

# Biodiversity, Stability, and Productivity in Competitive Communities

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Submitted February 8, 1999; Accepted June 14, 2000

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**ABSTRACT:** Three markedly different models of multispecies competition—one mechanistic, one phenomenological, and one statistical—all predict that greater diversity increases the temporal stability of the entire community, decreases the temporal stability of individual populations, and increases community productivity. We define temporal stability as the ratio of mean abundance to its standard deviation. Interestingly, the temporal stability of entire communities is predicted to increase fairly linearly, without clear saturation, as diversity increases. Species composition is predicted to be as important as diversity in affecting community stability and productivity. The greater temporal stability of more diverse communities is caused by higher productivity at higher diversity (the “overyielding” effect), competitive interactions (the “covariance” effect), and statistical averaging (the “portfolio” effect). The relative contribution of each cause of temporal stability changes as diversity increases, but the net effect is that greater diversity stabilizes the community even though it destabilizes individual populations. This theory agrees with recent experiments and provides a degree of resolution to the diversity-stability debate: both sides of the longstanding debate were correct, but one addressed population stability and the other addressed community stability.

*Keywords:* covariance effect, diversity-stability hypothesis, diversity-productivity, portfolio effect, overyielding, temporal stability.

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The diversity-stability hypothesis has long been controversial. Work by MacArthur (1955), Elton (1958), Odum (1959), Margalef (1969), and others suggested that more diverse communities are more stable and more resistant to invasion. Then May (1972) showed that simple models of interspecific competition became less stable—as measured by their ability to return to multispecies equilibria

after perturbation—as the number of interacting species increased. May (1974*a*, 1974*b*) also showed that total community abundance could be less variable than individual species. Goodman (1975) reviewed the mostly theoretical evidence and concluded that there was no consistent dependence of stability on diversity. McNaughton (1977) strongly objected to the rejection of the diversity-stability hypothesis based solely on theory, but the idea that diversity decreased stability, or at least did not influence it, took hold in ecology.

During the next 2 decades, a variety of articles re-explored the diversity-stability hypothesis (e.g., King and Pimm 1983; Pimm 1984), and recent empirical tests of the hypothesis have seemingly supported it (McNaughton 1993; Tilman and Downing 1994; Tilman 1996). Though the interpretation of these studies is debated (Givnish 1994; Tilman et al. 1994; Tilman 1996, 1999; Grime 1997; Huston 1997), they have renewed interest in the ways that diversity might affect stability. Doak et al. (1998) recently provided a major theoretical insight—that statistical averaging may cause greater stability at greater diversity. Tilman et al. (1998) showed that such statistical averaging was not an inevitable consequence of higher diversity in ecological systems, as it is in statistical subsampling, but depended on properties of the ecological system. Hughes and Roughgarden (1998) and Ives et al. (1999) found the stability of community biomass to be relatively unaffected by the strength of competitive interactions, and Ives et al. (1999) discussed how diversity-stability relationships depend on individual species responding differently to fluctuations in the environment. Yachi and Loreau (1999) showed that under rather general conditions, increased species diversity should not only reduce the variability of community properties such as productivity but also increase the temporal means of those properties.

Here we examine these ideas further, analyzing three markedly different models of exploitatively competitive communities—a mechanistic model, a phenomenological model, and a probabilistic model—to understand better how community and population properties, specifically productivity and temporal or fluctuational stability, de-

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pend on diversity. Throughout the article, we use “diversity” to mean simply the total number of species in a community. Despite the differences among the models, all revealed consistent effects of diversity on temporal stability: community variability decreased and population variability increased as species diversity increased. Moreover, all three models revealed similar underlying causes of decreased community variability with greater diversity.

### Various Definitions of Stability

Stability has a multiplicity of meanings in ecology, both qualitative and quantitative. Pimm (1984, 1991), for instance, identified five alternative uses of the term, multiplied by three levels of complexity and three levels of organization—giving potentially 45 variations in the meaning of stability. Different meanings of stability can give different conclusions, so the multiplicity of meanings has clouded diversity-stability debates. Stability can mean any of the following: the tendency to return after perturbation; the time for a perturbation to decay to a specified fraction of its initial size (resilience, Pimm 1991); how much a measurement fluctuates over time (variability, Pimm 1991); how long a condition lasts before it changes (persistence, Pimm 1991); how little a measurement is changed by a given disturbance (resistance, Pimm 1991); how likely it is that a system will continue functioning (reliability, Naeem 1998); what magnitude of perturbations a system can tolerate (domain of attraction, Holling 1973); and more. Elton (1958) and other early investigators explicitly considered stability to be related to variability, though in some cases they took stability to be persistence (Pimm 1991). In contrast, May (1972) and others generally defined stability as the return to equilibrium (or to another invariant condition such as a limit cycle) as determined by eigenvalues of a mathematical system. That use matches the definition long established in mathematics, physics, and population genetics (Lewontin 1969) but does not directly match the notions of variability used by Elton (1958) and others. Thus arose the difficulties in comparing conclusions among different investigators.

### Definition of Temporal Stability

Given the many possible variations in meaning, it is essential to define clearly at the outset exactly which type of stability one is addressing. We shall use a measure called “temporal stability” (Tilman 1999) that is related to variability. This measure may correspond with the way early contributors thought of stability (e.g., MacArthur 1955; Elton 1958, pp. 146–150). This we compare with “eigenvalue stability”—the return to equilibrium as determined

by eigenvalues of the Jacobian matrix—and show how these two contrasting definitions help clarify past conflicts in the diversity-stability debate.

Simply put, when two series of abundances are graphed versus time, each having been normalized by dividing by its respective mean abundance, we take the “more stable” case to be the one with the smaller normalized fluctuations. More precisely, we define “temporal stability,”  $S$ , as the mean abundance,  $\mu$ , divided by the standard deviation,  $\sigma$ , that results from temporal variation in that abundance. That is,  $S = \mu/\sigma$ . If there were no variation at all, temporal stability would be maximal (infinite). When variation is large relative to the mean, temporal stability is small (near 0). An analogous measure could be defined for variation across space.

Temporal stability,  $S$ , is equal to 100 divided by the coefficient of variation of statistics, but in our case the variance represents actual changes through time in species abundances, not sampling error. It is similar to the “signal-to-noise ratio” of information theory and is also similar to the reciprocal of the “root mean square relative fluctuation” described by May (1973). It is the reciprocal of certain measures we have used elsewhere (Tilman 1996; Tilman et al. 1998).

There are several reasons we use this particular measure of stability. First, it measures whole-system nonlinear dynamics, in contrast with eigenvalue stability, which follows from linear approximations to nonlinear systems. Second, it is intrinsically a nonequilibrium measure—useful because populations are rarely observed in equilibrium. Indeed, multispecies equilibria and associated eigenvalues do not even exist for some systems (DeAngelis and Waterhouse 1987), including the first and third models in this article, yet temporal stability is still well defined. Third, it is dimensionless and scale invariant. That is, its value does not change as units change. Fourth, its magnitude is larger for more stable communities—that is, for those with smaller average temporal variation, relative to the mean. This is in contrast to related measures such as the coefficient of variation, whose magnitude approaches 0 for more stable communities. Fifth, it is asymptotically linear in the simplest analytical case. Finally, it is readily observable in nature. In contrast, one cannot easily observe the eigenvalues of, say, a prairie community. In the remainder of this article, we use the term “temporal stability” or “temporally stable” when we refer to this measure.

### Components of Temporal Stability

The temporal stability of an individual species, which we denote by  $S_i$ , depends on the species’ mean abundance and the standard deviation in its abundance (on  $\mu_i/\sigma_i$ ), both of which are influenced by the dynamics of interspecific

interaction in a community. The relationship for the temporal stability of the total community, which we denote by  $S_T$ , is more complex, and its structure defines how diversity can affect temporal stability. The necessary definitions are given in appendix A, where it is shown that the numerator of the temporal stability criterion is just the summed biomasses of all the constituent species, but the denominator includes both the summed variances of all the constituent species and the summed covariances of all possible ordered pairs of species. Specifically, the temporal stability of total community abundance is

$$S_T = \frac{\mu_T}{\sigma_T} = \frac{\sum \text{Abundance}}{\sqrt{\sum \text{Variance} + \sum \text{Covariance}}}. \quad (1)$$

Because many different combinations of species may be able to coexist in a multispecies community, the temporal stability measure is taken as an average over many different communities. This eliminates bias arising from specific combinations of species. As can be seen from equation (1) (or app. A; eq. [A2]), for temporal stability to increase with diversity, the summed abundances (total community biomass) could increase with diversity, or the summed variances could decrease, or the summed covariances could decrease, or various combinations of these could occur. In this article, we explore, for three different models, how each of the three terms in equation (1) depends on diversity—and thus how and why diversity affects temporal stability.

#### *The Portfolio Effect*

Diversity can affect the summed variances in equation (1). Variance measures the average squared deviation from a mean. From this it follows mathematically that, if a random variable  $x$  is reduced by half, its variance is reduced to one-fourth or, more generally,  $\text{Var}(x/n) = \text{Var}(x)/n^2$ . This leads to the intriguing suggestion that if increasing biodiversity tends to reduce mean abundance of individual species, then those reduced abundances may provide greater than proportional reductions in variance (Doak et al. 1998). Hence, when the reduced variances of individual species are summed to calculate variance in total community abundance for equation (1), the ecosystem may be temporally stabilized purely on statistical grounds. We have called this the “portfolio effect” (Tilman et al. 1998) because in economics it has long been known to occur when a fixed financial investment is diversified across a portfolio of stocks. On average, the relative fluctuation in a diversified portfolio is smaller than the relative fluctuation in the constituent stocks. Similarly, if a community is diversified among many species, the relative fluctuation

in biomass of the entire community may be much smaller than the relative fluctuation in the biomass of the constituent species.

