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THE ROLES OF HARSH AND FLUCTUATING CONDITIONS IN THE DYNAMICS OF ECOLOGICAL COMMUNITIES

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Abstract.—Harsh conditions (e.g., mortality and stress) reduce population growth rates directly; secondarily, they may reduce the intensity of interactions between organisms. Near-exclusive focus on the secondary effect of these forms of harshness has led ecologists to believe that they reduce the importance of ecological interactions, such as competition, and favor coexistence of even ecologically very similar species. By examining both the costs and the benefits, we show that harshness alone does not lessen the importance of species interactions or limit their role in community structure. Species coexistence requires niche differences, and harshness does not in itself make coexistence more likely. Fluctuations in environmental conditions (e.g., disturbance, seasonal change, and weather variation) also have been regarded as decreasing species interactions and favoring coexistence, but we argue that coexistence can only be favored when fluctuations create spatial or temporal niche opportunities. We argue that important diversity-promoting roles for harsh and fluctuating conditions depend on deviations from the assumptions of additive effects and linear dependencies most commonly found in ecological models. Such considerations imply strong roles for species interactions in the diversity of a community.

In a series of influential works, Gause (1934), Hutchinson (1959), and MacArthur and Levins (1967) suggested that species interactions such as competition are a major impediment to species coexistence and community diversity and that competition has a major role in shaping the structure of communities. Despite early enthusiasm for these ideas, many ecologists have since argued that population densities are often low, because of harsh conditions resulting from physiological or resource stress or from mortality caused by disturbance, predators, or pathogens. They reason that competition therefore is weak or infrequent and consequently does not have appreciable effects on properties of communities such as species composition, diversity, and niche overlap (Wiens 1977; Grime 1979, 1985; Huston 1979; Menge 1979; Greenslade 1983; Strong 1983; den Boer 1986; Zobel et al. 1994). A common extension of such reasoning is that community properties are largely determined by chance and history (Hubbell and Foster 1986*a;* Cornell 1993).

A related argument is that competition only structures communities at equilibrium. Proponents of this view have argued that environmental fluctuations, such

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as seasonal variation, vagaries of the weather, and disturbance, disrupt equilibria and prevent consistent effects of competition (Hutchinson 1961; Wiens 1977; Huston 1979; Ricklefs 1987). Unpredictable environmental fluctuations are sometimes also assumed to reduce selection for ecological divergence that may result from interspecific competition (Wiens 1977; Hubbell 1979; Connell 1980). Indeed, Hubbell and Foster (1986*a*) argue that high environmental uncertainty leads to ecological convergence, high niche overlap, and coexistence of many very similar species. Hutchinson (1961) suggests that environmental fluctuations of the right frequency can reverse competitive exclusion and allow persistence of a richer nonequilibrium community. However, ecologists have most often viewed environmental fluctuations as promoting extinctions and reducing species diversity (Pimm 1991).

The recent acceptance of the concept that multiple mechanisms are most likely involved in diversity of any community and that the ecological processes of most importance may vary with locality, trophic level (Menge and Sutherland 1987; Menge and Farrell 1989), or spatial scale (Cornell and Lawton 1992; Ricklefs and Schluter 1993; Levin 1994) has also been construed as indicating that competition or other density-dependent processes may often be unimportant. The unfortunate failure to emphasize that, at some spatial or temporal scale, niche differences are essential to species coexistence has allowed logical inconsistencies in the ideas described above to remain unnoticed. Thus, these ideas remain commonly accepted though they fail to identify correctly the circumstances in which harshness and environmental fluctuations can importantly influence community structure.

We reexamine the role of harshness, arguing that it does not necessarily diminish the importance of competition because harshness has direct negative effects on population growth that must be compared with the positive effects of lowered competition. As Holt (1985) has shown for density-independent predation in Lotka-Volterra systems, such harshness may make a population less tolerant of competition: although competition may be reduced, harshness also means that competitive exclusion can occur with weaker competition. Thus, harshness resulting from a regime of disturbance, mortality, or stress does not have a general consequence for communities. Although harshness need not have any effect on diversity, we discuss several ways in which it can, and we offer ways of understanding its effects for particular ecological communities.

We argue further that the effects of environmental variation depend on particular ecological circumstances. Although environmental fluctuations may keep a system away from a traditional equilibrium where species densities remain constant over time, environmental fluctuations need not reduce the average effects of competition nor the selective value of resource partitioning. Rather, environmental fluctuations can provide temporal niche opportunities, permitting species to be differentiated from each other in their relationships with specific environmental conditions that occur over time; therefore, species can coexist by having complementary relationships with the temporally varying environment, for example, by having different periods of maximum growth and quiescence or dormancy. Competition may shape such complementary patterns by competitive ex-

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clusion within groups of ecologically similar species or by coevolutionary adjustments between coexisting species. Environmental fluctuations provide opportunities for temporal niche partitioning but do not fundamentally change the impact of interspecific competition.

Although we express much of our argument in terms of competition for resources, the conclusions apply also to other density-dependent population interactions that have the potential to generate ecological opportunities for species, that is, that can serve as niche dimensions (Levin 1970). It has long been recognized that shared natural enemies may have such a role. For instance, MacArthur (1970) discussed the concept of predator partitioning where members of a community are limited by predation; and the analogy between the effects of competition and shared density-dependent mortality from natural enemies is recognized in the concepts of ''apparent competition'' (Holt 1977) and ''competition for enemy free space'' (Jeffries and Lawton 1984).

Our arguments are developed by means of a general mathematical model that permits us to examine the logic of the ideas summarized above. The model includes as special cases the Lotka-Volterra model in a variable environment (Turelli 1981) and the lottery model with nonoverlapping generations (Chesson and Warner 1981) but is much more general than either of those models. We do not present this general model because we believe it has broad application; we will argue below that it does not. However, the model includes the elements that commonly enter discussions of the effects of harsh and fluctuating conditions, and comparison of this model with others highlights the ecological conditions under which harsh or fluctuating environments can play a significant role in diversity and community structure.

We begin with a study of the general model, which demonstrates that, at best, harsh and fluctuating conditions have severely limited roles in the maintenance of diversity when common premises apply. We then use these results to examine the views of Hutchinson (1961), Grime (1985), Hubbell (1979), and Huston (1979), arguing that in general these authors have presented inadequate, inconsistent, or improbable explanations for the role of competition in the maintenance of species diversity. Finally, we examine models that deviate in important ways from the general model, incorporating realistic features of nature that allow harsh and fluctuating conditions to promote strongly the maintenance of species diversity.

A GENERAL MODEL

Consider a guild of several potentially competing species. If $N_i(t)$ is the population size of species i at time t, then the per capita population growth rate (r) over discrete units of time can be defined as

$$r_i(t) = \ln[N_i(t + 1)/N_i(t)] = \ln N_i(t + 1) - \ln N_i(t), \tag{1}$$

or simply the change per unit time in the natural log of the population size. We assume that the growth of a population can be represented by the difference of two general sorts of effects, density-independent effects measured by a quantity

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$E_i(t)$ (which we refer to as the *environmental response*) and multispecies density-dependent effects measured by a quantity $C_i(t)$ (*competitive response*). Thus, in simplest terms our model is

$$r_i(t) = E_i(t) - C_i(t). \tag{2}$$

The density-independent effects accounted for by $E_i(t)$ include the effects of the physical environment and also any biotic effects that do not depend on the density of the population, for example, mortality by a predator or a pathogen whose dynamics and behavior are not strongly linked to species of the guild in question. Biotic effects linked to the species in this guild are accounted for by $C_i(t)$ and can be expected to depend on the densities of these species. In this sense these effects are density dependent. They include competition and density-dependent disease or predation (apparent competition; Holt 1977), although for simplicity our discussion is framed in terms of competition alone.

The competitive response may be defined as the total effect on the growth rate of both intra- and interspecific competition. It is not a competition coefficient, which measures the per unit effect of a species' density on the per capita growth rate of a species. The competitive response measures, instead, the total reduction in the per capita growth rate because of competition. Although similar to Goldberg's (1990) terminology, our usage applies at the population rather than the individual level and is the actual reduction in growth rather the relationship between growth and resource availability.

The environmental response can fluctuate over time because of fluctuations in the weather, fluctuations in predators and pathogens, and fluctuations in mortality rates because of disturbance. The competitive response may also fluctuate over time. It may do this because population densities fluctuate, because inputs of resources to the system fluctuate, because environmental factors modify resource uptake rates (Abrams 1984), or because environmental conditions modify the number or size of individuals competing for resources (Chesson and Huntly 1988).

To understand how different species respond to competition, we assume that the competitive response of a species can be broken down into responses to m distinct factors, with magnitudes $F_1(t), F_2(t), \ldots, F_m(t)$. In the Lotka-Volterra model (app. A), the species themselves are the competitive factors, and the $F_1(t)$, $F_2(t), \ldots, F_m(t)$ are the species' densities. Each species is considered to contribute some amount of competition of a particular sort to the system, depending on the rates at which it consumes particular resources, and this amount of competition is assumed proportional to the species' density. In more mechanistic models (e.g., Tilman 1982), the competitive factors could be resources, and $F_l(t)$ would then be a measure of the shortage of resource l.

We assume here that the competitive response depends linearly on the competitive factors:

$$C_i(t) = \sum_{l=1}^{m} b_{il} F_l(t). \tag{3}$$

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Thus, the response of species i to factor l is $b_{il}F_l(t)$, and the combined response to all factors is just the sum of the response to each factor separately. The constants b_{il} give the per unit response of species i to factor l, and we shall refer to b_{il} as the sensitivity of species i to factor l.

Stable species coexistence occurs without difficulty in a model of this sort when there are at least as many competitive factors as species (Levin 1970), as then different patterns of sensitivity to these factors (MacArthur 1970) mean that the species have distinct resource niches. Harshness and fluctuations are believed to allow coexistence with just a few or even just one competitive factor (one resource niche). Can this be so?

Arguments that there are many fewer competitive factors than species are common in the literature. For example, it is claimed that space may represent a single-competitive factor in some plant communities (Hubbell and Foster 1986*a*), as space brings the resources required by plants, which may be summarized broadly as nutrients, water, and light (Grubb 1986). If the species in a guild have similar dependence on resources, then such a single-factor summary is adequate. In Lotka-Volterra competition with a single competitive factor, the species collectively form the factor, which is measured as a weighted sum of the densities of the species (app. A), the weights being the competitive effect (sensu Goldberg 1990) of each. With just a single competitive factor, equation (2) can be expressed as

$$r_i(t) = E_i(t) - b_iF(t), \tag{4}$$

where $F(t)$ is the common competitive factor, and b_i is the sensitivity of species i to this factor.

