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THE MAINTENANCE OF SPECIES DIVERSITY BY DISTURBANCE

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ABSTRACT

Hypotheses that relate disturbance to the production and maintenance of species diversity are reviewed. The hypotheses have been classified traditionally by the effect of the disturbance on the community: those that involve selective mortality, which maintains the species diversity of a community in equilibrium, and those that invoke events causing random, localized, mass mortality, which prevent the community from reaching an equilibrium. Regardless of this difference, most hypotheses predict that the greatest number of species will occur at intermediate levels of disturbance.

We develop graphical models for equilibrium and nonequilibrium situations, which we show to differ only in respect to temporal and spatial scale. We maintain that the usual outcome—the greatest number of species at intermediate levels of disturbance—can be explained by assuming that there are trade-offs in species-specific abilities that place constraints on immigration to, and extinction in, patches. Changes in immigration and extinction, the processes that govern patch diversity, depend on species-specific abilities to fend off competitors or to endure disturbances. Members of a species can resist competitors or resist disturbance, but they cannot excel at both. If this trade-off does not exist, then the highest level of species diversity will not occur at intermediate levels of disturbance. Furthermore, we show that if this assumption is relaxed or if interactions between the frequency and magnitude of disturbances are considered, other unexpected outcomes are possible.

INTRODUCTION

BIOLOGISTS have long been fascinated by the diversity of plants and animals within natural communities. Many have com-

mented on the astounding species richness of tropical forests, coral reefs, and planktonic and benthic communities (Hutchinson, 1961; Grasse and Sanders, 1973; Connell, 1978; Hubbell, 1979). Close examination has also revealed considerable diversity in seemingly species-sparse communities such as mussel beds (Suchanek, 1979) and coniferous forests (Peet, 1978). Past efforts have focused on quantifying the

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numbers of species and their relative abundance in communities and on determining causes of temporal and spatial variation in these quantities within and among communities. On the one hand, to explain changes in diversity that have occurred over geological or evolutionary time spans, scientists from a wide range of disciplines have invoked speciation, macroevolution, and large-scale disturbances, such as continental shifts and island formation (e.g., Crepet, 1984; Valentine, 1985). On the other hand, ecologists have described changes in diversity that occur in "ecological time," that is, within the context of current processes (e.g., Connell, 1978).

Variation in the diversity of species over ecological time scales presents a puzzle for modern ecologists. The dogma that diversity is regulated by competition between species has become central to ecology (see Schoener, 1982, and Jackson, 1981, for comments on this idea). It originated in the early theoretical work of Volterra (1928), who concluded that species utilizing resources in an identical fashion are unlikely to stably coexist. The experimental studies of Gause (1934) reinforced this idea, showing that two species do not coexist, at least not in a simple system, on the same limiting resource. The work of Gause and others gave rise to what has become known as the competitive exclusion principle (Hardin, 1960). Although recent studies have shown that competitive exclusion arises from the restrictive assumptions of the Lotka-Volterra competition model (Armstrong and McGehee, 1980), variation in species richness within an ecological time scale is still most often seen as a problem requiring a special explanation involving processes that dampen the effects of competition.

Disturbance and predation are usually considered the main mechanisms underlying the maintenance of species diversity in the face of strong competitive interactions (but see Hay, 1985, 1986). Many explanations of how disturbance operates have been advanced (see Pickett and White, 1985), but most hypotheses fall into two general classes: those involving selective mortality and those that invoke events that are sometimes catastrophic, causing random, localized, mass mortality. Predation is often evoked as the chief mechanism causing selective mortality. Predation promotes diversity

among competing prey species when predators most strongly affect the superior competitor (predator-mediated coexistence). The cause of selective mortality need not necessarily be predation, however; anything causing a disproportionate share of deaths among individuals of species with superior competitive ability will have the same effect whether it is predation or some other factor, such as disease. This is the *compensatory mortality hypothesis* of Connell (1978), who sees it as an equilibrium model in which the ability of one species to displace another is counterbalanced by deaths owing to causes other than competition.

Diversity hypotheses that invoke catastrophic mortality, on the other hand, view such events as preventing the ecosystem reaching an equilibrium. Mass mortality eliminates all or most of the species from an area and opens that area to recolonization. Thus the competitive exclusion of species is delayed or never occurs because some fraction of the ecosystem is routinely set back by catastrophes. Diversity is the result of a balance between the frequency of disturbances that provide opportunities for species to recolonize, and the rate of competitive exclusion, which sets the pace of species extinctions within patches. The most successful of the hypotheses linking localized, catastrophic mortality to the maintenance of species diversity is the *intermediate disturbance hypothesis*, so named because it predicts that the highest diversity will be at intermediate levels of disturbance. If the disturbance is too mild or too rare, then patches will approach equilibrium and be dominated by a few species that are able to outcompete all others. If the disturbance is too harsh or too common, then only a few species that are resistant to the disruption will persist.

In general, there has been an effort to link selective mortality with equilibrium hypotheses and catastrophic events with nonequilibrium hypotheses. While, at first glance, the distinction between equilibrium and nonequilibrium phenomena seems straightforward, there is some confusion over the classification of selective versus random processes. Connell (1978) makes the distinction on the basis of changes in species composition. Nonequilibrium hypotheses assume species composition to be rarely at equilibrium; high diversity is maintained only when composition is continually changing. Besides the intermedi-

ate disturbance hypothesis, Connell lists the *equal chance hypothesis* (Sale, 1977; Hubbell, 1979) and the *gradual change hypothesis* (Hutchinson, 1961) in this category. The equal chance hypothesis assumes that the colonizing abilities of species are very similar and individuals are only killed by a disturbance. Species composition then depends on a scramble for resources after a disturbance in which all the propagules of a species have an equal chance. Hubbell (1979, 1980) considers the equal chance hypothesis to be a special kind of scramble in which a species' success — that is, its ability to reproduce and invade — is proportional to its abundance before the disturbance. The gradual change hypothesis differs from the intermediate disturbance hypothesis only in degree: gradual changes, rather than catastrophic events, prevent competitive exclusion. Under Connell's grouping, equilibrium hypotheses are those that assume species composition is usually at equilibrium and unchanging. Of the three hypotheses Connell lists in this category — *niche diversification*, *circular networks* and *compensatory mortality* — only the compensatory mortality hypothesis assumes the action of a disturbing agent, such as predation. Grassle and Sanders (1973: 651) make a similar but not identical distinction between "short-term, nonequilibrium, or transient high diversity [which is] induced by unpredictable physical or biological perturbations or stress resulting in biological 'undersaturation' of the environment," and "long-term, equilibrium, or evolutionary high diversity [which is] a product of past biological interactions in physically stable, benign and predictable environments." Grassle and Sanders stress that these are not simple alternatives.

In this review, we examine some equilibrium and nonequilibrium hypotheses that relate disturbance to the production and maintenance of species diversity over ecological time. Ecologists have consistently set up these two classes of hypotheses as opposites even though both predict the greatest number of species at intermediate levels of disturbance (but see Caswell, 1978). In reviewing these explanations, we will show that equilibrium and nonequilibrium in disturbance-diversity models are aspects of a single phenomenon. The lack of agreement among explanations arises from differences in scale, from inconsistent terminology

and, most importantly, from the difficulties of differentiating causes from effects.

The central question is: Why do both equilibrium and nonequilibrium hypotheses predict the highest diversity to be at intermediate levels of disturbance or predation? We believe that compensation is the key and that all explanations depend on a trade-off in species-specific abilities. Members of a species can resist competitors or resist disturbance but cannot excel at both. If the assumption of this trade-off is not met, then all models fail to show the highest level of diversity at intermediate disturbance. Furthermore, we will show that if the assumption of trade-offs is relaxed other, unexpected, outcomes are possible.

We will first develop graphical approaches to both equilibrium and nonequilibrium models, and then show how the two types of models differ only by the choice of scale. We will also show how different sorts of outcomes depend on biases in what we mean by harsh versus mild disturbances. Our backgrounds have led us to emphasize examples from the studies of intertidal seashores and of terrestrial plant communities. We have made no attempt to provide a complete review of the studies treating the effects of disturbance on diversity; we refer the reader to sources in Pickett and White's book (1985).

DEFINITIONS

There is not a consistent set of terms and definitions in the literature of ecological disturbance. Disturbance is widely agreed to be "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985: 7); these events include such things as the presence of dead bodies and feces, which are not commonly thought of as disturbances (Grassle and Sanders, 1973). However, terms like *severity*, *frequency* and *intensity* are often used to describe these *relatively discrete* events without any explicit definitions. Some of the confusion in the literature is the result of this state of affairs and, before we begin, it seems prudent to provide definitions. For the most part we have followed the terminology given by White and Pickett (1985, their Table 1).

Size, *area*, *magnitude*, and *patch* are often used

TABLE 1

Examples of multiplicative, damped and enhanced effects of disturbance frequency and size on species number

Either species C or Z can exclude species E in the damped case, but C or Z are required for the persistence of B in the enhanced case.

Size of Disturbance	Multiplicative Disturbance Frequency			Damped Disturbance Frequency			Enhanced Disturbance Frequency		
	Rare	Common		Rare	Common		Rare	Common	
Small	ABC	AB	A	ABC	AB	A	ABC	AB	A
	XYZ	XYZ	XYZ	XYZ	XYZ	XYZ	XYZ	XYZ	XYZ
Large	ABC	AB	A	ABC	AB	A	ABC	A	A
	XY	XY	XY	XY	XYE	XYE	XY	XY	XY
	ABC	AB	A	ABC	AB	A	ABC	A	A
	X	X	X	X	XE	XE	X	X	X

interchangeably to refer to the total area disrupted by a disturbance or by predation. We will use only the term *size* for this meaning. Following Miller's (1982) convention, we define *disturbance size as the amount of area disrupted per disturbance event*. This is independent of the number of individuals, since a single small disturbance may kill one or many individuals or, in a clonal organism, destroy only part of an individual. Our simple notion of size does not distinguish the ways in which an area may be disrupted. A fire and a hailstorm sweeping across ten hectares have the same size, even though their effects are clearly different. Hubbell (1979) equates size with the number of individuals killed, but this ignores sublethal effects. One solution is to define *size* as the amount of resource that is renewed by the disturbance event (Paine and Levin, 1981). This works best in systems for which space is the most crucial resource, where the size of disturbance is the amount of space cleared of previous occupants.

