Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization

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It is in changing that things find repose. [Heraclitus]

Succession refers to the changes observed in an ecological community following a perturbation that opens up a relatively large space. The earliest studies described the sequence of species that successively invade a site (Cowles 1899; Cooper 1913; Clements 1916); more recent studies have described changes in other characteristics such as biomass, productivity, diversity, niche breadth, and others (see review in Odum 1969). In this paper we will discuss only changes in species composition.

Clements (1916) proposed a theory of the causes of succession so satisfying to most ecologists that it has dominated the field ever since (see Odum 1969). Although doubts were raised earlier (Gleason 1917; Egler 1954), queries and objections have recently increased in number (McCormick 1968; Connell 1972; Drury and Nisbet 1973; Colinvaux 1973; Niering and Goodwin 1974, etc.). This paper will review the theory and the evidence and propose alternative testable models. We consider first the mechanisms which determine the changes during succession and second the relationships between succession and community stability and organization.

The mechanisms producing the sequence of species have not been elucidated for several reasons. First, direct evidence is available only for the earliest stages when many species are short lived and amenable to experimentation (Keever 1950). The sequence later in succession has not been directly observed for the obvious reason that these later-appearing species persist for much longer than the usual ecological study or even than the investigator. Therefore, the later sequence has had to be reconstructed from indirect evidence of various sorts, such as by tabulating the vegetation found on sites abandoned after cultivation at various past times (Oosting 1942) or by dating the living and dead trees on one site (Cooper 1913; Henry and Swan 1974).

Second, some possible mechanisms have been ignored, particularly the effects of grazing animals. The study of succession has in the past been carried out mainly by persons working solely with plants. This can be justified, in the sense

that plants not only are the primary producers but also usually constitute both the greatest amount of biomass and the structural form of a community (sessile animals also play this role in many aquatic communities). However, it has meant that the mechanisms conceived have usually been restricted to the interactions of plants with the physical environment or with other plants (Langford and Buell 1969). The interactions with organisms that consume plants have always been included as one of the many factors influencing succession, but again most of the attention has been given to the consumers involved in the cycling of mineral nutrients, particularly the decomposers such as microorganisms and fungi, rather than to animal herbivores.

The result has been to focus attention on the resources of plants so that the biological interaction regarded as being of overriding importance is competition. This has coincided with the development of a theory of community structure based almost entirely on competition (Hutchinson 1958; MacArthur 1972 and previous work; Levins 1968; Vandermeer 1972; for a contrasting view, see Connell 1975). As a result the most recent critical reviews of ecological succession have designated physical stresses to plants and competition for resources between plants as the main mechanisms determining the course of succession (Drury and Nisbet 1973; Colinvaux 1973; Horn 1974). In this paper we suggest that in addition to the competitive interactions between plants or sessile animals, interactions with herbivores, predators, and pathogens are of critical importance to the course of succession.

Third, the mechanisms that determine succession have not been defined clearly or stated in the form of hypotheses testable by controlled field experiments. In this paper we have tried to do this as well as to suggest certain experiments as tests.

We will direct our attention here to the succession of species that occupy the surface and modify the local physical conditions, e.g., plants and sessile aquatic animals. Other organisms, such as herbivores, predators, pathogens, etc., will be included only when they affect the distribution and abundance of the main occupiers of space. Species that depend upon the shelter of the larger occupants (e.g., understory species of plants, various animals such as those that live beneath mussel beds, etc.) will not be dealt with. We define a community as the set of organisms that occur together and that significantly affect each other's distribution and abundance. It is the interactions that make a community a unit worthy of study. Lastly, we will consider only those changes in species composition that would occur in the absence of significant trends in the physical regime, or in Tansley's (1935) terminology, "autogenic" succession.

MECHANISMS DETERMINING THE SEQUENCE OF SPECIES

Three Alternative Models

Figure 1 describes three different models of mechanisms that would bring about a successional change after a perturbation, assuming no further significant changes in the abiotic environment. Between the first two steps in the

A. A disturbance opens a relatively large space, releasing resources.

1

2,3

B. Of those species that arrive in the open space, only certain "early succession" species can establish themselves.

Of those species that arrive in the open space, any that are able to survive there as adults can establish themselves.

w

2

3

w

C. Early occupants modify the environment so that it becomes less suitable for subsequent recruitment of "early succession" species but more suitable for recruitment of "late succession" species.

Early occupants modify the environment so that it becomes less suitable for subsequent recruitment of "early succession" species but this modification has little or no effect on subsequent recruitment of "late succession" species.

Early occupants modify the environment so that it becomes less suitable for subsequent recruitment of both early and late succession species.

x

2

3

x

D. The growth to maturity of juveniles of later succession species is facilitated by the environmental modifications produced by the early succession species. In time, earlier species are eliminated.

Juveniles of later succession species that invade or are already present grow to maturity despite the continued presence of healthy individuals of early succession species. In time, earlier species are eliminated.

As long as individuals of earlier colonists persist undamaged and/or continue to regenerate vegetatively, they exclude or suppress subsequent colonists of all species.

y

2

3

y

E. This sequence continues until the resident species no longer facilitate the invasion and growth of other species.

This sequence continues until no species exists that can invade and grow in the presence of the resident.

