

MECHANISMS OF MAINTENANCE OF SPECIES DIVERSITY

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■ **Abstract** The focus of most ideas on diversity maintenance is species coexistence, which may be stable or unstable. Stable coexistence can be quantified by the long-term rates at which community members recover from low density. Quantification shows that coexistence mechanisms function in two major ways: They may be (a) *equalizing* because they tend to minimize average fitness differences between species, or (b) *stabilizing* because they tend to increase negative intraspecific interactions relative to negative interspecific interactions. Stabilizing mechanisms are essential for species coexistence and include traditional mechanisms such as resource partitioning and frequency-dependent predation, as well as mechanisms that depend on fluctuations in population densities and environmental factors in space and time. Equalizing mechanisms contribute to stable coexistence because they reduce large average fitness inequalities which might negate the effects of stabilizing mechanisms. Models of unstable coexistence, in which species diversity slowly decays over time, have focused almost exclusively on equalizing mechanisms. These models would be more robust if they also included stabilizing mechanisms, which arise in many and varied ways but need not be adequate for full stability of a system. Models of unstable coexistence invite a broader view of diversity maintenance incorporating species turnover.

INTRODUCTION

The literature is replete with models and ideas about the maintenance of species diversity. This review is about making sense of them. There are many commonalities in these models and ideas. The ones that could work, that is, the ones that stand up to rigorous logical examination, reveal important principles. The bewildering array of ideas can be tamed. Being tamed, they are better placed to be used.

The most common meaning of diversity maintenance is coexistence in the same spatial region of species having similar ecology. These species are termed here “the community,” but are in the same trophic level and may be described as belonging to the same guild, a term that commonly means species having overlapping

resource requirements (124). Another meaning of diversity maintenance refers not to coexistence of fixed sets of species but to the maintenance of species richness and evenness over long timescales, necessitating consideration of speciation and extinction rates, and infrequent colonizations (35, 74). The primary concern of this review is with diversity maintenance as species coexistence.

Many models of species coexistence are thought of as models of coexistence in some defined local area. However, to make any sense, the area addressed must be large enough that population dynamics within the area are not too greatly affected by migration across its boundary (103). At some spatial scale, this condition will be achieved, but it may be much larger than is considered in most models and field studies. There is a temptation to consider diversity maintenance on small areas and to treat immigration into the area as part of the explanation for coexistence (81), but that procedure becomes circular if immigration rates are fixed and are not themselves explained. Species that continue to migrate into an area are found there even if the habitat is a sink. Continued migration of a suite of species into a local area depends on diversity maintenance in the areas that are the source of the immigrants. Thus, nothing is learned about diversity maintenance beginning with the assumption that migration rates into local areas are constant.

STABLE COEXISTENCE

Species coexistence may be considered as stable or unstable. Stable coexistence means that the densities of the species in the system do not show long-term trends. If densities get low, they tend to recover. Unstable coexistence means that there is no tendency for recovery and species are not maintained in the system on long timescales. In early approaches to species coexistence, stable coexistence meant stability at an equilibrium point. These days, it is commonly operationalized using the invasibility criterion or related ideas (7, 13, 36, 51, 83, 94, 133). The invasibility criterion for species coexistence requires each species to be able to increase from low density in the presence of the rest of the community. A species at low density is termed the invader, with the rest of the community termed residents. In calculations, the residents are assumed unaffected by the invader because the invader's density is low. The important quantity is the long-term per capita growth rate of the invader, \bar{r}_i , which is referred to here as the "long-term low-density growth rate." If this quantity is positive, the invader increases from low density. This criterion has been justified for a variety of deterministic and stochastic models (36, 51, 94), and has been shown in some cases to be equivalent to more ideal definitions of coexistence such as stochastic boundedness (36). Most important, the long-term low-density growth rate can be used to quantify species coexistence (27).

For a species to have a positive, \bar{r}_i , it must be distinguished from other species in ecologically significant ways (34). Indeed, the question of stable species coexistence is largely the question of the right sorts of ecological distinctions for the given circumstances. The Lotka-Volterra competition model is a useful beginning

for discussing the basic principles. For this reason, it continues to have an important place in text books and also in the primary literature where it has roles approximating, interpreting, or describing the outcome of more sophisticated models (37, 104, 127, 130), as submodels (16), with variations on it increasingly fitted to field data (15, 42, 92, 115, 139). Unfortunately, textbooks muddy the water by parameterizing Lotka-Volterra competition in terms of carrying capacities and relative coefficients of competition. In terms of absolute competition coefficients, the two-species Lotka-Volterra competition equations can be written as follows (30):

$$\frac{1}{N_i} \cdot \frac{dN_i}{dt} = r_i(1 - \alpha_{ii}N_i - \alpha_{ij}N_j), \quad i = 1, 2, j \neq i. \quad 1.$$

The quantities α_{ii} and α_{ij} are, respectively, absolute intraspecific and interspecific competition coefficients, and the defining feature of Lotka-Volterra competition is that per capita growth rates are linear decreasing functions of the densities of each of the species. Parameterized in this way, species i can increase from low density in the presence of its competitor resident in the community if $\alpha_{jj} > \alpha_{ij}$, which may be read biologically as “species j cannot competitively exclude species i if the effect that species j has on itself is more than the effect that species j has on species i .” The criteria for species coexistence in a two-species system are therefore $\alpha_{11} > \alpha_{21}$ and $\alpha_{22} > \alpha_{12}$, which can be read very simply as “intraspecific competition must be greater than interspecific competition.” This criterion is equivalent to requiring the relative coefficients β of Bolker & Pacala (16), which equal α_{ij}/α_{jj} , to be less than 1. Unfortunately, the usual relative competition coefficients of textbooks (1), which equal α_{ij}/α_{ii} , are not instructive because they compare how the growth of a species is depressed by the other species with how much it depresses its own growth.