#### *The Covariance Effect*

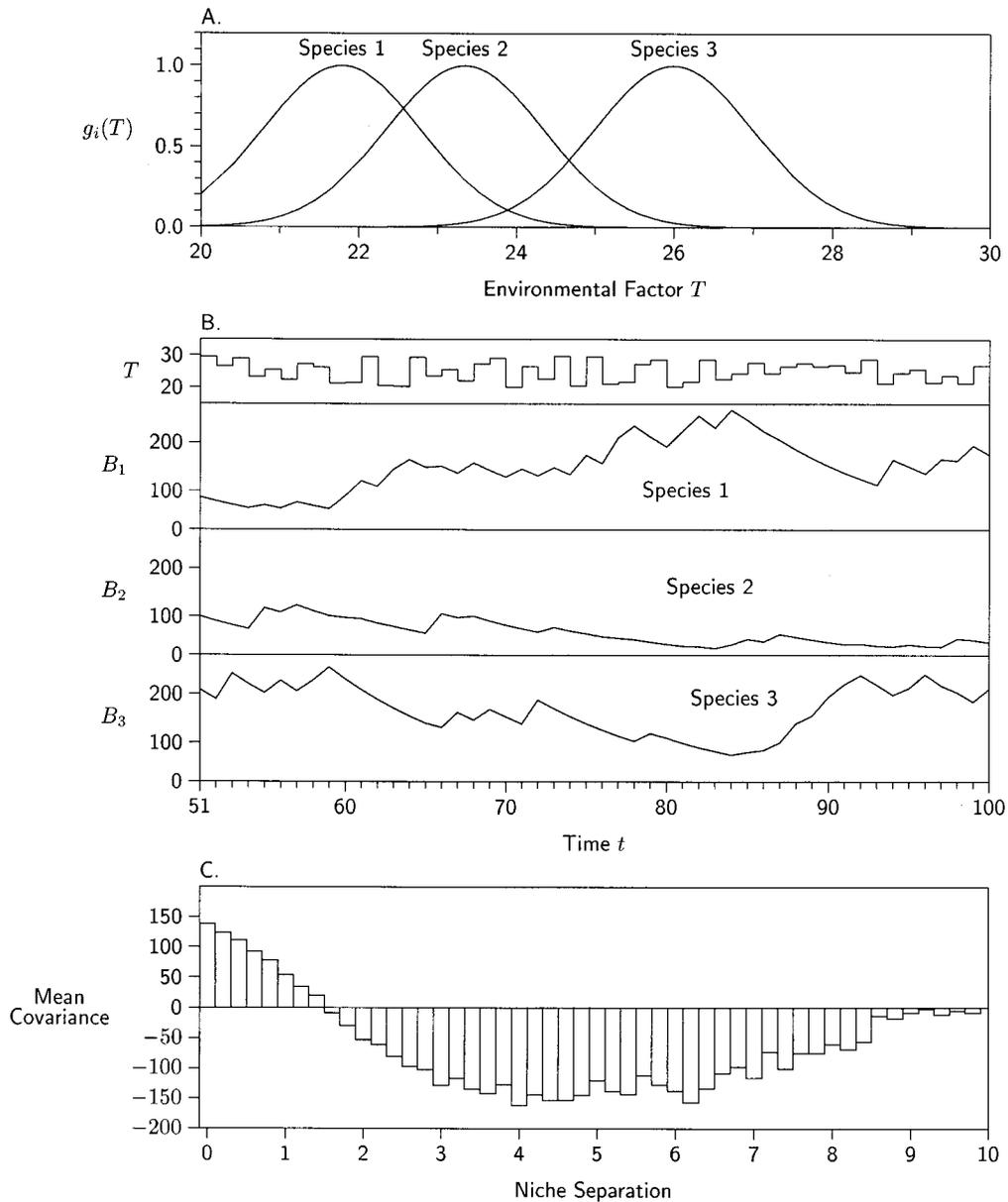
Community temporal stability also depends on the summed covariances in equation (1). Covariance,  $\text{Cov}(B_i, B_j)$ , measures how two species  $i$  and  $j$  vary jointly. If a covariance is positive, then the two species tend to increase and decrease together. If negative, one species tends to increase when the other decreases. If 0, then neither case is true—for example, they vary independently or do not vary. Thus, covariance provides a measure of species interactions, tending to be negative for competitors, positive for mutualists, and near 0 for noninteracting species. If summed covariances become smaller (i.e., more negative) as diversity increases, this covariance effect will make the total community temporally more stable, as seen by inspection of equation (1).

For  $n$  species, the covariances between pairs of species occupy the off-diagonal elements of the symmetric  $n \times n$  covariance matrix. The variances of individual species occupy the diagonal elements. The net variance in total community biomass is the sum of all elements of the matrix, that is, it is the sum of the variances of the individual species (all diagonal elements) plus the sum of the covariances between species (all off-diagonal elements). Roughly speaking, the portfolio effect results if the summed variances decrease as diversity increases, whereas the covariance effect results if summed covariances do so.

#### *Overyielding*

Overyielding occurs when the average total biomass of a community increases with diversity (Harper 1977; Naeem et al. 1995; Tilman et al. 1996, 1997a; Hector et al. 1999). Because biomass occurs in the numerator of equation (1), if all else were equal, overyielding would tend to temporally stabilize a community (reduce relative temporal variation) as diversity increased, giving an overyielding effect on temporal stability.

Because the relationship between diversity and summed variances, summed covariances, and total community biomass depends in turn on the mechanisms of interactions in a community, we examine three different models of interspecific competition to determine the dependence of temporal stability on diversity.



**Figure 1:** Simulations of the resource model. The system is that of equation (2) using parameters of table 1. A, Maximal growth rates of three species as a function of the environmental factor  $T$  for one of the 1,200 simulations. Here the points of maximal growth are approximately  $\tau_1 = 21.78$ ,  $\tau_2 = 23.35$ , and  $\tau_3 = 26.00$ . B, Sample trajectory for the above three species competing. The top curve shows the environmental factor as a function of time (a driving variable); the lower three curves show biomass of individual species (response variables). The first 50 time units in all the resource simulations allowed the system to settle but did not take part in further calculations. C, Covariance as a function of niche separation. Each histogram bar represents the mean covariance for species separated by the corresponding distance class. Results are drawn from communities of two to 12 species.

### Nonequilibrium Resource Competition

Let us consider species competing for a single resource, such as plants consuming nitrogen, but living under the

influence of a fluctuating physical factor, such as temperature. Resource-based models of competition (e.g., Tilman 1980) can be modified to have each species' resource-dependent growth rate depend on a time-varying physical

factor (eq. [2]). We let each species have its optimal competitive ability (minimal  $R^*$  value and maximal per capita gross productivity) at some value of the physical factor and have its productivity fall off as a bell-shaped curve away from this value (fig. 1A):

$$\frac{dB_i}{dt} = \left[ g_i(x) \frac{R}{R + K_i} - m_i \right] B_i,$$

$$\frac{dR}{dt} = \alpha(S - R) - \sum_{i=1}^n Q_i g_i(x) \frac{R}{R + K_i} B_i, \quad (2)$$

$$g_i(x) = r_i \exp \left[ -\frac{1}{2} \left( \frac{x - \tau_i}{w} \right)^2 \right].$$

Here  $R$  is the amount of resource,  $B_i$  is the biomass of species  $i$ ,  $x$  is the variable physical factor (e.g., temperature),  $\tau_i$  is the value of  $x$  at which species  $i$  has optimal competitive ability,  $w$  is the width of environmental tolerance, the product  $Q_i g_i$  is the temperature-dependent maximum resource assimilation rate,  $m_i$  is the sum of respiration and mortality rates of species  $i$ ,  $r_i$  is the maximal gross productivity rate of species  $i$  at its optimal temperature  $\tau_i$  and with unlimited resource,  $K_i$  is the half-saturation constant of the resource limitation function,  $S$  is the supply point of the resource, and  $\alpha$  is the supply rate of the resource. This model is similar to ones that have predicted competitive dynamics in a variety of habitats (e.g., Tilman 1976, 1977, 1982; Grover 1997).

In an unchanging environment, this system would exhibit competitive exclusion. The species with the lowest  $R^*$  would draw the resource down to that level (Tilman 1982), at which point its biomass would be constant and all other species would be driven toward local extinction. Thus, the only equilibrium is a single-species equilibrium. In a variable environment, however, many species may persist (fig. 1B). The abundance of all species constantly varies, and this variation allows coexistence (Chesson 1986, 1994). This resource model thus presents nonequilibrium conditions (DeAngelis and Waterhouse 1987) in which multiple species cannot coexist at fixed densities.

