

## Notes and Comments

### Diversity and Stability in Communities Structured by Asymmetric Resource Allocation

Yssa D. DeWoody,<sup>1,\*</sup> Robert K. Swihart,<sup>1,†</sup> Bruce A. Craig,<sup>2,‡</sup> and Jacob R. Goheen<sup>1,§</sup>

1. Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907-2033;

2. Department of Statistics, Purdue University, West Lafayette, Indiana 47907-1399

*Submitted September 4, 2002; Accepted April 11, 2003;  
Electronically published October 16, 2003*

---

*Keywords:* biodiversity, broken-stick model, community, competition, Dirichlet, stability.

---

MacArthur (1955) first proposed a hypothesis regarding the relationship between diversity and stability by claiming that diverse communities enhance ecosystem stability. This hypothesis was based on Odum's (1953) qualitative notion that stability increases as the number of links in a food web increase. MacArthur reasoned that more choices lead to less dependence on a particular path and thus more stability. A variety of views on the diversity-stability hypothesis ranging from agreement to opposition have been argued from numerous theoretical (May 1972, 1973; Doak et al. 1998; Tilman 1999; Yachi and Loreau 1999; Lehman and Tilman 2000) and empirical (McNaughton 1993; Tilman 1994, 1996; Ives et al. 1999; McGrady-Steed and Morin 2000; Wootton 2001) perspectives. Although several studies support the claim that biodiversity regulates stability, no clear consensus on the validity of the hypothesis has yet been reached (Cottingham et al. 2001).

Part of the controversy over the diversity-stability hypothesis stems from the multitude of meanings assigned to stability (Pimm 1984). Mikkelsen (1999, p. 483) argued

that several of these more stringent definitions (e.g., the mathematical notion of neighborhood stability) create a "severe a priori bias" against the diversity-stability hypothesis but that definitions of stability based on temporal variation avoided this bias. And, indeed, most of the current research on this debate has focused on this general notion of stability rather than notions based on equilibrium population dynamics (McCann 2000).

Many contend that the answer to the diversity-stability debate depends on the organizational level at which stability is measured: community or population (see review by Cottingham et al. 2001). In essence, the temporal stability of a population reflects the variation in abundance (biomass) of a particular species, while the temporal stability of a community reflects variation in summary or aggregate properties such as total abundance (biomass). Thus, a community with high temporal stability would be characterized by low aggregate variability (*sensu* Micheli et al. 1999). Lehman and Tilman (2000) argued that temporal stability at the community level responds differently to changes in species richness than at the population level. Specifically, they showed that species diversity increased the stability of a community but reduced the stability of individual populations within a community structured by symmetric competition.

Another point of contention in the diversity-stability debate has been the relative importance of species richness versus species composition. Tilman (1997) and Tilman et al. (1997) demonstrated theoretically that both influence ecosystem productivity and hence stability, noting that experimental systems should be designed to separate effects due to these two factors.

Here, we ask how competitive asymmetries alter the response of temporal stability to increasing diversity at both the community and population level. First, we alter a broken-stick model by mediating resource allocation among species through competition parameters that decline geometrically. We then examine the effect of limiting community size and hence species richness by imposing

\* E-mail: yssa@fnr.purdue.edu.

† E-mail: rswihart@fnr.purdue.edu.

‡ E-mail: bacraig@stat.purdue.edu.

§ Present address: Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131; e-mail: jgoheen@unm.edu.

Am. Nat. 2003. Vol. 162, pp. 514–527. © 2003 by The University of Chicago. 0003-0147/2003/16204-0203\$15.00. All rights reserved.

threshold resource requirements for species competing for finite resources under asymmetric competition.

### Defining Temporal Stability

In this note, we define temporal stability as mean abundance (biomass), normalized by the standard deviation of this abundance (biomass),  $S = \mu/\sigma$  (Lehman and Tilman 2000). Let  $S_i(n)$  and  $S_{\text{com}}(n)$  refer to the temporal stability of a population of species  $i$  and the total community, respectively, in a particular  $n$ -species community. Furthermore, let  $B_i(n)$  be the biomass (or abundance) of the  $i$ th species and  $B_{\text{com}}(n)$  be the total biomass in this community. In a stochastic environment, these quantities will vary. If distributional properties of the biomass are known, such as the mean ( $\mu_i/\mu_{\text{com}}$ ) and variance ( $\sigma_i^2/\sigma_{\text{com}}^2$ ), then temporal stability of a population of species  $i$  is

