and processes. (Adapted from* Trends in Ecology and Evolution, *Vol. 4, Pickett, S. T. A., and M. J. McDonnell, Changing perspectives in community dynamics: a theory of successional forces, pages 241–245, copyright 1989, with permission from Elsevier Science.)*

modeled and considers some mechanisms that might drive successional patterns.

QUANTITATIVE MODELS OF ECOLOGICAL SUCCESSION

Markov Models of Species Transitions

Henry Horn (1974, 1975) used a simple mathematical framework to model transitions from early- to late-successional species in eastern deciduous forests of the United States. The approach involves some simple matrix algebra, and models species replacements as transitions from one species to another on a particular site. A forest is assumed to represent a honeycomb of sites, with each site, or cell, in the honeycomb occupied by a single mature tree. Each tree is assumed to have a probability of being replaced by a tree of the same or different species with a probability that depends on the biology of the interacting species. The sequence of species transitions at each tree-occupied site is referred to as a **Markov chain**, and the models are termed **Markov models**.

Matrix models provide one way to simulate forest succession.

The approach uses the following formalism. Species composition is described by a vector of abundances of each species, $c_0 = (N_1, N_2, N_3, \ldots, N_s)$, summed over all of the available sites at a particular starting point in time. The change in species composition after a period of time corresponding to the death and replacement of every tree in the forest is calculated by multiplying this initial community composition vector by a matrix of transition probabilities. Each probability, or entry in the matrix, describes the probability that an individual of some species will be replaced by the same species or by some other species.

In a simplified example based on Horn's work, assume there are only four important species: gray birch (GB), black gum (BG), red maple (RM), and beech (BE). Assume that you can also estimate the probability of transition to the same or different species. In practice, you might do this by assuming that the replacement of an existing tree depends on the relative abundance of different species of seedlings beneath that tree. By counting the number of seedlings of each tree species beneath each mature tree, the relative abundance of each species in the seedling pool beneath each tree species provides an estimate of the transition probabilities. For example, if there are 100 seedlings beneath a sample of gray birch trees, and only 5 are gray birch seedlings, the probability of gray birch replacing gray birch is 5/100 = 0.05. For the same sample, if 50 seedlings are of red maple, the probability that maple replaces birch is 0.50. A simple example of a four-species transition matrix is shown in Table 13-2. Elements in each row describe the probability that a tree of the species listed in that row will be replaced by the species corresponding to each column. So, for GB, the first row, the probability of replacement by GB is 0.05, by BG is 0.36, by RM is 0.50, and by BE is 0.09. This means that seedlings of BG and RM are much more common under GB than conspecifics or seedlings of BE.

To find the relative composition of the forest in the next time period, the species composition vector, c_0, is post-multiplied by the transition matrix using standard rules of matrix algebra. In this case, the first element of the new species composition vector is given by the product of the species composition vector and the first column of S. The vector product is obtained by summing the products of the corresponding vector elements. For this example, assuming we start with a pure stand of 100 GB, that vector product is

$$\begin{aligned}&(100,\ 0,\ 0,\ 0)\times(0.05,\ 0.01,\ 0.0,\ 0.0)'\\&\quad=(100\times0.05)+(0\times0.01)+(0\times0.0)+(0\times0.0)=5\end{aligned}$$

For the transition to BG, the corresponding vector product is

$$\begin{aligned}&(100,\ 0,\ 0,\ 0)\times(0.36,\ 0.57,\ 0.14,\ 0.01)'\\&\quad=(100\times0.36)+(0\times0.57)+(0\times0.14)+(0\times0.01)=36\end{aligned}$$

For the transition to RM, the corresponding vector product is

$$\begin{aligned}&(100,\ 0,\ 0,\ 0)\times(0.50,\ 0.25,\ 0.55,\ 0.03)'\\&\quad=(100\times0.50)+(0\times0.25)+(0\times0.55)+(0\times0.03)=50\end{aligned}$$

For the transition to BE, the corresponding vector product is

$$\begin{aligned}&(100,\ 0,\ 0,\ 0)\times(0.09,\ 0.17,\ 0.31,\ 0.96)'\\&\quad=(100\times0.09)+(0\times0.17)+(0\times0.31)+(0\times0.96)=9\end{aligned}$$

Therefore, the species composition vector in the next generation is (5, 36, 50, 9).

Notice that the forest contains the same number of trees (occupied sites). What has changed is the relative distribution of species among those sites. If we take the new species composition vector, c_1, and post-multiply it by the transition matrix, the next species composition vector is given by $c_2 = (1, 29, 39, 31)$. After many iterations, the community attains a stable composition consisting of (0, 5, 9, 86), indicating that the forest consists mostly of BE, with a few BG and RM. This end result does not depend on the initial value of the composition vector used to describe the starting conditions. The final community composition depends only on the transition probabilities given in the matrix, S.