2

F. At this stage, further invasion and/or growth to maturity can occur only when a resident individual is damaged or killed, releasing space. Whether the species composition of this community continues to change depends upon the conditions existing at that site and on the characteristics of the species available as replacements.
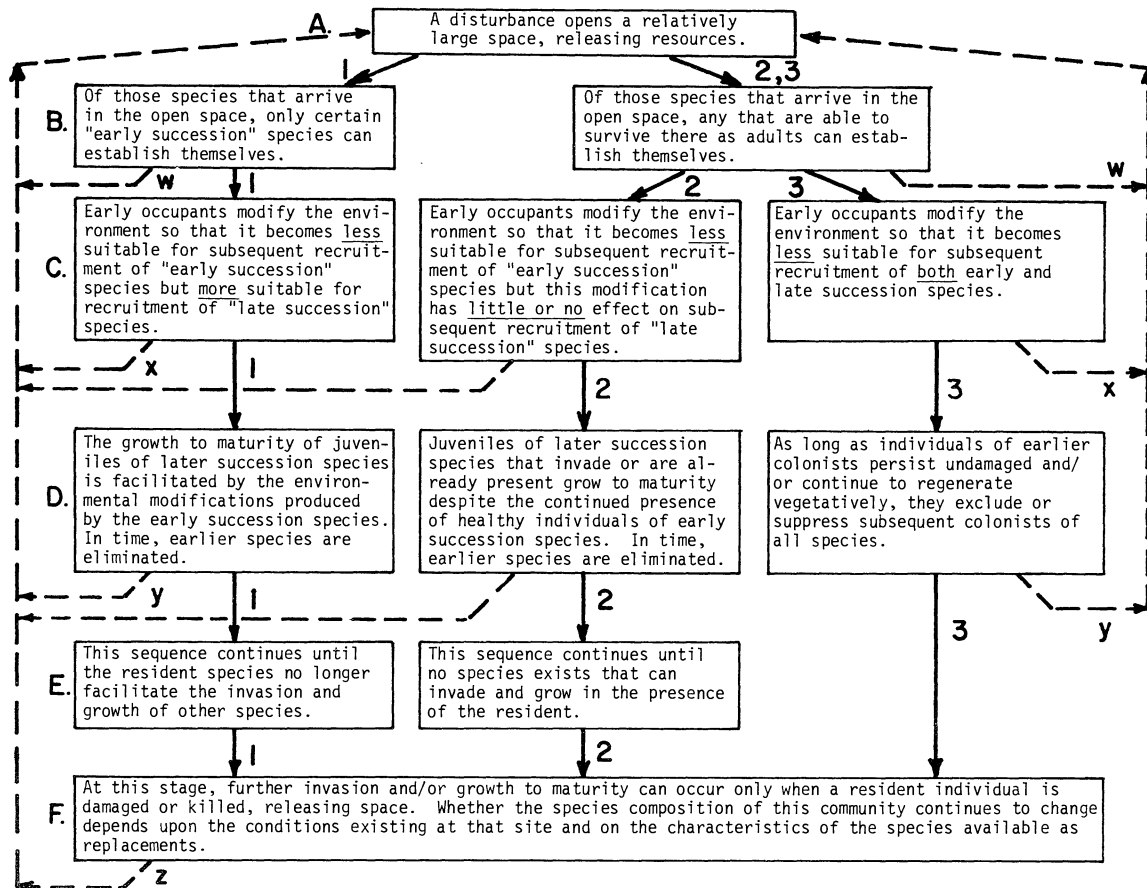
z

FIG. 1.—Three models of the mechanisms producing the sequence of species in succession. The dashed lines represent interruptions of the process, in decreasing frequency in the order w, x, y, and z.

diagram (A to B) there is a major dichotomy between alternative models of succession. Model 1 assumes that only certain "early successional" species are able to colonize the site in the conditions that occur immediately following the perturbation. Models 2 and 3 assume that any arriving species, including those which usually appear later, may be able to colonize. Egler (1954) was the first to distinguish this latter process, which he calls "initial floristic composition," from the "relay floristics" of model 1. This dichotomy emphasizes the fundamental difference between the original conception of succession proposed by Clements (1916) and the alternative ones described here. We will refer to model 1 as the "facilitation" model.

Up to this point all models agree that certain species will usually appear first because they have evolved "colonizing" characteristics such as the ability to produce large numbers of propagules which have good dispersal powers, to survive in a dormant state for a long time once they arrive (Marks 1974), to germinate and become established in unoccupied places, and to grow quickly to maturity. They are not well adapted to germinating, growing, and surviving in occupied sites, where there is heavy shade, deep litter, etc., so that offspring seldom survive in the presence of their parents or other adults. Thus in all models, early occupants modify the environment so that it is unsuitable for further recruitment of these early-succession species.

Where the models differ is in the mechanisms that determine how new species appear later in the sequence. In the facilitation model the early-succession species modify the environment so that it is more suitable for later-succession species to invade and grow to maturity (steps C and D in fig. 1). In describing how the exposed surface of a landslide may be recolonized, Whittaker (1975, p. 171) outlined the steps of the facilitation model: "One dominant species modified the soil and microclimate in ways that made possible the entry of a second species, which became dominant and modified environment in ways that suppressed the first and made possible the entry of a third dominant, which in turn altered its environment." This sequence continues until the resident species no longer modifies the site in ways that facilitate the invasion and growth of a different species (step E).

In model 2, the modifications wrought on the environment by the earlier colonists neither.increase nor reduce the rates of recruitment and growth to maturity of later colonists (steps C and D). Species that appear later are simply those that arrived either at the very beginning or later and then grew slowly. The sequence of species is determined solely by their life-history characteristics. In contrast to the early species, the propagules of the later ones are dispersed more slowly and their juveniles grow more slowly to maturity. They are able to survive and grow despite the presence of early-succession species that are healthy and undamaged. As stated by MacArthur and Connell (1966, p. 168), "In the case of forest succession, each species is able to stand deeper shade than the previous one, and as the forest grows the canopy becomes thicker and casts an even deeper shade. In this new, deeper shade other species are more successful . . . . [T]olerant species are those that are successful in shade. As expected the climax forests are composed of the most tolerant species." The end

point is reached when the most shade-tolerant species available occupies the site and casts shade so deeply (or removes other resources to such a low level) that its own offspring cannot survive. Although we have used shade tolerance as an example here, tolerance to other environmental factors, such as moisture, nutrients, allelochemicals, grazing, etc., may be equally or more important in other circumstances. We will refer to this as the "tolerance" model. It serves as an intermediate case between the first and third models.

In contrast to the first model, the third holds that once earlier colonists secure the space and/or other resources, they inhibit the invasion of subsequent colonists or suppress the growth of those already present. The latter invade or grow only when the dominating residents are damaged or killed, thus releasing resources (steps C and D). We will refer to model 3 as the "inhibition" model.

At this point (step D) in model 3, the possibility exists that the very first colonists, by interfering with further invasion, may have prevented any further succession. In contrast to the other two, in model 3 the species of individual that replaces a dying resident need not have life-history characteristics different from the original resident. It need not be a different species adapted to conditions modified in a particular way by former residents (model 1) or one that is more tolerant of reduced levels of resources (model 2). This being the case, it is possible that a resident may be replaced by another of the same species or of a different species also having "early succession" characteristics. Then the traditional successional sequence won't occur. If, on the other hand, the replacement happens to be a species having "late succession" characteristics, then the traditional successional sequence will be observed. Since the early-succession species are shorter lived, they will be replaced more often than would the longer-lived late-succession species. If propagules of these later species are available for invasion, then after several years of transitions the latter species will tend to accumulate, with the result that the early species will gradually decrease in relative abundance. In model 3, the great tolerance of late-succession species is of importance, not in allowing net growth beneath earlier species (as suggested in model 2), but in allowing the late species to survive through long periods of suppression. In effect, tolerance compensates for lower vagility of propagules, increasing the chances that a seedling of a late species will be available on the site to replace a dying earlier individual. In this way the operation of the inhibition model 3 will produce a succession of species leading from short-lived to long-lived species, as is commonly observed.