$$S_i(n) = \frac{\mu_i}{\sigma_i}, \quad (1)$$

and the temporal stability of the community is

$$S_{\text{com}}(n) = \frac{\mu_{\text{com}}}{\sigma_{\text{com}}}. \quad (2)$$

However, if distributional properties of the biomass are not known, then they must be estimated. In this case, consider a specific  $n$ -species community. Let  $\bar{B}_i(n)$  represent the  $i$ th species' mean biomass and  $\text{Var}[B_i(n)]$  represent the variance estimated from the  $B_i(n)$ . Then the population stability of species  $i$  is

$$\hat{S}_i(n) = \frac{\bar{B}_i(n)}{\sqrt{\text{Var}[B_i(n)]}}, \quad (3)$$

and the community stability is

$$\hat{S}_{\text{com}}(n) = \frac{\sum_i \bar{B}_i(n)}{\sqrt{\sum_i \text{Var}[B_i(n)] + \sum_{i \neq j} \text{Cov}(B_i, B_j)}}. \quad (4)$$

Thus, according to this definition, temporal stability increases if either mean biomass increases or total variability declines. An advantage of this definition of temporal stability is flexibility; temporal stability of nonequilibrium systems can be quantified while using wholly nonlinear dynamics. Therefore, models need not possess equilibria, nor do field studies have to assume that a community is in a state of equilibrium.

### Asymmetric Resource Partitioning among Competitors

MacArthur's (1957) original broken-stick model was constructed to predict the relative abundances of species in a community. Lehman and Tilman (2000) altered this model to study stability under the assumption that resources were randomly partitioned among competitors. This variation stems from the notion that competition at its most basic level represents the allotment of a limited resource among species. If one represents the limiting resource as a stick of unit length, then one can partition this resource among  $n$  species by randomly breaking the stick  $n$  times. This produces  $n + 1$  pieces of stick: one piece of resource for each species, and a leftover piece of unused resource. Stability can then be calculated by assuming that the relative abundance of each species is proportional to its piece of the resource stick (Lehman and Tilman 2000). We extend this notion of breaking a resource stick into  $n + 1$  portions by modeling the process with a Dirichlet distribution (Wilks 1962; Pielou 1981).

Dirichlet distributions are characterized by  $n + 1$  parameters,  $D(a_1, a_2, \dots, a_n, a_{n+1})$ . If  $x_i$  is the random variable designating the length of the  $i$ th subinterval, then the mean, standard deviation, and covariance with  $x_j$  are given by equations (5), (6), and (7), respectively:

$$\mu(x_i) = \frac{a_i}{\sum a_k}, \quad (5)$$

$$\sigma^2(x_i) = \frac{a_i(\sum a_k - a_i)}{(\sum a_k)^2(\sum a_k + 1)}, \quad (6)$$

$$\sigma(x_i, x_j) = \frac{-a_i a_j}{(\sum a_k)^2(\sum a_k + 1)}. \quad (7)$$

By definition, each parameter,  $a_i$ , of the Dirichlet distribution is proportional to the subinterval it defines. By assuming that the  $i$ th species' ability to capture resources is expressed by parameter  $a_i$ , variation in this parameter set implies interspecific asymmetries in resource partitioning. This fact makes the Dirichlet model ideal for studying stability under the general assumption of asymmetric competition (Buss 1980; Roxburgh and Bastow 2000). Similarly, the allocation of resources as unused is accomplished by assigning a parameter,  $a_{n+1}$ , to represent the inefficiency with which the community uses resources. Thus, the unused resource is functionally analogous to a pseudospecies in our model. This congruence is important because community stability can be computed solely in terms of the unused resource when one assumes a fixed limiting resource (i.e., the stick always has unit length):

$$S_{\text{com}}(n) = \frac{\mu_{\text{com}}}{\sigma_{\text{com}}} = \frac{1 - \mu_{\text{ur}}}{\sigma_{\text{ur}}} = \frac{1 - \mu(x_{n+1})}{\sigma(x_{n+1})}, \quad (8)$$

where  $\mu_{\text{com}}/\mu_{\text{ur}}$  and  $\sigma_{\text{com}}/\sigma_{\text{ur}}$  refer to the mean and standard deviation of the captured resources within the community and the unused resource, respectively, and  $\mu(\cdot)$  and  $\sigma(\cdot)$  are given by equations (5) and (6). As evident from equation (8), there are numerous ways to allocate resources asymmetrically among  $n$  species that result in the same community stability, as long as the communities' unused resource is the same. However, the role of asymmetric competition is realized in the different population stabilities of the species.