Even if one accepts the definition of disturbance size as the amount of renewed resource, this only pushes the problem to another level. Organisms require many different resources, and different types of disturbance do not have the same effect on the renewal of each resource. To the extent that we cannot define a common currency among species and resources, it is difficult to imagine how the sizes of different types of disturbances can be equated. This appears to us to be an open question, and we believe that approaches like that of Armstrong (unpubl.), who defines disturbance size as the

proportion of propagules that originate locally, should be explored further.

We take a *patch* to be a *contiguous area in which the effect of a disturbance is uniform and the subsequent dynamics are similar*. By this definition, which is similar to Whittaker and Levin's (1977), an area in which different contiguous sections have been affected by one disturbance is not a single patch. Each uniform section is a patch, and the total area affected by the disturbance (i.e., the size of the disturbance) is a collection of different patches. Yet, this definition is not without problems. Single, large individuals such as adult trees can occupy many small patches that differ in many ways — for example, nutrient availability and dynamics. This definition, however, removes the confusion of equating the area affected by a disturbance event to the patch itself.

The sampled area — the plot under observation — may be larger or smaller than the area disrupted by a disturbance. Predation may create small patches within a sampled area; catastrophic events usually cover areas much larger than sampling plots. Thus the sampled area may be either totally contained within a single patch or composed of many patches.

The patch affected by a disturbance and the area sampled may be open or closed to immigration (Caswell, 1978). Open systems have an input of species from outside; the availability of these species is not controlled by the species composition within the patch. Closed systems have no such input, and the changes in species composition are entirely determined by the dynamics within the patch. Equilibrium

systems are often seen as closed, nonequilibrium as open; for example, this is implicit in Connell's (1978) classification of hypotheses explaining diversity. We will follow Caswell's (1978) convention and will not link our usage of open and closed to the notions of equilibrium and nonequilibrium.

The *frequency of a disturbance* is the number of events per unit of time. The *frequency*, then, is the *unweighted rate of a disturbance*. This is a source of confusion in the literature, since the term *rate* has been used to mean the area disturbed per unit of time rather than simply the number of events per unit of time (Miller, 1982). For the total area disturbed per unit of time we will use the term *intensity* or overall intensity. We define *disturbance intensity* as the *weighted rate of disturbance*—i.e., *disturbance size (area per event) times frequency (events per unit of time)*. By defining intensity as size times frequency, we avoid some problems but create others. We are assuming that all disturbances within any particular system under observation, regardless of intensity, cause the same level of damage per unit area per unit time—that is, they are equally severe. Our definition does encompass sublethal effects, but only if they are of similar severity among disturbances.

Species diversity is often measured by an index that is a function of both the number of species and their relative proportions, but most models have focused on the number of species. We will consider *diversity* to be the *number of species within a patch or a sampled area regardless of their relative abundances*. Our diversity, applied to a patch, is identical to Osman and Whitlatch's (1978) definition of alpha diversity. Since the number of species is partly a function of the area sampled, geographic region, and taxonomic group, we will assume in our comparisons that we are dealing with species in sampled areas of the same size and within the same region and taxonomic group. We will use the terms *species number*, *diversity* and *richness* interchangeably.

Finally, we believe compensatory mechanisms underlie most of the disturbance-generated phenomena that have been described and so the meaning of compensation must be made clear. *Compensation* refers to the *assumed trade-off between competitive ability and resistance to disturbance or predation*. According to this assumption, competitive superiority counter-

balances, or compensates for, susceptibility to disturbance or predation. We will use the term *competitively dominant species* for species that show these characteristics. Likewise, competitively inferior species are more resistant to disturbance and predation or can recover more quickly after a disturbance. Viewed at the community level, compensation refers to disproportionality in the effects of disturbance or predation on different species. These effects fall most heavily on species that are good competitors; their increased mortality in disturbed situations is coupled with the improved survival and recruitment of other species that are resistant to disturbance.

EQUILIBRIUM MODELS

Equilibrium models describe the effects of disturbance or predation on a community when these processes are balanced against the effects of colonization and competition. The system is seen to be in a steady state—that is, the rates of all processes are fast enough to appear continuous in the time interval over which observations are made. In this situation the area sampled is much larger than the area affected by the largest possible disturbance.

In the simplest case, the sampled area is assumed to be composed of a large, but fixed, number of available positions, and each position can be either empty or occupied by one individual. The dynamics can then be expressed simply as the rates at which species are recruited or eliminated. Now imagine that the sampled area is continually colonized by new species from a large pool of potential recruits from outside, such as planktonic larvae or seeds. The pool of recruits is controlled by regional processes and this situation is known as gamma diversity (Whittaker, 1960; Osman and Whitlatch, 1978). Now let species be eliminated by competition among individuals of the species present in the community. The model is, in essence, identical to Greene and Schoener's model (1982), although they were concerned with successional changes (i.e., with transient states) while we are addressing the number of species present at equilibrium.

The dynamics of the system can be most clearly understood if it is modeled as a pure birth-and-death process (Feller, 1957). This is the approach used by MacArthur and Wilson in their formulation of the processes control-

ling species richness on islands (MacArthur and Wilson, 1967). Following Feller, let us assume that we look at changes over a small number of time units, h , so small that only one species can be gained or lost. Suppose there are S species present. Let the probability that the system changes from S to $S + 1$ species in one time unit be λ_S and the probability that the system goes from S to $S - 1$ species be μ_S . If we assume that the probability of more than one change occurring during the time interval is very small, then $P_S(t + h)$, the probability of finding the system with S species at time $t + h$, is

$$P_S(t + h) = P_S(t)[1 - \lambda_S h - \mu_S h] + \lambda_{S-1} h P_{S-1}(t) + \mu_{S+1} h P_{S+1}(t). \tag{1}$$

This is identical to Feller's formula for a pure birth and death process (1957, his equation 5.1, p. 454) and MacArthur and Wilson's formula for immigration and extinction of species (1967, their equation 3-3, p. 33). MacArthur and Wilson called λ_S and μ_S rates of immigration and extinction, but to avoid confusion we will call them probabilities (Parzen, 1962, calls λ_S and μ_S intensities of transition). The probability of immigration and extinction can be functions of the number of species present and are measures of changes within the sampling area; for example, immigrants must be viewed as arrivals into the sampling area, not as the number of potential recruits that are available outside the sampling area.

The changes in the system can be diagrammed as a compartment model plotted over time and species number (Fig. 1). As the system moves through time, the empty positions within the sampling area fill up and filled positions may be emptied by extinction. The tally of species present is not the same as the number of filled positions; the model therefore documents only the addition and loss of new species. The model allows only one species to arrive in any one time interval, but that single species may colonize many positions. Conversely, an established species may occupy many positions within the sampling area, yet it may go extinct only if removed from every position. Whether a system is defined as open or closed depends on what we define as inside and outside of the sampling area and thus is arbitrary; however, a system is closed when λ_S

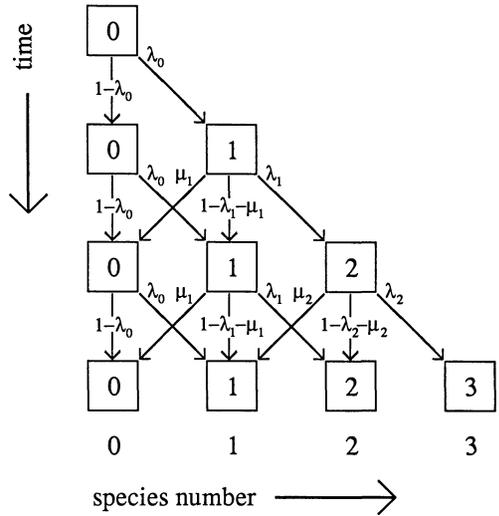


FIG. 1. COMPARTMENT MODEL OF THE CHANGES IN SPECIES NUMBER OVER TIME

The number of species (S) is given within the boxes and the changes over time are defined by λ_S and μ_S , the probabilities of immigration and extinction.

is zero and is open when λ_S is greater than zero.

Now suppose that the probability of immigration is a function of species number and decreases as species number increases (Fig. 2A). Although a linear decline is a simplification, the decline, regardless of its shape, may occur for two reasons. First, even if all species have the same probability of immigrating, λ_S is the probability of a new arrival—that is, the probability of a single arrival times the probability that that arrival represents a new species. Until extinction becomes important, the probability that an arrival does represent a new species will decline as the number of potential new species in the pool available for immigration declines by one with each arrival of a new species; thus the probability of immigration will decline as S , the number of species, present increases.

The probability of immigration may also decrease with increasing species number owing to inhibition by species already present. If each species present can inhibit colonization by several other species, then the probability of immigration will fall as the number of species within the patch increases, as long as each species does not inhibit the same set of potential

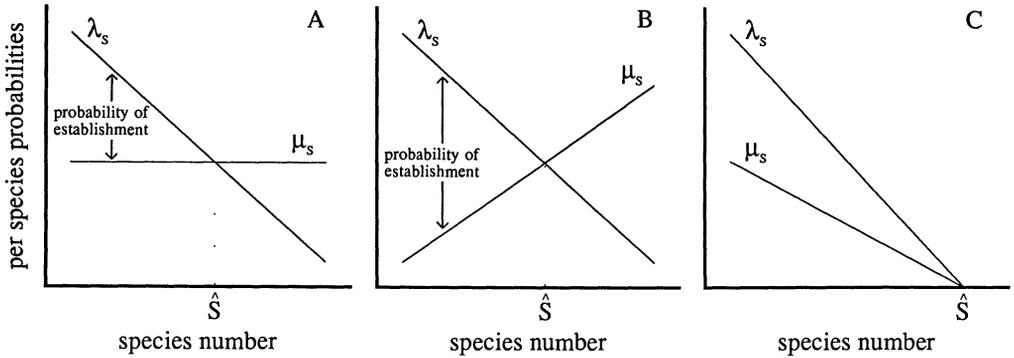


FIG. 2. THE SPECIES NUMBER AT EQUILIBRIUM (\hat{S}) AS DETERMINED BY THE PROBABILITIES OF IMMIGRATION AND EXTINCTION

The probability of establishment of a new species is the difference between the probabilities of immigration and extinction, and the system is at equilibrium where these curves cross. Examples A and B are open systems; C is a closed system. Both extinction and immigration are dependent on species number in examples B and C but not A.

recruits. There is evidence that established species may enhance colonization by others (e.g., Kitching, 1937; Bayne, 1964; Seed, 1969; Dayton, 1971; Reiners, Worley, and Lawrence, 1971; Menge, 1976; Osman and Haughness, 1981; Smedes and Hurd, 1981; Lubchenco, 1983; St. Clair, Webb, Johansen, and Nebeker, 1984; Petraitis, 1987). If the number of species inhibited is greater than the number facilitated, however, an overall decline will occur.