In summary, the mechanisms producing the sequence of species observed are as follows. In all models the earlier species cannot invade and grow once the site is fully occupied by their own or later species. However, the models differ in the way later species become established after their propagules arrive. In the "facilitation" model 1, the later ones can become established and grow only after earlier ones have suitably modified the conditions. In the "tolerance" model 2, later species are successful whether earlier species have preceded them or not; they can become established and grow to maturity in the presence of other species because they can grow at lower levels of resources than can earlier ones. In the "inhibition" model 3, later species cannot grow to maturity in the

presence of earlier ones; they appear later because they live longer and so gradually accumulate as they replace earlier ones. Another distinction between the models is in the cause of death of the early colonists. In models 1 and 2, they are killed in competition with the later species. The latter grow up and shade or otherwise deprive the former of resources. In model 3, however, this cannot happen; the early species are killed by local disturbances caused by physical extremes or natural enemies such as herbivores, parasites, or pathogens. We will now consider the evidence for each model.

Evidence

The mechanisms of the facilitation model probably apply to most heterotrophic successions of consumers feeding on carcasses, logs, dung, litter, etc. Savely (1939) pointed out that certain insect species that bore into logs must precede others that attack the inner tissues. Similarly some species of insects appear in dung and carcasses only after these have been decomposed to a certain degree by earlier colonists (Payne 1965). No experimental investigation has been carried out to demonstrate the details of the process, but the evidence seems to support the application of this model. In the absence of primary producers such localized successions finally exhaust the energy source.

Evidence in support of model 1 for autotrophs comes from primary successions on newly exposed surfaces. For example, Crocker and Major (1955) and Lawrence et al. (1967) have suggested that the characteristics of soils newly exposed by a retreating Alaskan glacier probably make the establishment of plants extremely difficult. However, those "pioneer" species that are able to colonize will ameliorate these conditions, reducing pH, increasing nitrogen content, adding a layer of organic soil over the hardpan, reducing desiccating winds, etc. Seedlings of spruce trees then appear in these new conditions, seldom if ever in the original exposed sites (Reiners et al. 1971). Therefore it is reasonable to conclude that the spruce could not have invaded until the pioneers had ameliorated the original conditions. A second example of the operation of model 1 in primary succession is the colonization of sand dunes on lake shores (Cowles 1899; Olson 1958). The pioneer plants stabilize the moving sands which otherwise would not be suitable for colonization by later-appearing species. More conclusive evidence would require a set of field experiments, manipulating separately the various factors to determine which contributed most to the establishment of the later successional species. However, even without such experiments these cases seem to support model 1.

Field experimental tests of the facilitation model are few. The only terrestrial example we have found involves the giant saguaro cactus. Experimental broadcasting of seeds, transplanting of seedlings, and observations of survival of natural seedlings showed that they survive only in the shade of other species of "nurse plants," or, in a few instances, in the shade of rocks (Niering et al. 1963; Steenbergh and Lowe 1969; Turner et al. 1969). As in the other instances described, the mechanisms of model 1 apply in the early stages of colonization of very rigorous extreme environments. Whether this model applies to replace-

ments at later stages of terrestrial succession remains to be seen; we are not aware of any such evidence at present.

In a review of marine benthic successions, Connell (1972) searched for evidence from field experiments supporting model 1. The only evidence he found was that of Scheer (1945), whose experimental evidence indicates that sessile marine animals (hydroids) probably attached more readily to glass plates immersed in the sea if these had previously been coated by bacteria in the laboratory. Another possible example of this model is provided by the mussel *Mytilus* which seldom appears very early in recolonization of rocky shores. Bayne (1965) and others have noted that larval mussels often attach preferentially to filaments provided by previously settled algae, hydroids, etc. However, Seed (1969) has found that they do not require such organisms and will attach to rough surfaces or crevices in bare rock. Harger and Tustin (1973) suggest that the large alga *Eklonia* may colonize only after filamentous organisms have become established. In none of the many other marine examples reviewed (Connell 1972) was there evidence that earlier species facilitated the establishment of later ones.

The evidence in support of the first step (B in fig. 1) in models 2 and 3 is that late successional species of land plants are often able to become established without any preparation of the site by earlier species (Egler 1954; Drury and Nisbet 1973). The later steps (C to E) of model 2 require that later species be able to invade and grow at lower levels of resources than earlier species. This is usually expressed in terms of greater tolerance by later species to shade or to reduction in other resources. In effect, this model specifies that later species are superior to earlier ones in exploiting resources. Even if the earlier ones reduce resources enough to depress the rate of growth of the later species, the latter will still be able to grow to maturity in the presence of the former. Necessary and sufficient evidence in support of model 2 would consist of observations or experiments showing that invasion and growth to maturity of later species neither require conditions produced by earlier species (model 1) nor are inhibited by them (model 3). Although this is theoretically possible, we have found no convincing examples. In the invasion and growth to complete dominance by mussels on marine rocky shores, no experiments have been performed testing the effects of the previous occupants on this process. The observation of Bayne (1965) cited above suggests that they may fit model 1; experiments would be welcome. Likewise in terrestrial successions, the effects of previous residents have not been elucidated. In fact, if the more shade-tolerant species are intolerant to full sun, as with saguaro cactus, they may be examples of model 1.

Evidence supporting model 3 consists of observations that early species suppress the establishment of later ones, inhibit their growth, and reduce their survival. Keever (1950) and Parenti and Rice (1969) have shown experimentally that early-colonizing land plants reduce the rates of germination and growth of other species arriving later. Niering and Egler (1955) and Niering and Goodwin (1974) found that a closed canopy of shrubs prevented the invasion of trees for periods up to 45 yr. Webb et al. (1972) found that 12 yr after an

experimental clearing in montane rain forest, the sprawling shrub *Lantana* had occupied a large area, excluding and suppressing tree species. Besides these data from land plants, there is also evidence from marine organisms living on hard substrates, that the first colonists prevent later ones from attaching. O'Neill and Wilcox (1971) got opposite results from those of Scheer (1945) in marine species; on glass plates, a thick coating of bacteria apparently inhibited attachment of diatoms. Likewise, Sutherland (1974) found that once sedentary marine invertebrates had covered the undersurface of tiles suspended from a wharf, other species invaded only after the occupants had died and sloughed off.

Field experimental demonstrations showing that early species exclude or suppress later ones come from several sources. For the earliest stages, McCormick (1968) found that removing the pioneering annual plants resulted in faster growth and earlier flowering of perennials. As yet no data from this unique study have been published. In an experimental study in the marine rocky intertidal zone, W. P. Sousa (unpublished manuscript) has found that removing early succession algae resulted in a much greater abundance of later succession algae.