#### Numerical Solutions

To determine the effects of diversity on productivity and on temporal stability, we solved equations (2) at many levels of diversity, with randomly assembled communities of species identical in all respects (table 1) except for their optimal temperatures,  $\tau_i$ . The species pool contained species of all possible  $\tau_i$  between  $x_0$  and  $x_1$ , with all values of  $\tau_i$  having equal probability. We randomly selected  $n$  species

from the pool (i.e.,  $n$  values of  $\tau_i$ ) and allowed them to compete in a randomly varying environment. In our solutions of equations (2),  $x$  changed at the beginning of each "year" to a new random value chosen from a uniform distribution on the interval [20, 30]. After allowing the system 50 yr (generations) of growth to adjust to the varying environment, we recorded annual year-end biomass, year-to-year variance in biomass, and covariances for all species pairs over the next 50 yr. We solved the equations using Mathematica (Wolfram 1996) for communities of one through 12 species, with 100 independent selections of species and random environments each, yielding a total of 1,200 simulations.

#### Effects on Productivity

As expected, environmental variability allowed multispecies persistence. Mean biomass of a species depended on the species' niche position, being lowest at the extremes of the range but positive throughout. On average, total community biomass rose toward an asymptote with increasing biodiversity (fig. 2A) because a greater number of species provided better "coverage" of the varying temperature conditions. Average abundances of individual species decreased as diversity increased but declined more slowly than simple dilution (fig. 2B). There was large variation in biomass among different communities of the same diversity, which was not sampling noise but resulted from different species compositions (i.e., from different randomly chosen combinations of  $\tau_i$ ). Interestingly, the upper bound of this variation increased with diversity, meaning that no monocultures were as productive as some two-species combinations, no two-species combinations were as productive as some three-species combinations, and so forth. This greater total community biomass, indicative of overyielding, was directly related to lower average resource levels caused by more complete resource use at higher diversity. Similar patterns are predicted by models that incorporate other "niche differentiation" mechanisms of competition (Huston 1997; Tilman et al. 1997b; Yachi and Loreau 1999). Such patterns also have been observed experimentally (e.g., Naeem et al. 1994, 1995; Tilman et al. 1996, 1997a; Hector et al. 1999) and, as noted by McNaughton (1993) and Kareiva (1996), were seen in the nineteenth century by Charles Darwin.

#### Effects on Temporal Stability

On average, temporal stability of total community biomass (eq. [1]; app. A; eq. [A2]) increased monotonically and rather linearly with increasing biodiversity (fig. 2C), indicating that the community became increasingly less variable at higher diversity. Such lessened variability matches

**Table 1:** Parameter values for resource simulations

Parameter	Symbol	Value
Resource supply rate	$\alpha$	1
Width of environmental tolerance	$w$	1
Half-saturation of resource use	$K_i$	10
Mortality and respiration	$m_i$	.1
Biomass conversion coefficient	$Q_i$	2
Maximum gross productivity	$r_i$	1
Resource supply point	$S$	100
Beginning time	$t_0$	0
Time when monitoring began (yr)	$t_1$	50
Ending time (yr)	$t_2$	100
Lowest value of environmental factor	$x_0$	20
Highest value of environmental factor	$x_1$	30
Mean value of environmental factor	...	25
Variance in environmental factor	...	8.3
Lowest tolerable resource level	$R^*$	1.1

the predictions Yachi and Loreau (1999) made when they analyzed two different cases of competition. There was large variation in temporal stability among randomly assembled communities of the same diversity (*small dots*, fig. 2C), indicating that species composition, as well as diversity, was a major determinant of temporal stability, as it was in the case of productivity. In figure 2C, 59% of the variance in temporal stability can be attributed to species composition and 41% to diversity.

Note that temporal stability of the community (fig. 2C) continued to increase even as total biomass (fig. 2A) leveled off. Temporal stability of individual species (fig. 2D) decreased as diversity increased. How could the entire community become less variable with increasing diversity even though every species in the community becomes more variable?

The answer lies in the components of temporal stability—the variances, covariances, and abundances—and how these components depend on diversity. As diversity increased, the summed variances for the community (the sum of the diagonal elements of the covariance matrix) rose to a maximum and then dropped (fig. 3A), while the summed covariances (the sum of all the off-diagonal elements) fell to a minimum and then rose again (fig. 3B). The sum of these two curves (fig. 3A, 3B) is the net variance in total community biomass (fig. 3C), which decreased monotonically with increasing diversity. Net variance declined as diversity increased from one to four species because of a covariance effect (increasingly negative summed covariances). Beyond four species, when summed covariances started to rise, net variance continued to decline because the summed variances (the portfolio effect) decreased more than the summed covariances increased. This monotonic decrease in net variance with increasing diversity would have been sufficient to increase the tem-

poral stability of total community biomass even if total community biomass were constant. However, overyielding at higher diversity (fig. 2A) temporally stabilized the community further. The continuing decrease in net variance maintained an increase in temporal stability of total community biomass even after total community biomass leveled off. Although total community biomass became temporally more stable as diversity increased, the biomass of individual species became temporally less stable (fig. 2D), much as predicted by May (1972).

Thus, in this resource competition model far from equilibrium, species composition had a major effect on temporal stability, but on average, individual species became relatively more variable with increasing diversity while the community as a whole became relatively less variable. In other words, on average, diversity decreased the temporal stability of individual species yet increased the temporal stability of the entire community. This is just as Tilman (1996) observed in grassland communities.

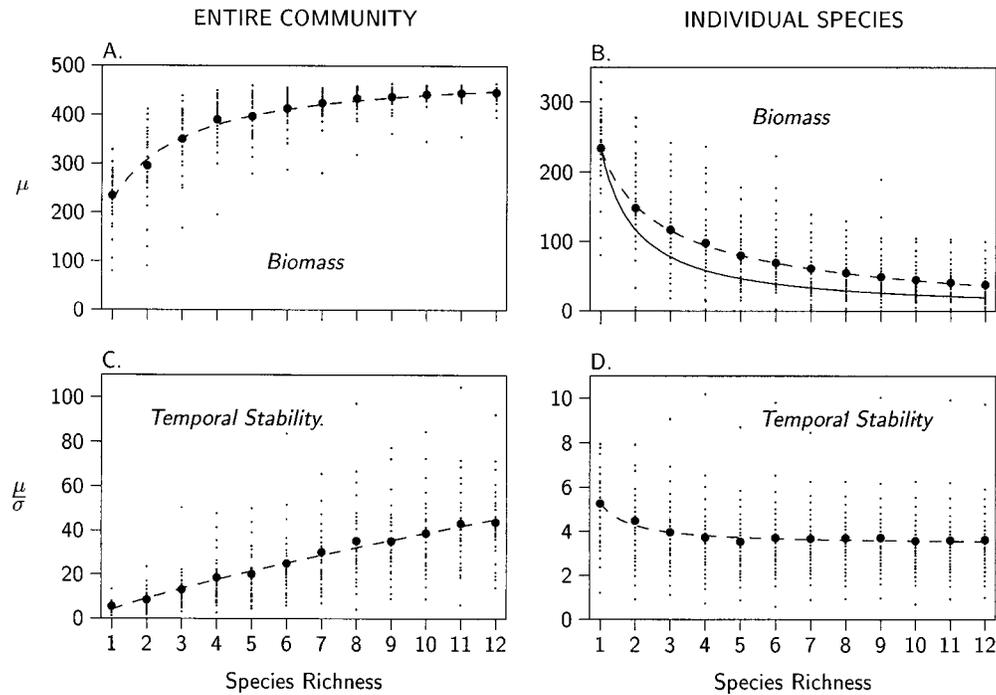
#### Covariance and Species Interactions

In this resource model, as in nature, species that compete most strongly might be expected to have the strongest negative effects on each others' abundances. Likewise, species with very different requirements should have a negligible effect on each other. Such an effect was apparent in the simulations, where the covariance between two species  $i$  and  $j$  depended on the distance  $|\mu_i - \mu_j|$  between the midpoints of their environmental tolerances (fig. 1C). However, the effect was not uniformly negative. Species whose optimal growth rates occur at nearby values of the variable environmental factor were positively correlated. At intermediate distances, species tended to fluctuate independently of one another, whereas at greater distances, they became negatively correlated. At larger distances still, the negative correlation tended to vanish, so very dissimilar species tended to fluctuate independently. Even though very similar species might inhibit each other strongly, they also flourish under similar environmental conditions, and that leads to positive covariance for similar species under this kind of temporal coexistence.

#### Lotka-Volterra Competition

Next let us consider a more phenomenological model in which any number of species can stably coexist at equilibrium—the Lotka-Volterra competition equations:

$$\frac{dB_i}{dt} = r_i B_i \frac{K_i - \sum_{j=1}^n \alpha_{ij} B_j}{K_i}, \quad (3)$$



**Figure 2:** Productivity and temporal stability in the resource model. Large dots represent the means of 100 sample communities. Small dots show variation about the mean, with small dots separated by approximately four percentiles. Dashed lines are fitted curves showing the trends and are used to compute  $R^2$  values. In all cases, the proportion of variance not explained by diversity,  $1 - R^2$ , is caused by species composition. A, Biomass of the entire community. For the fitted curve,  $R^2 = 0.67$ . B, Biomass of individual species.  $R^2 = 0.55$ . The solid line traces the simple dilution curve,  $\mu(0)/n$ , along which community biomass would be independent of diversity. C, Temporal stability of community biomass.  $R^2 = 0.41$ . D, Temporal stability of individual species biomass.  $R^2 = 0.05$ .