The dynamics of competitive factors, whether single (eq.[4]) or multiple (eq. [3]) can be complex, but all we need to know is that competitive factors prevent indefinite increase in population densities. We assume that if a species i is sensitive to factor l, then an increase in the density of species i tends to increase factor l (e.g., makes the resource less available). We assume that such density dependence prevents indefinite growth of a population, even if it operates with a time lag. In other words, we assume that populations are stochastically bounded from above (Chesson 1982).

GENERAL PREDICTIONS OF THE MODEL

There are several ways of considering harshness in the model. Lower values of the environmental response, $E_i(t)$, higher values of the b_{il}, and lower values of resource supply (which affects $F_l(t)$) all indicate harsher conditions. Thus, we can use the model to ask, How does harshness affect community dynamics, the coexistence of species, and the rate of approach to extinction? What is the role of fluctuations over time in environmental responses and competitive factors?

The quick route to answering these questions is through the special case of the model with a single competitive factor (eq. [4]), which is the object of study for the rest of this section and appendix B (stochastic analysis). The conclusions, however, extend to the case of several competitive factors (app. C). With just

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one competitive factor, an equilibrium analysis would predict that species loss must occur until just one species survives (Armstrong and McGehee 1980). Fluctuations in $E_i(t)$ can mean that competition occurs only infrequently, and with low average values of the environmental responses, average levels of competition are weak (fig. 1). Can competition be important in such circumstances? Can competitive exclusion still occur? Will exclusion be delayed for a very long time? The answers can be found by studying the dynamics of a measure of relative abundance.

We define the relative abundance of some species i compared with another species j as the scaled difference in log population sizes

$$R_{ij}(t) = [\ln N_i(t)]/b_i - [\ln N_j(t)]/b_j, \tag{5}$$

with scaling factors b_i and b_j representing different magnitudes of response to the common competitive factor. Dividing by the b's in equation (5) allows for species operating on different timescales because $1/b$ is proportional to the time for a given magnitude of response to a given level of competition. The most important property of $R_{ij}(t)$, however, is that it can be used to study competitive exclusion: indefinite increase in $R_{ij}(t)$ means that species j must be heading toward extinction. (Indefinite increase in species i cannot occur, and so cannot explain indefinite increase in $R_{ij}(t)$). Equivalently, if $R_{ij}(t)$ decreases indefinitely, then species i must be heading toward extinction.

Combining equations (4) and (5) reveals the change in $R_{ij}(t)$ from one time to the next:

$$R_{ij}(t + 1) - R_{ij}(t) = E_i(t)/b_i - E_j(t)/b_j, \tag{6}$$

which leads to the surprising conclusion that the dynamics of relative abundance do not involve the competitive factor $F(t)$ and, thus, do not depend on the amount of competition. Hence species are not limited relative to each other by the amount of competition. The role of competition is instead to limit the community as a whole. Does this observation mean that competitive exclusion cannot occur? We shall see below that the truth is exactly the opposite: competitive exclusion takes place independently of the amount of competition.

The Importance of Averages and the Role of Competition

Equation (6) can be summed over time to reveal the total change in relative abundance from time 0 to some time T as

$$R_{ij}(T) - R_{ij}(0) = T \cdot (\overline{E}_i/b_i - \overline{E}_j/b_j), \tag{7}$$

where $\overline{E}_i$ and $\overline{E}_j$ are respectively the averages of $E_i(t)$ and $E_j(t)$ over the time period $t = 0$ to $t = T - 1$ (app. B). This expression of total change in relative abundance in terms of average environmental responses, with no terms for variance in these environmental responses, leads to the second surprising conclusion: the change in relative abundance over any period of time depends only on average environmental responses for the given period of time and is independent of fluctuations about these average values.

As discussed below in the section on the role of fluctuations, the average en-

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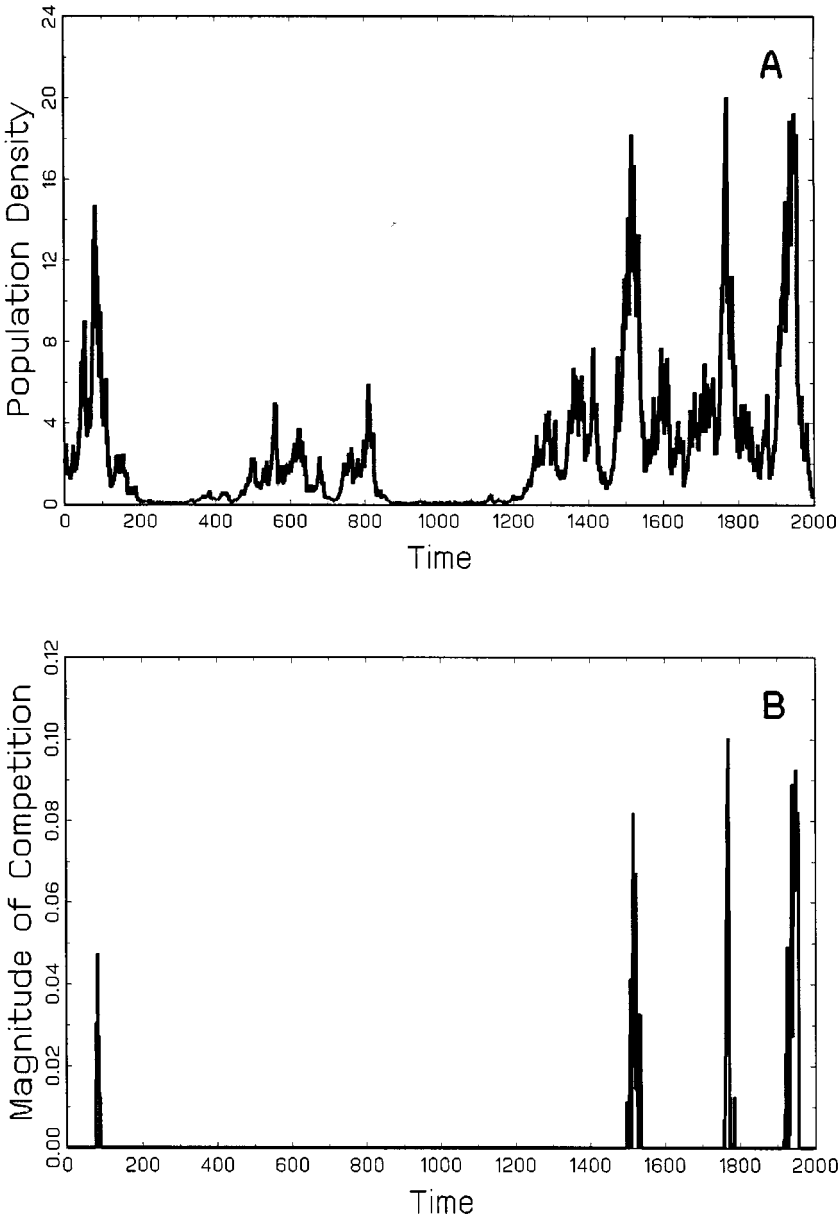

FIG. 1.—*A*, Fluctuations in population density for the dominant species of a three-species system experiencing random disturbances. Competition only occurs when population exceeds 10. *B*, Fluctuations in the magnitude of competition experienced by the population in *A*. Without disturbance, the equilibrium value of competition is 0.13. In the presence of disturbance, competition is infrequent and has an average value of only 0.0026, or 2% of the equilibrium value. The simulation is based on equation (4) of the text, with $F(t) = \max\{0, \sum_j 0.01N_j - 0.1\}$, $b_i = 1$. Fluctuations in $E_i(t)$ are independent over time, normal but with values above the mean truncated to the mean. The normal variance is 0.102 (chosen to give the 2% value for competition) and the mean for the dominant is 0.13.

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vironmental responses, $\overline{E}_i$ and $\overline{E}_j$, themselves may change with the interval of time T over which they are calculated, but in a variety of circumstances, for example, if the environment varies randomly over time, or regularly (e.g., seasonally), or is a combination of both, then $\overline{E}_i$ and $\overline{E}_j$ are approximately constant for large T in accordance with the law of large numbers (Feller 1968). Denoting these constant values by μ_i and μ_j, equation (7) becomes

$$R_{ij}(T) - R_{ij}(0) \approx T \cdot (\mu_i/b_i - \mu_j/b_j), \tag{8}$$

showing that relative abundance changes approximately linearly with time, except in the unlikely event that $\mu_i/b_i = \mu_j/b_j$. Thus, species must grow steadily apart in abundance with time. Indeed, relative abundance must approach plus infinity ($\mu_i/b_i > \mu_j/b_j$) or minus infinity ($\mu_i/b_i < \mu_j/b_j$), and so we must conclude that species i, species j, or both become extinct. Indeed, in a community of k species having differing values of μ/b, only that species with the highest value of μ/b will persist in the system because the relative abundances of other species must converge on minus infinity, signaling their extinction. Thus, the system has a dominant species that eliminates all other species. This is the case even though competition may be weak on average, which is so when the dominant has a low value of μ (fig. 2). As anticipated, competitive exclusion takes place independently of the magnitude of competition, independently of fluctuations in the environmental responses, and independently of the dynamics of competition beyond the assumption above that competition prevents any species from increasing indefinitely.

The Nature and Role of Ecological Dominance

As dominance in this system is determined by the ratio μ/b, a species can be dominant by having a large value of μ—a measure of the average effect of density-independent factors—or a small value of b (sensitivity to competition). The competitive dominant is not necessarily the species whose growth rate is least affected by competition, that is, the species least sensitive to competition. Rather, a species can be dominant by having a high μ, due, for example, to short development times, high fecundity, or low mortality in a particular environment. In Lotka-Volterra models, however, the commonly assumed trade-off between r and K does imply that the dominant is the species least sensitive to competition (app. A).

The ratio μ/b can be thought of as tolerance of competition or, more precisely, tolerance of the competitive factor, because μ/b is equal to the average value of the competitive factor F that leads to zero average growth over time for a species, as can be seen by taking the average of both sides of equation (4). A larger average F than this means negative average growth and convergence to extinction. A smaller average F means an increasing population. Corresponding to Tilman's R^* rule (Tilman 1982), the species that dominates is indeed the one able to tolerate the most competition.