Per capita growth rates are linear functions of density in Lotka-Volterra models, which makes Lotka-Volterra models special and may bias their predictions (1, 30, 68, 121). However, models with nonlinear per capita growth rates can be written in the form of Equation 1 by making the competition coefficients functions of density [$\alpha_{ij} = f_{ij}(N_i, N_j)$], and the results above remain true, provided the competition coefficients are evaluated for the resident at equilibrium and the invader at zero.

Lotka-Volterra models and their nonlinear extensions may be thought of as models of direct competition (56): Individual organisms have immediate direct negative effects on other individuals. However, they may also be derived from models with explicit resource dynamics (104, 120). Such multiple interpretations mean that these models are phenomenological: They are not defined by a mechanism of competition. A mechanistic understanding of competition usefully begins with Tilman’s resource competition theory in which species jointly limited by a single resource are expected to obey the R^* rule (127). For any given species, R^* is the resource level at which the species is just able to persist. The winner in competition is the species with the lowest R^* value. A species’ R^* , however, reflects not the ability of members of the species to extract resources when they

are in low concentration, but their ability to grow and reproduce rapidly enough, at low resource levels, to compensate for tissue death and mortality, which are affected by such factors as grazing and predation. A species experiencing low grazing and mortality rates will have a lower R^* than other species, all else being equal (30). In essence, it is the overall fitness of a species that leads to its R^* value.

Tradeoffs play a major role in species coexistence: Advantages that one species may have over others are offset by compensating disadvantages (129, 136). However, examined in relation to the R^* rule there is clearly more to stable coexistence. With just a single resource as a limiting factor, tradeoffs may make the R^* values of different species more nearly equal, but that would not lead to stable coexistence. This conclusion is amply illustrated in the case of a special linear form of this resource limitation model (13, 30, 141) where the long-term low-density growth rate of an invader i competing with a resident, s , is

$$\bar{r}_i = b_i \left(\frac{\mu_i}{b_i} - \frac{\mu_s}{b_s} \right), \quad 2.$$

with the μ_s representing mean per capita growth rates of the species in the absence of resource limitation, and the b_s representing the rates at which the per capita growth rates decline as resources decline in abundance (30). In this system, the ratios μ/b measure the average fitnesses of the species in this environment, and they have the appropriate property of predicting the winner in competition (13, 30): The species with the larger μ/b is the winner (has the smaller R^*). Tradeoffs may lead to similar values of μ/b for different species. However, such similarity in average fitness does not lead to stable coexistence as Formula 2 necessarily has opposite sign for any pair of species, meaning that only one of them can increase from low density in the presence of the other.

Coexistence with resource partitioning contrasts with this. Using MacArthur's mechanistic derivation of Lotka-Volterra competition (6, 26, 104), the per capita growth rate of an invader can be written in the form

$$\bar{r}_i = \frac{1}{N_i} \cdot \frac{dN_i}{dt} = b_i(k_i - k_s) + b_i(1 - \rho)k_s, \quad 3.$$

where the k_s correspond to the μ/b_s and ρ is a measure of resource-use overlap of the two species. [The k_s are the $h' - m'$ of (30), and b_i is $b_i\sqrt{a_{ii}}$ of (26, 30).] The first term on the right in Equation 3 is the average fitness comparison of Equation 2 and therefore has opposite sign for the two species. Whenever, $\rho < 1$ (resource overlap is less than 100%) the last term in Equation 3 is positive for both species. This last term is therefore a stabilizing term that offsets inequalities in fitness expressed by the first term. The two species coexist if the stabilizing term is greater in magnitude than the fitness difference term because then both have positive growth as invaders. Alternatively, note that $\alpha_{is}/\alpha_{ss} = (k_s/k_i)\rho$, which means that to satisfy the coexistence requirement that intraspecific competition exceed interspecific competition, ρ must be less than 1, and the smaller ρ is,

the easier it is to satisfy the condition, i.e. the larger the difference in k values compatible with coexistence (26, 30).

The stabilizing term in Equation 3 arises through a tradeoff in resource use. The assumptions of the model entail that doing well on some resources means doing less well on others. Each species has density-dependent feedback loops with its resources that limit it intraspecifically and limit other species interspecifically. However, limited resource overlap and tradeoffs in resource benefits mean that intraspecific limitation is enhanced relative to interspecific limitation. This concentration of intraspecific effects relative to interspecific effects is the essence of stabilization. Tradeoffs associated not with resource use, but for example, with mortality rates (30, 68), may minimize the fitness difference term, making it easier for domination by the stabilizing term, but such tradeoffs cannot create stability alone.

Equation 3 generalizes to multispecies communities involved in diffuse competition, that is, where competition between species involves comparable interaction strengths for all pairs of species. In a variety of different models of diffuse competition (including stochastic models), the following common approximation to the long-term low-density growth rate is found:

$$\bar{r}_i \approx b_i(k_i - \bar{k}) + \frac{b_i(1 - \rho)D}{n - 1}, \quad 4.$$

where n is the number of species in the system, the k s are again measures of fitness of individual species, \bar{k} is the average fitness of residents (the competitors of species i), ρ is again niche overlap, but not necessarily strictly defined in terms of resource use (27), and D is a positive constant. Like Equation 3, the first term is an average fitness comparison and the second term is a stabilizing term. Without this term, the first term of necessity leads to loss of all species but the most fit on average, which in the context of Tilman's R^* rule would be the species with the lowest R^* value. However, if the stabilizing term is larger in magnitude than the relative average fitness term for the worst species, then all species coexist. These two general terms may involve different mechanisms. Those reducing the magnitude of the fitness difference term will be referred to as *equalizing mechanisms*, while those increasing the magnitude of the stabilizing term will be referred to as *stabilizing mechanisms*. In the absence of the stabilizing term, equalizing mechanisms can, at best, slow competitive exclusion; but in the presence of stabilizing mechanisms, equalizing mechanisms may enable coexistence. Stabilizing and equalizing mechanisms are concepts applicable beyond diffuse competition, but their implementation and their sufficiency may differ for different competitive arrangements. For example, invasion of species occupying a one-dimensional niche axis means that neighboring species on the niche axis would be most important to the invader (105, 112), whereas the diffuse competition formula (Equation 4) implies that only the number of species and their average fitnesses matter to the invader. In addition, some mechanisms, as we shall see below, have both stabilizing and equalizing properties.