In this note, we introduce asymmetric competition among species by assuming that a species' ability to capture resources declines geometrically according to its rank in a community comprised of  $n$  species (May 1975; Magurran 1988). Let  $p_i$  be the proportional amount of resources that species  $i$  can capture. Then assume that

$$p_i = q(1 - q)^{i-1}, \quad i = 1, \dots, n, \quad (9)$$

where  $i$  is the rank and  $0 < q < 1$  is the shape parameter controlling the degree of asymmetry in the geometric decline. This functional form allows us to explore a continuum of communities in which species' abilities range from extreme asymmetry (high  $q$  value) to evenness (small  $q$  value) all within the same setting. This set of parameters,  $\{p_i\}$ , directly determines the Dirichlet parameters,  $\{a_i\}$ , for the model (fig. 1).

How are communities of competitively asymmetric species assembled? We will consider two approaches: systematic entry of species into the community according to competitive rank and random entry of species.

To facilitate the comparison between systematic entry and random entry, we propose the following normalization of Dirichlet parameters. The set of parameters  $\{p_i\}$  from a community with species richness  $n$  is transformed into the set of Dirichlet parameters,  $\{a_i\}$ , through a scaling that constrains the sum

$$\sum_{i=1}^{n+1} a_i = n + 1. \quad (10)$$

This normalization allows us to simplify the equations for stability of a community of  $n$  species,

$$S_{\text{com}}(n) = \sqrt{\frac{(n + 1 - a_{n+1})(n + 2)}{a_{n+1}}}, \quad (11)$$

and stability for the population of species  $i$ ,

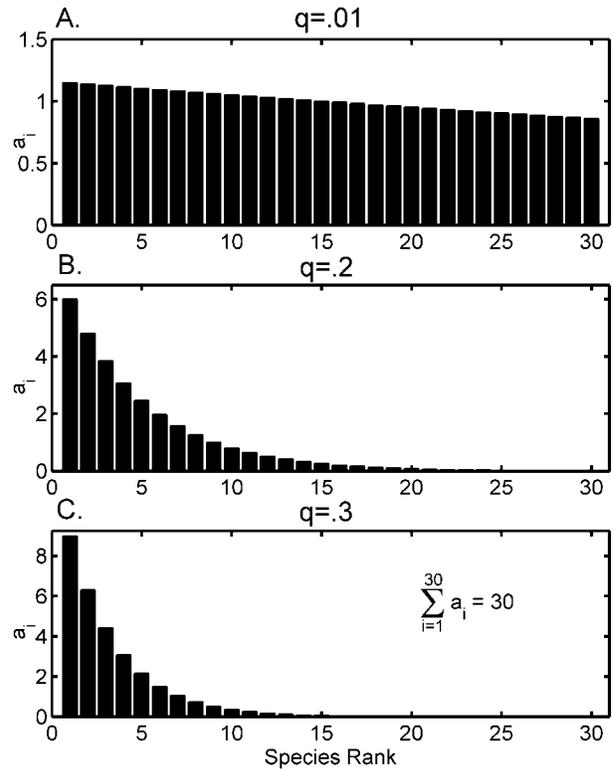


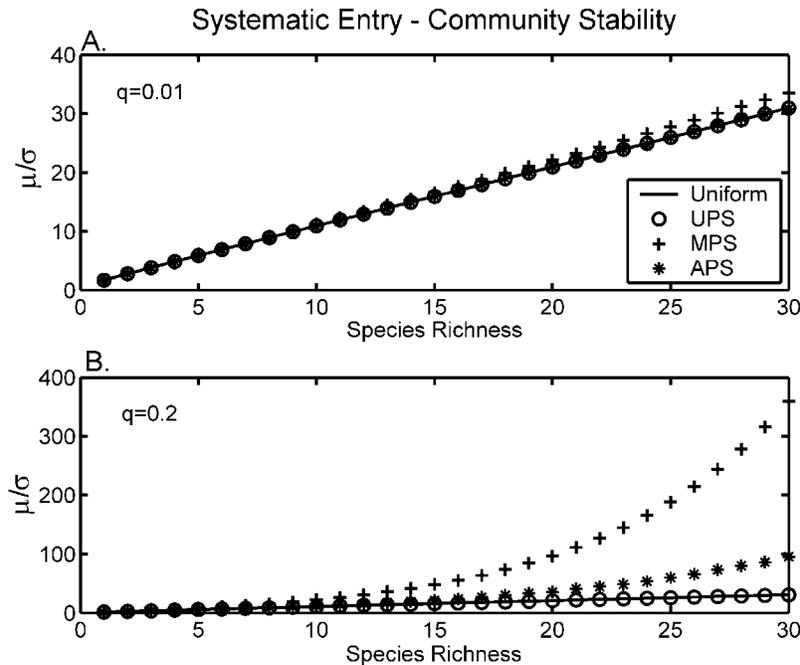
Figure 1: Role of asymmetry in the normalized Dirichlet parameters as a function of the shape parameter  $q$ .