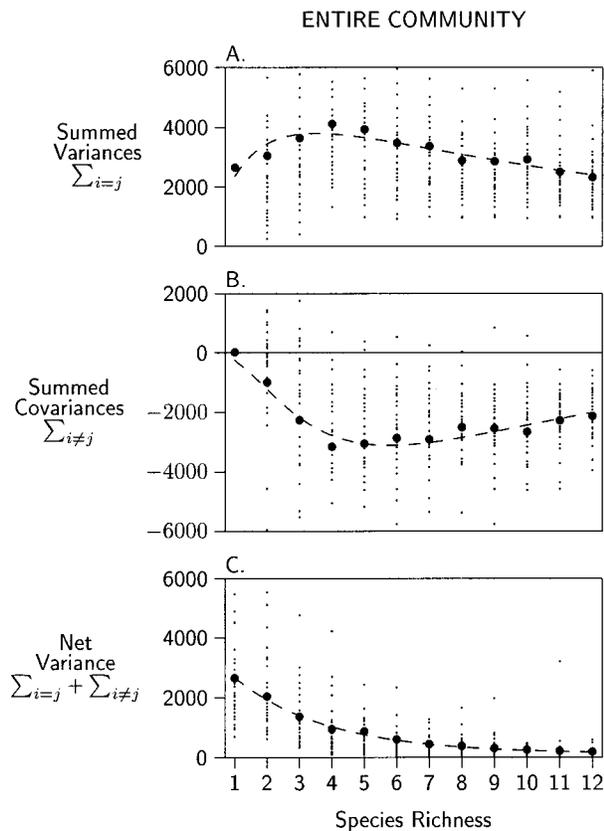
where  $B_i$  is the biomass of species  $i$  at time  $t$ ,  $r_i$  is the growth rate of species  $i$  under ideal conditions,  $K_i$  is the carrying capacity for species  $i$ ,  $\alpha_{ij}$  are competition coefficients, and  $n$  is species diversity. We first consider a case in which species are similar in their interactions, with identical growth rates ( $r_i = r$ ), carrying capacities ( $K_i = K$ ), and competition coefficients ( $\alpha_{ii} = 1$ ,  $\alpha_{ij} = v$ , with  $0 < v < 1$ ). Such similarity reduces the effect of species composition and makes it easier to see effects attributable to species richness alone. Here individuals compete more strongly with members of their own species than with members of other species, and any number of species can stably coexist at equilibrium ( $B_i > 0$  for all  $i$ ).

#### *Eigenvalue Stability of the Deterministic System*

In appendix B, we derive the local stability of the multi-species equilibrium using the eigenvalues of the Jacobian matrix (e.g., May 1972). For this model, all the eigenvalues are negative (app. B; eq. [B3]), so the equilibria are locally stable at all levels of diversity. However, as the number of

species in the community increases, the dominant eigenvalue becomes less negative, indicating that the strength of return by individual species to the  $n$ -species equilibrium decreases as diversity increases. That is, individual species become less resilient. Nonetheless, total community biomass returns to its steady state value after small perturbations at a rate that is independent of diversity (app. B; eq. [B6]), much as May (1974a) and later Ives et al. (1999) showed for other cases of Lotka-Volterra competition.

Furthermore, after an average small perturbation from equilibrium, biomass of the entire community (app. C; eq. [B6]) returns to its steady state more rapidly than do the biomasses of individual species (app. B; eq. [B5]; fig. 4). It might seem paradoxical that total abundance returns more rapidly than the parts that make it up, but this follows from the very nature of competition. Consider, for example, a two-species community in which one of the species is elevated above its equilibrium abundance. Its elevated abundance inhibits both its own growth and that of the other species. A higher abundance of one species thus induces a compensating lowered abundance of the



**Figure 3:** Community variance, covariance, and net variance in the resource model. Large dots represent the means of 100 sample communities. Small dots show the variation about the mean, with small dots separated by approximately four percentiles. Dashed lines are fitted curves showing the trends. A, Summed variances (the sum of the diagonal elements of the covariance matrix). B, Summed covariances (the sum of all the off-diagonal elements). C, Net variance in community biomass (the sum of all elements).

other, and this keeps the total abundance of the two species near the steady state level, even though both species may be far from their equilibria. The above points are derived mathematically in appendix B.

#### Stochastic Environments

For this Lotka-Volterra model, how do effects of diversity on eigenvalue stability compare to the effects of diversity on temporal stability? To address this, we performed stochastic simulations of equation (3), letting the carrying capacity of each species fluctuate about an average value of  $K$ . That is, we let  $K_i(t) = K + \gamma_i(t)$ , where  $\gamma_i(t)$  is background noise that varies randomly and uniformly in the interval  $[-\kappa, +\kappa]$ . At any instant, the carrying capacity

for a given species can be as low as  $K - \kappa$  or as high as  $K + \kappa$ , or anywhere in between.

We keep the noise  $\gamma_i(t)$  for species  $i$  independent of the noise  $\gamma_j(t)$  for species  $j$ . That is intended to simulate different species responding to different components of the varying environment. Covariance effects appear because different species respond differently to the environment (see Ives et al. 1999; Yachi and Loreau 1999). Indeed, if all species responded in exactly the same way, then they would all behave as a single species, all covariances would become variances, and hence the only effect of diversity on temporal stability would come from overyielding.

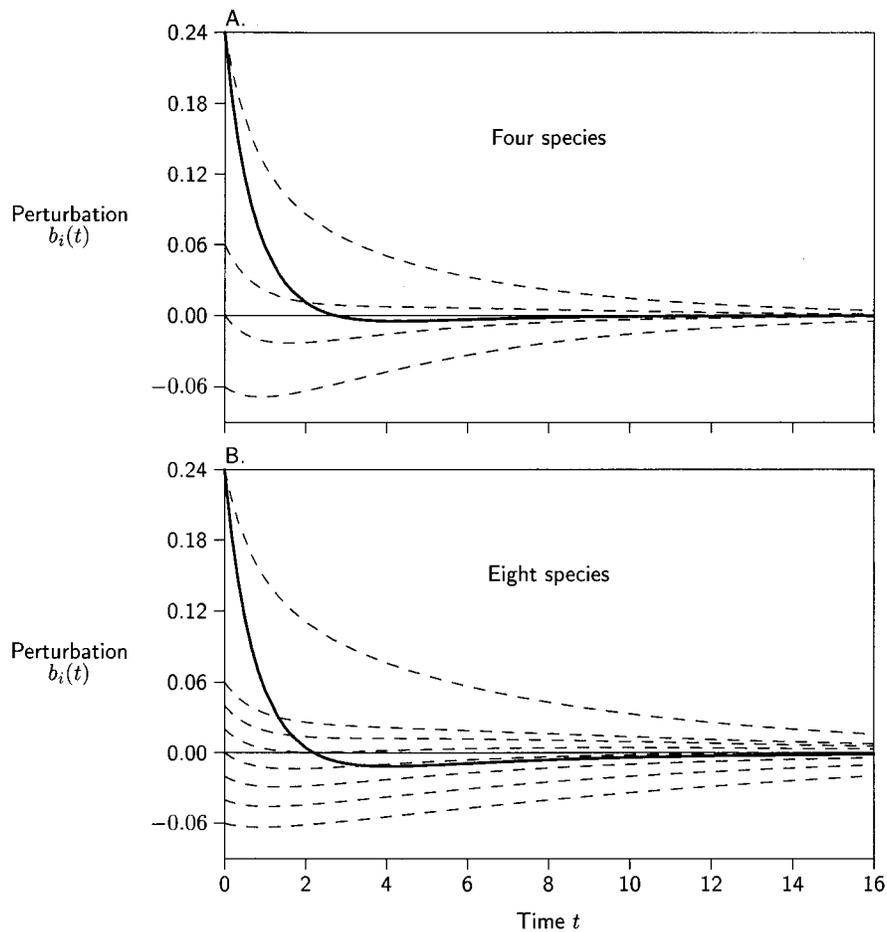
For these simulations, we let  $K = 1/2$  (e.g., a monoculture occupies half the available habitat) and  $v = 1/2$  (these parameters allow easy comparison with our next model). Then, from equation (B1) of appendix B, the equilibrium biomass of an individual species (solid curve, fig. 5B) is  $\hat{B}_i = 1/(n + 1)$ , and the total biomass in a community of species diversity  $n$  (solid curve, fig. 5A) is  $\sum_{i=1}^n \hat{B}_i = n/(n + 1)$ .

Using parameters shown in table 2, we ran stochastic simulations for communities of from one to 12 species. Each species was started at its deterministic equilibrium,  $\hat{B}_i$ . A new value of  $K_i$  was randomly selected for each species at each time step. The system ran 50 “years” (5,000 time steps) to allow it to settle into its normal behavior, then it was examined once per year for the next 950 yr of competition. All species coexisted, but the stochastic carrying capacity caused the biomasses of individual species to fluctuate.

In these stochastic simulations, mean total community biomass increased with diversity, and individual species biomass declined, as occurred in the deterministic equilibrium version of this model and also as occurred in the nonequilibrium resource competition model. Mean total community and individual species biomass under stochastic conditions approximated the equilibrium biomass predicted for a constant environment ( $n/[n + 1]$  and  $1/[n + 1]$ , respectively) but remained consistently lower (fig. 5A, 5B). This is because of the nature of the nonlinearities in the system (e.g., May 1972).

Temporal stability of the entire community increased steadily with diversity (fig. 5C). In contrast, temporal stability of individual species decreased with diversity (fig. 5D). Again, with respect to variability in biomass, increases in biodiversity stabilized the community but destabilized individual species.