Now assume that, owing to competitive interactions, the probability of extinction is a function of species number (Fig. 2B). This assumes that more species being present translates into more competitive interactions taking place and into a higher potential for extinction. Models that assume overgrowth by individuals in adjoining positions will give this pattern; evidence for overgrowth of patches by neighbors comes mainly from coral reefs (Karlson and Jackson, 1981), forests (Trimble and Tryon, 1966; Hibbs, 1982; Runkle, 1982) and grasslands (Rapp and Rabinowitz, 1985).

The net probability of establishment of species within a community is the difference between the immigration and extinction curves. The number of species within the community will reach an equilibrium when immigration and extinction are matched. This is the equilibrium species number, \hat{S} , in an undisturbed community (Fig. 2). Hubbell (1979, 1980) calls this balance a stochastic equilibrium when both

rates are greater than zero (as in Figs. 2A and 2B). Note that the probability of either immigration or extinction being independent of species number leads to the net probability of establishment declining with increasing species number.

In equilibrium models, disturbances must be viewed as occurring on the same scale as the processes of immigration and extinction. Small, frequent disturbances may be either biotic (predation or herbivory) or abiotic (e.g., physical stress). Our usage of the word "disturbance" encompasses all types. For the moment, assume that disturbance, by altering rates of mortality, affects all species in the same way and is independent of the number of species. Under these assumptions, any increase in the intensity of disturbance will always increase μ_s and thus decrease the equilibrium species number (Fig. 3).

For the equilibrium species number to follow the increasing phase of the familiar humped curve predicted by the compensatory mortality hypothesis, moderate-intensity disturbance must result in a feedback that leads to either smaller μ_s or larger λ_s relative to low-intensity disturbance. Competitively dominant species, in fact, may play a role in both processes, since they can normally inhibit the colonization of a patch by a large, untapped pool of species (keeping λ_s small) or quickly eliminate species established after disturbance (by keeping μ_s

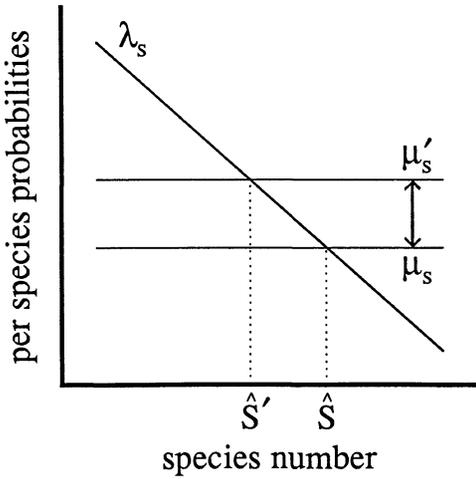


FIG. 3. A SMALLER NUMBER OF SPECIES EXISTS AT EQUILIBRIUM AT S' THAN AT S OWING TO A HIGHER PROBABILITY OF EXTINCTION AT μ'_s THAN AT μ_s .

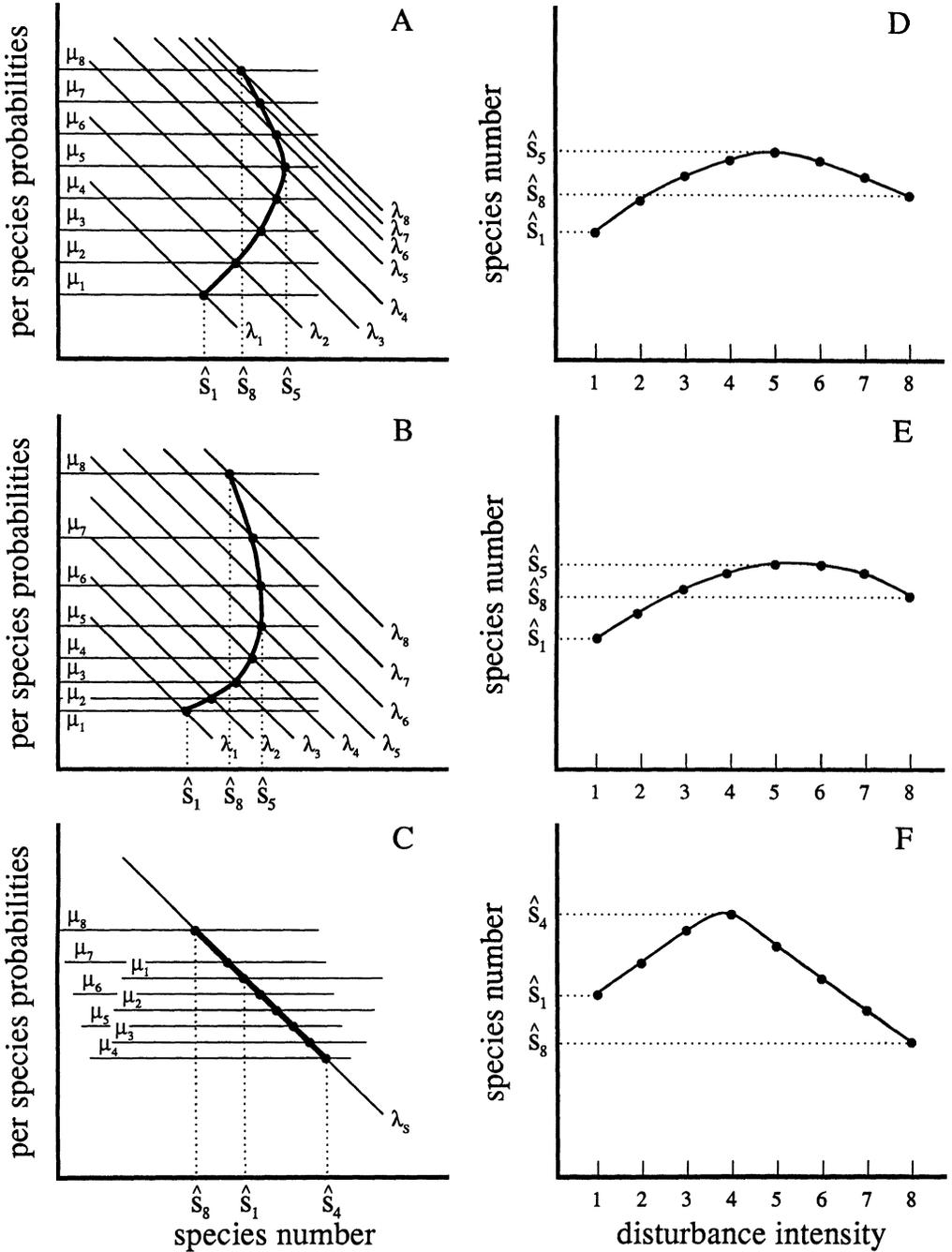
large). If disturbance is intense enough to keep individuals of a competitively dominant species out of a patch, the competitive effects among the individuals in the patch may be less and the recruitment greater than in a patch where the competitive dominant species is present. The result is a difference in both λ_s and μ_s between patches with different disturbance intensities. This is what Connell (1978) has termed compensation—the adverse effect of disturbance on competitively dominant species out of proportion to their numbers. There must be an upper limit to compensation for two reasons: (1) the pool of potential recruits is finite, meaning fewer and fewer new species will be available to recruit as species number increases; (2) disturbance increases μ_s and, if severe enough, would kill off all species.

Under this scheme, the slope of the curve describing the equilibrium species number is positive at low intensities of disturbance—but only if there is a compensatory effect—and is negative at higher intensities of disturbance because of mortality induced by disturbance itself (Fig. 4). In the increasing phase, μ_s must

decrease or λ_s must increase as a result of the release of competitive forces that offset local extinction induced by the disturbance. Moving to higher and higher disturbance intensities must be coupled with either smaller shifts in λ_s (Fig. 4A), larger shifts in μ_s (Fig. 4B), or a “bottoming out” followed by an increase in μ_s (Fig. 4C). Thus the equilibrium species number is smaller at low and high disturbance intensities than at intermediate intensities (Figs. 4D, 4E, and 4F).

Other outcomes are possible and depend on the patterns of the λ_s and μ_s curves. In general, small shifts from a lower to a higher disturbance intensity cannot compensate for higher local extinction resulting from the disturbance, but larger shifts can do so. The patterns of the λ_s and μ_s curves thus affect the shape of the species number curve. For example, if there is little or no difference between low disturbance intensities in their effect on species number, but higher intensities are coupled with larger differences in either λ_s (Fig. 5A) or μ_s , a reversed curve would occur. This could happen if a competitively dominant species was moderately resistant to disturbance. As the level of disturbance moves from low to moderate levels of disturbance, the competitively dominant species is not eliminated; the equilibrium species number decreases since other species would be absent at larger μ_s whereas the competitive dominant would remain as a bottleneck to new recruitment. At higher intensities of disturbance the competitively dominant species also would be absent; the community would be open to recruitment and establishment of a different suite of species (i.e., λ_s would be larger). At still higher intensities of disturbance, there would be still fewer competitively dominant species and more colonizing species. The pattern, to this point, would be the reverse of what is predicted by the intermediate disturbance hypothesis. Moving to higher and higher disturbance intensities, the pool of available recruits would be diminished, local extinction caused by disturbance would no longer be matched by compensatory changes in λ_s , and

FIG. 4. THE COMPENSATORY MORTALITY HYPOTHESIS SHOWN AS DIFFERENCES IN EQUILIBRIUM SPECIES NUMBER (THICK LINES) BETWEEN DISTURBANCE REGIMES OF DIFFERENT INTENSITIES, DRIVEN BY COMPENSATORY DIFFERENCES IN THE PROBABILITIES OF EXTINCTION AND IMMIGRATION. In A and D, the higher species number at S_2 than at S_1 occurs through a compensatory decrease in immigration moving from λ_1 to λ_2 that offsets the effects of increasing extinction from μ_1 to μ_2 . Immigra-



tion cannot offset losses caused by higher extinction at higher disturbance intensities because the pool of recruiting species is finite. In B and E, a similar pattern is produced where higher disturbance intensities are coupled with disproportionately higher extinction. C and F also show the humped species number curve without differences in the per species probability of immigration between disturbance intensities. Moving from lower to higher disturbance intensities, μ_s decreases as mild disturbance removes competitive dominants, allowing higher immigration; μ_s then increases where local extinction caused by disturbance itself is too high to be compensated by the competitive release of immigration.