The key question to be addressed below is how mechanisms with stabilizing properties arise in various situations. The theoretical literature supports the concept that stable coexistence necessarily requires important ecological differences between species that we may think of as distinguishing their niches (34, 95) and that often involve tradeoffs, as discussed above. For the purpose of this review, niche space is conceived as having four axes: resources, predators (and other natural enemies), time, and space. In reality, each axis itself is multidimensional, a feature that does not intrude on the discussion here. A species' niche is not a Hutchinsonian hypervolume (95), but instead is defined by the *effect* that a species has at each point in niche space, and by the *response* that a species has to each point. For example, consider the resource axis. A species consumes resources, and therefore has an effect on resource density (54, 95). Individuals of a species may also reproduce, grow, or survive in response to resources (54, 95).

The essential way in which stabilization occurs is most clearly seen with resource competition. If a species depends most on a particular resource (strong response), and also reduces that resource (strong effect), then it has a density-dependent feedback loop with the resource and is limited by it. If a second species has a similar relationship with a different resource, then even though the species each consume some of the resource on which the other depends most strongly (limited resource overlap), each species depresses its own growth more than it depresses the growth of other species (60, 127). The result is stable coexistence. This conclusion, however, depends on explicit and implicit assumptions, which if varied, alter the conclusion. A symmetric situation in which each resource is equally rich and each species is equally productive, would lead to identical average fitnesses, and therefore Equation 3 would have only the stabilizing term. However, asymmetries, in which one resource is much richer (127), one species produces more per unit resource, or has a lower mortality rate (30, 68), would mean that $k_i - k_s$ would not be zero, and if sufficiently large, this fitness difference would counteract the stabilizing effect of low resource overlap, causing competitive exclusion. This result would occur because the advantaged species would be at such high density that it would consume too much of the resource on which the other species depends. An equalizing mechanism would then be necessary to reduce $k_i - k_s$ before coexistence were possible.

Another implicit assumption in the argument above is that the resources have independent dynamics apart from consumption by common species. However, that is not true if, for example, the resources are simply two stages of the same food species (17) or light intercepted at different heights in a forest canopy (31, 89), requiring special conditions to allow each species to be partially independently limited by the resource supply on which they depend (17, 89). The idea that species must be somewhat independently limited is critical to their depressing their own growth rates more than they depress the growth rates of other species. And it is critical also that this phenomenon involves a density-dependent feedback loop from the species to itself, either directly through some form of interference or indirectly, as discussed here, through a resource. Predators and other natural enemies may also provide density-dependent feedback loops for their prey (8, 70, 77). Space

and time may modify such feedback loops applicable to the community as a whole in ways that intensify intraspecific density dependence relative to interspecific density dependence.

FLUCTUATION-DEPENDENT AND FLUCTUATION-INDEPENDENT MECHANISMS

Stable coexistence mechanisms may be fluctuation dependent or fluctuation independent (27). Examples of fluctuation-independent mechanisms are resource partitioning (6, 60, 118, 127) and frequency-dependent predation (53, 77). Community dynamics in both of these cases are commonly modeled by deterministic equations that have stable equilibrium points and are sometimes termed “equilibrium mechanisms.” However, these mechanisms can function in the presence of environmental fluctuations. Indeed, incorporating environmental variability in Lotka-Volterra models by making the per capita rate of increase fluctuate with time need not change the conditions for species coexistence in any important way (27, 133, 134). Thus, we can think of the operation of the mechanism as independent of the fluctuations in the system. The tendency to dismiss such mechanisms because populations in nature fluctuate is not supported by the results of models.

Some stable coexistence mechanisms critically involve the fluctuations in the system, that is, without the fluctuations, the mechanism does not function. Thus, they are termed *fluctuation dependent* (27). In the case of temporal fluctuations, these mechanisms can be divided into two broad classes: *relative nonlinearity of competition* and *the storage effect*.

Relative Nonlinearity of Competition or Apparent Competition

The per capita growth rate of a population is commonly a nonlinear function of limiting factors, such as limiting resources [e.g. the light saturation curve of plant productivity (137)], or predators [e.g. if predators interfere with one another (45)]. Stable coexistence may result from different nonlinear responses to common fluctuating limiting factors (9, 13, 18, 27, 50, 76, 101, 125). As first thoroughly investigated by Armstrong & McGehee (13), for the case of a single limiting factor, the per capita growth rate of a species takes the form

$$r_i(t) = E_i(t) - \phi_i(F), \tag{5}$$

where $E_i(t)$ is the maximum per capita growth rate as a function of possibly fluctuating environmental conditions (an environmental response), F is the limiting factor, for example the amount by which resources are depressed below their optimal values, and $\phi_i(F)$ is the response defining the dependence of the per capita growth rate on F (27). The departure of the function ϕ_i from a linear function is its nonlinearity, which is measured by a quantity τ (27). For example, a type II