For intermediate stages the best evidence comes from some of the first controlled field experiments ever done, trenching in forests. During the earlier stages of succession in forests with trees less than 50 yr old, more light penetrates to the ground than in old climax forests. However, several series of trenching experiments in these early succession forests showed that young trees grew only when the root competition with older trees was removed by trenching (Fricke 1904; Toumey and Kienholz 1931; Korstian and Coile 1938). Thus even with the greater light levels of early succession forests, the late succession seedlings are suppressed by root competition.

These observations and experiments indicate that in many instances the high tolerance of later succession species to low levels of resources still does not allow them to grow to maturity if they are dominated by a stand of early species. Studies by Vaartaja (1962), Grime and Jeffrey (1965), and others have shown that late species maintain themselves in the presence of dominating earlier species by having a lower metabolic rate, by repairing damages, and by fending off attacks of herbivores, soil pathogens, etc. The later species simply survive in a state of "suspended animation" until more resources are made available by the damage or death of an adjacent dominating individual.

Even though earlier species may continue to exclude or suppress later ones for long periods, the former eventually are damaged or killed and are then replaced. For example, in succession on prairies, annual weeds and grasses are gradually replaced by perennial ones. In Oklahoma, an annual species of grass lasted up to 15 yr before a perennial species of bunchgrass replaced it, to survive and dominate for another 50 yr as others slowly invaded (Booth 1941). The perennial never grew more rapidly than the annual at any level of mineral nutrients (Rice et al. 1960), so it could not displace it by exploitation competition as required by model 2. Rather it presumably simply filled in the space opened up by the death of the annual and held it thereafter. The seedlings of

sugar maple, one of the dominant late succession species in North American deciduous forests, become established mainly in the light gaps opened up when trees die (Bray 1956; Westman 1968).

This evidence suggests that in many situations, early and mid-succession life forms (e.g., perennial grasses and shrubs, green algae, etc.) may quickly secure the space opened up after a disturbance and then hold it, excluding typical late-succession species. This is especially true when the former can propagate vegetatively as well as sexually. The opportunities for a new seedling of any species to become established in a dense perennial grass sward or shrub thicket are virtually zero. By vegetative reproduction the dominant species can persist for a very long time.

PREDICTIONS AND TESTS ON THE MODELS

We predict that the facilitation model 1 will commonly apply to situations in which the substrate has not been influenced by organisms beforehand. It should apply to many primary successions, since soils newly exposed by receding glaciers, shorelines, etc., may have extreme properties of nutrients, structure, pH, etc., that render them difficult for most species to invade. In contrast, in secondary succession the soils have already supported plants and so present fewer difficulties to colonists. Therefore, we predict that models 2 and 3 apply to most secondary successions. If the previous occupation has not influenced the substrate (e.g., on marine rock surfaces), however, model 1 may apply. The facilitation model should also hold in heterotrophic successions in logs, corpses, etc., where there are barriers to initial penetration through bark or skin, so that specialist scavengers must bore through these barriers before other species can enter.

Rather than the purely observational evidence that is usually adduced, much better tests of the models could be made with controlled field experiments. For example, the best test of the hypothesis given in step B in figure 1 would consist of excluding early species from sites to see whether late species could colonize. The only published account of such an experiment is that of McCormick (1968), but no data were included.

Experimental tests of later stages are more difficult, because of the longer life spans of later species. However, the processes at step D, figure 1, could be investigated in the following way. Seeds and/or seedlings of later species could be transplanted and grown with and without earlier species. If later species grew better when early species were absent, models 1 and 2 would be rejected; if much worse, models 2 and 3 would be rejected; if there were little or no difference, models 1 and 3 would be rejected. The trenching experiments described earlier indicate that the first alternative (models 1 and 2 rejected) seems to apply to many forests in the intermediate stages of succession.

Model 3 could be tested by observing whether later succession species could invade a stand of early species that was either left intact (protected from fire, grazing, etc.) or in which gaps were created by removing some early individuals.

If later species invaded and grew only in the gaps, model 3 would be supported, models 1 and 2 rejected.

Careful experimental study of the early stages of primary successions would be particularly welcome. Present evidence suggests that here is where the traditional facilitation model 1 may be expected to apply most closely. Broadcasting and planting of seeds and transplanting seedlings of later-succession species are crucial field experiments that are feasible on such places as recently exposed moraines of receding glaciers, lava and ash beds from recent volcanic eruptions, newly exposed sand bars and dunes, recent landslides, and newly uncovered rocky shores. Such introductions with and without associated early-succession species would test the different models. If the later species become established without the early ones being present, the facilitation model will be rejected. If not, further field experiments could be done to determine what sort of modifications of the environment are necessary to ensure their establishment.

These field experiments were suggested by the statements in figure 1, which in most instances were stated as testable hypotheses. Some guidelines to the proper design and limitations of controlled field experiments have recently been described by Connell (1974).

SUCCESSION AND COMMUNITY STABILITY

In many communities, major disturbances occur frequently enough that succession will usually be cut short and started all over again, as indicated by pathways x and y in figure 1. Under what circumstances would we expect this to happen? Disturbance by man dates back to preneolithic cultures. In Britain, prehistoric man set fires to drive out game and cut vegetation to clear land for agriculture (Smith 1970; Turner 1970). Other disturbances not associated with man are natural fires, landslides, severe storms, and various biological causes such as intense grazing (e.g., the bison on North American plains) or predation on sessile marine organisms. For example, within the past several thousand years much of the forest of North America has been badly damaged or destroyed by fire at least once every few hundred years, within the life span of the dominant conifers (Heinselman and Wright 1973). These major sources of perturbation are so widespread as to suggest that even before man's interference became common, in relatively few natural communities did succession ever stop.

After a severe disturbance or during a short respite from normally heavy and continuous grazing or predation, there is usually a burst of regeneration that, once established, suppresses later regeneration. Thus a single age-class emerges that may dominate the scene for long periods. Henry and Swan (1974) found that the white pine trees that got established after catastrophes in the late seventeenth century dominated the forest for 200 to 250 yr thereafter, suppressing almost all later tree invasion. Similar waves of regeneration of a single age-class have been demonstrated in forests after large grazers were reduced

(Peterkin and Tubbs 1965) and after spruce budworm epidemics (Morris 1963). The existence of dominant, widely spaced age-classes resulting from such episodic regeneration after perturbations is an indication that succession has not yet stopped in an equilibrium assemblage.

If no such catastrophes have intervened we will have arrived at an assemblage of long-lived individuals that would usually be regarded as late-successional, or "climax," species, step F in figure 1. We will now consider the second question posed at the beginning, "Under what conditions will the species composition remain in a steady-state equilibrium?"

Theory

Stated simply, a system is stable if it persists despite perturbations. It is impossible to discover whether a system is stable if it is not tested with a disturbance. In real communities this is not a problem because challenges are being continually offered to the system's stability in the form of variations in physical conditions, invasions of competing species, natural enemies, etc.