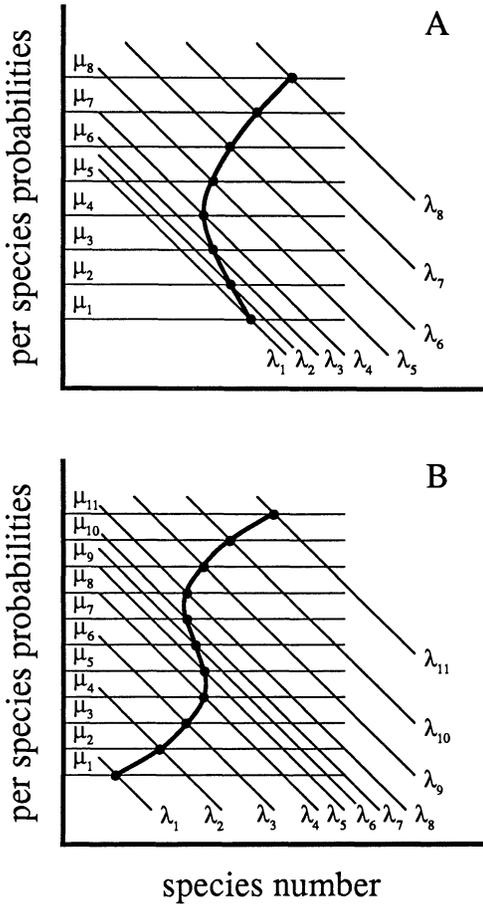


FIG. 5. ALTERNATIVE PATTERNS OF DIFFERENCES IN SPECIES NUMBER WITH DIFFERENT DISTURBANCE INTENSITIES

A shows a case where the differences in immigration increase from low to high intensity disturbance regimes; the result is a reversed pattern in species number with the lowest diversity at intermediate intensities of disturbance. B shows a complex pattern in which species number rises, declines and rises again moving from low to high intensity disturbance.

the result would be a declining number of species at equilibrium.

This pattern hinges on a community consisting of a set of species that are moderately resistant to disturbance and that can inhibit the establishment of new species. Lubchenco and Menge (1978, their Table 9) point out that the mussel *Mytilus edulis*, the alga *Chondrus crispus*,

and the barnacle *Semibalanus balanoides* in the rocky intertidal of New England all show some of these attributes.

It should be clear that a curve with multiple peaks is also possible if there were mutually exclusive sets of species with differing abilities to resist disturbance and to recruit successfully into the community (Fig. 5B). For example, in some parts of central and southeastern North America, either grasses (and scattered pines) or broadleafed forest may occupy sites of intermediate soil moisture (Bragg and Hulbert, 1976; Platt, Evans, and Rathbun, 1988). Certain grasses and pines have highly flammable litter that tends to burn frequently with low-temperature fires of short duration, killing forest species but not harming prairie or savanna species that display numerous adaptations such as post-fire crown sprouting and fire stimulated seed germination. Forest vegetation may become established on areas with sufficient moisture if fire frequency declines below some threshold. The presence of the forest vegetation itself may then keep fire frequency low because its litter is shaded and densely packed and thus retains moisture (Streng and Harcombe, 1982).

Our model rests on the balance between the probabilities of immigration and extinction. As such, the system is open to new arrivals replacing species that go extinct. This equilibrium differs from the common-sense notions of how predator-mediated coexistence and compensatory mortality maintain diversity, although we believe both these processes are special cases of our model. Compensatory mortality is concerned with the effects of disturbance in easing extinction, although from our presentation it should be clear that compensation can occur by means of either mortality (μ_S) or recruitment (λ_S). In considering predator-mediated coexistence, it is assumed that predation promotes an increase in diversity by reducing competitive interactions among prey species without driving them to extinction. The probability of extinction is zero and, in order for the system to be in equilibrium, the probability of immigration must match that of extinction and also be zero. The number of species at equilibrium is thus the special case where the probabilities of immigration and extinction are not only matched but also equal zero (see Fig. 2C).

Like disturbance, predation also may increase the probability of immigration by reducing the preemption of space by common species. Both processes, however, involve compensation. Predation on some species is offset by improved survival and recruitment of others.

NONEQUILIBRIUM MODELS

In nonequilibrium models, the system is repeatedly set back so that an equilibrium is never achieved. The process is usually conceptualized as changes in immigration and extinction rates over time, but within a patch in which a disturbance has simultaneously set back the whole patch and, in the most extreme case, all individuals within a patch have been killed. Because the dynamics within the patch are of interest, the area sampled is either equal to or less than the area affected by the smallest disturbance. While the situation within the sampled area can be described in the same way as the equilibrium case—that is, as a number of positions that are either occupied or empty—the processes of interest are the rates of immigration and extinction over the whole area sampled. The dynamics are controlled by three rates. The first two are the rate of immigration, $I(t)$, which is the number of arrivals of new species per unit of time per sampled area; and the rate of extinction, $E(t)$, which is the number of extinctions per unit of time per sampled area (these rates are not simple multiples of the probabilities of immigration and extinction, which are the probabilities of arrival or extinction of a single species per species present). The third rate is the frequency of disturbance, or how often the system is set back to initial conditions. Disturbance in this model is seen as a relatively infrequent and catastrophic event, but it is still expressed as a rate—the number of events per unit of time per sampled area.

The rates of immigration and extinction change as a newly disturbed patch ages, and these rates determine the number of species. Immigration declines and extinction rises as the patch fills up with individuals of different species and the species composition changes. In the absence of further disturbance, the number of species depends on the age of the patch and is the summation over time of the difference between the rates of immigration and extinction. In integral form this is

$$S(t) = \int_0^t \{I(t) - E(t)\} dt. \quad (2)$$

Without disturbance intervening, there are two distinctly different outcomes that depend on changes in the rate of extinction. First, the number of species may increase to a point and then remain constant. At that point, the rate of extinction matches the rate of immigration, and every extinction is balanced by the immigration of a new species. This implies that the area or resource freed by an extinction is not completely filled or used by individuals, either immigrants or locally produced offspring, of a species already present. The number of species reaches an equilibrium, although the species composition is constantly shifting (see Figs. 6A and 6D). The rates of immigration and extinction can be zero, in which case the species composition would be fixed (Figs. 6B and 6E). But recall that the rate of immigration is the number of *new* species entering the system. Openings within the area sampled which, in this case, occur without the extinction of a species, could be filled either by new species or by species already present. If the openings are quickly filled by individuals of species already present (regardless of the origin of the propagules) then the area would appear to be closed to immigration and the species in the sampled area would be at competitive coexistence.

Alternatively, the number of species may rise and then drop as the patch ages (Figs. 6C and 6F). In this case, the rate of extinction must overshoot the rate of immigration. From this time on, any positions within the sampled area opened by an extinction are filled by propagules of a species already present, and thus the number of species drops. At some point the rates of immigration and extinction are matched, and the number of species remains constant thereafter.

Disturbance may wipe out all individuals in a patch, as often happens in marine systems, or it may strike mainly at one or a few dominant individuals, as in a forest treefall. In either case, disturbance resets the system to an earlier state and the patch is no longer in equilibrium. If we now assume that disturbances occur randomly and at a lower rate than immigration and extinction, then the species com-