As in the nonequilibrium resource competition model, the steady increase in temporal stability of the community as species richness increases is caused both by a decrease in net variance (fig. 6C) and an increase in total community biomass (fig. 5A). Although summed variances rose as diversity increased from one to 25 species (fig. 6A),



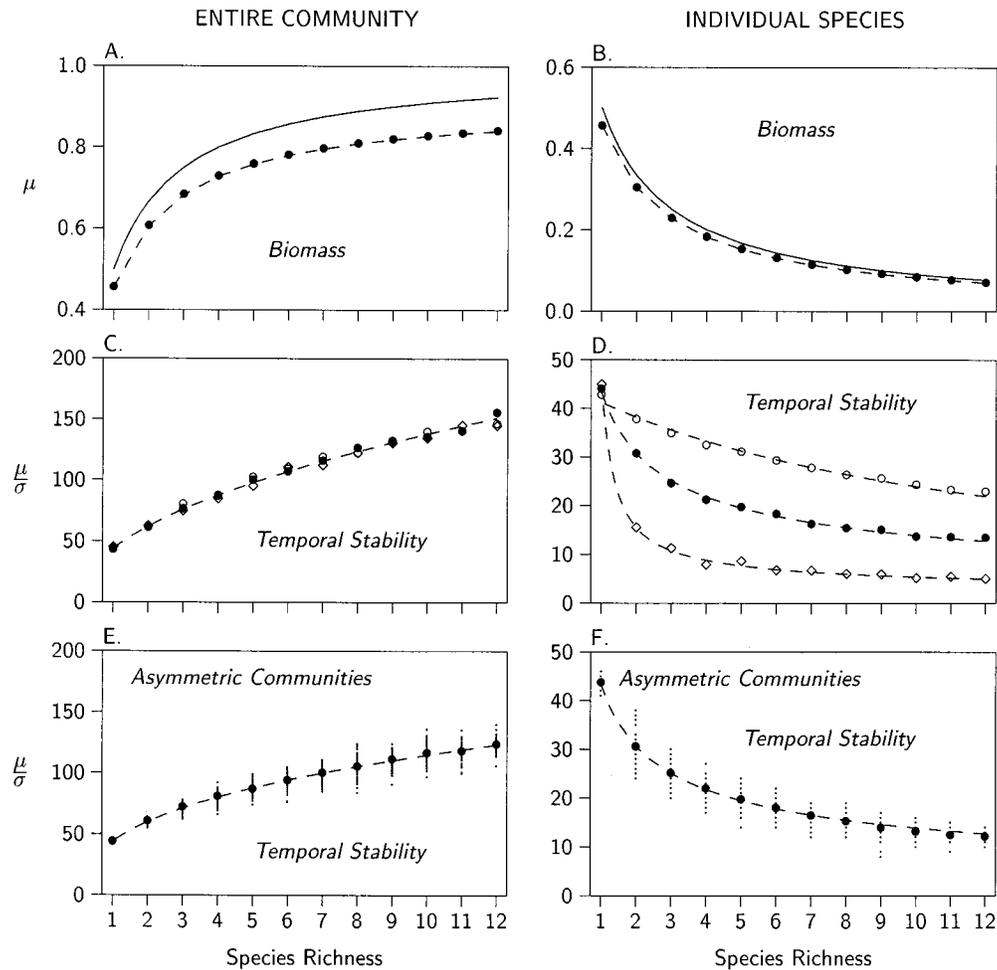
**Figure 4:** Return to equilibrium in the deterministic Lotka-Volterra system. An initial perturbation, shown on the vertical axis, is applied at  $t = 0$ , then the system returns under its own nonlinear dynamics. Total community biomass (*solid curves*) returns to steady state more rapidly than do individual species biomasses (*dashed curves*). Moreover, return of total biomass is not strongly affected by diversity, but individual species return more slowly in more diverse communities. These conclusions follow from the linear stability analysis near equilibrium (app. B), but they continue to apply in the large deviations depicted here, where individual species biomass is elevated up to three times its equilibrated level. Parameters  $r$ ,  $v$ , and  $K$  are those of table 2. *A*, Four-species community. Note that even though species 3 (third *dashed line* from the top) is not perturbed initially, competitive effects soon drive it away from equilibrium. *B*, Eight-species community. The four new species are perturbed in such a way as to keep the total perturbation the same as in *A*. Total biomass returns only slightly slower than in *A*, but individual biomasses return much more slowly.

the summed covariances declined even more (fig. 6B), causing net variance to decline (fig. 6B) and thus total community biomass to be temporally stabilized (fig. 5C). Beyond about 25 species, summed covariances started to rise, but then summed variances underwent a more rapid decline, causing net variance to continue declining and thus total community biomass to be further temporally stabilized as diversity continued to increase. Thus, this parameterization of the Lotka-Volterra model behaved much as did the previous model, with community temporal stability increasing with diversity first because of covariance effects and then because of the portfolio effect.

The overyielding effect added to temporal stability for all levels of diversity but in diminishing amounts when diversity was high. In this model, however, negative covariances remain an important factor of temporal stabilization to a much higher level of diversity than in the resource model.

#### *Temporal versus Eigenvalue Stability*

In this Lotka-Volterra formulation, there is a qualitative correspondence between temporal stability and eigenvalue stability, but this need not occur in general. A decreasingly



**Figure 5:** Productivity and temporal stability in Lotka-Volterra model. *A–D*, Symmetric communities. Each solid dot represents a single simulation with  $v = 1/2$  averaged over 950 “years.” Solid lines in *A* and *B* represent the analytical equilibria that would be achieved if stochastic fluctuations were suppressed. Dashed lines are fitted curves showing the trends. Compare with figures 2 and 7. *C, D*, Diamonds and open circles indicate how temporal stability depends on the strength of competition. Diamonds represent strong competition ( $v = 0.9$ ); open circles represent weak competition ( $v = 0.2$ ). *E, F*, Asymmetric communities with competitive exclusion. Small dots show the range of variation in individual stochastic simulations; large dots represent means. In each simulation, the competition coefficients  $v_{ij}$  were selected randomly from a uniform distribution with mean one-half and range plus or minus one-fourth. Each simulation was averaged over 950 “years” as in *A–D*.

negative dominant eigenvalue always means decreasing local eigenvalue stability, but it can lead to either an increasing or decreasing degree of fluctuations in population abundances, depending on how stochasticity enters the system (e.g., Loreau and Behera 1999; also cf. May 1974*a*, 1974*b*, 1974*c*; Feldman and Roughgarden 1975; Roughgarden 1975; Turelli 1978*a*, 1978*b*). Indeed, even the mathematical foundations for integrating stochastic systems are not free of ambiguity (e.g., Karlin and Taylor 1981, pp. 346–347). Eigenvalue stability of equilibria is well understood mathematically and is widely taught and used, yet it is difficult to measure in natural ecosystems, which may never go to equilibrium. A deeper knowledge of the re-

lationship between these two forms of stability would be worthwhile.

#### Variations in Competitive Interaction

How does the strength of interspecific competition affect the temporal stability of the community and of its constituent populations? As derived in appendix B, the equation describing the return of individual species biomass to equilibrium (eq. [B5]) is a function of the competition coefficient,  $v$ , but that describing the return of total community biomass (eq. [B6]) is independent of  $v$ . This suggests that temporal stability of individual species will be

**Table 2:** Parameter values for Lotka-Volterra simulations

Parameter	Symbol	Value
Growth rate per year	$r$	1
Deterministic carrying capacity	$K$	.5
Beginning time	$t_0$	0
Years before monitoring begins	$t_1$	50
Years per simulation	$t_2$	1,000
Simulation steps per year	$1/\Delta t$	100
Range of variation in $K$ per simulation step	$\kappa$	$\pm .25$

sensitive to the strength of competition but temporal stability of the entire community will not.

Figures 5C and 5D illustrate this as the results of stochastic simulations for three different intensities of competition. Parameters are those of table 2. Filled circles represent the intermediate level of competition described above ( $v = 0.5$ ), diamonds represent stronger competition ( $v = 0.9$ ), and open circles represent weaker competition ( $v = 0.2$ ). Qualitatively, all three cases were similar: community temporal stability increased with increasing diversity while population temporal stability decreased. However, while there were distinct differences in temporal stability among populations in communities with different strengths of interspecific competition (fig. 5D), there was no significant difference in temporal stability of the communities themselves (fig. 5C). Diversity still temporally stabilized the community while destabilizing individual populations, but the strength of competition had little effect on the magnitude of stabilization of the community. This is consistent with results derived for different stability measures from discrete-time analysis (Hughes and Roughgarden 1998; Ives et al. 1999).