This idealized model of succession captures the interesting biology involved in species transitions in the probabilities in the matrix S. For

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instance, failure to become established in the shade of other trees would appear as low probabilities for transitions to shade-intolerant species. In contrast, shade-tolerant superior competitors should have larger transition probabilities. The final species composition is always fixed for a given *S*, regardless of initial values of c_0. The approach can be varied somewhat by including different transition matrices to describe altered probabilities associated with different environmental conditions (say, alternations of harsh and benign climate, represented by the transition matrices *D* and *S*). Succession over two sequential favorable transitions followed by one harsh period is given by the product of $c_0 \times S \times S \times D$.

Horn's matrix approach makes many simplifying assumptions about how species replacements occur during succession. One of the more unrealistic assumptions is that the replacement probabilities are density independent; that is, they do not depend on the abundances given in the species composition vector. The approach also assumes that species transition probabilities remain constant over time unless different transition matrices are included in the successional sequence to account for possible changes. Despite these oversimplifications, the late-successional composition predicted by the model comes fairly close to the patterns seen in old wood lots in New Jersey.

Other, much more complex, simulation models have been developed to explore patterns of vegetation change in different well-studied systems. The models typically approach forest succession as a tree-by-tree replacement process and keep track of the growth and survival of a large number of individual trees within a simulated plot of forest. Early simulation models that are known by the acronyms FORET (Shugart and West 1977, 1980) and JABOWA (Botkin et al. 1972) provide reasonably good agreement between simulated patterns of forest succession and patterns reconstructed from historical information. More recent efforts such as the SORTIE model of Pacala et al. (1996) use information about seed input, light-dependent growth, and growth-dependent mortality to explore successional patterns in forests. The SORTIE model does a reasonable job of predicting the general successional trends expected in forests of the northeastern United States and has the advantage of being based on a series of basic ecological attributes of tree species that can be readily measured in the field. An example of the kind of succession predicted by SORTIE is shown in Figure 13.3.

Complex simulation models include more biological details, and make fairly realistic predictions.

The Resource Ratio Model of Succession

Tilman (1985) has extended his mechanistic model for resource competition among plants to describe how vegetation might change in an orderly fashion during succession. The model assumes that plants compete for two limiting

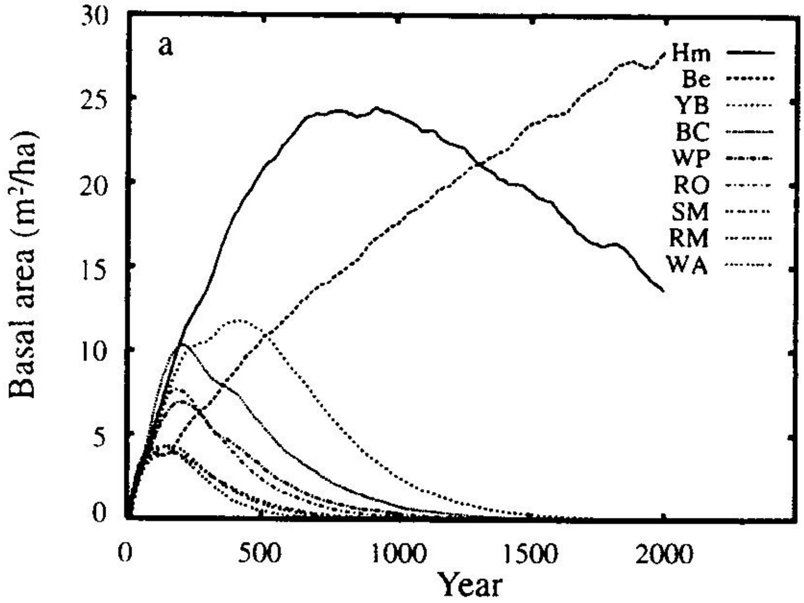
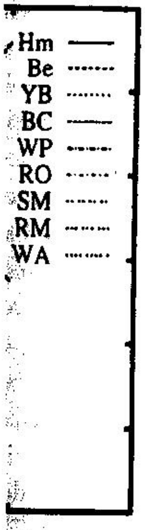


FIGURE 13.3. *Patterns of forest succession predicted by the SORTIE model. The model predicts replacement of shade-intolerant species by the shade-tolerant species eastern hemlock and American beech. Key to species: Hm = eastern hemlock, Be = American beech, YB = yellow birch, BC = black cherry, WP = white pine, RO = red oak, SM = sugar maple, RM = red maple, WA = white ash. (Reprinted from Pacala et al., 1996, with permission of the Ecological Society of America.)*

Succession as a consequence of changing resource ratios through time.

resources. The model also assumes that resource supply rates change in some orderly fashion during succession, as a result of consumption, biogeochemical processes, or disturbance. Finally, the model assumes that competition for these resources is what drives the replacement process in communities. Each plant species is assumed to be a superior competitor at a particular ratio of limiting resources.