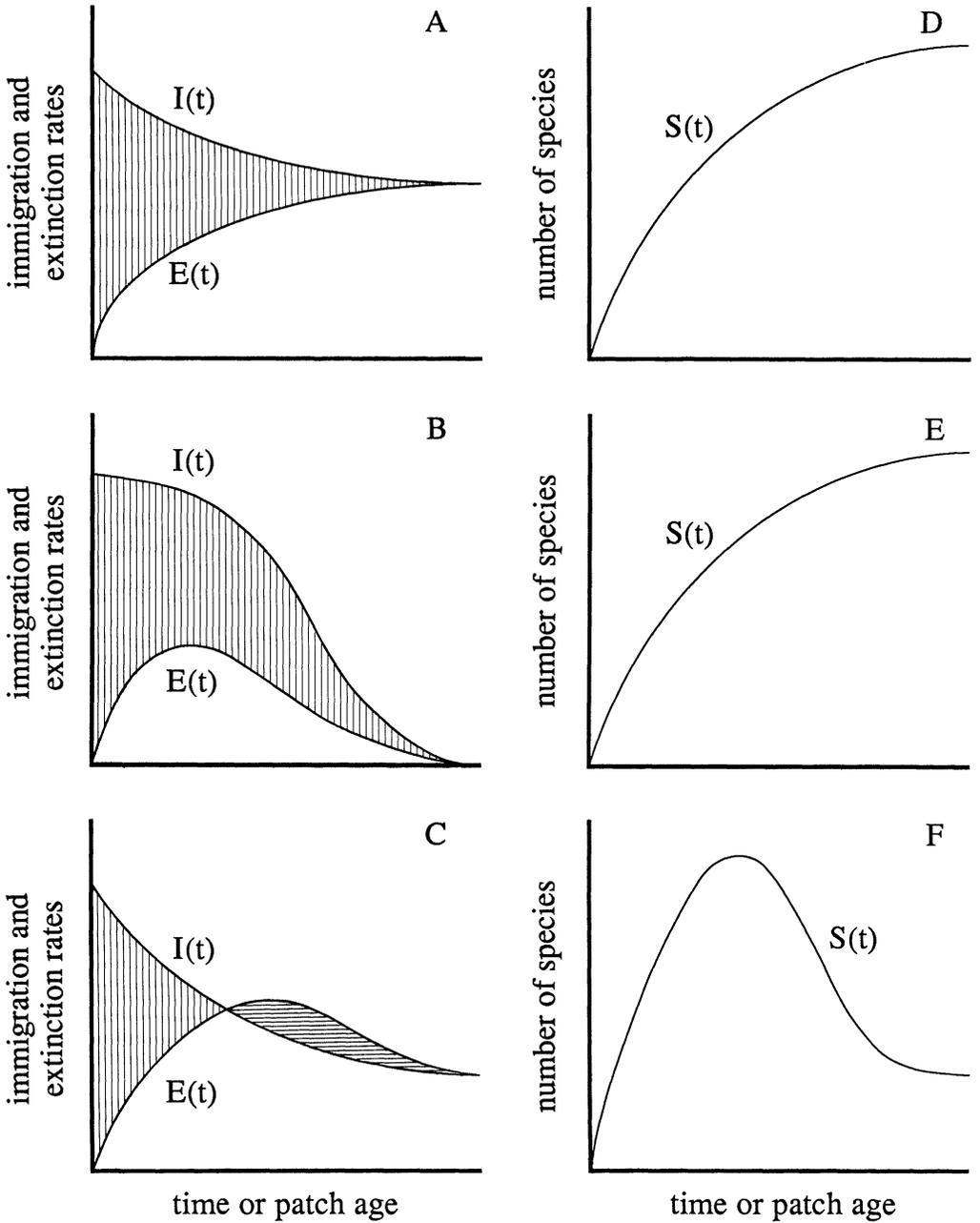


FIG. 6. TEMPORAL CHANGES IN RATES OF IMMIGRATION AND EXTINCTION AND THEIR EFFECTS ON SPECIES NUMBER

The number of species is the integral of the difference between the rates of immigration and extinction [see Equation (2)]. The abscissa, *time*, gives not only the age of the patch but also the time between disturbance events, with frequent disturbances keeping patches relatively young. D, E and F are plots of the number of species represented by the shaded areas in examples A, B and C, respectively. Where $E(t)$ is greater than $I(t)$, as in C, there is a decline in species number. When $E(t)$ and $I(t)$ are matched, the system is at equilibrium. A and C are open to immigration but B is not.

position of a patch is simply a reflection of the patch's age. If, on average, disturbances occur once every "t" time units, then we would expect patches to contain, on average, $S(t)$ species as defined by Equation (2).

Not all patches are necessarily the same age or of the same species composition. If we sample a number of patches, each of which has been randomly hit by a disturbance of the same size sometime in the past, then we should find a distribution of ages of patches. Even if disturbances do not alter immigration and extinction rates, the species richness of an area composed of many patches should be determined by the distribution of patch ages. Overall, a system of patches is constantly changing as new patches are created and older patches age; this is the "shifting mosaic" (Aubréville, 1938; Watt, 1947). Alternatively, there could be many small patches, each with only a few species (low within-patch or alpha diversity) but each with a different set of species (high between-patch or beta diversity). This has been called contemporaneous disequilibrium (Richerson, Armstrong, and Goldman, 1970).

The relationship of species number to disturbance frequency depends on the shapes of the immigration and extinction curves. When species number rises to an asymptote, as in Figs. 6D and 6E, higher disturbance frequencies will be coupled only with lower species numbers. The more frequent the disturbance, the younger the average age of patches and the fewer the species. In such situations, species richness is never greatest at intermediate levels of disturbance frequency. In contrast, if the within-patch extinction rate is sometimes greater than the immigration rate (as in Fig. 6C) it is then possible for a disturbance regime of moderate frequency to generate the highest levels of species richness across patches. In both cases, differences in disturbance frequency appear to generate differences in the rates of immigration and extinction. In fact, differences in disturbance frequency cause differences in the age distribution of patches and not in the rates directly.

Under the intermediate disturbance hypothesis, the rise and fall of species number across patches is seen as a consequence of temporal changes in the rates of immigration and extinction within patches (Figs. 6C and 6F). Species number across patches is higher in a very low

frequency disturbance regime than in an undisturbed area because even the rare disturbance event reduces the average age of patches. With rare disturbance, the last few extinctions never occur and the average number of species in patches is greater than with no disturbance. The average species number in patches continues to increase moving from lower to higher frequencies of disturbance (from right to left in Figs. 6C and 6F) to the point where the extinction and immigration curves cross. Species richness is maximum within a patch at this patch age. The average species richness in patches declines moving from this point to higher disturbance frequencies, where the average patch age is smaller.

This is the simplest scenario of the intermediate disturbance hypothesis as outlined by Connell (1978). The processes that drive the within-patch dynamics (immigration and extinction) are assumed to depend only on disturbance frequency and not on historical effects, for example, seasonal variation in immigration rates or spatial differences in nutrient availability. Our nomenclature does not exclude such effects since we define a patch as a homogeneous area. Whether such effects are included or not, in Connell's scenario the greatest richness of species occurs where disturbances are moderately frequent because of changes in the rates of immigration and extinction that are dependent on patch age.

We view the changes in the rates of immigration and extinction as compensatory because the decline in richness in older patches depends on extinction rates overshooting the early buildup of species that is due to immigration. The rise in extinction in middle-aged patches is due to the loss of early successional species that are good colonizers but poor competitors. If these species were prevented from entering the patch after a disturbance then initial immigration would be low and the patch would slowly fill with the few later successional species that were competitively dominant. Disturbance exacts the heaviest toll on later successional species which take the longest to recover, thus allowing early colonizers to persist. This is a compensatory effect because it hinges on a trade-off in the abilities of species. If the assumed trade-off did not exist or if early colonizers were prevented from entering, we would expect immigration to be lower initially and the extinc-

tion curve never to cross the immigration curve, as seen in Fig. 6C.

The distinction between young patches and old patches with the same species richness depends on which processes dominate the system. Young patches are dominated by immigration whereas older patches are dominated by extinction. Some benthic ecologists have emphasized "supply-side" communities as if they were distinct from systems dominated by such internal processes as predation and competition (Connell, 1985; Gaines and Roughgarden, 1985; Roughgarden, Iwasa, and Baxter, 1985; Gaines and Roughgarden, 1987). The distinction has also been tied to the notion of open and closed systems; supply-side systems are driven by immigration processes which are seen as entirely external. We feel it is more useful to realize that processes such as immigration, which is measured in terms of new arrivals, are controlled partly by local factors, such as predation and competition. We suspect that in different communities, and even in the same community but in patches of different ages, immigration and extinction differ in their importance.

EQUIVALENCE OF MODELS

Are equilibrium and nonequilibrium models two sides of the same coin? Clearly equilibrium models, such as compensatory mortality, focus on the steady-state condition, whereas nonequilibrium models, such as the intermediate disturbance hypothesis, emphasize the maintenance of transient states by disturbance. On the one hand, it is not difficult to imagine predation affecting patches in the same way as would a disturbance. Predation can be an infrequent but catastrophic event. On the other hand, it is not clear under what conditions small, frequent disturbances mimic the compensatory effects of predation. It seems reasonable to ask whether nonequilibrium models converge with equilibrium models when the disturbance is small and frequent and thus acts in a manner similar to predation.

At first glance nonequilibrium and equilibrium models appear to be quite different. Apparent differences have arisen because the processes have been examined on differing temporal and spatial scales. Ecologists who study disturbances covering areas larger than the sampling unit see a nonequilibrium world (see

Shugart and West, 1981, for a discussion of the relationship between equilibrium and the scale of disturbance). By contrast, predation is usually seen as a process operating on the same temporal and spatial scale as competition, and thus compensatory mortality is justly viewed as an equilibrium between opposing processes.

We believe that nonequilibrium and equilibrium models embody the same types of processes even though the spatial and temporal scales differ. Simple nonequilibrium models, in the absence of disturbance, do reach an equilibrium (see Fig. 6). At the very least it seems reasonable to ask: If patches are near equilibrium, do disturbances and predation affect the system in a similar fashion? (Addressing this question experimentally would not be easy since, in comparing systems influenced by disturbance with those influenced by predation, it would be vital to control for differences in the spatial extent of patches, in the kinds of sessile organisms present, and in the characteristics of the areas sampled.) The crucial question is: Under what assumptions can disturbance and predation be viewed as similar? Answering this question first involves showing the relationship of the rates of immigration and extinction, $I(t)$ and $E(t)$, to the probabilities of immigration and extinction, λ_s and μ_s , and then showing how events that alter the probabilities of immigration and extinction can be related to changes in the rates. Much of the following argument is identical to Feller's (1957) demonstration of the relationship between birth-and-death processes and Markov chains, and is similar to Diamond and May's (1977) derivation of species turnover rates.

We can begin by examining the definitions of $I(t)$ and $E(t)$, the rates of immigration and extinction, respectively, for a given area. In the nonequilibrium situation, what we observe is the change in species number from one census to the next. This is proportional to the difference between the two rates, $I(t) - E(t)$. Now if the expected numbers of species at two successive censuses, which are H time units apart, are $M(t)$ and $M(t + H)$, we can estimate the difference between $I(t)$ and $E(t)$ as

$$I(t) - E(t) = \frac{M(t+H) - M(t)}{H}. \quad (3)$$

The expected change in species number per time unit, $I(t) - E(t)$, is thus estimated from

the difference in species number over H time units. Note that we assume our sampling area to be completely within a homogeneous patch. Now if we let H approach zero, then

$$I(t) - E(t) = \frac{dM(t)}{dt}. \tag{4}$$

If the time interval is small enough, the instantaneous rate of change in species number, $dM(t)/dt$, is equal to the difference between immigration and extinction.

The expected number of species, $M(t)$, depends on the probability distribution of species numbers. If we assume the probability of finding exactly i species at time t is $P_i(t)$, then the expected number of species, $M(t)$, is

$$\sum_{i=0}^{\infty} iP_i(t).$$

We can rewrite the change in species number as

$$\frac{dM(t)}{dt} = \sum_{i=0}^{\infty} i \frac{dP_i(t)}{dt}. \tag{5}$$

The probabilities, $P_i(t)$, and their derivatives are functions of the probabilities of immigration and extinction. Equation (1) gives the probability of finding S species at time $t + h$, and its derivative is

$$\begin{aligned} \frac{dP_S(t)}{dt} &= (-\lambda_S - \mu_S)P_S(t) \\ &+ \lambda_{S-1}P_{S-1}(t) + \mu_{S+1}P_{S+1}(t) \end{aligned} \tag{6}$$

(Feller, 1957).

Substituting these derivatives into Equation (5), we find

$$I(t) - E(t) = \sum_{i=0}^{\infty} \lambda_i P_i(t) - \sum_{i=0}^{\infty} \mu_i P_i(t) \tag{7}$$

(note: $\mu_0 = 0$ by definition).