$$S_i(n) = \sqrt{\frac{a_i(n + 2)}{n + 1 - a_i}}. \quad (12)$$

We considered three models under systematic and random species entry, each differing in how it deals with the unused component of the resource stick (i.e.,  $a_{n+1}$ ).

### Systematic Entry

In this first approach, species were admitted systematically into the community according to competitive rank. Thus, a community of five species was comprised of species with abilities given by  $\{p_1, p_2, p_3, p_4, p_5; p_{\text{ur}}\}$ , where  $p_{\text{ur}}$  refers to unused resource. This approach had the advantage of being analytically tractable but had the disadvantage of not being able to isolate the effects of diversity and composition on stability. Two types of communities were simulated (fig. 1): one type consisted of species that were approximately uniform in their competitive abilities ( $q = .01$ ), whereas the other type of community was characterized by pronounced asymmetry ( $q = .2$  and  $q = .3$ ). Figures 2 and 3 display results from our models under the assumption of systematic entry for these communities.



**Figure 2:** Predicted effects of asymmetric resource capture based on four versions of the broken-stick model with systematic entry; that is, species were added to the community according to their rank. Solid line represents uniform distribution of resources among the species on the basis of uniform capture of resources by species (Lehman and Tilman 2000). Circles represent model UPS in which an average of  $1/(n+1)$  of resources are unused but species capture resources according to the geometric decline. Plus signs represents model MPS in which the least abundant species in the sample was chosen as the unused resource pseudospecies. Stars represents model APS in which the pseudospecies was chosen randomly from the sampled species. Community stability increased with species richness. This effect was heightened and became nonlinear as the asymmetry increased for both the MPS and APS models.

#### Uniform Pseudospecies (UPS)

This model assumes that on average the unused resource totals  $1/(n+1)$  of the resource stick, whereas all the species share  $n/(n+1)$  of the total resources. We termed this the “uniform pseudospecies” (UPS) model because it assumes that the unused portion is the same as any species’ portion under the assumption of a uniform resource distribution. In this case, the resource efficiency of the community is independent of species composition. If the species follow the geometric decline given by equation (9), then the normalized Dirichlet parameters (see eq. [10]) are as follows:

$$a_i = \frac{nq(1-q)^{i-1}}{1-(1-q)^n}, \quad i = 1, \dots, n,$$

$$a_{n+1} = 1.$$

From equation (11), one can see that the temporal stability for the community is

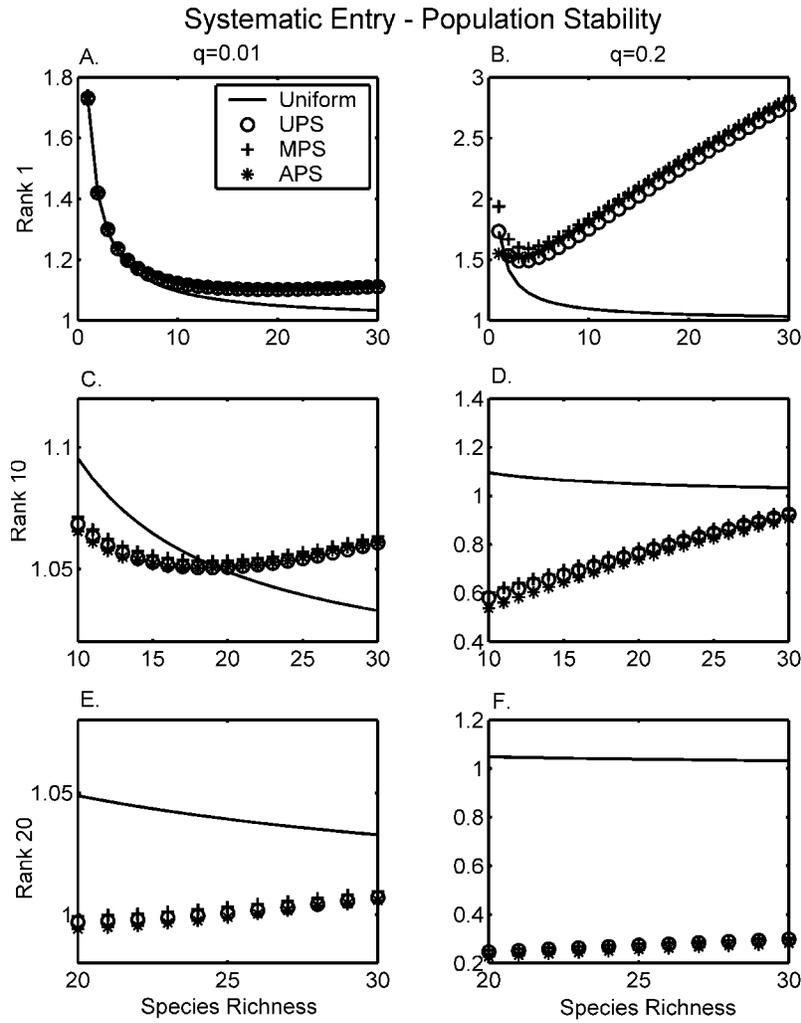
$$S_{\text{com}}(n) = \sqrt{n(n+2)}.$$

Thus, the temporal stability increases at a rate that is slightly greater than linear as the number of species increases. It is worth noting that this is the same expression for community stability derived by Lehman and Tilman (2000) from their stochastic model that assumed each species was competitively equivalent. Although they did not couch their broken-stick model in terms of a Dirichlet distribution, it is equivalent to the Dirichlet described by  $D(1, 1, \dots, 1, 1)$ . Note that our UPS model and the model of Lehman and Tilman (2000) both satisfy the conditions

$$\sum_{i=1}^n a_i = n,$$

$$a_{n+1} = 1.$$

Indeed, any Dirichlet model satisfying this condition will give rise to the same community stability (see eq. [11] for verification) regardless of competitive asymmetries. Thus, for the UPS model, there is no difference in the aggregate stability of communities with varying degrees of asym-



**Figure 3:** Predicted effects of asymmetric resource capture based on four versions of the broken-stick model with systematic entry; that is, species were added to the community according to their rank. The population stabilities of different species for models UPS, MPS, and APS were qualitatively similar and increased with species richness. This result is qualitatively different than what is predicted if the resources are distributed uniformly among species. The rate of increase and the value of stability are dictated by the shape parameter  $q$  and the rank of the species.

metry since the unused resource is always modeled with the constant 1 (fig. 2).

From equation (12), one can derive the following expression for the population stability of species  $i$ :

$$S_i(n) = \sqrt{\frac{n(n+2)q(1-q)^{i-1}}{(n+1)[1-(1-q)^n] - nq(1-q)^{i-1}}} \quad (13)$$

This expression clearly depends not only on the species' rank,  $i$ , but also on the asymmetry of competition,  $q$ . Consider this equation under the following assumptions:

In the case of  $q \rightarrow 0^+$ , the species are approaching a state

in which they are all competitively equivalent (fig. 1A). After applying L'Hopital's rule,

$$\lim_{q \rightarrow 0^+} S_i(n) = \sqrt{\frac{n+2}{n}}$$

Thus, uniform resource allocation results in the temporal stability of any individual species asymptotically approaching 1 as species richness increases. This is the same result for the population stability of a species that Lehman and Tilman (2000) derived from their stochastic model that assumed uniform competitive abilities.

In the case of  $0 < q < 1$ , there is a dominance hierarchy among the species that becomes more pronounced as  $q$  increases. For large  $n$ , the population stability of each species is

$$S_i(n) \approx \sqrt{\frac{nq(1-q)^{i-1}}{[1-q(1-q)^{i-1}]}}$$

If  $i = 1$ , then this expression simplifies so that the temporal stability for the dominant species for large  $n$  behaves as

$$S_1(n) \approx \sqrt{\frac{nq}{1-q}}$$

Thus, a systematic entry of species according to rank allows the population stability of each species to grow unchecked, provided there is no limit to the number of species that can be further packed into the community. The rate of increase in stability is regulated by both the decay parameter  $q$  and the rank of the species; dominant species stand to gain the most from increases in richness (fig. 3).