Tilman argues that random or positively correlated changes in resource supply rates should not produce the orderly changes in species composition that are usually associated with succession. The reason is that neither of these patterns leads to a consistent trajectory of resource supply rates across the regions corresponding to different competitive outcomes (Figure 13.4). In contrast, negative correlations among resource supply rates over succession will produce trajectories that cut across regions corresponding to dominance or coexistence by multiple species (Figure 13.5). Negative correlations might arise as simple consequences of plants competing for resources such as light and nutrients.



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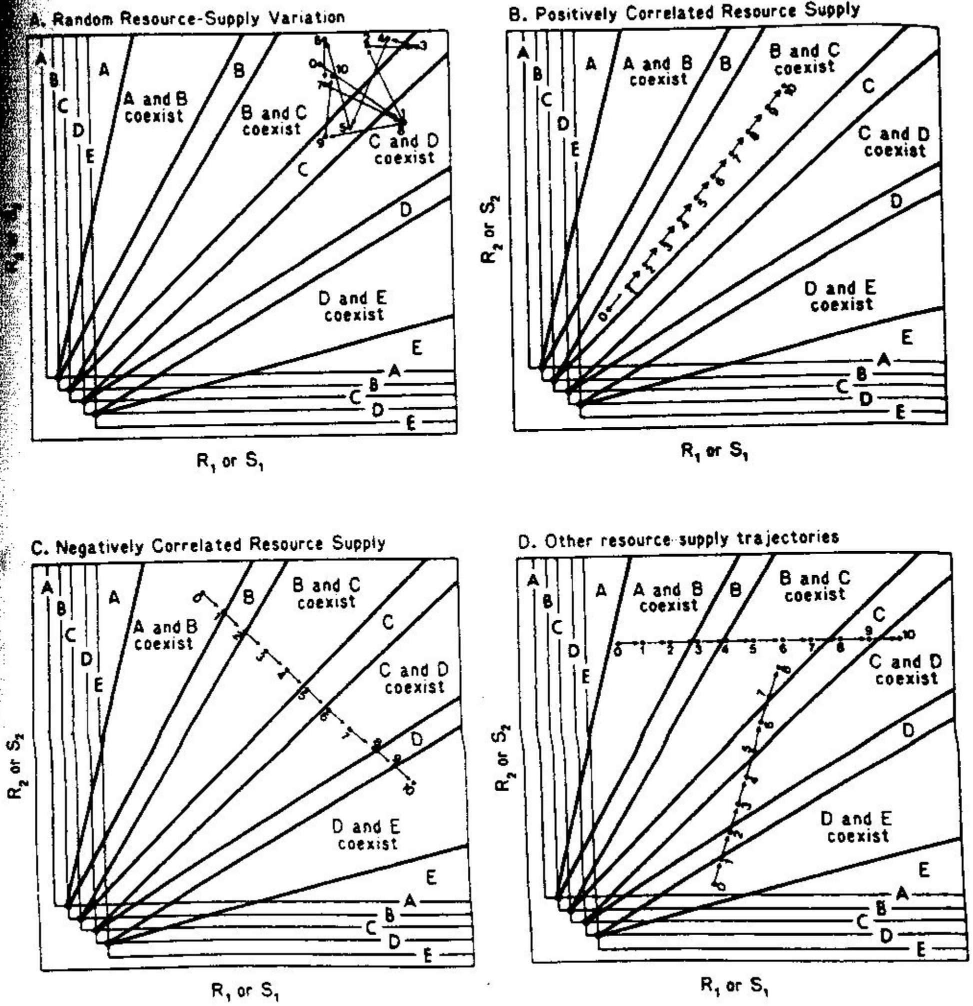
A. Random Resource-Supply Variation

B. Positively Correlated Resource Supply

C. Negatively Correlated Resource Supply

D. Other resource supply trajectories

FIGURE 13.4. *Tilman's (1985) resource ratio framework for ecological succession. Plants are assumed to compete for two resources. Succession occurs when there is a change in the supply rates of both resources through time such that supply rates are negatively correlated. Random temporal changes or positively correlated changes in resource supply rates do not produce a predictable sequence of species transitions over time. (Reprinted from Tilman, 1985, with permission of the University of Chicago Press.)*

Observational studies of patterns of light and nutrient availability in old agricultural fields of different ages support a negative correlation between light and nutrients (Inouye et al. 1987). Early in primary succession, as plants first become established, light is abundant but nutrients are in short supply. As plants become abundant and nutrients accumulate, light at the soil surface decreases and nutrients increase. This process could create the kind of negative correlation that would lead to an orderly transition of species during suc-