Rates of Approach to Extinction

Rates at which nondominant species are excluded from the system are available by rearrangement of equation (8). If species 1 is the dominant, that is, has

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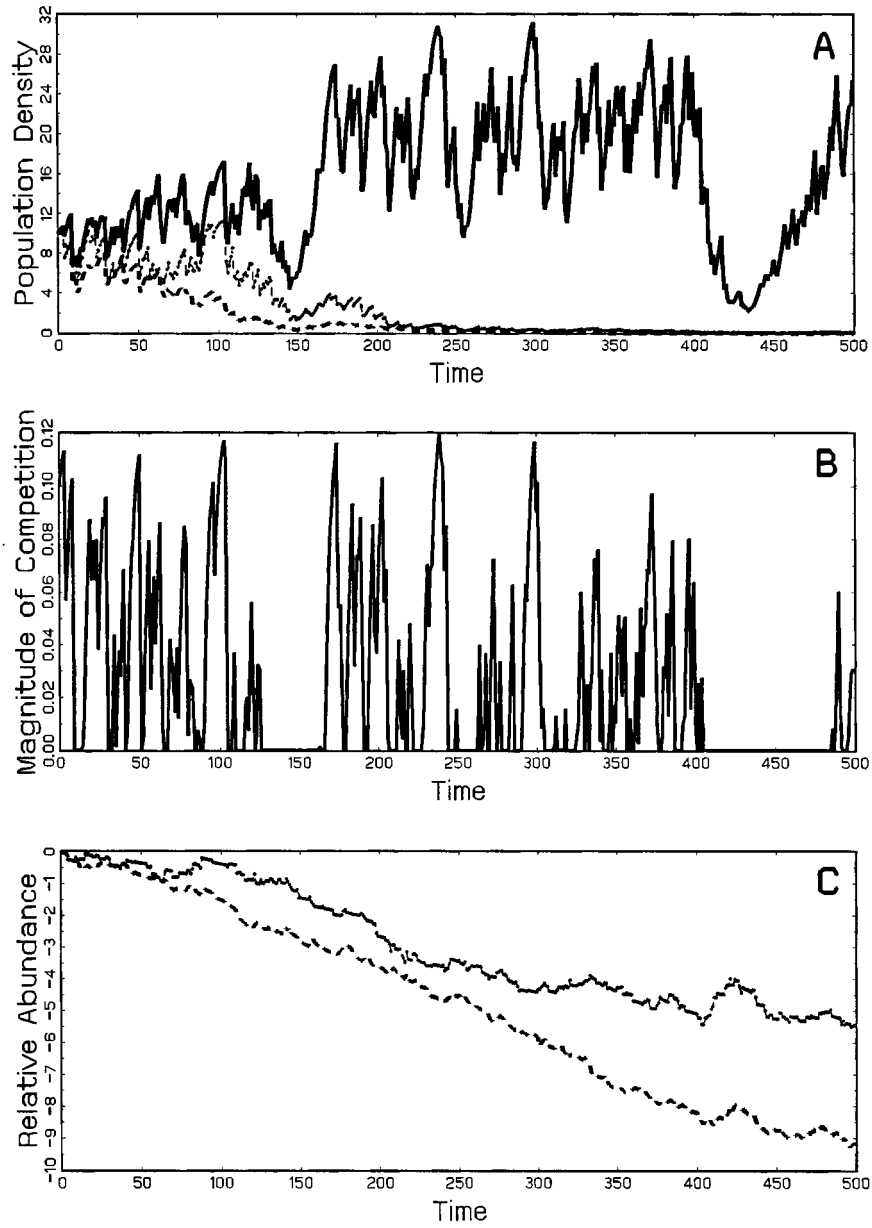

FIG. 2.—*A*, Fluctuations in the population densities of three species experiencing random disturbance and common competition. *B*, Fluctuations in the magnitude of competition. *C*, Relative abundances of the two subordinate species relative to the dominant. Note that relative abundances decline approximately linearly even though competition fluctuates a great deal. The simulation is based on equation (4) of the text, with $F(t) = \max\{0, \sum_j 0.01N_j - 0.2\}$, $b_i = 1$. Fluctuations in $E_i(t)$ are independent over time, normal but with values above the mean truncated to the mean. The normal variance is 0.07, with correlations between species of 0.9. The mean is $0.14 - 0.01i$, $i = 1, 2, 3$.

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the highest value of μ/b, then dividing equation (8) by T, with $j = 1$, yields

$$\overline{R}_{i1} = \bar{r}_i/b_i - \bar{r}_1/b_1 \approx \mu_i/b_i - \mu_1/b_1, \tag{9}$$

where $\overline{R}_{i1}$, $\bar{r}_i$, and $\bar{r}_1$ are the averages of $R_{i1}(t)$, $r_i(t)$, and $r_1(t)$ over the time period 0 to $T - 1$. For large T, the average per capita growth rate, $\bar{r}_1$, of the dominant approaches 0, as the dominant can show no long-term trend in abundance (see, e.g., Chesson 1994). It follows that

$$\bar{r}_i \approx \mu_i - \mu_1 b_i/b_1. \tag{10}$$

The rate of convergence to extinction is just the negative of $\bar{r}_i$, a fact that we now use to draw conclusions about the potential effects of various kinds of harshness on rates of competitive exclusion.

HARSHNESS AND RATES OF APPROACH TO EXTINCTION

The general results above show that harshness cannot alter the conclusion that there must be a competitive dominant that drives the other species extinct, except in the unlikely event that harshness leads to equal tolerances of competition (μ/b). Even then, as we shall see below in the section on fluctuations, competitive exclusion of all but one species is still the most likely outcome. Harshness, however, can alter the rate at which exclusion is approached and it can alter the dominance ranking in a system. To see when and how these effects may occur we examine several possible sorts of harshness.

High Mortality Rates or Metabolic Costs

High mortality rates because of disturbance, density-independent disease, or predation all lead to low values of the environmental response, $E_i(t)$, and hence low values of μ_i, the time average of $E_i(t)$. In small mammals and birds, low temperatures, which require high metabolic rates to maintain body temperature, may be another way in which environmental responses are lowered. To understand how rates of approach to extinction may be affected by such harshness, let δ_i be the decrease in μ_i with the imposition of harshness, which we may regard as the sensitivity of species i to harshness. Equation (10) implies that the change in the rate at which species i approaches extinction is

$$\delta_1(b_i/b_1) - \delta_i, \tag{11}$$

which means that species i's rate of approach to extinction declines with harshness if

$$\delta_i/b_i < \delta_1/b_1. \tag{12}$$

Thus, species i's rate of approach to extinction declines with harshness if the ratio of species i's sensitivity to harshness and its sensitivity to competition is less than this ratio for the competitive dominant.

If harshness is due to indiscriminate mortality, as might occur with disturbance or nonselective predation, then the δ's are similar and extinction will be slowed simply if $b_i > b_1$, that is, if the growth rate of species i is more sensitive

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to competition than is the growth rate of the competitive dominant. Thus, in those cases when dominance is caused by low sensitivity to competition, indiscriminate mortality reduces rates of approach to extinction. If dominance results instead from a larger μ, harshness would not affect extinction rates or would increase them if the dominant were more sensitive to competition than other species.

In some situations mortality may fall selectively on the dominant. For example, the dominant may have a higher value of μ than other species because it invests less heavily in defenses against predators or harsh environmental conditions. Thus, it would be more sensitive to harshness than other species would, with the consequence that extinctions are slowed by harshness. At some level of harshness, however, the rank order of dominance would change so that the previous dominant goes extinct. Further increases in harshness from this point would hasten the extinction of the original dominant. Thus, though competitive exclusion may be slowed, it is never eliminated; eventually one species dominates.

Why Reduced Competition Need Not Delay Competitive Exclusion

Harshness that lowers the average environmental response does lead to reduced competition on average. We can see this from the fact that a persisting dominant must have a long-term average growth rate close to zero, that is, $\bar{r}_1 \approx 0$ for large T. Because r is just the difference between E and C, we must have, in the long run,

$$\bar{E}_1 \approx \bar{C}_1 . \tag{13}$$

As a consequence, a lowering of the average environmental response must be accompanied by a lowering of the average competitive response. Since $C_1 = b_1 F$, equation (13) means that

$$\bar{E}_1 \approx b_1 \bar{F} \tag{14}$$

or

$$\bar{F} \approx \bar{E}_1 / b_1 \approx \mu_1 / b_1 . \tag{15}$$

As $C_i = b_i F$, we see that

$$\bar{C}_i \approx \mu_1 (b_i / b_1) . \tag{16}$$

Thus, how much reduction in competitive response a nondominant species gains from lowered environmental responses depends on its sensitivity to competition relative to the dominant. When these sensitivities are the same, a nondominant species experiences exactly the same reduction in competitive response as does the dominant. If, in addition, the nondominant species' environmental response is reduced identically to that of the dominant, there is no net change in long-term growth rates of any species. Competitive exclusion occurs at the same rates, and the order of dominance is unchanged.

When sensitivities to environment and competition differ between species, a species may experience a net gain or a net cost from harshness, according to the

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details discussed above, but such gains or costs cannot be predicted from the reduction in competition alone. The effect of a lowered environmental response is a reduction in the ratio μ/b (tolerance to competition). Thus, although there may be a benefit from harshness in terms of reduced competition, a species is made less tolerant of competition by that same harshness. Whether a species gains a net benefit from harshness depends on how its tolerance to competition changes relative to that of the dominant species.

Physiological Stress: Slow-Growth Harshness and the Question of Temporal Scale

Until now we have assumed that harshness had its effect on the environmental response, $E_i(t)$, alone. However, physiological stress, for example, because of cold temperatures in plants and ectothermic animals, would slow down growth processes generally and thus lead to a reduction in μ and b by the same factor. Although the growth rates, $r_i(t)$, would be smaller in magnitude, the ratio μ/b would not be affected regardless of the extent to which different species were affected by the stress. Hence, the dynamics of the relative abundance measure, R_{ij}, would not change. A change would occur in the absolute rate of competitive exclusion, as given by expression (10), which would be slower simply as a reflection of the slower dynamics of the species. In effect, the timescale would be stretched without altering the events that occur.

Resource Harshness: Unproductive Environments and the Question of Spatial Scale

Finally, consider resource harshness. Resource harshness is defined as a low rate of replenishment of depleted resources. Resource harshness may be caused by uniformly low replenishment in time and space or by patchy resource supply. In arid environments, water resources may be temporally patchy because rain is sporadic. Resources may also be supplied patchily in space, which may lead to a patchy distribution of a community in space.

Although resource harshness derives from the environment in which organisms live, it does not alter μ because it does not have a direct effect on the species. The effect, instead, is indirect through the resources. The results of the analysis above do not involve the dynamics of resources. Rather, they are wholly dependent on the mean direct environmental response, μ, and the sensitivity to competition, b. Neither of these quantities is affected by resource harshness, and therefore, it appears that the rank order of competitive dominance, the extinction of all but the dominant species, and the rates at which extinction is approached are all unaffected by resource harshness. How can this be?