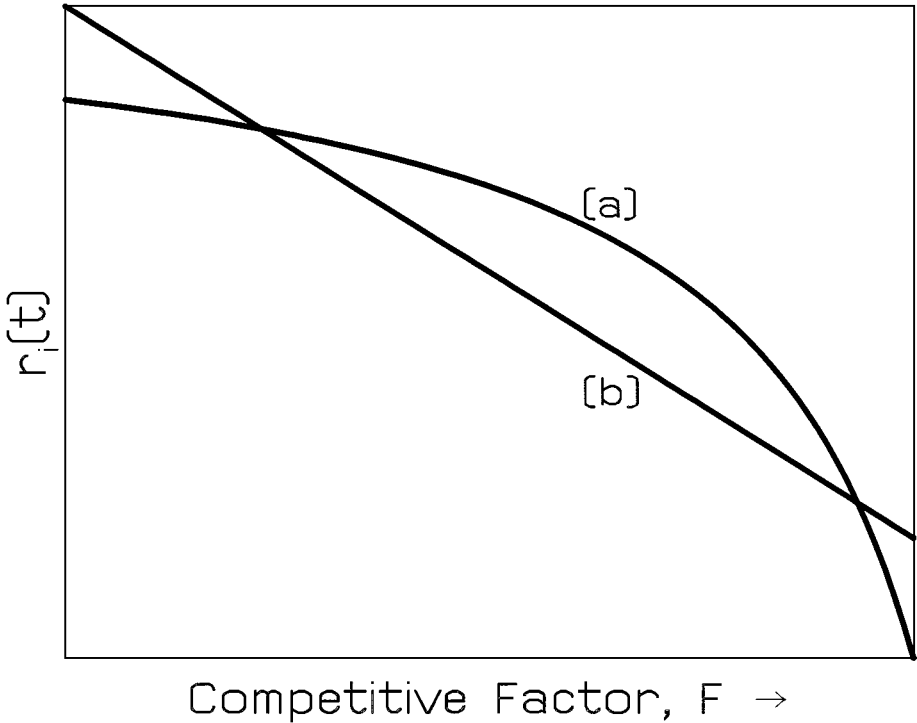


Figure 1 Per capita rates of growth of two species (*a* and *b*) as functions of a common limiting factor. In the case where the limiting factor is shortage of a resource, larger F means less resource, and curve *a* with positive τ would be generated by a type II functional response, while curve *b* with zero τ would occur with a linear response.

functional response to a limiting resource gives a positive τ , while a linear functional response gives a zero τ (Figure 1). Two species with different values of τ may coexist stably provided the species with the larger value of τ (*a*) has a mean fitness advantage in the absence of fluctuations in the limiting factor and (*b*) experiences lower fluctuations in the limiting factor when it is an invader than when it is a resident. Armstrong & McGehee showed that condition (*b*) may arise naturally with resource competition because a large value of τ may cause resources to have large-amplitude cycles over time.

These conditions for stable coexistence can be understood from the following general approximation to the long-term low-density growth rate of a species, *i*, in the presence of its competitor, *s*:

$$\bar{r}_i \approx b_i(k_i - k_s) - b_i(\tau_i - \tau_s)V(F^{-i}), \quad 6.$$

where the first term is the fitness comparison in the absence of fluctuations in the

limiting factor, $\tau_i - \tau_s$ measures relative nonlinearity, and $V(F^{-i})$ is the variance of the limiting factor calculated for invader i and resident s (27). In contrast to Equation 3 for the Lotka-Volterra model, the second term of this equation is not positive for both species but changes sign when resident and invader are exchanged. The species with more positive nonlinearity (larger value of τ) is disadvantaged by fluctuations in the limiting factor. However, if it is also the species with higher average fitness as measured by the first term, then this mechanism can have an equalizing role decreasing the advantage that a species gains from the first term. The fact that $V(F^{-i})$ may vary depending on which species is the invader means that it is possible for this mechanism to have a stabilizing role too. An algebraic rearrangement of Equation (6) clarifies these stabilizing versus equalizing roles. Defining B to be the average of $V(F^{-i})$ for each species as invader and A to be half the absolute value of the difference between these values, and assuming that the species with the smaller τ experiences larger $V(F)$ as an invader, then

$$\bar{r}_i \approx \{b_i(k_i - k_s) - b_i(\tau_i - \tau_s)B\} + b_i|\tau_i - \tau_s|A. \quad 7.$$

The term in braces becomes the equalizing term—it is the relative fitness taking into account fluctuations in the limiting factor, and has opposite sign for the two species. The final term has the same sign for both species and is therefore a stabilizing term. Thus, relative nonlinearity (nonzero $\tau_i - \tau_s$ combined with variance in F) can have both stabilizing and equalizing roles. However, the stabilizing role might be negative, viz destabilizing if the species with the larger value of τ also has the larger value of $V(F^{-i})$, as then A in Equation 7 must be replaced by $-A$, which moves both species, long-term low density growth rates closer to zero promoting competitive exclusion (or apparent competitive exclusion if F relates to common predation on the two species).

Although there is a generalization of Equation 6 to multiple limiting factors (27), relative nonlinearity in the presence of multiple limiting factors has been poorly investigated. Huisman & Weissing (76), however, have demonstrated enormous potential for this mechanism with multiple competitive factors. For the dynamics of phytoplankton in lakes they use a model of competition for essential resources (98, 127) that has strong nonlinearities in a multidimensional sense. Fluctuations in these essential resources driven by their interactions with phytoplankton species appear to stabilize coexistence very strongly. This result contrasts with the feeble effects of relative nonlinearity on coexistence of phytoplankton previously demonstrated for the case of a single limiting factor (57–59).