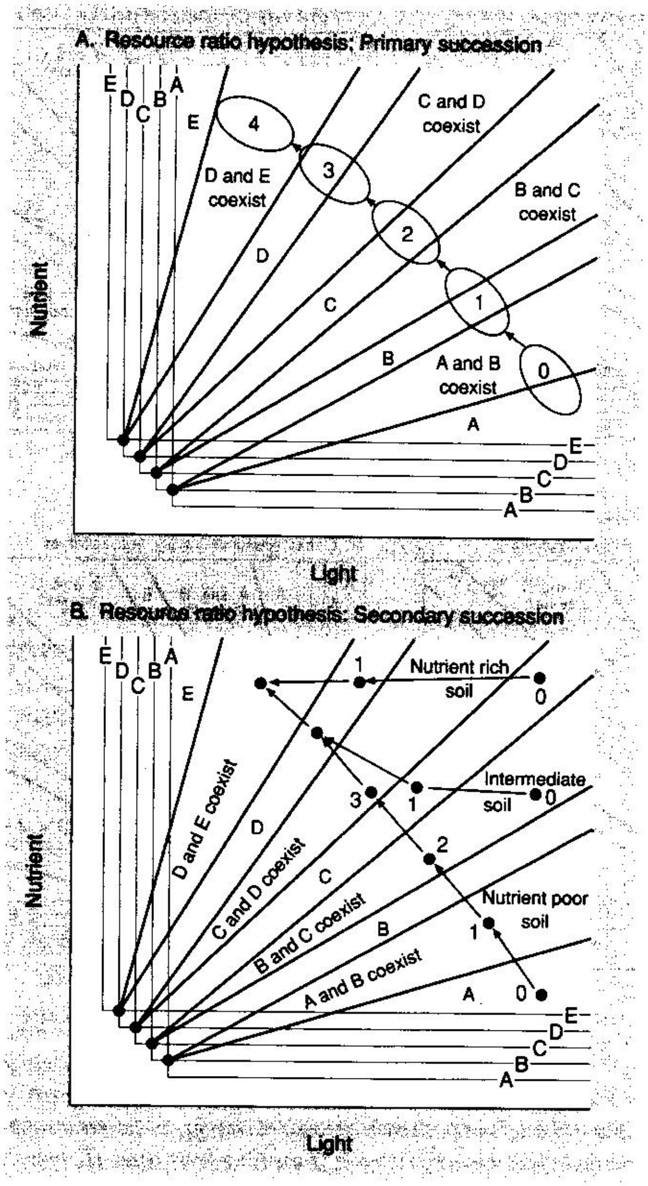

FIGURE 13.5. *Possible differences in successional pathways during primary and secondary succession that result from different initial values and rates of change for resource supply rates. (Adapted from Tilman, 1985, with permission of the University of Chicago Press.)*

cession. Tilman suggests that primary succession and secondary succession on nutrient-poor soils should show similar patterns, whereas succession on nutrient-rich soils should be rapid and should involve fewer species (see Figure 13.5). Rapid succession on nutrient-rich soils might happen because starting conditions occur at a location in resource supply space that allows fewer possible transitions in dominant species.

Experimental tests of the resource ratio succession hypothesis (Tilman 1987) focus mainly on the consequences of nutrient additions for plant species composition in different situations. For example, Tilman (1987) added nitrogen fertilizer at nine different rates, ranging from 0 to 27.2 $\mathrm{g\,m^{-2}\,yr^{-1}}$, to fields of four different successional ages and followed the patterns of community change for four years. Basic responses of the community to nitrogen addition showed that plant biomass increased as light declined, supporting a negative correlation between the supply rates of these two resources. Plant species richness also tended to decline over time, and the decline was most rapid in plots with the highest rate of nutrient supply. This result is qualitatively similar to the predictions of the graphical mechanistic theory.

CASE STUDIES OF SUCCESSION IN DIFFERENT KINDS OF HABITATS

Although the majority of concepts and systems considered in this chapter have focused on succession in temperate terrestrial plant communities, succession happens in any situation in which a disturbance creates opportunities for establishment and subsequent species transitions. One of the more illuminating studies of species replacement mechanisms comes from the rocky intertidal zone of California (Sousa 1979a). After a disturbance creates a patch of bare rock in the intertidal zone, a succession of different algal species occupy the site. Because the transitions are relatively rapid, occurring over just a few years, it is possible to observe how changes in the abundance of early-successional species influence the establishment of later ones.

Sousa created opportunities for algal succession by removing all algae from small patches of rock. He was then able to observe how removals of early-successional species influenced the establishment of late-successional species. Removals of early-successional species tended to enhance establishment of late-successional species (Figure 13.6). This result is consistent with inhibition of species replacement by established species (Connell and Slatyer 1977), but not with either facilitation or tolerance. Sousa concluded that algal succession in his system was accelerated when disturbances or herbivores removed early-successional species and allowed late-successional species to become established.