First of all, note that availability of resources need not be low in the presence of resource harshness, because availability represents the net result of supply and consumption over time. Resource harshness is low supply, but this low supply is compensated by low total consumption if population densities are low. Low consumption as a result of low population densities can lead to high resource availabilities. As the competitive factor represents a measure of resource shortage, resource harshness does not automatically lead to high values of the

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competitive factor. For the dominant to persist, resource shortage must not, on average, be higher than μ_1/b_1, the tolerance of the dominant species. This average value is implied by the persistence of the dominant and is achieved by negative feedback. If resource shortage should remain higher than μ_1/b_1 for any period of time, the growth rate of the dominant would tend to be negative, and the dominant would tend to decline in density. This outcome would reduce resource consumption and lessen resource shortage.

Conversely, values of resource shortage lower than μ_1/b_1 lead in the long run to higher densities of the dominant, hence higher resource consumption and higher resource shortage. In essence, long-term matching of average values of resource shortage with μ_1/b_1 depends on population densities of the dominant and the resource renewal rate. With resource harshness, lower densities of the dominant achieve the same levels of resource shortage. There is no reason for the relationships between the dominant and other species to change as the species are ranked on the basis of tolerance of resource shortage. Thus, the only change in the system is a lower density of the dominant species. We may think of resource harshness as a stretching of the spatial scale: nothing would look any different if the system were simply viewed from further away.

THE ROLE OF FLUCTUATIONS

In the analysis of harshness above, the environment was considered to be fluctuating, but fluctuations played no role in the conclusions. The role of fluctuations in the linear-additive modeling framework is necessarily quite small. The rate of divergence of relative abundances given by equation (7) depends just on the averages, $\bar{E}_i/b$ and $\bar{E}_j/b_j$, and not on fluctuations about these average values. The only issue is whether the ratios settle down to constant values (μ/b) with time (converge) and differ between species. Above, we used the preliminary assumption that the environment was some arbitrary mixture of random and regular variation to justify convergence (settling down). More generally, convergence occurs with stationary time series (Wei 1990). To say that a time series is stationary is to say that its probabilistic properties (frequencies with which various states and sequences of states are predicted to be found) do not change with time. Stationary time series cover a wide range of the various kinds of ''noise'' (red, white, and blue) commonly encountered in ecological discussions of environmental variation (Nisbet and Gurney 1982). Thus, the analysis above remains valid in all these cases, the critical issue being only that the final values of the $\bar{E}/b$ (μ/b, say at $T = \infty$) differ between species. In reality, this will always be so, as there are bound to be quantitative differences in species' properties, but these differences could be small, in which case the differences between the $\bar{E}/b$ will be dominated by random variation.

Even in the case where the dynamics are dominated by random variation, most of the conclusions above about harshness are preserved (app. B). The abundances of different species still move apart. The presence of any randomness over time in the differences of the E/b values guarantees this. When the μ/b values do not differ appreciably between species, equation (7) express-

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ing the change in relative abundance between times 0 and T still applies, but, because its values are dominated by random variation, we must examine its standard deviation to understand the fate of the community. The standard deviation describes the rate at which abundances move apart by a process of random walk, an accumulation of steps that by chance alone favors one species over others. The conclusions in this case differ in detail but not in main thrust from the conclusions when the μ/b differ appreciably between species (app. B). The important differences are as follows. First, the surviving dominant species is not predictable on the basis of greater tolerance of competition a priori but is the one better able to tolerate competition given the actual sequences of environmental states occurring over time. Second, the trend to extinction is not linear in time but linear in the square root of time—a slower rate of approach to extinction but nevertheless an inevitable approach to extinction. Finally, fluctuations still do not slow competitive exclusion; instead, they hasten it.

In general, the rate of approach to extinction consists of the sum of a linear rate, coming from the difference between μ/b values, and a square root rate, coming from the stochastic element of fluctuations in E/b values. The linear rate just depends on average effects and dominates when it is present (unless species differences are slight or populations are very small), while the square root rate depends entirely on unpredictability of the fluctuations in the environmental responses and leads to slower extinction with less predictability. Regular fluctuations in the environment do not contribute to the square root rate of extinction, as they quickly average out. See appendix B for details.

The above arguments all depend on an environment that can be approximated as a stationary time series. What if the environment is not approximately stationary, for example, if the environment follows some of the more exotic noise processes that some believe realistic in ecological settings (Halley 1996)? In such cases, the most likely scenario is that divergence of relative abundances is faster than linear. With a nonstationary environment, the differences in $\overline{E}_i/b_i - \overline{E}_j/b_j$ may show directional change with time. Thus, $T(\overline{E}_i/b_i - \overline{E}_j/b_j)$ will change rapidly, signaling rapid extinction.

Fluctuations in competition have played no role in the development above because the competitive factor plays no role in the dynamics of relative abundance, as revealed by equation (6). Species diverge based on differences between their values of E/b, and these differences are unrelated to competition. The average level of competition and fluctuations in competition are affected in a major way by the actual, as opposed to relative, values of the E/b, especially those of the dominant species (see, e.g., eq. [13]). Fluctuations in competition can indeed be a major cause of population fluctuations, but they have no role in relative fluctuations while species are affected linearly by a common competitive factor. They neither slow nor speed competitive exclusion. Rather, they limit the community as a whole, not any species in relation to others.

In conclusion, however, we look at this linear-additive model, with a single competitive factor, the system must ultimately be dominated by a single species. Fluctuations in the system do not weaken this conclusion. In fact, they may strengthen it.

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CONTRARY PERSPECTIVES

Hutchinson's Hypothesis: When Do Environmental Fluctuations Promote Coexistence?

Our analysis of linear-additive models sheds light on an influential hypothesis put forward by Hutchinson (1961). He assumes that environmental fluctuations alter the rank order of competitive superiority. Without introducing any features that take him beyond the general model analyzed above, he concludes that species coexistence is possible if the timescale for competitive exclusion in a fixed environmental state is comparable to the timescale of environmental change. Under conditions where the environment changes much faster or much slower, he concludes that competitive exclusion must still occur.

If the dynamics of such a system are described by the Lotka-Volterra equations or any other additive linear model, then Hutchinson's conclusions are in error. Both on the short and the intermediate timescales of environmental change that he discusses, exclusion will take place at rates given by average favorabilities of the environment for the species, as determined by average environmental responses. Fluctuations in the system are irrelevant. There is no a priori reason to expect that the average environmental responses of different species should lead to similar tolerances to competition, and so linear rates of approach to competitive exclusion are to be expected. Average environmental responses would lead to a system closer to neutrality, with slower competitive exclusion, than if the environmental responses were fixed in a particular environmental state favoring one species over others. There is no reason, however, to invoke fluctuations to arrive at these conclusions.

Deviations from the modeling framework that we have assumed here, though not part of Hutchinson's arguments, are critical for environmental variability to have a role in diversity maintenance, as we shall see below. Although it has been claimed that Hutchinson's hypothesis is obviously true (Huston 1979), we have shown that in detail it is wrong; missing from his arguments are the most important premises capable of leading to the conclusion that diversity can be maintained by fluctuations. We discuss these important premises in a later section (''Alternative models'').

Huston's Model: When Does Disturbance Promote Coexistence?

Using Lotka-Volterra competition models, Huston (1979) concludes that an intermediate frequency of disturbance is favorable to species coexistence provided the various species have similar values of their intrinsic rates of increase. He does not predict indefinite coexistence but slow competitive exclusion. The imposed disturbances are pulses of mortality recurring at regular intervals of time and, hence, harshness from high average mortality rates (low average environmental responses). Slowing of competitive exclusion occurs in Huston's model by lowering all species' tolerances to competition to near zero, taking them all to the edge of existence (app. A). Similar intrinsic rates of increase are essential for indiscriminate mortality to have this effect. Long-term population dynamics are very slow as the $\overline{E}$'s and $\overline{C}$'s are very small in magnitude. Short-

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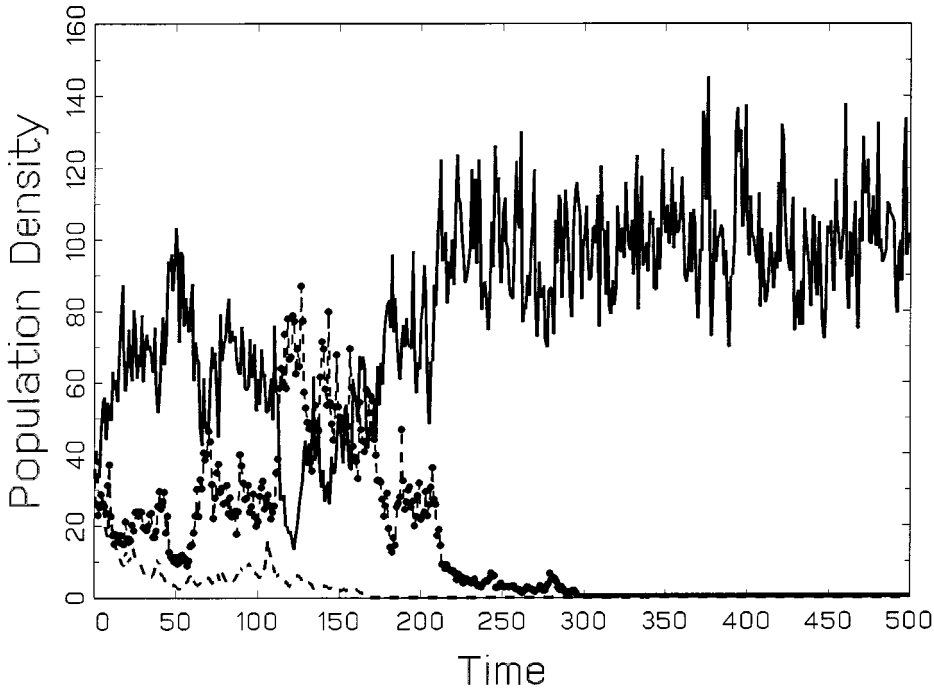

FIG. 3.—Simulation of a three-species equal-carrying-capacity Lotka-Volterra model in a random environment. In the absence of environmental fluctuation, the system has neutral stability, and species relative abundances remain constant. If environmental fluctuations have random components that do not affect the species identically, random drift must take all but one species to extinction, as depicted. The simulation is based on equation (A1) of appendix A with $\alpha_{ij} = 0.01$, $r_i^0 = 1$, and the ϵ_i independent white noise processes with variance per unit time of 0.04.

term dynamics are not slow, however: large increases are followed by large deterministic declines. As shown above, because the model is linear and additive, these highly varying deterministic dynamics on the short timescale are irrelevant to the long-term outcome. Because the mortality fluctuations are regular, the identical result would be achieved by constant mortality with the same average value.