Margalef (1969) pointed out that systems persist either by giving way to the perturbation and subsequently recovering to the original state or by not giving way at all. He suggested that these could be called, respectively, "adjustment or lability," vs. "conservatism, endurance, or persistence." Since we have equated stability with persistence, we will refer to the two sorts of mechanisms as adjustment and resistance, respectively. In his discussion of the application of the theory of stability to ecological systems, Lewontin (1969) discussed the nature of the field of transformations in which the system moves. If there exists a point at which the transformation vector is zero, so that the system does not change, it is called a stationary point. Whether it is also a stable point can be decided only by observing that, in the region nearby, all the transformation vectors point toward it. If the system returns to a stable point from any other point in the vector field, i.e., after any degree or extent of perturbation, it is globally stable. If it returns to it only after small perturbations and to another stable point after a large perturbation, the system exhibits only neighborhood stability. Each stable point has its own basin of attraction, the neighborhood in which the system returns to the original point.

In Margalef's (1969) terminology, the process of succession represents "adjustment" stability. If all successions on a site led to a similar species composition at equilibrium, as postulated by Clements (1916), this would be global stability. If quite different species compositions were reached, the system would have multiple stable points. Only by observing the process of adjustment after perturbation can such judgments be made.

If a community resists perturbation, there will be no succession since there is no change. Therefore, we need not consider this mechanism in detail, except to point out that individuals resist perturbations by defenses against stresses from physical factors, attacks by natural enemies, and invasions by competitors.

Succession as Adjustment Stability: The Importance of Scale

In recovery from a perturbation, it is the maintenance of species composition that we are considering. However, before the stability of any real community can be discussed, three scales must be specified: the time, space, and intensity of perturbations. In other words, to judge stability we need to decide how long and over what space the present species composition must persist in the face of a given intensity of perturbation. The reason for this proviso can be illustrated by the following example: Horn (1974, p. 28) states, "Early successional patches are by definition ephemeral, while tracts of the climax remain relatively unchanged for several generations." But this statement holds only under certain scales of time and space. In a small area of forest, early-succession stages are individually ephemeral because the species are short lived and seldom persist for many generations. But if the early-succession species are not to go extinct, somewhere either disturbances must occur close enough in time and space to provide open sites or else such sites must exist continually (e.g., ridges with much drier conditions than the surrounding forest) in which they can produce successive generations and so perpetuate their species. Therefore a large enough tract of forest must be included in the system under consideration so that the kind of habitat recognized as "early succession patches" remains in existence, somewhere, for generations.

In contrast, the assertion that tracts of the climax remain unchanged for several generations is supported only by general impressions. The long-enduring climax tree lends an air of permanence, but as Frank (1968) points out, this implies nothing about self-perpetuation. So on the scale of generation times and over a large enough tract, if both early- and late-succession stages persist despite perturbations, both are stable.

Thus, to be able to judge the degree of stability of the species composition of a community, the following site characteristics must be met: (1) an area large enough to ensure either sufficient site diversity or that disturbances opening up new sites occur at intervals no longer than an early succession species persists (including the period that the seeds lie dormant [Marks 1974]). This ensures that the early-succession species are able to persist somewhere in the system. (2) An observation period at least as long as the longest generation time of any of the species and also long enough so that the whole range of kinds and intensities of perturbations will have had a chance to occur. This would allow enough time to see how much the species composition varied over at least one complete turnover of generations.

These requirements may be so stringent as to make it virtually impossible to determine the stability of communities composed of long-lived species. But unless these scales of time, space, and intensity of disturbance are defined in relation to the organisms comprising the community, any pronouncements about stability are of limited value.

We have already incorporated variations in the frequency of disturbance in figure 1; pathways *w, x, y,* and *z* represent a sequence of decreasing frequency of major disturbances. Let us now consider the general effects of varying the

TABLE 1

The Effect of the Size of Area Disturbed and Intensity of Disturbance
on the Course of Succession

Intensity of Disturbance	
Extreme	Slight

Large area:
   I. *A long succession*: Assuming no survivors, all colonists must come from outside, so will consist mainly of early succession species with high vagility of propagules. Since late-succession species have low vagility, they will spread in slowly from the borders. Meanwhile the early species may go through several generations.
 	
 Small area:
   III. *Some succession*: Surrounding adults colonize, with propagules or vegetative growth. Propagules of distant early-succession species also colonize, but since resources are reduced by the neighboring adults, the early species may not grow as quickly as usual.
	Large area:
	   II. *A moderate amount of succession*: The area will be refilled: (*a*) by individuals growing from propagules that arrived from distant early-succession species or those that were present in the soil before the disturbance; (*b*) by growth of surviving juveniles of late-succession species that before had been living suppressed in the shade of the adults; and (*c*) by resprouting of damaged adults.
	
	 Small area:
	   IV. *No succession*: The small gap is refilled by growth of surrounding adults and/or of previously suppressed offspring of the late-succession species.

scales of intensity of disturbance and size of area disturbed (see table 1). First, if the disturbance is both intense and also extends over a large area, such as extensive cultivation, or a large fire severe enough to kill all of the plants in the forest, all recruitment must come from outside. The pioneer species with highest vagility of propagules will then secure and hold the ground for a long time, with the climax species only slowly spreading in from the edges. Obviously, return to the original forest will take a long time. Similarly, observations of colonization on very extensive new surfaces exposed in the sea, such as on new sea walls, show an initial colonization within a few weeks of diatoms and green algae, whereas the larger long-lived algae may not appear for 2 or 3 yr (Moore 1939; Rees 1940).

Second, if the disturbance is less severe but affects a very large area, such as extensive damage from a hurricane which often kills large trees but not the undergrowth, regrowth of survivors as well as recruitment from seeds will occur. Opportunists, whose seeds have either been present in the soil or newly arrived from surrounding areas, may germinate and rapidly grow up, suppressing the seedlings of climax species that have survived either as seeds or seedlings from the original forest. Alternatively, surviving shrubby undergrowth may suppress these seedlings. However, some members of the climax species may have survived as taller saplings or as portions of adults that send up sprouts. These may be too tall to be suppressed by the pioneers (Webb et al. 1972). Thus the

return to the original state will not be delayed as much as in the first case by the dominance of early-succession species.