Tilman (1983, 1984, 1987) showed that differences in nutrient availability have major effects on early patterns of succession. In his system, additions of nitrogen increase rates of successional change while decreasing the number of coexisting species (Figure 13.7). One fascinating complication in this study is

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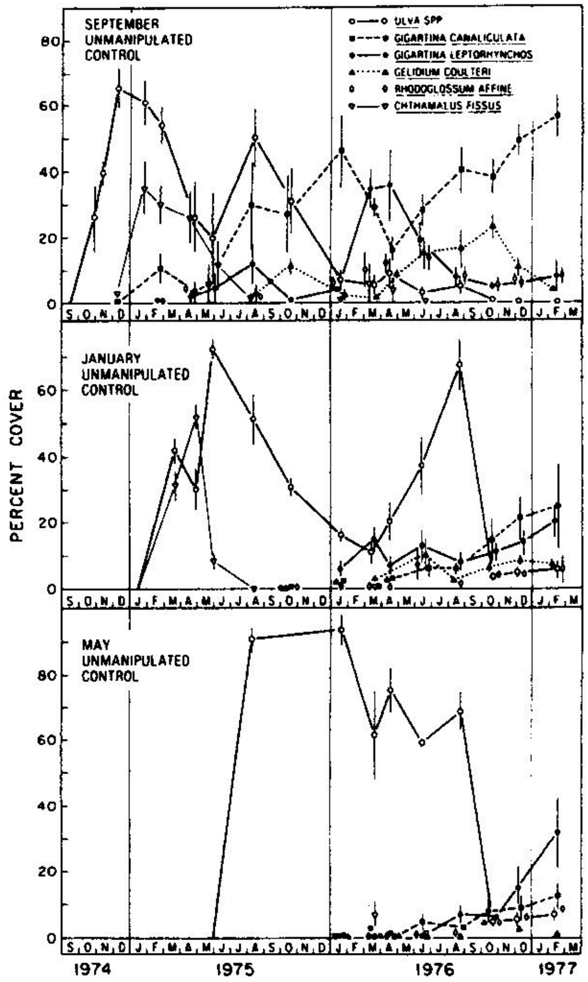

FIGURE 13.6. *Successional transitions among rocky intertidal algae that colonize open substrate at different times of the year. Early-successional species such as* Ulva *tend to slow recruitment by late-successional species. (Reprinted from Sousa, 1979a, with permission of the Ecological Society of America.)*

that herbivores, in this case subterranean-feeding pocket gophers, differentially attacked plots with high levels of nitrogen addition and high standing stocks of biomass. Unlike the situation in marine systems, herbivory seems to slow rather than speed succession in terrestrial situations (Tansley and Adamson 1925; Hope-Simpson 1940). There is abundant anecdotal evidence that strong herbivory on woody seedlings is sufficient to slow or arrest the establishment of woody species, especially in situations in which natural enemies of the herbivores are rare or absent. This is the current situation in portions of the northeastern United States, where abundant populations of white-tailed deer inhibit the establishment of woody species or select for par-

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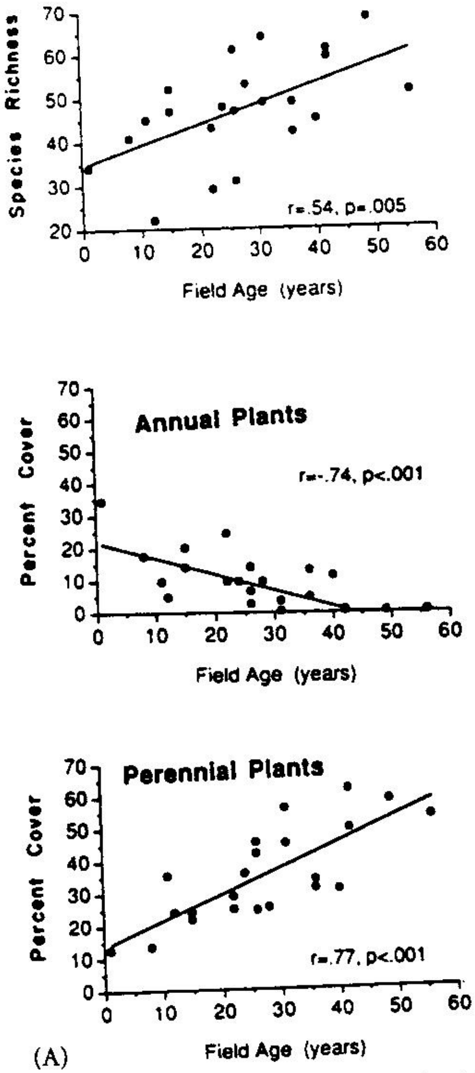

FIGURE 13.7. *(A) General trends in species richness and species composition in a chronosequence of old field communities. (Reprinted from Inouye et al., 1987, with permission of the Ecological Society of America.) (B) Effects of nitrogen addition on patterns of plant species composition in old fields in Minnesota. (Reprinted from Tilman, 1987, with permission of the Ecological Society of America.)*

ticularly unpalatable ones. It is surprising how few careful studies of the effects of herbivory on terrestrial succession have been done.