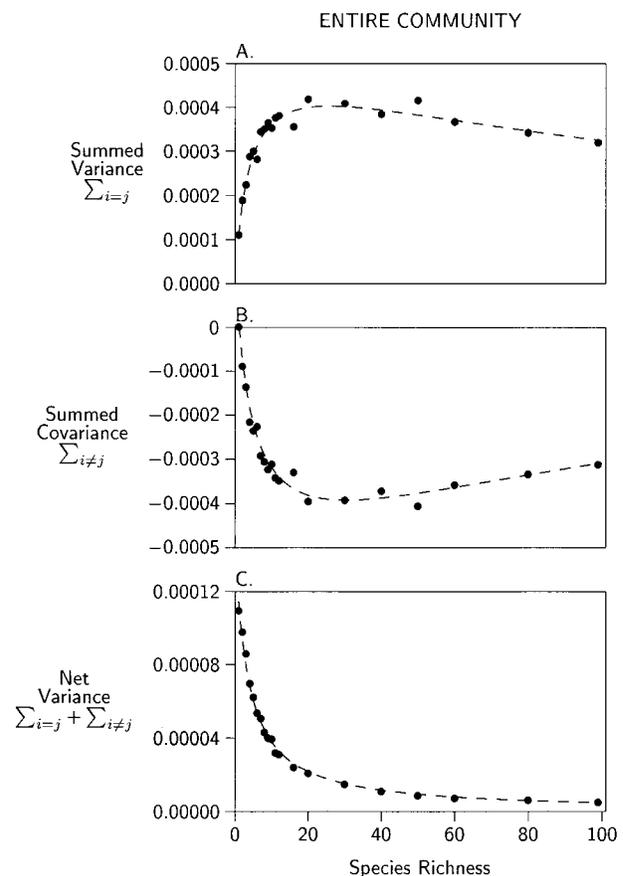
The distinction between community and population temporal stability arises because two effects compensate and keep temporal stability of the community relatively invariant. First, greater interspecific competition (e.g.,  $v = 0.9$ ) produces more negative covariances among species, tending to increase temporal stability of the community. Second, however, greater interspecific competition leads to less overyielding, tending to decrease the temporal stability of the community (see eq. [1]; app. A; eq. [A2]). These two effects roughly cancel. Given sufficiently strong overyielding, net community variance could actually increase at low levels of diversity without causing temporal stability to decrease.

#### *Asymmetric Competition*

In the symmetric Lotka-Volterra communities considered thus far, any number of species coexist at equilibrium. When all species affect each other identically with  $v < 1$ , there is no upper bound on species packing in this system.

The question arises: Does temporal stability depend in the same way on diversity when the species do not affect each other identically?

We examined this question by constructing random community matrices in which the diagonal elements were always 1 but in which the off-diagonal elements differed. For comparison with the symmetric communities above, we used the parameters of table 2 but selected off-diagonal elements independently from a uniform random distribution with mean one-half and with range plus or minus one-fourth. We then ran approximately 1,000 stochastic simulations for communities with a range of species richnesses, using the same simulation protocols described above for the symmetric communities. We allowed 500 yr for the system to settle and then monitored it for 1,000 yr. A species was considered competitively excluded if its abundance at the end of the simulation (i.e., after 1,500 yr) was less than  $10^{-6}$ .



**Figure 6:** Community variance and covariance in the Lotka-Volterra model. Each large dot represents a single simulation averaged over 950 “years.” Dashed lines are fitted curves showing the trends. Compare with figures 3 and 8.

**Table 3:** Analytical properties of the broken-stick model

Temporal stability of entire community (fig. 7C; eq. [C12])	$\sqrt{n(n+2)}$
Temporal stability of individual species (fig. 7D; eq. [C11])	$\sqrt{1+2/n}$
Summed community variance ( <i>diagonal</i> , fig. 8A; eq. [C7])	$\frac{n^2}{(n+1)^2(n+2)}$
Summed community covariance ( <i>off-diagonal</i> , fig. 8B; eq. [C8])	$-\frac{n(n-1)}{(n+1)^2(n+2)}$
Net community variance (fig. 8C; eq. [C10])	$\frac{n}{(n+1)^2(n+2)}$

With that criterion, many species were excluded. Communities with 12 surviving species, for example, developed from communities initially containing as many as 50 species with an initial mean of 21.8 species. Figure 5E and figure 5F show the resulting temporal stabilities for randomly assembled communities and their constituent populations compared to their final diversity. Large dots represent means; small dots show the variation about the means. These means correspond to the large dots in figure 5C and figure 5D, which represent perfectly symmetric communities.

Qualitatively, the same pattern appears. The mean temporal stability of individual populations in the randomly assembled communities (fig. 5F) is close to that in the symmetric communities (fig. 5D). The mean temporal stability of the community rises with increasing diversity but more slowly than for symmetric communities (cf. fig. 5E with fig. 5C). This slower rise is due in part to dominance by a few individual species in randomly assembled communities that thus have lower diversity in terms of the Shannon diversity index. Thus, the analytical results derived for these Lotka-Volterra communities are not restricted strictly to the symmetric form analyzed.

Increasing temporal stability with increasing diversity in the cases above might seem to conflict with the idea that fluctuating environments tend to favor less diverse communities—for example, the idea that the tropics are more diverse than temperate zones, in part because the tropical environment is less variable (e.g., Abrams 1976; Nisbet et al. 1978). However, the cases reported here do not address that question, which concerns limits to packing in fluctuating environments. None of the communities considered here is “overpacked” with species. The kinds of communities represented in figure 5C and 5D have no hard upper limit on species numbers, while those represented in figure 5E and 5F are communities that have been randomly assembled from larger communities that underwent competitive exclusion. How temporal stability behaves under transient conditions as overpacked communities are

losing species is an interesting question but not one addressed here.

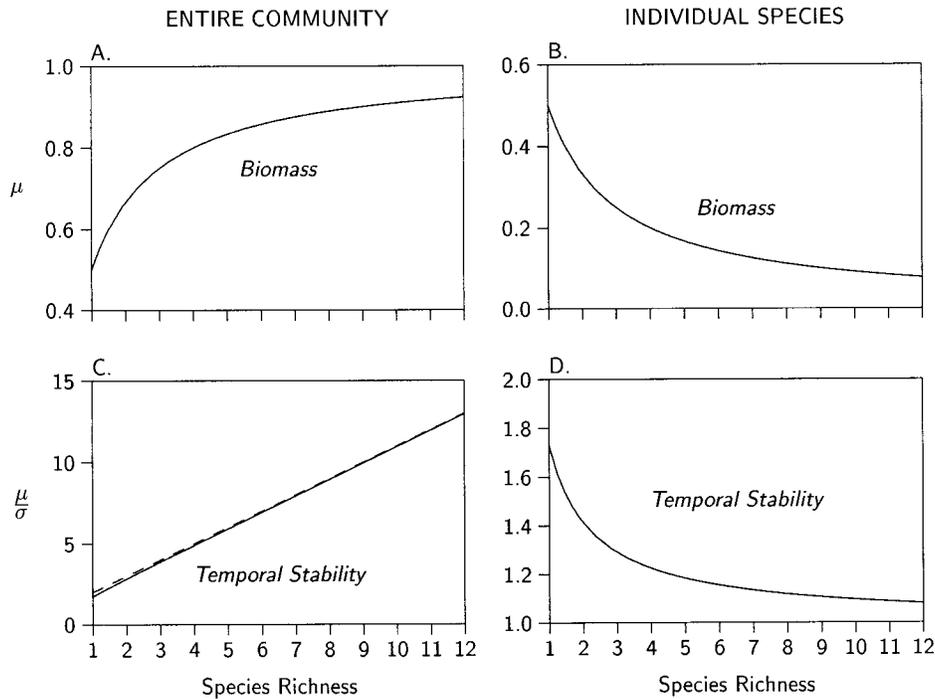
### A Statistical Model of Competition

A cost of greater realism is greater complexity. In the previous two models, increased diversity temporally stabilized total community abundances, but neither model was amenable to complete analytical solution. We now explore a highly abstracted model in hope of capturing the underlying processes that cause diversity to affect population and community temporal stability.

The essence of interspecific competition is the partitioning of limiting resources among species. In simplest form, let us assume that each year a fixed limiting resource is randomly and independently partitioned among competing species—a variation on the broken-stick theme of MacArthur (1957, 1960). Though the assumption of random partitioning might seem to be an overly strong caricature of nature, we shall show that it has surprising similarities to the two previous more realistic models and has the benefit of being analytically tractable.

#### Analytical Solution

Let the unit interval  $[0, 1]$  represent a fixed resource that can be divided up among competing species, with the relative abundance of a species determined by the length of the subinterval it occupies. Simultaneously break the unit interval at  $n$  random points selected from a uniform distribution on this interval. The length of the leftmost subinterval represents the amount of resource seized by species 1, the length of the second subinterval from the left represents the same for species 2, and so forth. The length of the rightmost subinterval, beyond the  $n$ th point, represents unused resource—for example, bare ground or unconsumed soil nitrate. Let this process of random resource partitioning be repeated each year. As shown in appendix C, it is then possible analytically to calculate the average abundance of each species (i.e., the average length of each subinterval), the year-to-year variance in abundance of each species, and the covariances among species abundances. Where  $n$  is the number of species in a community, the average biomass of an individual species is  $1/(n+1)$  and the average total community biomass is  $n/(n+1)$ . This is an example of a model for which there is no equilibrium state at all, stable or unstable (see DeAngelis and Waterhouse 1987), and for which eigenvalues are not even defined. Temporal stability is defined, however, and for total community biomass is equal to  $\sqrt{n(n+2)}$  (app. C).



**Figure 7:** Productivity and temporal stability in the broken-stick model. Solid curves represent analytical long-term averages derived in appendix C. The dashed line in C is a linear asymptote, which is approached very quickly. Compare with figures 2 and 5.