Third, if the disturbance is severe over a small area, such as a lightning strike that kills all individuals in a small space, recruitment must come from outside, either by seeds or vegetative growth of neighbors. Because the area is small, seeds of both low vagility from nearby climax trees and greater vagility from more distant early-succession species will colonize the gap. In small gaps resources of light and soil nutrients are reduced by the neighboring trees so that the early-succession pioneers may not grow quickly enough to suppress the growth of the climax offspring. Climax seedlings may even grow faster than those of earlier stages in small gaps; data in Horn (1971, p. 33) suggest this. A similar case has been demonstrated on marine rocky shores (Pyefinch 1943). A quite small area of surface was cleared in the midst of a bed of large long-lived algae; offspring of these large species soon became established and filled in the gap within the first year, in marked contrast to their slow invasion on extensive new surfaces as described above.

In the fourth case, the disturbance is slight over a small area, such as when a single adult dies. Light and soil water and nutrients are only slightly increased over a small area, and few individuals are killed by the disturbance. The gap is filled either by vegetative growth of the surrounding adults or by replacement of the dead adult by growth of offspring of late-successional species that are already present as suppressed individuals. Few early-succession species invade successfully because the area is small and the level of resources is low. In this case the whole process takes place within step F, figure 1.

Patterns of Stability Following Recovery from Major Disturbances

Succession, as represented by steps A through F in figure 1, is the process by which a community recovers from a perturbation. Two questions are relevant here: (1) What determines the rate of recovery after major perturbation, and (2) how closely will the species composition return to the original state?

Regarding the first question, the three models produce different rates of recovery. In the facilitation model 1, early-succession species enhance the invasion and growth of late-succession species, so the former increase the rate of recovery. In the tolerance model 2 the early species reduce the rate of recovery since they suppress the rates of invasion and growth of late species. In the inhibition model 3, the early species prevent recovery completely until they die or are damaged. Thus the rate of recovery, i.e., degree of stability, drops in the order of models 1, 2, and 3.

In terms of the management of either natural or disturbed sites, the correct plan to encourage a quicker recovery from perturbation depends on the type of community it is desired to develop and upon the likely model pathway that succession would follow. Assuming that a situation like the original community is desired, and if model 1 tends to operate, early succession species should be encouraged. If model 2, they should probably be discouraged, and if model 3, they must be discouraged. In the latter two, the best plan would be to replant

the species that were there originally and remove any early ones that invade. In fact, it may be necessary, in order to preserve some communities, to tolerate some events that ordinarily would be regarded as unmitigated catastrophes. The long-term maintenance of alluvial redwood groves may depend upon the Heraclitean forces of fire and flood to remove the trees that suppress young redwoods (Stone and Vasey 1968). Person and Hallin (1942) pointed out that natural regeneration of redwood requires removal of competing species. The second question is, how closely will the species composition tend to return to the original state? In the four cases just described (see table 1) we suggest that the probability of a close return increases in the order I, II, III, IV. Considering a large tract of land, the more extensive and/or intense the disturbance, the longer the succession and the less probable that the final composition will resemble the original.

Does the Species Composition Ever Reach a Steady-State Equilibrium?

Let us now consider communities that are subjected only to slight disturbances over small areas (step F, fig. 1). Here the future course of events will consist of a series of very small-scale changes as individuals die and are replaced. We now ask the question, does the species composition remain constant over several generations? We will answer this on two different spatial scales. The smallest scale is the individual organism, so we will first discuss how species may vary during a plant by plant replacement process. Second, we will consider whole tracts of land containing a number of species.

The pattern of small-scale changes will depend upon whether individuals are more likely to be replaced by a member of their own or another species. The species of replacing individual will depend upon how the conditions at the spot had become modified during the previous occupation. In relation to the success of their own offspring, three types of conditions could be produced in the immediate vicinity of the individual being replaced.

In the first, the conditions are such that offspring of the same species will be favored over those of other species. That is, offspring of the same species may be concentrated near the adult so that when it dies there is a very high probability that it will be replaced by one of them. Such precise self-replacement would mean that not only the species composition but also their relative abundance and spatial pattern would remain constant. This would represent the highest possible degree of stability.

The most likely instance of this occurring would be one in which the late-succession species reproduce vegetatively from root or stump sprouts. The situation described by Horn (1975) in which, at the calculated equilibrium state, American beech was strongly dominant may be an example, since every beech offspring was a root sprout. The same pattern occurs in other species such as *Tilia americana* and in Antarctic beech forests in Australia, the trees sprouting in circles around old stumps.

A second and opposite alternative is a species in which conditions in the

vicinity of a late-successional individual become modified in such a way that its offspring can no longer survive there. Then when the adult dies, it would be replaced by another species. For example, seedlings of the cedars of Lebanon "thrive under hardwood trees and shrubs but not under cedar trees, so that some disturbance is apparently necessary for cedar-forest regeneration" (Beals 1965, p. 694). Another example of this was indicated by Florence (1965), who suggested that in old-growth redwood forests conditions in the soil may change gradually for the worse as resistant portions of the litter (e.g., lignins) accumulate and, perhaps as a consequence, pathogenic microorganisms increase while saprophytes decrease. Thus redwoods, the epitome of the long-enduring climax species, may not replace themselves unless the soil environment is changed. Florence (1965) found that redwood seedlings grew poorly in soil from old redwood groves unless the microorganisms were killed by irradiation. He suggests that seedlings will persist and grow only if the inimical soil environment is changed, either by new soil being brought in by stream deposition (Zinke 1961) or by a set of hardwood species intervening between redwood generations. Such "soil fatigue" has been observed in other forests (see review in Florence 1965). Other examples in which soil microorganisms have been demonstrated or implicated in the death of seedlings in the vicinity of adults of the same species are from *Eucalyptus* forests (Florence and Crocker 1962; Evans et al. 1967) and, in a rain-forest tree, *Grevillea* (Webb et al. 1967).

If only a few species are available, a "cyclic succession" may occur, each species alternating with one or two others. The first examples of such cyclic successions were pointed out by Watt (1947); others have since been studied in Alaskan flood-plain vegetation (Drury 1956), old-growth redwoods (Florence 1965), etc. Aubreville's (1938) "mosaic theory of regeneration" in tropical rain forests seems to fit this model also. Unlike the first situation, which is stable in areas the size of an adult individual, stability in the second situation can only occur on a larger scale, minimally accommodating individuals of several species.

In the third alternative the site where the adult stood remains neither more nor less favorable for offspring of the same species. The species of replacing individual will depend upon the relative abundance of propagules arriving there or of suppressed individuals already present. Since its own offspring are not more disadvantaged than those of other species, it is highly likely that they will be the commonest young in the immediate vicinity of the adult. Only if the species produces very many highly dispersed offspring, as in the planktonic larvae of marine sedentary organisms, would this likelihood be reduced. Therefore this more closely resembles the first than the second alternative. Thus the first acts as an "absorbing sink," for, when conditions of either the first or the third type are associated with the replacing individual, the probability is very high that that species will continue to occupy that site for many generations.