Christopher Uhl (1987) has used factorial experiments to study the causes of successional patterns in tropical forests. Succession has been little studied in highly diverse tropical systems, and consequently we know little about factors that might be manipulated to accelerate the restoration of tropical forests that have been devastated by slash-and-burn agriculture. Uhl's

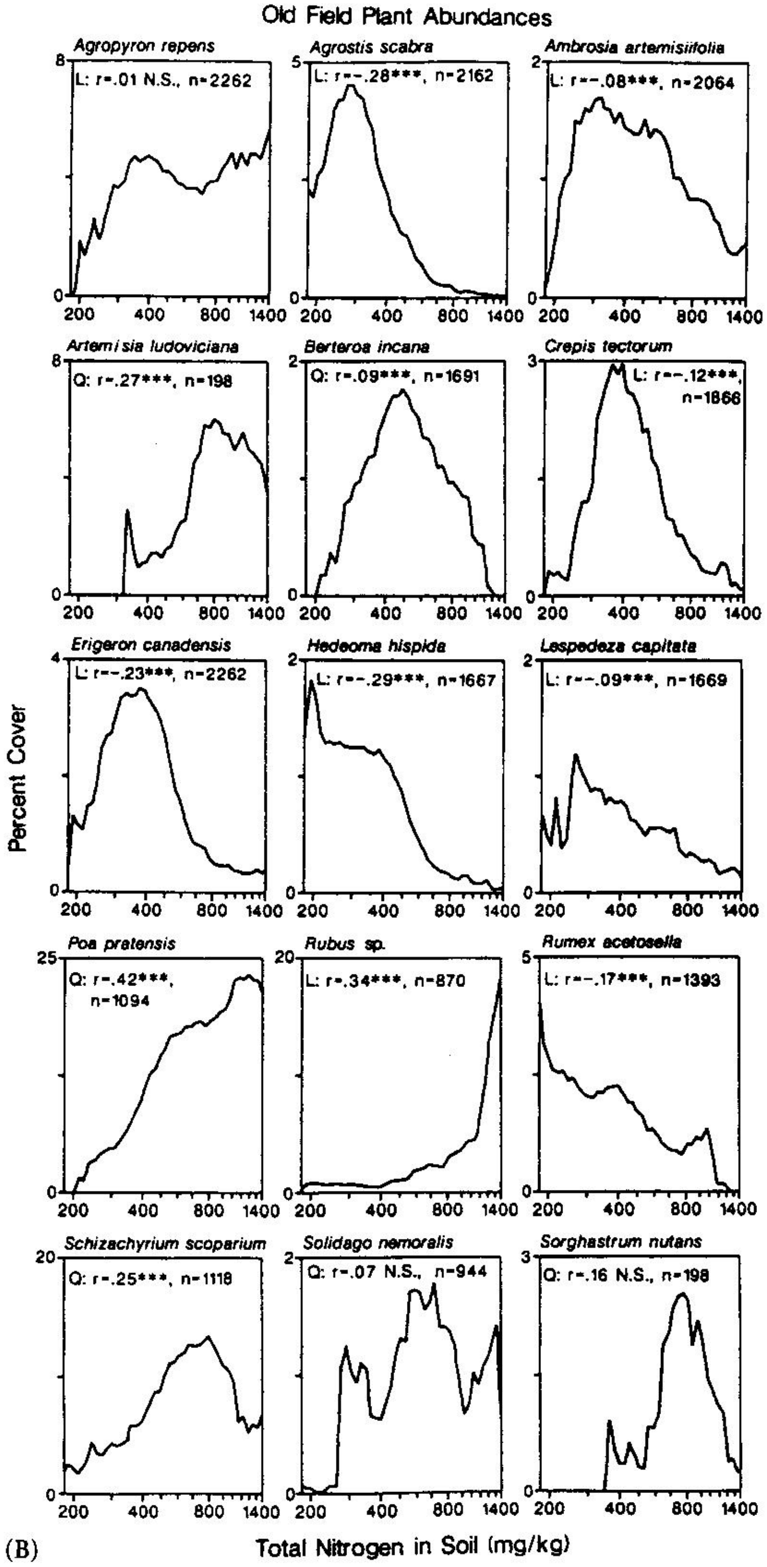

FIGURE 13.7. *(Continued)*

studies show that establishment of woody tropical forest species depends strongly on factors affecting propagule dispersal and herbivory.