#### *Effects on Productivity and Temporal Stability*

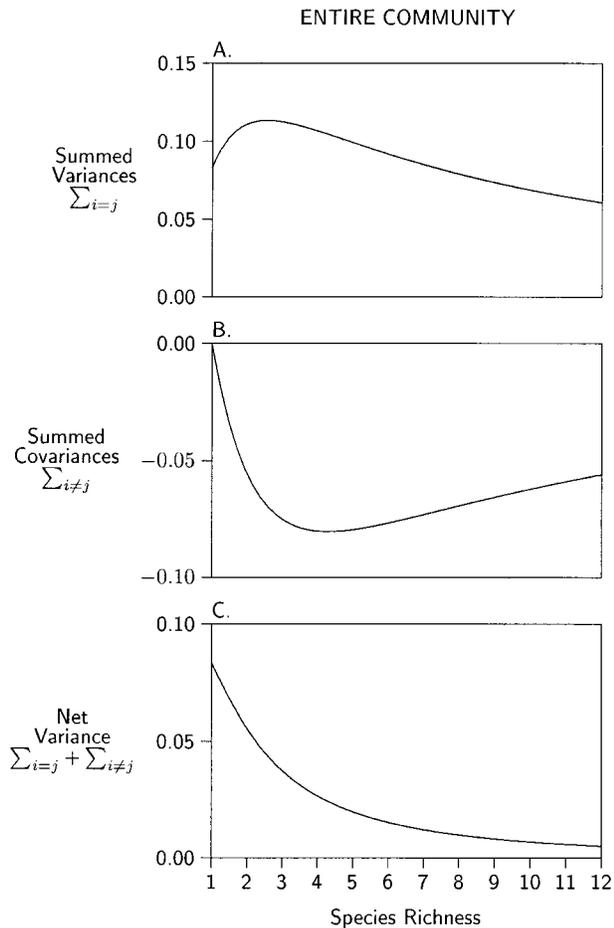
The formulas summarized in table 3 define how temporal stability depends on diversity in this modified broken-stick model. As in the first two models, total community biomass (summed abundances) increases asymptotically with increasing diversity (fig. 7A), while individual species abundances decrease (fig. 7B). Temporal stability of total community biomass increases as diversity increases (fig. 7C), and that of individual species decreases (fig. 7D), again indicating that the community becomes less variable and populations become more variable with increasing diversity. It is interesting that, in this highly abstracted model, the increase in community temporal stability is very nearly linear, and the analytical formula (app. C; eq. [C12]) shows that it approaches perfect linearity as diversity increases to large values. This is an important point because it shows that the temporal stabilization of community biomass continues to increase uniformly through all levels of diversity. The effect of diversity on temporal stability of the community never levels off.

The contributing components are qualitatively similar to the previous models. The summed variance (the sum of the diagonal elements of the covariance matrix) increases to a maximum at about three species, then decreases slowly toward 0 as the number of species in the

community increases (fig. 8A). Thus, the portfolio effect contributes to greater temporal stability for diversity greater than about three species. Summed covariance (the sum of all the off-diagonal elements) is always negative. As diversity increases from one to four species, the covariance effect adds to temporal stability, but then it subtracts from temporal stability as diversity increases beyond four (fig. 8B). The summed variance and summed covariance curves combine to give the net variance in total community biomass, which decreases steadily to 0 as diversity increases (fig. 8C). Overyielding also contributes to community temporal stability.

#### **Competition and Stability in a Natural Grassland**

Earlier research (Tilman and Downing 1994; Tilman 1996) reported that total plant community biomass was temporally more stable in areas with higher plant diversity. This greater temporal stability of community biomass occurred both in response to a major perturbation—a once-in-50-yr drought—and in response to more normal year-to-year variation in climate. Using data for the same 207 grassland plots analyzed in Tilman and Downing (1994) and Tilman (1996), we determined how temporal stability,  $S_T$ , depended on the average plant diversity of each plot.



**Figure 8:** Community variance, covariance, and net variance in the broken-stick model. Solid curves represent analytical long-term averages derived in appendix C. Compare with figures 3 and 6.

To do this, we used the mean and the year-to-year variance in total plant community biomass for each of the 207 plots, applying data from 1984 through 1998. We also determined the average plant species diversity of each plot. The 207 plots reside in four fields; plots receive different rates of nitrogen addition and have differing species compositions (Tilman 1996). Multiple regressions that included field, rate of nitrogen fertilization, mean species richness, and mean abundances of the three dominant plant species—*Schizachyrium scoparium* (little bluestem), *Agropyron repens* (quackgrass), and *Poa pratensis* (bluegrass)—as independent variables, and temporal stability,  $S_T$ , as the dependent variable, retained the rate of nitrogen addition (slope =  $-0.005$ ;  $P = .011$ ), abundance of *Schizachyrium* (slope =  $-0.0022$ ;  $P = .042$ ), and mean species richness (slope =  $0.051$ ;  $P = .0002$ ) as significant explanatory variables. The resulting overall multiple regression had  $F =$

$15.3$ ,  $df = 203, 3$ ,  $P < .0001$ , and  $r^2 = 0.18$ . The positive slope associated with mean species richness shows that the temporal stability of total community biomass,  $S_T$ , was significantly greater at higher plant species richness, even after controlling for effects of confounding variables. A similarly significant dependence was observed in the full multiple regression before elimination of nonsignificant ( $P > .05$ ) variables.

The greater temporal stability of more diverse communities in this grassland study is not caused by overyielding. Indeed, in this experiment, fertilization had two effects: it increased productivity and simultaneously decreased diversity. The higher temporal stability of higher diversity plots, which on average have lower plant biomass, thus represents covariance and portfolio effects strong enough to overcome an inverse-overyielding effect imposed by fertilization. An analysis of the dependence of summed variance and summed covariance on diversity in these plots (Tilman 1999) revealed patterns similar to those predicted here.

### Summary

All three models of competition examined here predict similar qualitative dependence of temporal stability on diversity; with respect to variation in biomass, diversity stabilizes the community but destabilizes individual populations. All three models also show productivity increasing as communities become more diverse. In addition, the resource model shows that the species composition of a community can be as important as diversity in determining temporal stability and productivity.

The three models differ markedly, one being a model of nonequilibrium competition, one being a stochastic phenomenological model, and one being almost completely probabilistic. Their common element is that all are structured by interspecific competition, and all make the same qualitative predictions. Hence it may be that these models are revealing common features of competitive communities. These models predict patterns like those observed in field and laboratory studies, where total community abundance is observed to be temporally stabilized by diversity (Tilman 1996; McGrady-Steed et al. 1997; Naeem and Li 1997), whereas individual species abundances are temporally destabilized (Tilman 1996). The temporal destabilization of individual species abundances at higher diversity is consistent with predictions originally made by May (1972, 1973, 1974a, 1974b, 1974c), who also suggested that whole system properties would be more stable than those of individual species. Our results extend this conclusion by demonstrating that the whole system does not just have greater temporal stability than individ-

ual species but indeed has the opposite dependence on diversity.

These results show that the temporal stabilizing effect of diversity on community biomass is caused by three interacting processes. As diversity increases from low to moderate levels, the major temporal stabilizing forces are the covariance effect and the overyielding effect. The portfolio effect is not operational at low levels of diversity because variance is scaling approximately linearly with abundance there. Further increases in diversity lead to increased temporal stability because of both the portfolio effect and the overyielding effect, which compensate for the increasingly less negative summed covariances. The same qualitative pattern of diversity-dependent contributions from the portfolio effect, the covariance effect, and the overyielding effect occurred in all three models.

In total, the models presented here suggest that a common feature of communities of exploitatively competing species is that total community biomass, and perhaps other total community attributes, have greater temporal stability in response to environmental stochasticity at higher diversity but that individual populations have decreased temporal stability at higher diversity. The similarity of these predictions to the patterns observed in a field study (Tilman and Downing 1994; Tilman 1996, 1999) adds credence to the conclusions.

The views presented here provide a partial resolution of the long-standing diversity-stability debate. Diversity increases temporal stability at the community level, in agreement with Elton and other early investigators, but decreases stability at the population level, in agreement with May and later investigators. Thus, each side of the debate was in essence correct. However, as is so often the case in science, a final resolution awaits further work, including extensions to multiple trophic levels.

**Acknowledgments**

We are grateful to B. Foster, S. Gaines, J. Haarstad, N. Haddad, L. Johnson, C. Klausmeier, N. Larson, R. McGehee, C. Neuhauser, K. Thomson, and two anonymous reviewers who helped and guided us in many ways during the preparation of this manuscript.

**APPENDIX A**

**Definition of Temporal Stability**

Let  $S_i(n)$  denote the temporal stability of the abundance of species  $i$  coexisting in a community of  $n$  competing species and  $S_T(n)$  denote the temporal stability of the total community. Let  $B_i(n)$  represent the biomass of species  $i$

in a specific  $n$ -species community. Because this biomass may vary through an interval of time, let  $\bar{B}_i(n)$  represent the mean biomass during that interval. Then the temporal stability  $S_i(n)$  of species  $i$  living in the average community of  $n$  species is the expected value (E) of mean biomass relative to its standard deviation, taken as the average over all possible communities (or a large representative sample of them):

$$S_i(n) = E \left\{ \frac{\bar{B}_i(n)}{\sqrt{\text{Var}[B_i(n)]}} \right\}. \tag{A1}$$

The biomass of an entire community is the sum of the biomasses of its constituent species. The variance of the sum of  $n$  variables is the sum of all elements in the  $n \times n$  covariance matrix, which includes not only all the individual variances but also the covariances between all possible ordered pairs of species. Thus, for the total biomass of a community,

$$S_T(n) = E \left\{ \frac{\sum_i \bar{B}_i(n)}{\sqrt{\sum_i \text{Var}[B_i(n)] + \sum_{i \neq j} \text{Cov}[B_i(n), B_j(n)]}} \right\}. \tag{A2}$$

Each species pair enters the formula twice, once as  $\text{Cov}(B_i, B_j)$  and again as  $\text{Cov}(B_j, B_i)$ , and because the covariance matrix is symmetric, the two are equal.