One can ask why the assumption of similar intrinsic rates of increase should be satisfied by the different members of a natural community; this situation seems unlikely. A system so highly dynamic on short-term scales also seems unlikely to be wholly deterministic. Thus, even accepting the assumptions of similar intrinsic rates of increase and average mortality rates, which would slow deterministic dynamics and delay competitive exclusion, one must face the reality that in nature mortality fluctuations are at least partly stochastic and such stochasticity is likely to dominate the long-term dynamics of the system (fig. 3), especially given the low tolerance of competition resulting from Huston's assumptions. Thus, the delay in competitive exclusion that is possible from Hus-

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ton's mechanism is limited. Indeed, Huston's model does not seem to provide a realistic mechanism of species coexistence. More plausible explanations of disturbance as a coexistence mechanism are discussed below in the section on the successional mosaic hypothesis.

The Ideas of Grime: Harshness and the Importance of Competition

Grime (1979) suggested that stress (defined as reduction of biomass accrual) and disturbance (defined as removal of biomass) are major factors affecting the organization of communities. He suggests that competition is important primarily in low stress, low disturbance conditions and, thus, that the importance of competition is reduced by either stress or disturbance. Although Grime used the word *competition* to refer to purely resource consumption, whereas we have adopted the more conventional population biologists' usage, our definitions of harshness cover Grime's definitions of stress and disturbance. Thus, our analysis shows that Grime's scheme does not show that population interactions, such as competition, are made less important in stressful environments or in those subject to disturbance.

Hubbell's Model: The Role and Likelihood of Competitive Equivalence

Slow rates of competitive exclusion have often been regarded as a sufficient explanation of high diversity and of the impotence of competition in shaping diversity patterns (Hubbell 1979; Huston 1979; Shmida and Ellner 1984; van der Maarel and Sykes 1993). Our objection to this conclusion has two parts. First, the conditions necessary for slow competitive exclusion are not robust. Second, slow decay of species diversity does not explain high diversity in the absence of a satisfactory mechanism for its origin. To the contrary, the situations implying slow decay of diversity seem to preclude a satisfactory mechanism for the origin of high diversity.

Huston's model, discussed above, is one proposal for achieving slow competitive displacement, but we have argued that it is implausible and not robust to stochastic fluctuations. A less extreme scenario for slow competitive displacement is even matching of competitive abilities of species (competitive equivalence; Hubbell 1979; Shmida and Ellner 1984) or, in our terminology, similar tolerance of competition. In the Lotka-Volterra model, this corresponds to species having similar carrying capacities, which in some instances can be achieved by the addition of harshness to a system (app. A). As shown in appendix A, however, the conditions necessary for this are quite restricted. In all cases, these systems exhibit nearly neutral stability, meaning that perturbations from a given state are neither reduced nor enlarged by the dynamic rules of the system. Such neutral stability is quite fragile. It can easily be turned around by something omitted from the model, even if that omitted factor is weak (Lewontin 1969). Discussion of Hubbell's (1979) rain forest model is instructive. Although Hubbell's model cannot be expressed in the form of our general model (eq. [2]), it is a prominent model in the discussion of slow competitive displacement.

Hubbell's (1979) model assumes space is the sole limiting resource, which means that, in our terminology, there is a single competitive factor, which is the

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inverse of space availability. In this model community, a single niche is occupied by all species. Briefly, the model works as follows.

Species have identical demographic parameters, death occurs at a constant rate, and recolonization of sites vacated by death occurs by a random draw from the species pool with the probability of recolonization by a particular species equal to its relative abundance. This is a special case of the lottery model (Chesson and Warner 1981), with the main special feature being the absence of environmental fluctuations.

As the species have identical demographic parameters, the model is neutrally stable and leads to a slow random walk to extinction because of demographic stochasticity. The suggestion that migration from outside the system (i.e, from ''regional species pools''; Hubbell 1984; Ricklefs and Schluter 1993) will maintain diversity indefinitely can only be the case if diversity is maintained in the areas from which the migrants originate. If there are truly no niche differences anywhere, there can be no greater expectation that diversity is maintained in areas outside the system than within it.

The assumption of equal demographic parameters seems very unlikely, even if differences between them are not discernable when the species are studied on a small spatial scale. Enlarging the spatial scale may reveal differences between species as changes in relative abundances on a regional scale. This observation is perfectly consistent with the hypothesis of subtle variation over space in the relative values of the demographic parameters of different species, which constitutes broadly overlapping but different spatial niches. Such subtle differences between niches can be sufficient for stable species coexistence when species have similar average adaptedness to the region, that is, when they have similar average demographic parameters (Chesson 1991; Tilman and Pacala 1993), as opposed to identical demographic parameters everywhere. In this scenario, local diversity is a product of regional diversity, but variation in space is critical to the maintenance of regional diversity. The system may look neutrally stable in that the differences between species are subtle and drift in local relative abundances occurs, but regionally it is not neutral. The subtle differences between species stabilize regional diversity.

If one accepted Hubbell's hypothesis that slow species extinction explains the persistence of highly diverse systems, difficulties would still remain. Slow rates of decay can only explain the slow loss of diversity, not the actual species diversity. In a model of community dynamics with slow decay of species diversity, the diversity observed at any time depends on the initial diversity, the rate of decay, and the amount of time elapsed. The initial diversity is of major importance, but natural communities do not just appear with some value of diversity, independent of the properties of the system. The closest one might come is the hypothesized spread of tropical forests from Pleistocene refugia at the beginning of the Holocene, where an initial diversity derived from those refugia might be reasonable (Flenley 1993). More commonly, we should not expect to be able to identify an initial diversity, and species are best regarded as arriving at the community continuously over time. The actual diversity achieved might then be thought of as some balance between arrival and extinction rates, as in the theory

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of island biogeography (MacArthur and Wilson 1967; Hubbell and Foster 1986*a*).

Speciation and establishment of new species within a neutrally stable system seem unlikely. If the species have not experienced selection pressures that would differentiate them ecologically, the conditions for a species split are greatly restricted. Chance mutation (e.g., polyploidy, translocations, etc.) that might lead to instant reproductive isolation (Tilman and Pacala 1993) is possible, but such reproductively isolated mutants have little hope of persistence unless they are at some advantage under some conditions, and such ecological differentiation would destroy neutrality. Thus, the chances for sympatric speciation consistent with neutral stability are slim, implausibly restricting the rate of speciation and the likelihood of highly diverse neutrally stable systems.

In summary, the hypothesis that diverse systems are neutrally stable seems highly implausible. Although tropical forests were the motivation of Hubbell's (1979) neutrally stable model, we note that empirical research in these systems has steadily revealed a variety of potential stabilizing mechanisms, including species-specific density-dependent seed and seedling mortality (Clark and Clark 1984; Connell et al. 1984; Hubbell and Foster 1990; Gilbert et al. 1994), spatial niches of various sorts (Hubbell and Foster 1983, 1986*b*), and recruitment fluctuations that may lead to the storage effect (Runkle 1989; Iwasa et al. 1993) as discussed below.

ALTERNATIVE MODELS

The linear-additive models that we have studied so far reveal the limitations of the common logic on the consequences of harsh and fluctuating conditions for community dynamics and diversity. These models emphasize the fact that the positive and negative effects of harshness and fluctuations may cancel out and have no net overall effect. When they do not cancel out in systems with linear and additive dynamics, they lead at best to neutral stability or at worst to more rapid competitive exclusion. Without invoking the effects of deviations from this logical framework, stronger conclusions about the role of harsh or fluctuating conditions are not valid.

It is clear that nature is much more complex than the linear-additive framework permits, and we shall see below that deviations from this framework do have major effects. However, the standard arguments that harshness and fluctuations allow maintenance of diverse communities do not simply become valid with more realistic assumptions. There are two reasons for this: the nature of the effects of harsh and fluctuating conditions depends on the specific deviation from the linear-additive, few competitive factors framework, and the magnitude of any such effect depends on the magnitude of the deviation. We now consider three examples of the kinds of ecological scenarios that permit major effects of harshness or fluctuations.

Harshness and Resource Partitioning

First we consider deviations from a few competitive factors. Multiple competitive factors can permit stable coexistence, but they do not have to: they are

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merely necessary for equilibrium coexistence in the standard competition models. Harshness can enable the potential coexistence arising from many competitive factors. This seems likely to be a common situation in nature, which we explore by means of MacArthur's (1970) mechanistic model of Lotka-Volterra competition based on competition for many resources.

Two important requirements must be satisfied for species coexistence in MacArthur's model. First, species must depend on different resources to different degrees, that is, they must have nonproportional resource use (Chesson 1990*b*). This is necessary so that the resources cannot be reduced to a single composite competitive factor. Second, and most significant for our discussion here, species cannot be too unequal in their potential for population growth or a species may monopolize all resources including those that are the mainstay of other species. The details of these phenomena for a system of two consumer species are developed elsewhere (Chesson 1990*b*) and are modified to address the issues of this article in appendix D.

Three important quantities determine coexistence: proportionality of resource use, ρ, maximum resource harvest rate, h_i', and the maintenance requirement, m_i'. The quantity ρ ranges from 0 to 1, with 0 meaning no overlap in resource use and a value of 1 meaning exactly proportional resource use. The value of m_i' represents the amount of resource that needs to be harvested per capita for zero population growth. The difference between the maximum harvesting rate and the maintenance requirement, $h_i' - m_i'$, is the net maximum harvesting rate. Like tolerance to competition, discussed above, both h_i' and m_i' are measured in units that facilitate comparisons between species and reduce complex formulas to simple ones (app. D). In terms of these quantities, a stable coexistence occurs if the following inequality is satisfied:

$$\rho < (h_i' - m_i')/(h_j' - m_j') < 1/\rho\,. \tag{17}$$

As ρ lies between 0 and 1, this represents a range of values for the ratio of net maximum harvesting rates $(h' - m')$ centered on the value 1. Thus, if the two species have equal net harvesting rates, a stable coexistence is guaranteed, provided only that $\rho < 1$, that is, that resource dependence is nonproportional. Coexistence will not occur if the ratio of the net maximum harvesting rates lies outside this range. Thus, species j will dominate and drive species i extinct if $h_j' - m_j'$ is too large compared with $h_i' - m_i'$, that is, if $(h_i' - m_i')/(h_j' - m_j') < \rho$. Harshness can alter the outcome by increasing resource maintenance requirements.