The Storage Effect

Models imply that temporal environmental fluctuations can have major effects on population and community dynamics. It has been widely noted that negative environmental effects may reduce population densities and therefore reduce the

magnitude of competition (55, 78, 79), but this possibility does not necessarily translate into less competitive exclusion (30). Instead, models in which stable coexistence results from environmental fluctuations are models of temporal niches: Species are not distinguished by the resources they use but by when they are most actively using them (2, 12, 30, 102). For stabilization to result, intraspecific competition must be concentrated relative to interspecific competition, and this requires three important ingredients, whose collective outcome is referred to as *the storage effect* (27). The most obvious of these is *differential responses to the environment*. Species from the same community may have different responses to their common varying environment. Environmental variation may be regular and deterministic, for example seasonal (12, 37, 47, 60, 86, 91, 102, 109, 140) or stochastic, attributable, for example, to weather on a variety of timescales (2, 27, 30, 32, 33, 36, 37, 51, 52, 62, 112, 123).

How can differential responses to the environment concentrate intraspecific density dependence relative to interspecific density dependence, and hence act as a stabilizing mechanism, when the physical environment is not altered by population densities? The answer is that population responses to the physical environment modify competition, as measured by the second essential feature of the storage effect, *covariance between environment and competition* (30, 33). Just as negative environmental effects may decrease competition, positive environmental effects may increase it. Covariance between environment and competition is measured by calculating the standard statistical covariance between the effects of the environment on the per capita growth rate of a population (*the environmental response*) and of competition (both intraspecific and interspecific) on the growth rate (*the competitive response*).

With covariance between environment and competition, and differential responses to the environment, intraspecific competition is strongest when a species is favored by the environment, and interspecific competition is strongest when the species' competitors are favored. The final ingredient, *buffered population growth*, limits the impact of competition when a species is not favored by the environment and is therefore experiencing mostly interspecific competition. Buffered population growth may result from a variety of life-history traits: seed banks in annual plants (29, 48, 49, 113, 114), resting eggs in freshwater zooplankton (22, 62, 63), and long-lived adults in perennial organisms (38, 86, 91, 96, 97, 112, 119). Organisms not having specific life-history stages with a buffering effect may be buffered in other ways. For example, desert rodents and herbaceous plants may have times of the year when they are dormant and therefore relatively immune to unfavorable environmental and competitive conditions (19, 37). Alternatively, subdivision of a population into different phenotypes, or local populations in space, with different exposure to environmental effects and competition, may also have a buffering role (33).

By diminishing the effects of interspecific competition when a species is not favored by the environment, buffered population growth, combined with the other two ingredients of the storage effect, leads to concentration of intraspecific effects

on population growth relative to interspecific effects, which is stabilizing. In a variety of models of diffuse interactions involving the storage effect, the long-term low-density growth rate can be given approximately in the form

$$\bar{r}_i \approx b_i(k_i - \bar{k}) + \frac{b_i(1 - \rho)(-\gamma)\sigma^2}{n - 1}, \tag{8}$$

where the symbols follow those in the general diffuse competition formula (Equation 4), with $D = (-\gamma)\sigma^2$ (27). Note that $(-\gamma)$ measures buffered population growth and is positive for buffering. The variance in the environmental response is σ^2 , and ρ is the correlation between the environmental responses of different species. This formula has a fitness comparison (here representing an average over all environmental states), which is opposed by a stabilizing term (here due to the storage effect) promoting stable coexistence.

Mechanisms in Combination Integrated over Temporal Scales

Two general factors, competition and the physical environment, drive the mechanisms above. Two-factor analysis of variance shows how the effects of two factors can be divided into their separate or “main” effects and their interaction (126). Applying this technique to population growth (27) expresses the long-term low-density growth rate as

$$\bar{r}_i \approx \bar{r}'_i - \Delta N + \Delta I, \tag{9}$$

where \bar{r}'_i is the effect of fluctuation-independent mechanisms, plus mean fitness differences (i.e. everything that is independent of fluctuations), ΔN is relative nonlinearity of competition, and ΔI is the storage effect. Formulae for \bar{r}'_i , ΔN , and ΔI can be found in Chesson (27), but examples of them are respectively Equation 4 and the second terms of Equations 6 and 8. The storage effect, ΔI , is the interaction between fluctuating environmental and competitive responses, which might serve as its formal definition. The other two terms arise from the main effects with adjustments to remove all fluctuation-independent effects from ΔN and ΔI , and place them in \bar{r}'_i .

Although the derivation of Equation 9 in (27) involves approximations (hence “ \approx ”), these approximations occur in the formulae for the components, not the division into three terms. The important assumption limiting the generality of the results is that there should be fewer limiting factors than community members so that competition experienced by a low density invader can be expressed as a function of competition experienced by the resident species. With this one caveat, Equation 9 shows that in models of temporally fluctuating environmental and competitive effects, three broad classes of mechanisms (fluctuation-independent mechanisms, relative nonlinearity, and the storage effect) are exhaustive: Any mechanism of stable coexistence must be one of these or a combination of them.

Although the storage effect and relative nonlinearity may appear to be rather involved, there are no simpler fluctuation-dependent stable coexistence mechanisms waiting to be discovered. In particular, no credence can be given to the idea that disturbance promotes stable coexistence by simply reducing population densities to levels where competition is weak (30, 141). More sophisticated views of disturbance (23–25, 39, 40, 64), however, have yielded important hypotheses, as discussed below under the spatial dimension.