The rates of immigration and extinction, $I(t)$ and $E(t)$, are not simple multiples of the probabilities. Rather, the rates are averages of the probabilities of immigration and extinction which are weighted by the probability distribution of species number at time t (see MacArthur and Wilson, 1967: 33-34; and Feller, 1957: 456-457). Moreover, from Equation (6), it can be seen that the probability distribution is itself a function of the probabilities of immigration and extinction. As t increases and the system reaches equilibrium, the probability distribution becomes stationary (Feller, 1957)

and the rates of immigration and extinction are then constant (see Fig. 6).

How does a small disturbance affect this system? Suppose we are observing a patch of age a and we introduce a small disturbance that has the effect of setting the patch back so it appears to be younger, to age b (Fig. 7A). Also suppose that as soon as the interval $a - b$ elapses, we allow the disturbance to occur again. If the disturbance is small and frequent enough, it would appear as if there were a balance maintained by disturbance. The fact that for this example we have made the disturbance occur at regular intervals makes no difference. If the disturbance has no effect on the rates of immigration and extinction, $I(t)$ and $E(t)$, and if the patch is near equilibrium, we would see no change in the species number just as we would expect if disturbance acted like predation but caused no compensation.

For a small disturbance to act like predation in the equilibrium models the rates must be altered. Recall that predation alters the probabilities of immigration and extinction and thus also may alter $I(t)$ and $E(t)$, which are functions of these probabilities. Only if a small disturbance alters the probabilities of immigration and extinction will it have an effect indistinguishable from the compensatory effects of predation. If, like predation, our small recurring disturbance affects the probability of either immigration or extinction then it will alter the shape of the $I(t)$ and $E(t)$ curves (Fig. 7B). The alteration changes the area between the two curves—that is, it affects the species number in a manner similar to the compensatory effect of predation. Both predation and disturbance affect not only the number of species at equilibrium but also the time-dependent probability distributions, and thus the approach of the system to equilibrium.

To the degree that predation, disturbance and other factors modify the probabilities of immigration and extinction, we must view all as similar phenomena. In our original formulation of the effects of disturbance in nonequilibrium situations, we assumed disturbance had no effect on $I(t)$ and $E(t)$. Because disturbance is rarely a non-selective agent of mortality (see Discussion, below), it seems reasonable to assume that the probabilities of immigration and extinction will be altered. If this is the case then the division between equilibrium and

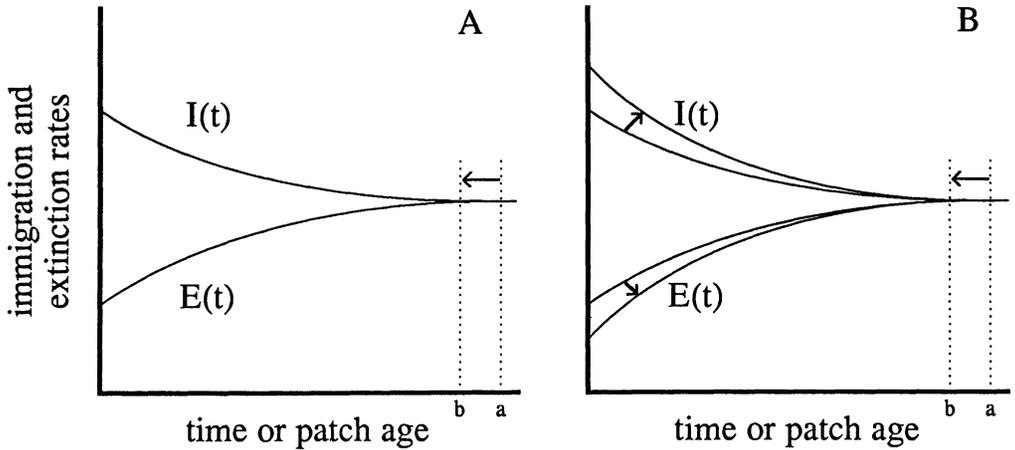


FIG. 7. THE EFFECTS OF DISTURBANCE, WHICH OCCURS AT REGULAR INTERVALS, ON THE NUMBER OF SPECIES.

In A, there is no change in species number when a disturbance that occurs with frequency $1/a$ is altered to a frequency of $1/b$. In B, the same change in disturbance frequency increases the number of species by altering the rates of immigration and extinction.

nonequilibrium models such as compensatory mortality and intermediate disturbance is simply a matter of convenience for ecologists who examine processes on different temporal and spatial scales.

INTERACTION OF DISTURBANCE FREQUENCY AND SIZE

The equivalence of equilibrium and non-equilibrium models raises the question whether changes in frequency and changes in size of disturbance have similar effects on the overall intensity of disturbance. Although disturbance intensity is defined as the total area disrupted per unit of time and is equal to size times frequency, different combinations of size and frequency that result in the same intensity may affect the number of species in profoundly different ways. The converse is also possible; changes in either size or frequency that alter overall intensity in the same way may affect species quite differently.

The effects of disturbance depend on the relationship of species number to both size and frequency of disturbance. To take the simplest case, suppose species number always decreases with disturbance. Lubchenco (1978, her Fig. 4D) reports this pattern for algal species on emergent surfaces grazed by the snail *Littorina littorea*, although Tilman (1982, his Fig. 85) believes Lubchenco's data can be explained more

easily as a humped curve that has been truncated. In either case, we assume, for simplicity, that species number always decreases with either increasing disturbance frequency or size. This is equivalent to our equilibrium model without compensation (see Fig. 3).

A plot of species number against both disturbance size and frequency forms a surface (Fig. 8). The effects of size and frequency, when taken together, give the overall intensity of the disturbance (intensity = size \times frequency). The interaction of size and frequency can be represented as a two-dimensional map with overall intensity plotted as isoclines. If the axes are log-scaled, a straight, diagonal line provides isoclines of equal intensity for different combinations of the two variables. The effects of disturbance size and frequency on species number may not be strictly multiplicative, however; that is, a change in size may not be the same as a proportional change in frequency, and thus the surface may bow out or bow in. The resulting surfaces—flat, convex or concave, which we call multiplicative, damped, and enhanced interactions—can be plotted as species number isoclines on the disturbance size-by-frequency plane (see Fig. 9).

The contours shown are not the only possibilities and may reflect our research biases but they illustrate the essential cases. The multiplicative case is expected when the effects

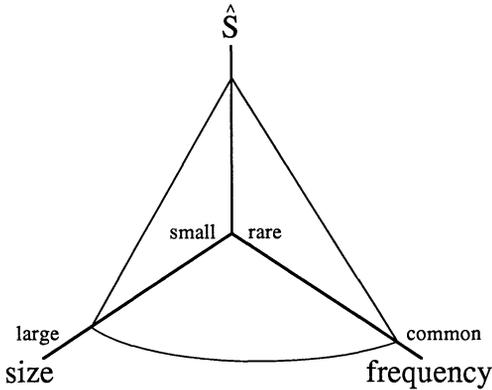


FIG. 8. SPECIES NUMBER AS A FUNCTION OF THE SIZE AND FREQUENCY OF DISTURBANCE

of disturbance size and frequency are interchangeable. This would occur if the effect of the frequency of a disturbance is independent of the effect of the size of that disturbance. Thus, an increase in either size (area disrupted per event) or frequency (the number of events per unit of time) would affect individuals in the same manner. In contrast, enhanced and damped species isoclines show an interaction between frequency and size. With damped isoclines, there is a decrease in the effect of a disturbance at a "mixed" combination of size and frequency. The isoclines bow out. The enhanced case shows an increased effect under these conditions, and the isoclines bow in.

Damped isoclines are likely to be common

when some species act as bottlenecks to further establishment until moderate and mixed levels of disturbance are reached. Bryozoans (Day and Osman, 1981), sponges (Kay and Keough, 1981), algae (Pyefinch, 1948; Menge, 1976; Hawkins, 1983; Petraitis, 1983; Underwood, Denley, and Moran, 1983), and sea anemones (Taylor and Littler, 1982) include some of the species that have been shown or are suspected to act as bottlenecks to the establishment of other species. The example in Table 1 is illustrative. Assume that one set of species, A, B and C, is affected only by disturbance frequency and another set, X, Y and Z, is affected only by disturbance size. (We know of no evidence that shows a species to be sensitive only to size or to frequency, but it seems reasonable that variation among species does exist. This is an area that needs further study.) Now suppose that species C and Z can exclude a seventh species, E. As shown in Table 1, the inhibition of E causes the combined effects of size and frequency on the species number to be damped. The pattern hinges on species C and Z which are moderately resistant to disturbance but in different ways and which have the ability to inhibit establishment of the same species.

The enhanced isocline example is merely the reverse situation. Again, assume that one set of species is affected by disturbance frequency while another is affected by disturbance size. Now assume that species B requires either species C or species Z in order to persist. The effects of frequency and size on species num-

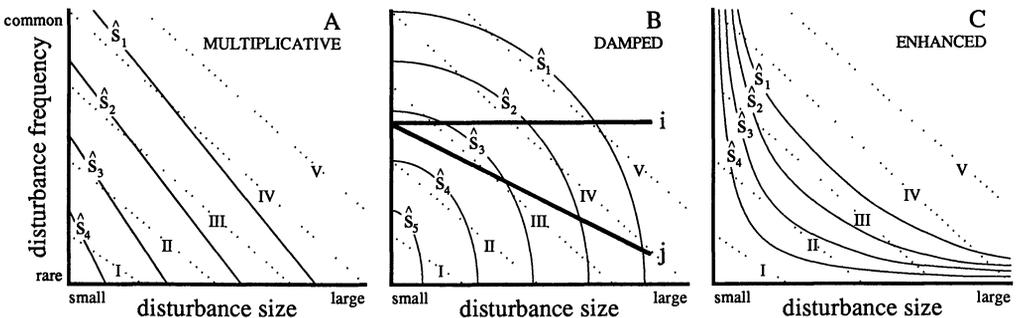


FIG. 9. PLOTS OF DISTURBANCE SIZE BY DISTURBANCE FREQUENCY, WITH SPECIES NUMBER AS A FUNCTION OF BOTH SIZE AND FREQUENCY

Species number isoclines are thin solid lines, isoclines of equal disturbance intensity are dotted lines, and lines representing observed covariation between disturbance size and frequency are thick solid lines. Axes are log transformed; since intensity is size \times frequency, this transformation generates straight lines representing intensities in the multiplicative case.

ber are then enhanced when in combination (Table 1). The ability of barnacles and algae to enhance the establishment of algae (Lubchenco, 1983; Petraitis, 1987) and mussels (Kitching, 1937; Bayne, 1964; Seed, 1969; Dayton, 1971; Menge, 1976) are well-known examples of this process.