Uhl explored the importance of herbivory and site characteristics on the persistence of plant propagules placed in either a natural forest gap or an abandoned farm site. For most species considered, few propagules survived longer than one month in the former farm site, whereas survival was considerably higher in the natural forest gap (Table 13-3). Apparently, animals that feed on seeds and fruits took a much larger toll in postagricultural sites, either because the diaspores were easier to locate or because more consumers frequented these sites. Larger propagules also tended to survive longer, suggesting that removals were the work of relatively small consumers. The implication is that restoration of forest species in these locations requires measures to reduce predation on plant propagules. However, simply reducing predation may be insufficient, since postagricultural sites also appear to be physiologically stressful to any propagules that do become established as seedlings.

Uhl also transplanted seedlings of rain forest trees into shaded and exposed sites in farmland that had been abandoned for different amounts of time. Most seedlings transplanted into open unshaded fields died within two days, due to the effects of intense tropical sunlight. In contrast, seedling survival in shady older fields was closer to 90% over the same time period. This result clearly suggests a positive effect of early colonists on the establishment of later ones. Similarly, after one year of growth, woody stems were approximately one order of magnitude more abundant in shady sites compared with exposed sunny sites. Uhl's work on tropical secondary succession suggests an important role for facilitation of later colonists by pioneering species that has not been documented in most studies of temperate terrestrial succession. It also emphasizes the striking effects of herbivores, which can greatly slow or limit the establishment of primary forest species if those species manage to disperse to postagricultural sites.

TABLE 13-3. Mortality of diaspores (fruits and seeds) of different primary forest tree species placed in either an open abandoned agricultural field or a natural forest gap.

Species	*Ocotea* (small)	*Jessenia* (small)	*Aldinla* (large)
Time	1 month	1 month	4 months
Farm	100%	100%	35%
Gap	88%	68%	6%

Source: Data from Uhl (1987).

Most studies of ecological succession have emphasized description of patterns without directly measuring the mechanisms responsible for species replacements or establishment. Consequently, the expected patterns of changing community composition are well known for a variety of sites, but the reasons for differences among sites, or for the replacement series seen within each site, remain poorly understood. Much important work remains to be done, particularly in understanding how interactions with other organisms, especially consumers and mutualists, alter the rate and pattern of community change over time. This information is crucial for situations in which it is desirable to reestablish particular kinds of communities after various kinds of natural or anthropogenic disturbances.

EFFECTS OF PLANT SUCCESSION ON ANIMAL ASSEMBLAGES

Well-known associations among certain kinds of vegetation and particular animal species are usually cited to suggest that successional changes in vegetation should generate differences in animal species composition (Lack and Venables 1939; Kendeigh 1948; Odum 1950; Johnston and Odum 1956). However, most explicit studies of succession focus on plants and pay little attention to concordant changes in other groups of organisms. Studies that attribute changes in animal species composition to successional changes in plant communities often do so indirectly and for very limited groups of species, primarily birds. In the eastern United States, declines in some bird species, such as eastern bluebirds that frequent agricultural fields, have been ascribed to the loss of extensive early-successional communities through secondary succession to woodlands. Other species, such as the red-cockaded woodpecker, are restricted to old-growth *Pinus plaustris* forests because the birds only nest in older longleaf pine trees that have been infected by a particular fungus that attacks the heartwood of the tree (Jackson 1977, 1986). Reasons for associations between particular plants typical of certain successional communities and other animal species are probably as numerous as the factors affecting the distributions of any organisms, and include physiological constraints, feeding preferences, and habitat selection driven by predator avoidance.

Studies of bird species composition in communities of different successional age do show important changes in species composition and species richness that accompany changes in plant community structure. In the piedmont of Georgia (United States), both bird species richness and the density of breeding pairs per unit area tend to increase through successional time (Johnston and Odum 1956; Figure 13.8; Table 13-4). These changes reflect some turnovers of species that occur in very early successional communities,