It is now commonly believed that spatial and temporal scale have major effects on the perception and functioning of diversity maintenance mechanisms (10, 14, 43, 44, 74, 78, 80–82, 100, 116, 143). An important finding is that fluctuation-dependent mechanisms can give community dynamics indistinguishable from those of fluctuation-independent mechanisms when viewed on a longer timescale than the period of the fluctuations (37, 91), as is illustrated in Figure 2. Similar effects are often apparent in spatial models (16, 46, 64, 84, 122), although not always explicitly noted by the authors. In this regard, the term \bar{r}_i in Equation 9 can be regarded as containing not just fluctuation-independent mechanisms, but also fluctuation-dependent mechanisms on timescales shorter than the fluctuations considered in the ΔN and ΔI terms. When this is done, Equation 9 can be viewed as an iteration allowing the effects of fluctuation-dependent mechanisms operating on different timescales to be combined to give their total effect on very long timescales (37).

THE SPATIAL DIMENSION

Nature is strikingly patchy in space. Naturally, if species live in different habitats and have no direct or indirect interactions with each other, they should have no difficulty coexisting in a region combining these separate habitats. However, species do not have to be strictly segregated in space for regional coexistence (16, 20, 38, 90, 93, 99, 112, 122, 123). Spatial variation is similar to temporal variation in its effects on species coexistence with some important differences (32, 38, 123). In particular, there is a spatial analog of Equation 9 expressing growth from low density in terms of fluctuation-independent mechanisms, spatial relative nonlinearity, and the spatial storage effect (28a). In addition, there is a fourth term in the spatial analogue of Equation 9 involving the spatial covariance of local population growth with local population density, which behaves like a spatial storage effect in some circumstances, but like spatial relative nonlinearity in others (28a).

Spatial storage effects commonly occur in spatial models when spatial environmental variation is included. There are two common ways in which the requirement of differential responses to the environment is met in such models. First, relative fitnesses of different species may vary in space (21, 32, 38, 85, 107, 112, 122, 131). For example, for plant species, the identity of the species with the lowest R^* value may vary spatially due to differential dependence of R^* on spatially varying

physical factors, such as temperature and pH (131). Second, there may be relative variation in dispersal into different habitats, for example, in marine habitats due to the complexities of spawning, currents, and developmental interactions (21, 32, 42, 85) and in insects potentially due to spatially varying habitat preferences (34, 84, 88). Such relative variation satisfies the requirement for differential responses to the environment.

Buffered population growth automatically occurs when populations are subdivided in space over a spatially varying environment (32, 38), but the strength of the buffering is affected by other aspects of the biology of the organisms, including their life-history attributes (28a). Covariance between environment and competition naturally arises when dispersal varies in space but not necessarily when relative fitnesses vary in space. The presence of covariance is easy to determine in a model, and is a powerful tool for determining if coexistence can be promoted by spatial environmental variation. For example, in models of sessile marine invertebrates with competition between adults and new settlers, but not among adults, spatial variation in adult death rates leads to strong covariance between environment and competition if the environmental differences between localities remain constant over time. Then adult densities build up in low-mortality locations, leading to strong competition from adults in such localities. Thus, covariance between environment and competition occurs, and regional coexistence by the spatial storage effect is possible (32, 107). However, if environmental differences between localities constantly change with time [i.e. environmental variation is spatio-temporal rather than purely spatial, *sensu* Chesson (32)], local population buildup occurs at best weakly before the environment changes. Covariance between environment and competition is weak or nonexistent, and so the storage effect is weak or nonexistent (32, 107).

There has been little explicit attention to relative nonlinearity of competition in spatial models, but Durrett & Levin (46) demonstrate coexistence in a spatial competition model dependent on spatial variation and different nonlinear competition functions that correspond biologically to different competitive strategies. The spatial Lotka-Volterra model of plant competition of Bolker & Pacala (16) does not have relatively nonlinear competition, as the per capita rates are linear. However, a similar nonlinear effect arises from covariance between local population density and competition. This covariance is due to chance variation in local population densities, which covaries with local competition in ways that give advantage, under some circumstances, to species with short-distance dispersal strategies. Similar phenomena have been found in other spatial competition models (93).

There are many other spatial models of competitive coexistence, few of which have been investigated within the framework presented here or a related framework (66, 89, 106, 117). Nevertheless, most do have some of the key elements of this framework, including nonlinearities, spatial covariances, and buffered growth rates, which appear actively involved in model behavior. From these other models, two ideas emerge as especially important: Tilman's resource-ratio hypothesis (127, 128), and colonization-competition tradeoffs.

The resource ratio hypothesis postulates that the ratio of the rates of supply of two limiting resources at a particular locality determines a unique pair of plant species from a given regional pool able to coexist at that locality. Given variation in space in the supply rate ratio, different pairs of species would be able to coexist at different localities in the absence of dispersal between localities. However, a full spatial model exploring this idea in the presence of dispersal has never been developed. Moreover, Pacala & Tilman (112) pointed out that under certain conditions, a given resource ratio may determine a particular best competitor that would dominate that site. With site-to-site variation in the resource ratio, this scenario leads to coexistence as a simple example of a spatial storage effect (112). Although there would be only one best species at any given locality, as determined by the resource ratio there, many species could be present at a locality due to dispersal from other localities.

Competition-colonization tradeoffs have been discussed in two distinct sorts of models. In one, a patch in space supports a local community that is destroyed at random by disturbance. It is then recolonized from other patches (24, 64). In other interpretations, a patch supports a single individual organism (87, 110, 130), whose death by some means (not necessarily disturbance) opens that locality for recolonization. Coexistence in these models requires the colonizing ability of different species to be ranked inversely to competitive ability, which therefore tends to drive a successional process in each locality. Localities becoming vacant randomly in space and time ensures a landscape in a mosaic of successional states. When vacant sites are interpreted as resulting from disturbance, this model provides perhaps the most satisfactory expression of the intermediate disturbance hypothesis (30), as diversity tends to be maximized at intermediate values of disturbance frequency (64).