Now suppose that the pattern of covariation in the size and frequency of disturbance observed in nature, which would normally be a cloud of points, could be represented as a line on the frequency-by-size map (Fig. 9). A linear pattern of covariation between frequency and size might lie in any direction on the interaction isocline map. The line of covariation provides two pieces of information. First, the intersections of the observed line of covariation with the isoclines of disturbance intensity shows the change in intensity as size and frequency co-vary. Second, the intersections of the line and the species isoclines gives the species number at a particular combination of size and frequency.

The effects of disturbance are now not so clear-cut. For example, moving along the intensity isocline labelled "III" on Fig. 9, which indicates changes in the mix of size and frequency but not in overall intensity, can give very different results. In the multiplicative case (Fig. 9A) there is a decline in species number as the disturbance shifts from a small, common disturbance to a large, rare disturbance. In contrast, the damped case, with the same shift in disturbance pattern (Fig. 9B), shows an increase, then a decrease, in species number even though there is no change in intensity. The enhanced case (Fig. 9C) shows a reversed curve; the highest number of species occurs when disturbances are small and common or large and rare.

It is also possible for different lines of covariation to give very different patterns of diversity even if the species number isoclines do not change. In Fig. 9B, for example, line *i* shows a decline in species number with increasing overall intensity of disturbance while line *j* gives the highest species number at an intermediate intensity. This difference in patterns of diversity occurs because disturbance size and frequency co-vary along lines *i* and *j* in different ways even though both show a monotonic increase in overall intensity. For line *i*, the disturbance becomes larger but not more com-

mon as intensity increases. In contrast, line *j* shows a pattern of rarer but consistently large disturbance as intensity increases.

There are no a priori reasons for the pattern of covariation to be linear or to be oriented in a particular way. In fact, it may be more profitable to assign each combination of size and frequency a probability and to visualize the disturbance regime as a probability map overlying the isoclines.

DISCUSSION

In this review we have tried to bring together several issues generally considered to be distinct. The links between nonequilibrium models, such as the intermediate disturbance hypothesis, and equilibrium models, such as the compensatory mortality hypothesis, have been ignored by most ecologists (for some exceptions, see Caswell, 1978; DeAngelis and Waterhouse, 1987). Adding to the confusion, some authors have not used terms consistently and most have not explicitly examined the relationship between the size and frequency of disturbance. We have attempted to resolve these problems, or at least define the limits of our ignorance, by clarifying the distinctions among such terms as disturbance size, sampling area and patch, and by stressing the commonality of processes that underlie all the models.

Much of the confusion can be traced to ambiguous usage of the term "patch." Clearly both a catastrophe and the predation of a single individual are mortality events although they are very different in scale. In a catastrophe, the patch may be congruent with the area affected by the disturbance event itself but, in predation, the patch is the area across which a predator forages. Moreover, catastrophes affect large areas that can be ecologically very heterogeneous. By focusing on the mechanism of disturbance, ecologists have allowed the event to define the scope of interest; in general, ecological studies have been colored by the scale of the event studied. This has led to confusion over what constitutes a patch and has allowed ecological events to manipulate researchers rather than the other way around. The problem can be resolved if we distinguish among the area that is sampled, the areal magnitude of the disturbance, and the size of a patch, and if we define them independently. We have chosen to define patch in a very narrow sense, that is, as

a homogeneous region in which the effects of a disturbance are similar (this definition runs into problems in situations where single large individuals, for example, trees or corals, occupy many smaller patches). A single disturbance may create one patch or many. A complex disturbed area such as a forest blow-down or even a single treefall may be a mosaic of disturbance patches displaying very different characteristics.

Once we distinguish among sample area, disturbance area, and patch area, then certain questions that have not been widely addressed by ecologists become obvious. For example, do the observed effects of disturbance in a sample plot made up of many patches differ from the observed effects in a sample plot contained within a single patch?

The confusion over what constitutes a patch or a disturbance also has led to defining disturbance in terms of characteristics of the patch. Osman and Whitlatch (1978: 42) define disturbance as "a mechanism or category of mechanisms which controls the age of a patch." From our discussion of equilibrium and nonequilibrium models, it should be clear that a disturbance is not a simple mechanism resetting patch age but a process that alters the birth and death rates of individuals present in the patch. The alteration can be direct or indirect. The disturbance can either kill individuals or affect competitors, natural enemies and resource levels in ways that alter survival and fecundity. Changes in the per capita rates of birth and death shift the patterns of immigration and extinction and thus give rise to the disturbance-diversity phenomena called, in ecologists' jargon, intermediate disturbance and predator-mediated coexistence.

The differences between nonequilibrium and equilibrium models tend to blur when the importance of shifts in per capita rates of birth and death and their effects on immigration and extinction are recognized. Equilibrium models address the maintenance of a steady state while nonequilibrium models address the approach to that steady state. The number of species present at any time, regardless of whether the system is at equilibrium, depends on immigration and extinction which, in turn, depend on per capita rates of birth and death. Furthermore, birth and death rates depend on both within- and between-patch characteristics, such as

microclimate and resource availability. While it seems that the most profitable area of research would be related to the effects of disturbance not only on the rates of immigration and extinction but also on the per-capita rates of birth and death, most work has addressed the effects of disturbance size on species composition.

Paine and Levin's (1981) study of patch dynamics after a disturbance provides a good example of how disturbance size may play a role in determining species diversity. In a rocky intertidal community on the coast of Washington State they found the rate of patch closure to be highly dependent on the size of the patch. Adults of the dominant occupier of space, the mussel *Mytilus californianus*, can move in from the edges of newly formed small patches of open space very quickly. Given that other species of sessile marine organisms must rely on the settlement of planktonic larvae, a disturbance that creates many small patches has a different effect from a disturbance of equal size that creates a few large patches. Paine and Levin's study relied on naturally occurring disturbances to create patches, and it could be argued that the patches differed in other ways besides size. Yet, Kay and Keough (1981) made three sizes of clearings on pilings covered by sponges and found, as Paine and Levin did, that the smaller clearings were rapidly filled in from the sides.

In a similar study, Sousa (1979a) details how species composition and number are dependent on the size of the disturbance. In the rocky intertidal of southern California, the barnacle *Chthamalus fissus*, the green alga *Ulva*, and four perennial species of red algae colonized the space on large clearings (165 cm²). Smaller clearings (100 cm²) made by scraping in the middle of beds of the dominant red alga *Gigartina canaliculata* were colonized only by *Chthamalus* and two species of red algae.

Barden (1981) found a similar effect in southern Appalachian forest gaps. He examined tree replacement in 118 small, single-treefall gaps and in 42 larger, multiple-treefall gaps and found that recruitment in all gaps was predominantly by 11 species ranging from moderately to very shade-tolerant but that 4 additional species, less shade-tolerant than the others, occasionally captured canopy space in the larger gaps. Runkle (1982) also showed a strong correlation between woody plant species number and gap area in old growth forests spanning

five of the eastern United States. Oliver and Stephens (1977) studied tree recruitment in gaps of wide size distribution in a forest in Massachusetts and found that recruits included new immigrants only in large disturbance patches; small patches were captured entirely by shade-tolerant juveniles already established at the time of disturbance.

Although not as well studied, the frequency of disturbance also has important effects. For example, the density of patches created by a disturbance across a landscape depends on the frequency of disturbance and thus frequency may affect immigration. Platt and Weis (1977) showed species number among plants colonizing badger mounds on an Iowa grassland to vary inversely with distance to other mounds. Persistence of species may depend on disturbance frequency; Paine (1979) found that the sea-palm, the alga *Postelsia palmaeformis*, persists only in intertidal areas on the Washington coast where disturbances occur above a threshold frequency. A high frequency of forest disturbance may favor tree species intermediate in tolerance of shade, since they can establish during one episode of canopy opening and persist in the understory through one or more periods of canopy closure, according to Runkle and Yetter (1987), who present evidence that many trees in southern Appalachian old-growth forests have survived several episodes of suppression before reaching the canopy. Brokaw (1982) found that the frequency of small treefall disturbances in Panama is higher in an old-growth forest than in a younger forest only 100 years removed from large-scale disturbance, resulting in higher species richness in the old forest owing to the recruitment of species regenerating only in gaps.

It is especially perplexing that the greatest number of species is usually seen at intermediate levels of disturbance since alternative patterns seem likely, given the large number of possible permutations of species' birth and death rates that may be affected differently by disturbance. There are two possible explanations. First, other patterns may have gone unrecognized, although at least one other, that of greatest diversity at the lowest level of disturbance, has been reported (Lubchenco, 1978; Lubchenco and Gaines, 1981). However, the pattern of the greatest number of species only at the lowest levels of disturbance is simply a

special case of our models. If there is no compensation in the rate of either immigration or extinction from lower to higher intensities of disturbance, then diversity will decline. This is most easily seen for the equilibrium case of our model (Fig. 3), but the same argument can be made for the nonequilibrium case (Figs. 6A and 6B). There is no need to invoke more complex scenarios, such as species-specific changes in competitive ability, as Lubchenco and Gaines (1981) do.

Second, and more intriguing, it is possible that other patterns are not common because species are severely constrained in their reactions to disturbance and predation. For example, if a species is unable to invade undisturbed patches because of competitive exclusion, its persistence may depend on an ability to invade and resist extinction at moderate levels of disturbance. We know of no data demonstrating that such trade-offs exist. We believe, however, that compensation in immigration and extinction may arise from such trade-offs in the "packaging" of different abilities into single species. Implicit in both disturbance and predation-mediated models is this notion of trade-off. Traditionally, disturbance has been thought to remove competitively dominant species, thus allowing other species to invade. Predator-mediated coexistence differs only in degree: predation removes individuals of the species with superior competitive abilities and therefore alters either birth or death rates or both. In each case, a species can be good at resisting either competition on the one hand or disturbance and predation on the other, but it cannot be adept at resisting both kinds of stresses. A major challenge to models of disturbance is the acquisition of data that will support or refute this contention.