Predation or harsh physical conditions selectively increasing mortality rates of the dominant species (Paine 1966; Lubchenco 1978) will increase m_j' because the increased mortality increases the amount of resource that must be harvested for zero population growth. Thus, the ratio of the net maximum harvesting rates of the two species could increase above ρ, enabling coexistence. If mortality on species j is too high, however, this ratio will exceed $1/\rho$, in which case species j will be driven extinct by the combined effects of competition and harshness. Unlike the case of a single competitive factor, here selective mortality can convert competitive exclusion into stable coexistence. The critical feature is the ex-

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istence of differences in resource use as indicated by a value of $\rho < 1$. With ρ different from 0, coexistence is not guaranteed because each species still has the capacity to reduce the resources available to the other species. If species *j* gathers too much of a resource on which species *i* depends, even if species *j* does not depend greatly on such a resource, species *j* can drive species *i* extinct. Note, however, that nonselective mortality, such as might occur with disturbance, need not have equal effects on the scaled maximum net harvesting rates (app. D). For example, there will be more effect on a species with a low intrinsic rate of increase than on a species with a high intrinsic rate of increase (cf. Lotka-Volterra section above and Lubchenco 1978).

The important stabilizing mechanisms in this example come from the different niches that the species have. This niche difference means that when a species is at low density it experiences reduced competition because intraspecific competition is reduced without interspecific competition increasing in compensation. In the absence of niche differences, increased interspecific competition would eliminate the advantage of reduced intraspecific competition. Density-independent mortality that results from predation or harsh physical conditions merely adjusts the existing stabilizing mechanisms rather than being a stabilizing mechanism. By reducing the density of the dominant, mortality reduces competition experienced by the subordinate, allowing it to have a positive growth rate when its own density is low and so persist in the system. A similar adjustment of stabilization by resource partitioning has been explored by Holt (1985), but Holt's proposal differs in an important respect: dependence of per capita growth rates on competitive factors is nonlinear, with different species having different nonlinear responses to the same factors (the species densities). Thus, in Holt's model nonselective predation can affect species' coexistence, making it more likely with some nonlinearities and less likely with others.

Predators as a Niche Dimension

In the above examples, density-independent mortality does not add any stabilizing effect in its own right as it does not cause population growth rate to increase as density falls. It simply allows the higher growth rate at low density to be positive. Density-dependent mortality, however, can directly stabilize coexistence, providing all or part of the stabilizing mechanism. For example, in a three-species system, two species may be limited mostly by specific resources on which they depend, and a third species may be limited by a predator imposing density-dependent mortality on that particular species. These species have distinct niches defined by how they are affected by the various density-dependent agents in the system, be they resources or predators.

A variation on this situation occurs where all species are limited by density-dependent predators. This situation may lead to coexistence by predator partitioning, in analogy with resource partitioning, as anticipated by MacArthur (1970) and as suggested for tropical forests by Janzen (1970) and Connell (1971). In addition, a single predator species can act as several limiting factors (Murdoch 1969; Levin 1970; Murdoch and Bence 1987) because predators may behave differently toward their prey species depending on the densities of other

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prey species. In particular, predation may be frequency dependent, leading to reduced predation on a species when it declines in relative abundance. In this way predation promotes recovery to higher densities, stabilizing diversity.

Predation can also stabilize diversity when it is coupled with spatio-temporal variation, as discussed below (''The successional mosaic hypothesis'' section). It is important to recognize, however, that the simple addition of mortality to a system is not sufficient for coexistence without the existence of separate niches for the various species (Chesson 1991). In particular, limitation of the total density of all species by predation is not sufficient to explain maintenance of species diversity.

Nonadditivity: The Storage Effect

We have seen that if the dynamics of a community are additive and linear, fluctuations in environmental and competitive responses are of minor importance. When competitive responses (C_i) are nonlinear functions of the underlying competitive factors, however, the average environmental responses ($\overline{E}_i$) of persisting species no longer determine the average competitive responses of other species (Chesson 1994). Fluctuations in the competitive factors affect the average values of the competitive responses and may favor species coexistence (Chesson 1994) according to a mechanism worked out by Levins (1979) and Armstrong and McGehee (1980). Removal of the assumption of additivity also allows fluctuations to maintain diversity. Then the average value of r_i is no longer determined by the average of the environmental response minus the average of the competitive response. Such nonadditivity may promote coexistence strongly and is the focus of our discussion below.

To see how nonadditivity together with fluctuations may affect species coexistence, we consider the following approximate formula

$$r_i(t) \approx E_i(t) - C_i(t) + \gamma E_i(t) C_i(t), \tag{18}$$

which applies to nonadditive models generally (Chesson 1994). The constant γ specifies the magnitude and type of nonadditivity. A negative value of γ indicates less than additive combined effects of environmental and competitive responses, which seems to be the most likely situation in nature (Chesson and Huntly 1988). It is expected when organisms have bet-hedging life-history strategies or have adaptations that allow them to avoid investment in situations where they are unlikely to do well. A negative γ arises naturally in a variety of ways, most obviously from population structure. For instance, the division of a population into juveniles and adults, which are sensitive to different degrees to the effects of environmental factors and competition (Chesson and Huntly 1988; Chesson 1990*a*) can lead to nonadditive population dynamics that buffer population growth against the harmful effects of competition and a poor environment but still permit strong population growth with a favorable environment and reduced competition.

To understand the ultimate fate of a population, we again look at its average growth rate over time, which is given here as

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$$\bar{r}_i \approx \overline{E}_i - \overline{C}_i + \gamma \overline{E}_i \overline{C}_i . \tag{19}$$

Thus, long-term population growth is determined by the average of three terms. But if long-term growth depends only on averages, how can fluctuations have an effect? The answer is that the average $\overline{E}_i \overline{C}_i$ depends on fluctuations in E_i and C_i because it is the average of the product of $E_i(t)$ and $C_i(t)$ over time, that is,

$$\overline{E}_i \overline{C}_i = \frac{1}{T} \cdot \sum_{t=0}^{T-1} E_i(t) C_i(t) . \tag{20}$$

Statistical theory (e.g., Hogg and Craig 1978) shows that the average of the product differs from the product of the averages ($\overline{E}_i \cdot \overline{C}_i$), according to the formula

$$\overline{E}_i \overline{C}_i = \mathrm{Cov}(E_i, C_i) + \overline{E}_i \cdot \overline{C}_i , \tag{21}$$

where $\mathrm{Cov}(E_i, C_i)$ is the covariance between $E_i(t)$ and $C_i(t)$, measuring the magnitude and sign of joint fluctuations in $E_i(t)$ and $C_i(t)$. (The covariance is equal to the correlation between $E_i(t)$ and $C_i(t)$ times the product of their standard deviations.) Fluctuations affect the average growth rate through this covariance. Thus, $\bar{r}_i$ is affected by the standard deviations of each of $E_i(t)$ and $C_i(t)$ and the correlation between them. If $E_i(t)$ and $C_i(t)$ are positively correlated (positive covariance between environment and competition), then fluctuations increase the average of the products, and because we assume a negative value for γ, fluctuations decrease $\bar{r}_i$. In contrast, if $E_i(t)$ and $C_i(t)$ are negatively correlated (negative covariance between environment and competition), then the product is decreased by fluctuations and $\bar{r}_i$ is increased.

Importantly, the covariance between environment and competition depends on the absolute and relative densities of the species. It is assumed that when the environmental response of a species increases, the species places more demand on resources. When a species is abundant relative to other species, it is the main consumer of resources and so fluctuations in its environmental response lead to positively covarying fluctuations in competition. As a species becomes less common relative to other species, there is no reason for a close correlation between its environmental response and competition, as other species contribute more to competition. Asynchrony in the environmental responses of the different species (temporal environmental niches) means that the environmental response of a species at low density may show little or even negative covariance with competition (Chesson and Huntly 1988). With negative γ, such changes in the covariance between environment and competition mean that a species at low density gains an average growth advantage over species at high density, promoting coexistence.

A particular nonadditive model that illustrates these findings is the lottery model (Chesson and Warner 1981). Although commonly considered with population sizes as a continuous variable, the results discussed here remain valid for populations of discrete size, provided the population is large (Chesson 1982). This is of particular importance as the forest model of Hubbell (1979), discussed above, is a special case of the lottery model with discrete population sizes

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(Chesson 1982). Hubbell's version of the lottery model does not have temporal variation in the environment and so describes slow species loss. With temporal environmental variation, stable coexistence of any number of species is possible. Indeed, that such variation may maintain diversity in tropical forests is now one of several serious alternatives for the maintenance of tropical diversity (Runkle 1989; Iwasa et al. 1993). In the lottery model, nonadditivity comes from the division of the life cycle into juveniles and adults with different sensitivities to environment and competition. The adult survival parameter, s, is assumed insensitive to environmental factors and competition, but recruitment of juveniles to the adult phase is highly sensitive to both.

In the lottery model, the net benefit that a low density species has in competition with other species is

$$\frac{s}{1 - s} \cdot \frac{\sigma^2(1 - \rho)}{n - 1}, \tag{22}$$

where $\gamma = -s/(1 - s)$, and $\sigma^2(1 - \rho)/(n - 1)$ is the difference between the environment-competition covariance for the low density species and the average of that of its competitors (Chesson 1994). The covariance difference is made up of the variance in the environmental response σ^2, the correlation ρ between the environmental responses of different species, and n, the number of species. The parameter ρ measures synchrony between species in their responses to the environment. A value of $\rho = 1$ means that the species environmental responses are perfectly synchronous and linearly related. Thus, the quantity $1 - \rho$ measures differences in the way species respond to the environment. Note that the benefit to a species at low density given by expression (22) increases in an unlimited way with the variance of the environmental response and therefore potentially permits stable coexistence of many species.

Although Hutchinson (1961) was correct in his expectation that environmental fluctuations have a role in maintaining species diversity, his discussion omits the critical roles of nonadditivity and covariance between environment and competition. It is not possible to conclude from Hutchinson's arguments that coexistence will be stable in the sense that species at low density have positive average growth rates when environmental conditions vary and favor different species at different times. Deviations from additivity, as discussed here, or of weaker effect (Chesson 1994), deviations from linearity, are needed for stable coexistence to arise.