PREDATORS, HERBIVORES, AND PATHOGENS

Predation is a common hypothesis for high biological diversity. However, the argument that predators maintain diversity by keeping populations below levels at which they compete is now known to be highly simplistic (4, 30). Predators may add density dependence to their prey populations through functional, numerical, and developmental responses to prey (108). In the absence of frequency-dependent functional responses or similar complications (65), a common predator of several prey is a single limiting factor with analogous effects to limitation by a single resource (67). One density-dependent limiting factor (the resource) is simply replaced by another (the predator). Indeed, there is a P^* rule exactly analogous to the R^* rule that says that the species with the highest tolerance of predation will drive other species extinct (69). Thus, if predation is so severe that it does eliminate competition, then competitive exclusion may be replaced by apparent competitive exclusion.

There are many ways in which predators may help species coexist, but it is far from an easy solution (7, 30, 65, 68, 70, 77, 135). Predators may promote species

coexistence when each species has its own specialist predators, or more generally, specialist natural enemies that hold down the density of each species independently. This idea, known as the Janzen-Connell hypothesis, is an important hypothesis for the coexistence of trees in tropical forests (11) where tree seeds and seedlings may be subject to density- or distance-dependent seed predation (41, 138). By providing or attracting species-specific seed and seedling predators, an individual tree would have a greater negative effect on a conspecific growing nearby than on a heterospecific growing nearby (all else equal), thus providing the critical requirement of a stabilizing mechanism.

Many systems support generalist predators or herbivores, which prey or graze on a range of species (65, 77, 108). Murdoch has emphasized that predators may have frequency-dependent functional responses (switching; 108), which are stabilizing mechanisms. More complex intergenerational learning responses of parasitoids may have similar effects (65). Alternatively, a predator may not be frequency-dependent but have unequal effects on prey species that are also limited by resources (135). For example, two competing prey species may coexist if one of them is more strongly limited by the resource and the other is more strongly limited by the predator (61). In all of the above instances, the role of predation is to generate feedback loops in which an individual prey species depresses its own per capita growth rate more than it depresses the per capita growth rates of other species, thus meeting the requirements of stabilizing mechanisms. However, when these density-dependent and frequency-dependent requirements are not met, a generalist predator may instead have an equalizing role by inflicting greater predation on the competitive dominant. If a stabilizing mechanism such as resource partitioning is present, then although the predator is not the stabilizing agent, stable coexistence may occur in its presence (30).

Predators are often invoked as biological disturbance agents inflicting mortality patchily in space and time. When mortality is not species specific, predators may be the agent of local extinction in the competition-colonization tradeoff models (23). If mortality is species specific, but density independent, then predators may have a role analogous to a spatio-temporally variable environment, which may lead to coexistence by the spatial storage effect (111). Thinking of predators as organisms, and the environment as the physical environment, invites generalizations of the storage effect to stable species coexistence in the presence of apparent competition. However, at present there is no theory of covariance between environment and apparent competition. As discussed above, predators can be fluctuating nonlinear limiting factors, but the potential of this mechanism has not been explored in any detail.

UNSTABLE COEXISTENCE

Hubbell (73, 74) has championed and steadily refined a model of community dynamics in which coexistence is not stable: The species compete for space but are ecologically identical and therefore have equal fitnesses under all conditions.

Thus, in Equation 4, both the average relative fitness term and the stabilizing term are close to zero, and the species in the system undergo a very slow random walk to extinction. To many people, a very slow loss of species is equivalent to indefinite coexistence, and it is certainly one model of how nature is (78, 79, 81, 123). Several objections have been raised against it. First, equal average fitnesses seem highly unlikely (28), and significant violation of this assumption destroys the conclusion of slow extinction (142) by creating nonzero average fitness difference terms for the species. Minor realistic variations on the model also lead to stabilizing components (28). Indeed, such features seem difficult to avoid in most systems (28, 142).

Other approaches to unstable coexistence have not assumed the extreme neutrality of Hubbell's model, and have sought means by which fitness differences may be minimized (78, 79, 81, 123). But these approaches have not recognized that stabilizing components are difficult to avoid (28), and may have overestimated the effectiveness of purported equalizing mechanisms (28). Nevertheless, there is undeniable merit in the question of unstable coexistence because it must be that in many systems at least some species are only weakly persistent because their fitness disadvantages are comparable in magnitude to the stabilizing component of their long-term low-density growth rate. At this point, the study of diversity maintenance needs to take account of macroevolutionary issues such as speciation and extinction, processes (35, 74), biogeographic processes of migration of species between communities on large spatial scales, and climate change on large temporal scales (37). Hubbell (74) argued that on such large scales, speciation, extinction, and migration processes are dominant, rendering the admitted oversimplifications of his neutral model unimportant. Independent data on the rates of these critical processes are needed to test this perspective.

NONEQUILIBRIUM COEXISTENCE

Stable and unstable coexistence is one view of the distinction between equilibrium and nonequilibrium coexistence (75). Another view is fluctuation-dependent versus fluctuation-independent coexistence (35). But equilibria are everywhere. For example, Hubbell's (74) model of unstable coexistence nevertheless has an equilibrium for species diversity on the large spatial scale. Thus, it seems best to ask, Is species coexistence stabilized or not? And if it is, Is that stabilization dependent on fluctuations or is it independent of fluctuations? The term nonequilibrium coexistence is better avoided.