**APPENDIX B**

**Lotka-Volterra Local Stability**

At the interior equilibrium of the Lotka-Volterra equations (3), where all  $n$  species coexist, abundances are defined by solutions to the  $n$  simultaneous linear equations  $K_i = \sum_{j=1}^n \alpha_{ij} B_j$ . With parameters as described in the text ( $r_i = r$ ,  $K_i = K$ ,  $\alpha_{ii} = 1$ ,  $\alpha_{ij} = v$ ),

$$\hat{B}_i = \frac{K}{1 + (n - 1)v} \tag{B1}$$

for all  $i$ . The Jacobian matrix, evaluated at this equilibrium, is

$$\mathbf{J}(n) = - \frac{r}{1 + (n - 1)v} \begin{bmatrix} 1 & v & v & \cdots & v \\ v & 1 & v & \cdots & v \\ v & v & 1 & \cdots & v \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ v & v & v & \cdots & 1 \end{bmatrix}, \tag{B2}$$

and its eigenvalues are

$$\lambda(n) = \begin{bmatrix} -r \\ -r(1-v)/(1-v+nv) \\ -r(1-v)/(1-v+nv) \\ \vdots \\ -r(1-v)/(1-v+nv) \end{bmatrix}. \quad (B3)$$

These eigenvalues are always negative, but the dominant eigenvalue,  $-r(1-v)/(1-v+nv)$ , approaches 0 as  $n$  increases.

Suppose the deterministic system is perturbed a small amount from equilibrium then allowed to return under its own dynamics in the absence of stochasticity. Let  $b_i(0)$  represent the initial perturbation of species  $i$  from its equilibrium, and let  $b_i(t)$  represent what that perturbation will have become at any later time  $t$ . That is, let  $b_i(t) = B_i(t) - \bar{B}_i$ . Then the linear equations constructed from the Jacobian matrix, which describe the decay of sufficiently small perturbations back to equilibrium, can be shown to have the solution

$$b_i(t) = \bar{b}(0)e^{-rt} + [b_i(0) - \bar{b}(0)]e^{-rt(1-v)/(1-v+nv)}. \quad (B4)$$

Here  $\bar{b}(0)$  is the initial perturbation averaged over all species in the community, that is,  $\bar{b}(0) = \sum_{i=1}^n b_i(0)/n$ . Equation (B4) can be simplified by examining the perturbation at time  $t$  relative to the initial perturbation at time 0 (i.e.,  $b_i(t)/b_i(0)$ ), then by examining the average solution over all possible perturbations. For any reasonable distribution (such as Gaussian) of initial perturbations,  $b_i(0)$ , it can be shown that the normalized average response of an individual species is, from equation (B4),

$$\text{Mean} \left[ \frac{b_i(t)}{b_i(0)} \right] = \frac{1}{n} e^{-rt} + \frac{n-1}{n} e^{-rt(1-v)/(1-v+nv)}. \quad (B5)$$

The corresponding solution for total community biomass can be found by summing all the individual perturbations,  $b_i(t)$ , in equation (B4), then normalizing by the initial total perturbation. When this is done, all terms containing  $n$  in equation (B4) nicely cancel out and the result is simply

$$\frac{\sum_{i=1}^n b_i(t)}{\sum_{i=1}^n b_i(0)} = e^{-rt}. \quad (B6)$$

Equation (B6) shows that the total community biomass returns to its steady state at a constant rate, which is independent of the number of species in the community and, by comparison with equation (B5), faster than the individual species return on average. The variance in the values described by equation (B5) can be large (un-

bounded for many distributions of  $b_i$ ), meaning that specific random perturbations can be very different from the mean. However, in the neighborhood of equilibrium where this linear analysis holds, the biomass of any individual species never recovers faster than the biomass of the entire community, and these linear dynamics remain good approximations for the nonlinear system far from equilibrium (fig. 4).

### APPENDIX C

#### Modified Broken-Stick Model

To model a system containing  $n$  species, select  $n$  random points on the unit interval and label them  $x_1, x_2, x_3, \dots, x_n$  from left to right. The first species occupies a portion  $x_1$  of the habitat and has an abundance proportional to this. The second occupies a portion  $x_2 - x_1$ , and the  $i$ th species occupies a portion  $x_i - x_{i-1}$ . The remainder,  $1 - x_n$ , is unused resource. Then repeat this selection to obtain a time series, with each successive selection of  $n$  points being independent of the previous.

Average abundances, variances, and covariances can be found by observing that the cumulative probability that the length of the leftmost subinterval is greater than some number  $x$ , where  $0 \leq x \leq 1$ , is the same as the probability that all  $n$  points fall in the interval  $[x, 1]$ . That probability is just  $(1-x)^n$ . Then, since the probability density function is the first derivative of the corresponding cumulative function, the density function follows by differentiating  $(1-x)^n$  with respect to  $n$ . Thus, the probability that the right endpoint of the first subinterval falls in the range  $[x - \Delta x, x]$  approaches

$$p(x, n)\Delta x = n(1-x)^{n-1}\Delta x \quad (C1)$$

as  $\Delta x$  approaches 0. This makes the average length of the leftmost subinterval equal to

$$\begin{aligned} \mu(n) &= \int_0^1 xp(x, n)dx, \\ &= \int_0^1 xn(1-x)^{n-1}dx, \\ &= \frac{1}{n+1}. \end{aligned} \quad (C2)$$

By a similar calculation, the variance in this length is

$$\begin{aligned} \sigma^2(n) &= \int_0^1 [x - \mu(n)]^2 p(x, n) dx, \\ &= \int_0^1 \left(x - \frac{1}{n+1}\right)^2 n(1-x)^{n-1} dx, \quad (C3) \\ &= \frac{n}{(n+1)^2(n+2)}. \end{aligned}$$

These two formulas are derived for the leftmost subinterval, but for reasons of symmetry, they apply (perhaps surprisingly) to all subintervals (see Feller 1971).

Covariances emerge from the following argument: the total resource in this model never changes—only the amount of unused resource varies from year to year. Therefore, in an expanded covariance matrix covering the entire community plus the unused resource, the sum of all the terms of that expanded matrix vanishes because the variance in the total resource is 0. Because all the variances are equal and (necessarily) positive, including unused resource, then the sum of the covariances must be negative, and by symmetry arguments, all covariances are identical. Moreover, in the expanded covariance matrix, including unused resource, there are  $n + 1$  variances and  $n(n + 1)$  covariances, which means

$$(n + 1) \text{Var}(n) = -n(n + 1) \text{Cov}(n), \quad (C4)$$

or

$$\text{Cov}(n) = -\frac{\text{Var}(n)}{n} = -\frac{1}{(n + 1)^2(n + 2)}. \quad (C5)$$

Thus, the complete covariance matrix is

$$\mathbf{M}(n) = \frac{1}{(n + 1)^2(n + 2)} \begin{bmatrix} n & -1 & -1 & \cdots & -1 \\ -1 & n & -1 & \cdots & -1 \\ -1 & -1 & n & \cdots & -1 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ -1 & -1 & -1 & \cdots & n \end{bmatrix}, \quad (C6)$$

where  $n$  is the number of species in the community. This means that the summed community variance (the sum of the diagonal elements of the covariance matrix) is

$$\frac{n}{(n + 1)^2(n + 2)}, \quad (C7)$$

and the summed community covariance (the sum of all the off-diagonal elements) is

$$-\frac{n(n - 1)}{(n + 1)^2(n + 2)}. \quad (C8)$$

The mean total community biomass in this model, in which all species are symmetric, is  $n$  times the mean individual species biomass (eq. [C2]), or

$$\mu_T = \frac{n}{n + 1}. \quad (C9)$$

Likewise, the total variance (the sum of all diagonal elements of eq. [C6]) is  $n^2/[(n + 1)^2(n + 2)]$ , and the total covariance (the sum of all off-diagonal elements) is  $-n(n - 1)/[(n + 1)^2(n + 2)]$ . These two added together become the variance in the biomass of the entire community, which is therefore

$$\begin{aligned} \sigma_T^2 &= \frac{n^2}{(n + 1)^2(n + 2)} - \frac{n(n - 1)}{(n + 1)^2(n + 2)} \\ &= \frac{n}{(n + 1)^2(n + 2)}. \quad (C10) \end{aligned}$$

(Note that the net variance in community biomass in this case is the same as the variance in individual species biomass, which may be seen more directly from the geometry of the subintervals.)

Finally, the temporal stability of an individual species in an  $n$ -species community is its mean (eq. [C2]) divided by the square root of its variance (eq. [C3]), which is

$$S_i(n) = \sqrt{1 + \frac{2}{n}}, \quad (C11)$$

and likewise the temporal stability of the entire community is its mean (eq. [C9]) divided by the square root of its variance (eq. [C10]), which is

$$S_T(n) = \sqrt{n(n + 2)}. \quad (C12)$$

That the temporal stability of the community (eq. [C12]) approaches a linear asymptote ( $y = n + 1$ ) can be seen by rewriting it as

$$S_T(n) = \sqrt{(n + 1)^2 - 1}. \quad (C13)$$

As  $n$  grows large, the term  $(n + 1)^2$  overwhelms the term  $-1$ , so  $S_T(n)$  approaches  $\sqrt{(n + 1)^2}$ , which is simply  $n + 1$ .

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