The Successional Mosaic Hypothesis

Spatial variation can have an important role in coexistence (Horn 1971), and when disturbance creates spatial variation it has great potential as a coexistence-promoting mechanism (Paine 1979; Sousa 1979; Tilman 1982). Discussions of disturbance by Caswell (1978), Connell (1979), and Hastings (1980) all assume that disturbance is patchy in space and that disturbance begins a successional sequence at any locality. Because disturbance is asynchronous in space, different localities are at different successional stages at any one time. Thus, on a regional

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scale, diversity can be high because species characteristic of a variety of successional stages are present. The magnitude and frequency of disturbance then determine the relative abundances of different species.

Competition may drive succession, and although this is not an essential requirement for succession to occur, such competition-driven successions do seem to be associated with the coexistence-promoting effect of intermediate disturbance (see app. E). Under this scenario, resources initially are abundant after disturbance (space and/or nutrients have been released), there is little competition (Tilman 1990), and species that are poor competitors but good colonizers are favored. Over time, late-successional species become more abundant by being better competitors for scarce resources or better holders of space in the face of competition. The successional process, trade-offs that cause species to do best at different stages of succession, and spatial asynchrony of disturbance all play important roles in this diversity-maintaining mechanism. Thus, rather than the intermediate disturbance hypothesis, which is not informative about the real mechanism, we shall refer to this idea as the successional mosaic hypothesis.

This successional mosaic hypothesis involves species differing fundamentally in their biology in order to occupy different successional stages. Disturbance does not simply lessen competition, preventing the most competitive species from dominating. For example, in appendix E we show that diversity is not maintained with inhibitional succession (Connell and Slatyer 1977), in which individuals are not displaced by competition from superior competitors, but hold space until death from other causes. The successional mosaic model deviates markedly from the general additive linear model and has nonadditive elements analogous to those found with the storage effect (P. Chesson, unpublished manuscript). In this case, there are spatial as well as temporal storage effects.

DISCUSSION

Our analysis of the general linear-additive model reveals serious errors in the argument that harshness promotes species diversity by lessening competition. A species is excluded from a system when its long-term population growth rate is negative. Harshness has a direct negative effect on that growth rate and lowers a species' tolerance of competition. Thus, the positive indirect effect of lowered competition may not be sufficient to make any difference to a species' persistence. Indeed, these indirect benefits may fall short of the direct negative effects, and harshness may hasten competitive exclusion.

We distinguish fluctuations from harsh conditions unless they are associated with average conditions that have direct negative effects on population growth rates. The linear-additive model gives no reason for expecting fluctuations to have particularly favorable or unfavorable effects on species coexistence or to lessen the importance of competition

Our results show that harshness can slow competitive exclusion in some circumstances, especially when the species show an *r-K* trade-off. However, this slowing of competitive exclusion has been overstated in the literature, for common models do not allow for effects of realistic environmental fluctuations.

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Moreover, this slowing of competitive exclusion does not reflect stabilizing mechanisms but, rather, near-neutral stability. Near-neutral stability does not explain diversity, for near-neutral systems lack mechanisms for building diversity; although the diversity of a near-neutral system may decay slowly, the origin of its diversity is unexplained. In addition, neutral stability seems quite unlikely in nature, as it can easily be overridden by factors that allow differential advantage to a species: we should expect evolution of species differences that destroy near-neutral dynamics.

Although harshness and fluctuations alone cannot stabilize coexistence, they can affect coexistence by their interaction with or generation of other mechanisms. These other mechanisms involve the critical elements of niche differentiation. Where harshness makes species more equal in demographic rates, stable coexistence may result more easily from classical resource partitioning or from species-specific responses to spatial patches. In these cases, harshness does not itself provide a stabilizing mechanism but merely adjusts the parameters of a system, potentially facilitating or broadening the effects of other diversity-stabilizing mechanisms. Temporal fluctuations also may form part of a stabilizing mechanism when species use ecological conditions that occur through time in ways that are nonadditive or nonlinear. The nonadditive or nonlinear responses of species generate the potential for costs and benefits realized at different times to combine in ways that do not cancel each other; net benefits promote coexistence and diversity.

Our results do not suggest a diminished role of competition in the presence of harshness or fluctuations, for we have seen that the direct effect of harshness makes a population less tolerant of competition. In other words a population subject to harsh environmental conditions can have a negative growth rate and become extinct at lower levels of competition. Even though the strength of competition may be reduced, the ability of competition to shape a community need not be diminished. Harshness may allow the effects of resource partitioning to be large enough to be an effective mechanism of coexistence. Competition shapes such a community, because only those species differing sufficiently in resource use can coexist. Moreover, in allowing coexistence, harshness creates the potential for coevolutionary adjustments, such as character displacement, among the coexisting species.

Similar considerations apply to the role of fluctuations, which we have examined specifically in relation to the storage effect and the successional mosaic hypothesis. The storage effect allows coexistence of species differing sufficiently in their responses to environmental conditions. Without this sufficient degree of difference, some species are excluded by interspecific competition. Again, the balance between interspecific and intraspecific competition among the coexisting species should lead to coevolutionary adjustment of the degree of specialization on environmental conditions.

In addition, competition is but one form of density-dependent limitation that can affect the relationships between species. The conclusions we have derived for competition apply also to predation and other forms of density-dependent limitation. For example, we can consider nonlinearity and nonadditivity in re-

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sponse to predators and the environment. Density-dependent limitation is inevitable. Differentiation in relation to density-dependent factors, either directly or indirectly via factors such as environmental fluctuations that interact with the density-dependent factors, is a critical component of all mechanisms of stable coexistence.

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APPENDIX A

Lotka-Volterra Models

A common formulation of the Lotka-Volterra competition model in a variable environment is

$$\frac{1}{N_i} \cdot \frac{dN_i}{dt} = r_i^0 \left(1 - \sum_{j=1}^{k} \alpha_{ij} N_j \right) + \epsilon_i , \tag{A1}$$

where k is the number of species, α_{ij} is the coefficient of competition for the effect of species j on species i, ϵ_i is an environmental perturbation to the per capita growth rate, and r_i^0 is the intrinsic rate of increase, that is, the per capita growth rate in the absence of competition and environmental perturbations. If this equation is integrated over the unit of time from t to $t + 1$, we obtain equation (2) of the text:

$$r_i(t) = E_i(t) - C_i(t) , \tag{A2}$$

where here

$$r_i(t) = \int_t^{t+1} \frac{1}{N_i(u)} \cdot \frac{dN_i(u)}{du} \, du = \ln N_i(t + 1) - \ln N_i(t) , \tag{A3}$$

$$E_i(t) = r_i^0 + \int_t^{t+1} \epsilon_i(u) \, du , \tag{A4}$$

and

$$C_i(t) = r_i^0 \sum_{j=1}^{k} \alpha_{ij} \int_t^{t+1} N_j(u) \, du . \tag{A5}$$

The competitive response $C_i(t)$ can be seen to be further structured as

$$C_i(t) = \sum_{l=1}^{m} b_{il} F_l(t) , \tag{A6}$$

with

$$F_l = \int_t^{t+1} N_l(u) \, du \tag{A7}$$

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and

$$b_{il} = r_i^0 \alpha_{il}. \tag{A8}$$

In the special case where a species has proportional effects on other species, α_{il} can be expressed as a product, $\alpha_i \beta_l$. Then we can define the common competitive factor as

$$F = \sum_{l=1}^{m} \beta_l \int_t^{t+1} N_l(u)\,du, \tag{A9}$$

and sensitivity to the competitive factor F can be defined as

$$b_i = r_i^0 \alpha_i. \tag{A10}$$

Equation (4) of the text applies to this special form of the Lotka-Volterra model.

Assuming that the average of ϵ_i over time is zero, tolerance of competition in this special form of the Lotka-Volterra model is equal to $1/\alpha_i$. This quantity is the carrying capacity of the environment for species i, where population densities are measured in the common units of the competitive factor—that is, rather than in numbers of organisms per unit area, the density of species i is measured in terms of the total competitive effect that it has.

The commonly assumed trade-off between r and K means here that a species with a low value of r_i^0 should have a large value of $1/\alpha_i$, and therefore a small value of $b_i = r_i^0 \alpha_i$ (sensitivity to competition). Thus, a high tolerance of competition may correspond to low sensitivity to competition.

The above discussion assumed that ϵ had a zero average over time. A nonzero average value over time is equivalent to changes in r_i^0 and α_i. For example, if the average of ϵ over time is $-\delta$, then

$$\frac{1}{N_i} \cdot \frac{dN_i}{dt} = (r_i^0)' \left(1 - \sum_{j=1}^{k} \alpha_{ij}' N_j\right) + \epsilon_i', \tag{A11}$$

where now $\epsilon_i' = \epsilon_i - \delta$, which does have a time average equal to zero, $(r_i^0)' = r_i^0 - \delta$, and $\alpha_{ij}' = r_i^0 \alpha_{ij}/(r_i^0 - \delta)$. Thus, having nonzero average environmental perturbation is equivalent to a Lotka-Volterra model with different parameters and zero time average for the environmental perturbation. In particular, average environmental harshness ($\delta > 0$) is equivalent to a lower r_i^0 and a lower carrying capacity, $K = 1/\alpha_i$, with no average environmental harshness. Note that r_i^0 determines the overall rate of population dynamics for species i and so lower r_i^0 means slower population dynamics. More on this topic can be found in earlier work (Chesson 1994).

Huston (1979) emphasizes slowing of competitive exclusion in the case where the r_i^0's are similar in value and competition leads to a common reduction for all species. This means that as the average mortality rate is increased, the dynamics of the system are uniformly slowed on a timescale equal to or greater than the intervals between disturbances, and accompanying this slowing is a reduction in carrying capacity to near-zero values.

Slowing of competitive exclusion without reduction of carrying capacities to zero is possible in the Lotka-Volterra model when tolerances to competition, and hence the carrying capacity, are made very similar by disturbance. Such a result occurs for just a very precise relationship between the parameters of the various species and the average mortality resulting from disturbance. To see how this occurs in the single factor form of the Lotka-Volterra model (i.e., where $\alpha_{il} = \alpha_i \beta_l$), we first rank species in order of their values of α_i (in inverse order of carrying capacity). Then for a given average value of disturbance δ, the following formula for r_i^0 defines the situation permitting a neutrally stable persistence of the community:

$$r_i^0 = \frac{\delta}{[1 - (1 - \delta/r_1^0)\alpha_i/\alpha_1]}. \tag{A12}$$

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This formula embodies an *r-K* trade-off as larger values of α_i (smaller values of K_i without disturbance) correspond to larger values of r_i^0. Note that this neutrality does not require the species to have zero values of $(r_i^0)'$ (or equivalently $\bar{E}_i$). In contrast to Huston (1979), this means of achieving neutral long-term community dynamics has the properties that carrying capacities need not be near zero and the weighted density of the whole community (the competitive factor F) is stable: perturbations above or below the equilibrium value of F are followed by return to this value. Relative abundances, however, remain at the values they have after perturbation.