LIMITING SIMILARITY

Unstable coexistence requires species to have very similar average fitnesses for long-term coexistence. Stable coexistence benefits from similar average fitnesses, but requires niche differences between species that intensify negative intraspecific

effects of density on population growth relative to negative interspecific density effects. This requirement of niche differences has often been referred to as limiting similarity (3, 112). It is clear that not any kind of niche differences between species will do. For example, the discussion of the storage effect above showed that species-specific responses to the environment, which are one sort of niche difference, lead to stability only if they are linked appropriately to density-dependent feedback loops. This condition applies generally, as has been emphasized here, but has not been studied in as much detail for most other mechanisms. The right sorts of niche differences might be called stabilizing niche differences. A precise limit to similarity implies a particular minimum value for stabilizing niche differences. It is clear there can be no such value (3, 5). For example, in the various equations above, the magnitude of the stabilizing term is naturally an increasing function of stabilizing niche differences (although this feature cannot be expected under all circumstances 6). The smaller the average fitness differences, the smaller the stabilizing niche differences can be. One may be tempted to suggest that average fitness differences can be zero, but there are plenty of reasons to expect them to differ from zero in most situations in nature, and as yet we have no theory that predicts average fitness differences. Thus, we cannot predict a particular limit to similarity, although the concept that niche dissimilarities of the right sort promote coexistence is generally supported (3).

Models of species on one-dimensional niche axes predict particular limits to similarity when one asks whether a species can invade between two particular resident's with a given niche spacing and given average fitness differences (105, 112). Such an invader is automatically at a disadvantage to the residents, however, because it has more competitors close to it than the residents do. Thus, this sort of analysis does not seem truly to answer the question of how close the niches of coexisting species can be, but it does emphasize that variation in the spacing of the niches of various species in a community, not just the average spacing, is an important factor in species coexistence (5). This feature is not captured by the simple equations for diffuse competition given here where there is no such variation in spacing.

Recently, particular limits to similarity were also claimed for coexistence by colonization-competition tradeoffs. However, the limit in question is the difference in colonizing ability of successively ranked competitors (87, 130). This difference has an equalizing effect because it compensates for a species' inferior competitive rank. It is not a stabilizing niche difference, but instead reduces average fitness inequalities that stabilizing niche differences must overcome. There should be no paradox in the idea that dissimilarities in niche differences of the stabilizing sort, which may be characterized as keeping species out of each other's way, promote coexistence, while differences in average fitness, which determine how much "better" one species is than another overall, favor competitive exclusion (14).

An objection that can be raised about all of the above analyses is that they take no consideration of the increasing sparseness of populations, and the decreasing absolute numbers of individuals in those populations, as more species are packed

into a community. Allee effects in sparse (low density) populations (71, 72) and stochastic extinction in small populations (132) both potentially limit how similar the niches of coexisting species can be when similar niches mean sparser or smaller populations. These possibilities deserve further study as they have the unique property that they would still work when species are equal in average fitness, that is, they potentially lead to the requirement that stabilizing mechanisms of a certain minimum strength (depending on population sizes supportable in the system) must exist for coexistence regardless of the strength of equalizing mechanisms.

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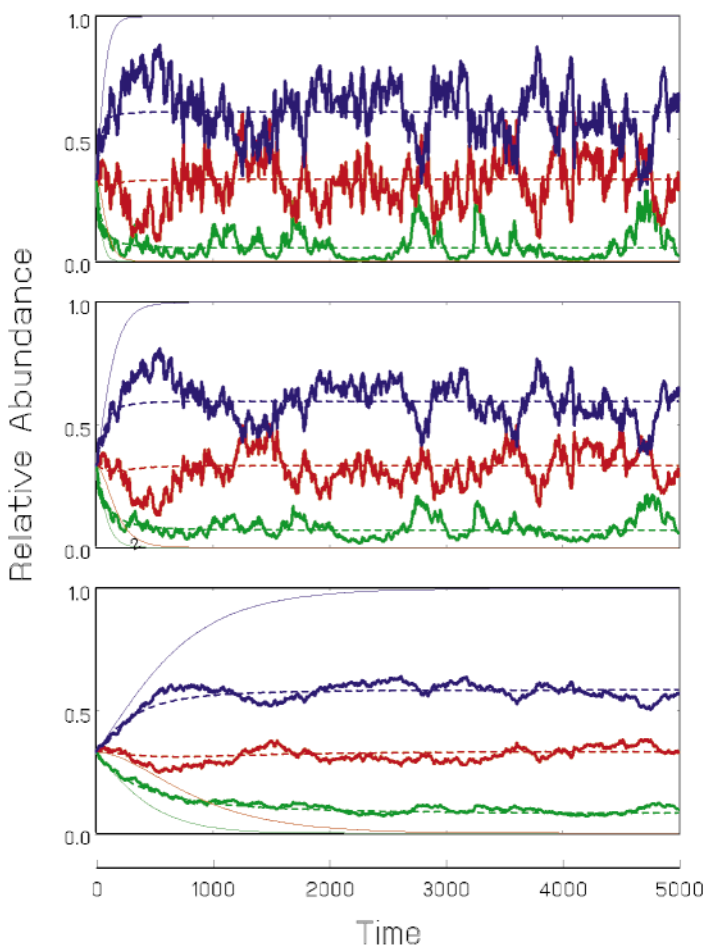


Figure 2 Community dynamics on a long timescale for three species coexisting by the storage effect (fluctuating lines) in the lottery model for intense competition for space (no space is left vacant, 37) compared with an approximating Lotka-Volterra model (37) modified for intense space competition (dashed lines) and the lottery model with no environmental fluctuations (solid smooth curves). The different panels are for mean adult longevities of 10, 20 and 100 respectively from top to bottom. Comparing the lottery model with and without fluctuations demonstrates the necessity of environmental fluctuations for species coexistence. The approximating Lotka-Volterra model from (37) shows that this mechanism can be mimicked by fluctuation-independent mechanisms with increasing precision as the longevity of the organism is increased. Lotka-Volterra models with noise added (133) give dynamics indistinguishable from the lottery model. The intraspecific and interspecific interaction coefficients in the Lotka-Volterra model are equal respectively to the variances and covariances of the environmental responses in the lottery model (37).



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