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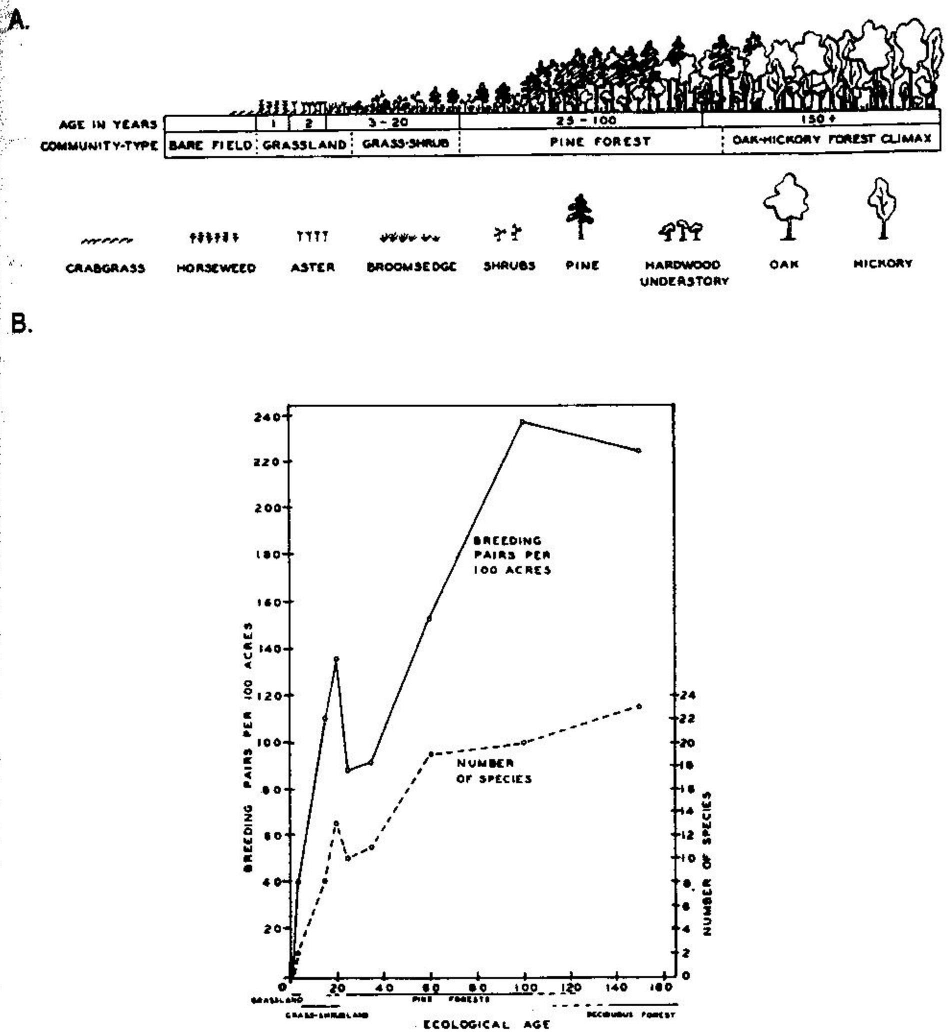

FIGURE 13.8. *(A) Schematic diagram of plant succession in the Georgia (United States) piedmont. (B) Changes in bird species richness and total numbers of bird breeding pairs in sites of different successional age in the piedmont of Georgia. (Reprinted from Johnston and Odum, 1956, with permission of the Ecological Society of America.)*

but not in later ones, as well as the addition of many species that occur only in forest communities.

It is unclear whether other groups of organisms, which are much more difficult to sample, display similar patterns along successional gradients. Other organisms, such as arthropods, sometimes show associations with plant species that are likely to translate into differences in animal community composition as plant communities change through time (Whittaker 1952), although the fidelity of those associations varies greatly among species (Futuyma and Gould 1979).

TABLE 13-4. Patterns in the density of different species of breeding birds occurring in different secondary successional sites in the piedmont of Georgia (United States). Numbers represent territories or pairs per 100 acres.

	Successional Stage and Age (in years)								
	Grass-Forb		Grass-Shrub		Pine Forest				Oak-Hickory
Species	1	3	15	20	25	35	60	100	150+
Grasshopper sparrow	10	30	25						
Eastern meadowlark	5	10	15	2					
Field sparrow			35	48	25	8	3		
Yellowthroat			15	18					
Yellow-breasted chat			5	16					
Cardinal			5	4	9	10	14	20	23
Eastern towhee			5	8	13	10	15	15	
Bachman's sparrow				8	6	4			
Prairie warbler				6	6				
White-eyed vireo				8		4	5		
Pine warbler					16	34	43	55	
Summer tanager					6	13	13	15	10
Carolina wren						4	5	20	10
Carolina chickadee						2	5	5	5
Blue-gray gnatcatcher						2	13		13
Brown-headed nuthatch							2	5	
Blue jay							3	10	5
Eastern wood pewee							10	1	3
Ruby-throated hummingbird							9	10	10
Tufted titmouse							6	10	15
Yellow-throated vireo							3	5	7
Hooded warbler							3	30	11
Red-eyed vireo							3	10	43
Hairy woodpecker							1	3	5
Downy woodpecker							1	2	5
Crested flycatcher							1	10	6
Wood thrush							1	5	23
Yellow-billed cuckoo								1	9
Black-and-white warbler									8
Kentucky warbler									5
Acadian flycatcher									5

Reprinted from Johnston and Odum, 1956, with permission of the Ecological Society of America.

CONCLUSIONS

Succession is a community-level phenomenon that results from the full panoply of interspecific interactions, historical effects, and spatial dynamics that operate in developing communities. The history of the study of succession is one of often heated debate about the best way to describe the phenomenon and the mechanisms of community change. Simple models can mimic the patterns of species replacement over time, with or without the inclusion of explicit mechanisms of species interactions. Most studies of succession have been largely descriptive, which means that the actual mechanisms of species replacement in most natural communities remain highly speculative.