In that case, why do any instances of the second type exist? The answer is that this situation is produced not by the species itself, nor by competing species, but by natural enemies that attack that species in preference to another. At

least two possible mechanisms could produce this result. Either the predators could be generalists that switch their attention to whichever species is commoner or else they are specialists attacking that particular species. The first mechanism might apply in instances where local patches of a single species are produced following the operation of replacement processes of the first and third type described above. This behavior has been predicted and verified in invertebrate predators by Murdoch (1969) and Murdoch and Oaten (1975). Similar studies of herbivores attacking plants would be welcome to see whether the same principles apply as in predator-prey interactions.

The second mechanism, specialist natural enemies, has been proposed for tropical forests by Janzen (1970) and Connell (1971), who have suggested that fallen seeds and young seedlings will be attacked more heavily near the parent tree than further away. Field experimental tests have rejected this hypothesis for seeds in four instances (Connell 1971, two species; Janzen 1972a; Wilson and Janzen 1972) and supported it in a fifth, involving an introduced insect seed predator in a disturbed habitat (Janzen 1972b). The hypothesis has been supported for seedlings by a field experiment (Connell 1971) and field observations (Janzen 1971). Thus in some tropical forests, the pattern of turnover of trees in climax stands may be caused by this mechanism.

Concerning changes in species composition on a larger scale, tracts bearing communities of several species, Horn (1974) states, "If stability is defined as the absence, or inverse, of species turnovers and of population fluctuations, then stability increases tautologically with succession. There is nothing magic about this invariable increase in stability because succession is defined as occurring when the specific composition of the community is changing, and it is defined as having stopped when the composition of the community is not changing."

Obviously, if in the plant-by-plant process the first alternative described earlier holds and every individual is replaced by another of the same species, the climax stage will possess both local and large-scale stability and, by Horn's definition, succession will have stopped. But if either of the other alternatives holds, so that individuals may be replaced by others of different species, then stability of species composition will not necessarily follow and so, by Horn's definition, succession may or may not ever stop. The only test of this has been performed by Horn (1975). His steady-state Markov extrapolation resulted in a species composition that resembled fairly closely an old-growth natural forest nearby. However the species that almost completely dominated both the simulated and real forest was American beech, which in Horn's example was reproducing entirely by root sprouts. If, as seems likely, these root sprouts grow to replace the main tree when it dies, this forest is composed essentially of immortal individual beeches, an extreme example of the first alternative described above.

We have found no example of a community of sexually reproducing individuals in which it has been demonstrated that the average species composition has reached a steady-state equilibrium. Until this is demonstrated, we conclude that, in general, succession never stops.

The three models of succession described earlier are based upon three quite different views of the way ecological communities are organized.

The Facilitation Model 1

The idea that the presence of later-succession species is dependent upon early ones preparing a favorable environment for them implies a high degree of organization in ecological communities. Although few modern ecologists would subscribe to Clements's (1916) analogy with an individual organism, the idea is widely held that the community is a highly integrated, well-adjusted set of species. A succinct summary of this view is given by Odum (1969):

> Ecological succession may be defined in terms of the following three parameters: (i) It is an orderly process of community development that is reasonably directional and, therefore, predictable. (ii) It results from modification of the physical environment by the community; that is succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets limits as to how far development can go. (iii) It culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow. In a word, the "strategy" of succession as a short-term process is basically the same as the "strategy" of long-term evolutionary development of the biosphere—namely, increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations. [P. 262]

The idea that succession is a process of "community development" led to the characterization of "immature" and "mature" stages of an ecosystem (Margalef 1963). Odum (1969) proposed a tabular model of the contrasting trends in energetics, structure, life history, nutrient cycling, selection pressure, and overall homeostasis to be expected in the developmental and mature stages of a community.

This model has been severely criticized in recent reviews by McCormick (1968), Drury and Nisbet (1973), and Colinvaux (1973). They point out that most of the proposed characteristics of "mature" communities are simply the consequence of the passage of time rather than of internal control. For example, in old-field succession biomass increases since trees take time to grow. More nutrients are tied up in the bodies of trees than in herbs. Starting from nothing, species diversity and biochemical diversity increase as colonizers arrive. As a consequence of these obvious trends others of necessity follow: changes in production/biomass and other ratios, increases in structural complexity, increase in importance of detritus in nutrient regeneration, etc.

Other predictions of the model derive from the apparently firmly held view that the mature community, like the adult organism, is a highly organized, stabilized system, with maximum homeostasis achieving maximum protection from perturbations from the environment. This view is based solely on the analogy, not, in our opinion, on evidence. Odum (1969, table 1) has proposed a series of trends. Mature communities (as contrasted to developmental stages) are presumed to have more weblike food chains, more well-organized stratifica-

tion and spatial heterogeneity, narrower niche specialization, longer and more complex life cycles, selection pressures "for feedback control (K-selection)" rather than "for rapid growth (r-selection)," low entropy, and high information content.

All or most of these predicted characteristics are not findings but deductions from the concept that the mature community is in fact in a steady state that is maintained by internal feedback control mechanisms. All have been questioned by one or other of the recent reviews (Drury and Nisbet 1973; Colinvaux 1973; Horn 1974). The bases of the doubts, which we endorse, are that since the embryology analogy is unsupported, and since there is no evidence that so-called mature communities are internally controlled in a steady state, such characteristics cannot be deduced from them.

Obviously the mechanisms determining the sequence of species of model 1 may apply, for example, to heterotrophic successions and certain primary successions, even if the high degree of positive integration described above does not hold in those same communities.

The Tolerance Model 2

This view holds that succession leads to a community composed of those species most efficient in exploiting resources, presumably each specialized on different kinds or proportions of resources. Connell (1975) pointed out that this model may hold in two sorts of circumstances: (a) for certain groups of animals that have evolved a high degree of independence from the rigors of both the physical and biotic environments (warm-blooded vertebrates, large predators, social insects, etc.); (b) where natural enemies are reduced but the physical environment is not so severe as to remove most organisms directly; then the populations may be limited by resources.

Several examples of the latter situation are described in Connell (1975); the winning competitors were species that were more effective in interference rather than more efficient in exploiting resources. Another example is from those areas on coral reefs protected from hurricane damage but where predators of corals are not common. In such an area at Heron Island, Queensland, the surface is almost completely occupied by those competitors that are most effective in interfering with their neighbors, colonies of "staghorn" corals that have grown up over all neighbors and now hold the space against invaders (Connell 1976). Elsewhere the reef is damaged by frequent hurricanes and the succession is kept in an earlier stage, exemplified in figure 1 by pathways x or y.