APPENDIX B

General Linear-Additive Models

In the text it is shown that relative abundances change according to the following formula:

$$R_{ij}(t+1) - R_{ij}(t) = E_i(t)/b_i - E_j(t)/b_j. \tag{B1}$$

Summing this formula for $t = 0$ to $t = T - 1$, and canceling terms on the left-hand side leads to the equation

$$R_{ij}(T) - R_{ij}(0) = \sum_{t=0}^{T-1} E_i(t)/b_i - E_j(t)/b_j \tag{B2}$$

$$= T \cdot (\bar{E}_i/b_i - \bar{E}_j/b_j), \tag{B3}$$

where $\bar{E}_i$ and $\bar{E}_j$ are respectively the averages of $E_i(t)$ and $E_j(t)$ over the time period $t = 0$ to $t = T - 1$.

To understand divergence of relative abundances, we need to examine both the mean and the variance of $R_{ij}(T)$. If $E_i(t)$ is a stationary time series, it has a theoretical mean μ_i, and $\bar{E}_i$ converges on this value with probability 1 as $T \to \infty$. (In the case of nonergodic stationary processes [Breiman 1968], we can take μ_i as a mean conditional on the invariant sigma field.) The deviation of $\bar{E}_i$ from μ_i has asymptotic variance proportional to T or more (Breiman 1968). Thus, as a conservative statement, the divergence in relative abundance can be written as

$$R_{ij}(T) - R_{ij}(0) = T \cdot (\mu_i/b_i - \mu_j/b_j) + \sqrt{T} \cdot W_{ij}(T), \tag{B4}$$

where $W_{ij}(T)$ is a random variable with mean 0 and bounded variance. Equation (B4) consists of a deterministic linear rate in T given by $\mu_i/b_i - \mu_j/b_j$ and a square root rate in T with a random and changing direction and magnitude. The deterministic linear rate will dominate whenever $\mu_i/b_i - \mu_j/b_j$ is of appreciable magnitude. However, in the circumstances where species have nearly identical tolerances to competition, the stochastic square root rate becomes important and ensures that relative abundances diverge even though species have identical tolerances to competition.

In Huston's (1979) model, disturbance is regular in occurrence, and therefore only the linear rate of approach to extinction is found in the long run—the asymptotic variance of $W_{ij}(T)$ is zero. Thus, when the linear rate is made nearly equal to 0, there is no possibility of the stochastic square root rate taking over and causing competitive exclusion. Indeed, the regular rate of disturbance in Huston's model gives the unrealistic impression of stabilization of densities by disturbance.

APPENDIX C

Multiple Density-Dependent Factors

If there are several competitive or, more generally, density-dependent factors but, nevertheless, still fewer density-dependent factors than species, the matrix b_{il} must have rank less

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than k, the number of species. It follows that there must be a nonzero vector $\mathbf{a} = (a_1, a_2, \ldots, a_k)$, such that

$$\sum_{i=1}^{k} a_i b_{il} = 0, \tag{C1}$$

for each i. Moreover, as each species must have some dependence on the limiting factors (by assumption) the vector $\mathbf{a}$ must also have at least two nonzero components. Defining

$$R(t) = \sum_{i=1}^{k} a_i \ln N_i(t), \tag{C2}$$

we see that

$$R(t + 1) - R(t) = \sum_{j} a_j E_j(t), \tag{C3}$$

which depends just on the environment. As in the case of R_{ij} for a single competitive factor in a stationary environment (app. B), this quantity will grow with time according to the sum of a deterministic linear rate and a stochastic square root rate:

$$R(T) - R(0) = T \cdot \sum_{i=1}^{k} a_i \mu_i + \sqrt{T} \cdot W(T). \tag{C4}$$

Except in the unlikely event that

$$\sum_{i=1}^{k} a_i \mu_i = 0, \tag{C5}$$

$R(T)$ must converge to plus or minus infinity. If, however, equation (C5) is satisfied, then the stochastic square root rate nevertheless ensures that R becomes arbitrarily large in magnitude in all realistic scenarios of environmental fluctuation. As no species can approach infinity, this can only mean that some species approaches zero (has log abundance approach minus infinity)—in other words, becomes extinct. Only when the number of species is reduced to the number of density-dependent limiting factors can this conclusion be avoided.

Equation (C3) can be rearranged to reveal the rate of approach to extinction. Suppose species i does not persist in the system, but the other species do; then in analogy with equation (10) of the text we obtain the expression

$$\bar{r}_i \approx \sum_{j} (a_j/a_i)\mu_j. \tag{C6}$$

Thus, when equation (C5) above is not satisfied, a linear rate of approach to extinction applies.

APPENDIX D

A Consumer-Resource Model with Added Mortality

An earlier study (Chesson 1990*b*) gives the following condition for two species coexistence from which equation (17) in the text is derived:

$$\theta\rho < (h_i - m_i)/(h_j - m_j) < \theta/\rho, \tag{D1}$$

where ρ is as defined in the text, and h_i and m_i have the same meanings as the primed quantities in the text but are measured in different units. The quantity θ given here accounts for the difference in units and is defined as

$$\theta = \sqrt{a_{ii}/a_{jj}}, \tag{D2}$$

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where the a_{ii} are defined in an earlier work (Chesson 1990*b*) as quadratic forms in resource consumption rates. Thus, θ represents an overall measure of the relative resource consumption rates of the two species and can be regarded as measuring a relative timescale of the dynamics of the two species. Dividing the quantities h_i and m_i by $\sqrt{a_{ii}}$ adjusts for this overall consumption rate difference, which then yields h_i' and m_i', and the coexistence condition (17) of the text.

How does density-independent mortality affect m_i'? To understand this, we first note that in the notation of that earlier work (Chesson 1990*b*),

$$r_i^0 = b_i\left(\sum_l c_{il} w_l K_l - m_i\right), \tag{D3}$$

where w_i is the value of one unit of resource l, K_l is the carrying capacity of resource l, c_{il} is the per capita rate of consumption of resource l by species i, and b_i is the number of units of species i resulting from the net consumption of one unit of resource value. The addition of an average mortality rate of δ to this system leads to a reduction of m_i by the amount δ/b_i, and therefore a reduction in m_i' by the amount $\delta/(b_i\sqrt{a_{ii}})$. Other than m_i, the parameters of this system that change with the species are b_i and c_{il}. Now $\sqrt{a_{ii}}$ scales proportionately to c_{il}. Hence except for m_i, those factors that vary r_i^0 between species, vary $\delta/(b_i\sqrt{a_{ii}})$ inversely. Hence, a smaller value of r_i^0 because of smaller b_i or c_{il} corresponds to a larger effect of common mortality on m_i'.

APPENDIX E

A Disturbance Model

In the standard metapopulation formulation of community dynamics (e.g., Hastings 1980), species presence at a site is the only information that is considered, and these data are summarized for the entire collection of localities in terms of proportional occupancy. In Hastings's (1980) disturbance model, only one species can occupy a site at a time; species are ranked in competitive ability with higher-ranked species able to invade sites occupied by lower-ranked species but not vice versa. This process leads to a succession at a site driven by competitive ability as successively higher-ranked species occupy a site until a disturbance vacates the site and allows the process to begin again. With an inverse ranking of competitive ability and colonizing ability, this process allows a stable coexistence of a diverse assemblage of species in the system as a whole.

To understand more fully the implications of a competitive hierarchy, we shall compare it with a null model in which we assume that rather than be displaced from a site by competition, species go extinct independently of each other and at random on individual sites at the species-specific rate ϵ_i'. This model makes most sense when a site can be occupied by at most one mature individual of any species so that ''extinction'' at a site is simple death of a mature individual. We retain local extinction by disturbance and assume that this operates independently of species and may occur simultaneously for sites that are spatially contiguous, at the rate ϵ per unit time. Competition for space still occurs in the model as preemptive competition, for an occupied site cannot be colonized by another species. Writing $\epsilon_i = \epsilon + \epsilon_i'$, we obtain the equation

$$\frac{dp_i}{dt} = -\epsilon_i p_i + b_i p_i\left(1 - \sum_{j=1}^{k} p_j\right), \tag{E1}$$

where p_i is the proportion of habitat occupied by species i and b_i is the rate of colonization of empty space per unit time per unit species i.

This system will become dominated over time by the species with the largest ratio of colonization to extinction (b_i/ϵ_i); for example, defining

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$$F = \sum_{j=1}^{k} p_j \tag{E2}$$

and recognizing that

$$r_i(t) = \frac{d \ln p_i}{dt} \tag{E3}$$

is the appropriate definition of the population growth rate in a metapopulation model, we find that

$$r_i(t) = -\epsilon_i + b_i - b_i F. \tag{E4}$$

From the theory in the text, we see that this is an additive model and that the system will ultimately be dominated by the species with the largest value of $(b_i - \epsilon_i)/b_i$ or, equivalently, the largest value of b_i/ϵ_i. Thus, we see that when succession is not driven by competitive rankings, regional diversity is not preserved by disturbance. This model does imply that succession takes place at disturbed sites, however, as we now explain.

The succession at a site has a highly stochastic quality but does qualify as a succession in the sense that when a large number of sites are disturbed together a directional change in species composition with time will be seen for these sites as a whole. To understand this, note that immediately following disturbance, sites are recolonized at the rate $c_i p_i$ for species i, and so it follows that the fraction of sites with first colonist equal to species i is equal to

$$\frac{c_i p_i}{\sum_{j=1}^{k} c_j p_j}. \tag{E5}$$

Before the next disturbance, with mortality unrelated to disturbance and continued colonization from the regional pool, the long-run fraction of occupied sites that contain species i is

$$\frac{c_i p_i/\epsilon_i'}{\sum_{j=1}^{k} c_j p_j/\epsilon_j'}. \tag{E6}$$

Note that the mean longevity of an individual of species i in the absence of disturbance is equal to $1/\epsilon_i'$, and so we see a shift in species composition following disturbance from domination by those species favored by colonization rate (high $c_i p_i$) to those species having a high ratio of colonization to death rate (high $c_i p_i/\epsilon_i'$) or, equivalently, those species having a high product of colonization rate and mean longevity. A succession of this sort corresponds to the inhibition model of succession of Connell and Slatyer (1977) as it represents accumulation in the system of longer-lived species for no other reason than their longevity. In such circumstances there is no reason to expect disturbance to be favorable to the maintenance of species diversity. It simply alters which species are favored.

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