Patterns of diversity may be limited in another way. We have shown how rates of immigration and extinction can be altered by the interactive effects of disturbance frequency and size. If only certain types of interactions of frequency and size are common, then the patterns of diversity across differing degrees of overall intensity (frequency \times size) may be limited. The explicit mapping of disturbance size and frequency suggests at least two possibilities (Fig. 9). First, size and frequency of disturbance may co-vary in only a small number of ways, and thus the direction of the trend of observed

co-variation would be very restricted. For example, if disturbance frequency and size show a strong positive correlation, then the number of species can only decline with increases in intensity. Second, the effects of disturbance size and frequency on species number may be very similar, and thus the species number isoclines would not bow very much. Both would limit the patterns of diversity. It should not be surprising that the alternative patterns we have proposed depend on a negative correlation between disturbance size and frequency and on very bowed species number isoclines.

This negative correlation may arise from the disproportionate effects of disturbance size and frequency on species. Miller (1982) suggests that the number of species in a patch may be dependent on the size of the disturbance. If this dependence exists, then changes in the intensity of a disturbance may cause species number to increase, decrease, or remain the same. The outcome depends on how size and frequency change and provides another possible explanation for why the species number isoclines might bow in or out as in Fig. 9.

There is, unfortunately, little experimental work that examines the relationship between disturbance size or frequency without using indicator species, in which a species' presence is used to define disturbance intensity without independently measuring the actual disturbance. Examples of independent measures are Dayton's (1971) "survivorship" curves for nails which were subject to wave battering in the rocky intertidal shore in Washington State and Beatty's (1984) frequencies of toothpick-toppling by frost heave on forest floor sites in New York, but it is not possible to infer a correlation between size and frequency from either set of data. To make matters more difficult, experimental work (Sousa, 1979b; Paine and Levin, 1981; Brokaw, 1982; Proffitt, 1983) and modeling (Abugov, 1982) suggest that, even if frequency and size are correlated, the timing of disturbance has an important role. Much more work needs to be done for a clear understanding to emerge on how disturbance size and frequency co-vary.

The relationship of species number to changes in both disturbance frequency and size is an even more difficult problem. Part of the problem is that the effects of size and frequency may be similar in some instances but not in

others. When disturbances are small in size and common in frequency, it may be reasonable to assume that a small increase in size would have the same effect as a small increase in frequency. Over the range of sizes and frequencies for which this is true, the species number isoclines will not be bowed, and increases in intensity, either through changes in size or in frequency, will cause a decline in species number (see Fig. 9A). Given that alternative patterns could be generated by the interaction between frequency and size of disturbance, this seems to be an area that requires more investigation.

We know of three experimental studies of species richness patterns in which both disturbance size and frequency were varied. Mook (1981) provides data from a fouling (marine, hard-bottom, sessile animal) community in Florida. He reports a change in species number when the size and frequency of an artificial disturbance was changed but the overall intensity was held constant. Fouling plates on which 25 percent of the surface was scraped every month averaged 10 species while plates on which 50 percent was scraped every two months average 14 species. Both controls (no scraping) and treatments of higher overall disturbance intensity (50% scraped monthly) averaged 12 species. The experiment was not properly replicated. Data collected by Proffitt (1983), in an experiment using artificial disturbance in a soft-bottom marine animal community, also in Florida, suggests the opposite trend. In experimental plots exposed to a similar overall intensity of disturbance, there was a tendency for more frequent, small disturbances to result in higher species richness than less frequent, larger disturbances. In an intertidal boulder field dominated by algae in southern California, Sousa (1979b) studied changes over time in species diversity on boulders overturned by waves, exposing unoccupied space. He found low diversity on both small, frequently disturbed boulders and large, infrequently disturbed boulders, and higher diversity on boulders of intermediate size and disturbance frequency. Sousa attempted to separate the effects of disturbance size from those of frequency by stabilizing some artificially denuded small boulders. After two years, the small boulders with infrequent disturbance had diversities as high as those of boulders of intermediate size with intermediate disturbance frequencies,

suggesting that disturbance frequency is more important than size in producing the diversity patterns he observed. All three studies were very narrow in scope. Full factorial experiments with adequate replication in a range of different communities are needed for a fuller understanding of the individual effects of disturbance size and frequency and their interaction.

The possibility of disproportionate changes in competitive interactions occurring with changes in the frequency and size of disturbance poses a difficult problem. Our argument concerning the changes in species number shown in Table 1 relies on the assertion that changes in disturbance frequency and size have a disproportionate effect on competitively dominant species. Species number at any given disturbance frequency and size is the result of a balance between competitive abilities of species and their resistance to different regimes of disturbance-induced mortality. There are other possible explanations. For example, there could be many intransitive interactions among competitors (Lubchenco and Gaines, 1981), with disturbance frequency and size altering these interactions and resulting in damped or enhanced effects. Alternatively, resource availabilities could be highly dependent on either the frequency or the size of disturbance; for example, light flux is higher in large forest canopy gaps than in small gaps (Marquis, 1965; Chazdon and Fetcher, 1984; Nakashizuka, 1985). Changes in the frequency or size of a disturbance also may influence the recovery of the system by means of changes in the levels of productivity or by other mechanisms; for example, gap size has been shown to be strongly related to the rate of growth in height of juvenile trees in a forest (Yetter and Runkle, 1986) and to the rate of successful colonization by annuals in an old field (McConnaughay and Bazaz, 1987).

Up to this point we have ignored complex interactions between disturbance and resources. In a review of how disturbance affects marine soft-bottom communities, Thistle (1981) mentions that disturbances may kill all the individuals in a patch in a soft-bottom community, but their bodies may remain in the patch and enrich the sediment. Depending on how species respond to different levels of enrichment, increases or decreases in species number that are induced directly by distur-

bance may be quickly altered by the amount of enrichment. Grassle and Sanders (1973) note that resource levels, even if they are not altered by a disturbance, can influence the recovery rate of a patch after a disturbance. They argue that resource levels in the deep sea are so low that competitive exclusion occurs very slowly. As a result, "a spatial mosaic emerges from local successional sequences that are out of phase" (p. 656). Huston (1979) restates this view as the converse: the rate of competitive displacement could be higher with higher levels of productivity (although he does not propose any link between disturbance and the level of productivity). Thus, he suggests, to maintain high species number in a highly productive system, frequent disturbances may be required.

Disturbance may alter the resource situation in a way that shifts competitive hierarchies among patches in a more complex manner than the simple dichotomy we have assumed between colonizing species and competitively dominant species (Hibbs, 1982; Tilman, 1982, 1984). This idea is similar to Hutchinson's (1961) explanation for the "paradox of the plankton," except that the competitive hierarchy here is varying among resource combinations in different patches instead of from one season to another. Tilman (1982: 226) views disturbance, not as "a process that periodically interrupts competition, but rather [as a] process that influences the relative supply rates of the resources for which competition occurs." For terrestrial plants, at least, disturbance may enrich a patch in one resource while either enriching, not affecting, or impoverishing the patch of other resources. For example, essential resources that occur in amounts limiting to the growth of forest trees and that change in response to disturbance include, at the very least, light (March and Skeen, 1976; Chazdon and Fetcher, 1984; Nakashizuka, 1985), soil moisture (Fletcher and Lull, 1963), and inorganic nitrogen and other essential mineral nutrients (Vitousek and Melillo, 1979; Allen, 1985). Although a disturbance in a terrestrial plant community generally causes enrichment of light at the surface, the effects of disturbance on soil moisture and minerals are not as clear-cut. The death of an adult tree stops its network of fine roots from taking up mineral-containing soil solution and accelerates the return of minerals to the soil by increasing the rate of decomposi-

tion of organic matter. Intuitively this should result in renewal of mineral nutrients in a treefall gap; ecologists, however, have gathered little evidence bearing on whether this actually happens (Collins, Dunne, and Pickett, 1985; Vitousek, 1985; Vitousek and Denslow, 1986). On the other hand, ecologists have documented decreases in soil moisture and in such highly soluble minerals as nitrate nitrogen in situations where large disturbances, involving the death of many trees, have occurred and there is consequent leaching, erosion and runoff (Nye and Greenland, 1964; Christensen, 1977; DeBano and Conrad, 1978; Vitousek and Melillo, 1979). From the small amount of evidence that is available, mainly from studies of the effects of clearcutting, it appears that disturbance may result in increases, decreases, or no change in the potentially growth-limiting availabilities of different minerals in different situations (Allen, 1985).

Complicating the problem still further, a terrestrial disturbance commonly generates several to many patches that differ markedly in resource availability. Treefalls, for example, create tip-up mounds of exposed mineral-rich subsoil, adjacent pits that collect water and dead organic matter, fallen logs that provide low-nutrient, high moisture environments, fallen crown areas of rotting branches and leaves, and areas relatively unaffected except by the death of the gap-maker's fine roots (Lyford and MacLean, 1966; Stone, 1975). Treefalls also make holes in the canopy that vary in size, shape and orientation with respect to the sun, the surrounding canopy, and the newly landscaped microhabitats on the forest floor; Marquis (1965) provides a geometrical analysis of canopy gaps showing how the amount of light reaching different parts of the gaps varies with their size, shape, and orientation. Wildfires vary locally in intensity and ash deposition, resulting in uneven distributions of liberated mineral nutrients (Christensen and Muller, 1975; Westman, O'Leary, and Malanson, 1981; Wilbur and Christensen, 1983). Some marine systems also are subject to com-

plex resource alteration by disturbance—for example, soft bottoms disturbed by the grazing activities of large animals (Thistle, 1981; Nerini and Oliver, 1983; Oliver, Kvitek, and Slattery, 1985), and intertidal hard bottoms, where disturbances of different types vary in whether they kill barnacles that provide attachment sites for mussels (Dayton, 1971). Moreover, different kinds of disturbances may interact in affecting resources. Collins and Uno (1983) and Collins and Barber (1985) describe a system of disturbances on grasslands in Oklahoma that includes grazing by large herbivores, fire, bison wallowing, and mound building by prairie dogs; they found that the species number of plants decreases within patches and increases across patches with increasing diversity in the types of disturbance.

We have shown that a fairly simple model of the interactions between disturbance frequency and size can produce a variety of patterns of species number. It appears to be essential that the effects of frequency, size, and overall intensity be teased apart if we are to understand the possible outcomes. The mechanisms underlying how disturbance and predation regulate the number of species also need to be examined in detail. The idea that compensatory effects derive from the inability of species to excel at resisting both disturbance and competitors is untested. Trade-offs must not only be shown to exist but they also must be shown to be important in driving observed changes in species number. Future comparisons among systems with disturbance regimes that differ in frequency and size but not in overall intensity may provide some of the best case studies of how disturbance regulates species number in a community.

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