In dense, light-limited forests, this tolerance model predicts that the set of species most tolerant (i.e., able to grow on the lowest level of resources) will eventually dominate the community at equilibrium. Predictions of the outcome of successional trends have been made for several forests. For example, Stephens and Waggoner (1970) extrapolated from transition probabilities directly measured over several decades in a forest undergoing succession. By assuming a stationary Markov process, they concluded that at equilibrium the moderately shade-tolerant species will be in the majority, rather than the forest progressing

inexorably toward the very shade-tolerant species as the model predicts. This is not a consequence of disturbance setting back succession, since the transition probabilities were estimated only from undisturbed plots.

Horn (1975) estimated transition probabilities of successive generations indirectly by recording the saplings underneath each species of mature trees. Assuming that each sapling has an equal probability of replacing that mature tree in the next generation of the canopy, he used the proportions of saplings of each species as transition probabilities. In the subsequent extrapolation, the forest at equilibrium was dominated by the very shade-tolerant beech, a different result from that of Stephens and Waggoner. This result apparently supports the model of increasing competitive ability. It is probably a consequence of the fact that, since every young beech recorded was a root sprout of an adult and since the adult probably contributes energy to the root sprout, these "offspring" have a great competitive advantage over independent saplings in the shade.

Thus the prediction of the competition model has so far not been verified in forests replacing themselves by independent offspring (Stephens and Waggoner 1970), but only in one that apparently is doing so mainly by vegetative reproduction.

The Inhibition Model 3

In this model no species necessarily has competitive superiority over another. Whichever colonizes the site first holds it against all comers. After all the empty space is filled, invasion is possible only if the new colonist brings along its own resources, such as a large seed with enough stored energy to sustain the seedling for awhile in an undisturbed stand of vegetation where no spare energy is available.

Since replacement occurs only when resources are released by the damage or death of the previous occupant, the species composition shifts gradually and inexorably (given no further major disturbances) toward species that live longer. This is not because these species are more likely to colonize; quite the opposite. It is because once a long-lived species becomes established, it persists by definition. This, as Frank (1968) has pointed out, is succession by tautology! No directional mechanism (as in models 1 and 2) need be invoked for model 3. Simply by these life-history characteristics, long-lived species eventually dominate the ecological scene.

The ability to survive a long time is a function of having defenses against all the inevitable hazards. Examples abound of the defensive adaptations that enable late-succession species to survive better than early species. Billings (1938) showed that, as compared to early-succession species, the juveniles of late-succession species develop deeper and more extensive root systems, allowing them to persist through drought periods better than early-succession species. Stone and Vasey (1968) point out that several species of trees that invade gaps and suppress young redwoods in alluvial groves are killed by fires or by the alluvium deposited by floods, whereas the redwoods are not harmed. The allocation of energy and matter into harder, denser wood must cause a tree to

grow more slowly. But harder wood is a better defense against storm damage and wood borers. Likewise, some species of corals produce a dense, massive skeleton at the expense of slower growth and occupation of space than other corals that produce a less dense, branched skeleton and quickly secure space. Connell (1973) found that two species of fast-growing corals had many more mollusks and sponges boring into and weakening their skeletons than did a slower-growing massive species.

Adaptations against natural enemies include various morphological (hard wood, spines, fibers, etc.) and chemical defenses (secondary substances such as alkaloids, tannins, etc.). Cates and Orians (1975) found that generalist herbivorous slugs ate early-succession species in preference to species that occurred in late-successional stages in the coniferous forests of the northwestern United States. In apparent conflict with these results, Otte (1975) found that generalist herbivorous grasshoppers preferred late-succession bushes, vines, and trees to early-succession herbs in Texas. This conflict may perhaps be resolved with the following argument. The grasshoppers studied by Otte were three species of *Schistocerca* that can disperse widely. In contrast to the forest habitat of slugs, such mobile insects are more characteristic of open savannah or xeric grassland. Thus the species of plants that persist in the grasshopper habitats may be herbs rather than shrubs and trees. The grasshoppers, along with other grazing insects and vertebrates, plus seasonal fires, may be eliminating shrubs and trees and preserving the herbaceous vegetation as the "climax" stage. In their own habitat they may be behaving in the same way that slugs do in their wet forest, attacking and eliminating certain species and not eating the climax, i.e., persistent, species.

Lest this reconstruction seem farfetched, we would like to emphasize that controlled field experiments have demonstrated in several instances that natural enemies have eliminated species which were superior competitors capable of holding space against invasion. Sea urchins often clear algal mats (Paine and Vadas 1969), and predatory starfish and snails eliminate mussels (Paine 1966, 1974; Dayton 1971). These natural enemies are important components of the community and often determine the species composition of the climax.

Model 3 emphasizes that "possession is eleven points in the law" (Cibber 1777, p. 121); once an individual secures the space it resists the invasion of competitors. Eventually it may be damaged or killed and invaders may replace it. In this model, early-succession species may be just as resistant to invasion by competitors as late species, so the "climax" species are those most resistant to being damaged or eliminated by fires, storms, natural enemies, etc.

SUMMARY

The sequence of species observed after a relatively large space is opened up is a consequence of the following mechanisms. "Opportunist" species with broad dispersal powers and rapid growth to maturity usually arrive first and occupy empty space. These species cannot invade and grow in the presence of adults of their own or other species. Several alternative mechanisms may then determine

which species replace these early occupants. Three models of such mechanisms have been proposed.

The first "facilitation" model suggests that the entry and growth of the later species is dependent upon the earlier species "preparing the ground"; only after this can later species colonize. Evidence in support of this model applies mainly to certain primary successions and in heterotrophic succession.

A second "tolerance" model suggests that a predictable sequence is produced by the existence of species that have evolved different strategies for exploiting resources. Later species will be those able to tolerate lower levels of resources than earlier ones. Thus they can invade and grow to maturity in the presence of those that preceded them. At present there exists little evidence in support of this model.

A third "inhibition" model suggests that all species resist invasions of competitors. The first occupants preempt the space and will continue to exclude or inhibit later colonists until the former die or are damaged, thus releasing resources. Only then can later colonists reach maturity. A considerable body of evidence exists in support of this model.

In the majority of natural communities succession is frequently interrupted by major disturbances, such as fires, storms, insect plagues, etc., starting the process all over again. However, if not interrupted, it eventually reaches a stage in which further change is on a small scale as individuals die and are replaced. The pattern of these changes will depend upon whether individuals are more likely to be replaced by a member of their own or another species. If the former, stability will be assured. However, in terrestrial communities, conditions in the soil in the immediate vicinity of long-lived plants may become modified in such a way that offspring of the same species are much less favored than those of other species. A likely cause is the buildup of host-specific pathogenic soil organisms near a long-lived plant. In this case, the species at each local site keep changing, producing local instability. Whether the average species composition of the whole tract does not change, exhibiting global stability, or whether it keeps changing has not yet been decided for any natural community.

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