In the case of  $q \rightarrow 1^-$ , two stability results follow immediately from equation (13). First, the population stability of all species except the most dominant goes to 0. Second, the population stability of the dominant species behaves like the stability of the community as  $q$  approaches 1; that is,

$$\lim_{q \rightarrow 1^-} S_1(n) = \sqrt{n(n+2)}.$$

This is reasonable, since the implication of  $q$  approaching unity is that the community is approaching a monoculture.

#### Minimum Pseudospecies (MPS)

In this model, the unused resource was treated as a pseudospecies whose competitive ability was inferior to all other species in the community. Under systematic entry, the unused resource in a community of  $n$  species is described by the next geometric parameter,  $p_{n+1}$ . We termed this the “minimum pseudospecies” (MPS) model. Functionally, the MPS model applies most readily to communities subjected to relatively minor and infrequent disturbances and structured principally by competition. Inclusion in these nearly equilibrium communities is dependent on efficiency of resource use; thus, species should pack relatively tightly into the available niche space, with the result that unused resources should occur at low levels (Pianka 1974; Huston 1994).

Although a full analysis of this model could be done,

we report here only the results as they compare with the UPS model. Since  $a_{n+1}^{\text{MPS}} \ll a_{n+1}^{\text{UPS}} = 1$ , then equation (11) implies

$$S_{\text{com}}^{\text{MPS}}(n) \gg S_{\text{com}}^{\text{UPS}}(n) = \sqrt{n(n+2)},$$

where the strength of these inequalities is heightened as the asymmetry in competitive abilities increases (fig. 2). Similarly, since  $a_i^{\text{MPS}} > a_i^{\text{UPS}}$  for all  $i = 1, \dots, n$  because of the normalization, then quantitatively

$$S_i^{\text{MPS}}(n) > S_i^{\text{UPS}}.$$

However, qualitatively the curves are nearly identical (fig. 3).

#### Average Pseudospecies (APS)

In this model, the unused resource was treated as a pseudospecies chosen randomly from the available species pool and thus was termed the “average pseudospecies” (APS) model. Unlike the MPS model, the APS model depicts communities subjected to substantial and frequent disturbances and clearly nonequilibrium conditions. Inclusion in APS communities is dependent less on efficiency of resource use than on responses to disturbance. This suggests that species should be packed less tightly into the available niche space and unused resources should occur at greater levels than in communities structured to a greater degree by biotic interactions (Pianka 1974; Huston 1994).

Since the unused resource was chosen randomly, we ran 5,000 trials at each species richness. Community and population stabilities were calculated for each trial. These results were then averaged at each species richness to compute the expected stability for an  $n$ -species community. Because of our normalization, the average value of a Dirichlet parameter is 1; that is,  $\bar{a}_i = 1$ . Thus, the relationship between the community stability of the model and the previous two can be explained as follows: since  $a_{n+1}^{\text{MPS}} \leq a_{n+1}^{\text{APS}}$  and  $\bar{a}_i = 1 = a_{n+1}^{\text{UPS}}$ , then

$$\begin{aligned} S_{\text{com}}^{\text{MPS}}(n) &> S_{\text{com}}^{\text{APS}}(n) = \overline{S_{\text{com}}(n, \bar{a}_i)}_{\text{over all } i} > S_{\text{com}}(n, \bar{a}_i) \\ &= S_{\text{com}}^{\text{UPS}}(n). \end{aligned}$$

To summarize, models' performance in terms of community stability follows the order MPS > APS > UPS (fig. 2).

Population stability for the APS model is qualitatively similar to both the MPS and UPS models, but there are slight quantitative differences between the models. Since  $a_i^{\text{MPS}} > a_i^{\text{APS}}$  for all  $i = 1, \dots, n$ , then

$$S_i^{\text{MPS}} > S_i^{\text{APS}}.$$

The species' relationship between the APS and UPS models is a bit more complicated because there is a point at which the inequality between species' parameters switches from  $a_i^{\text{APS}} < a_i^{\text{UPS}}$  for  $i = 1, \dots, j$  to  $a_i^{\text{APS}} > a_i^{\text{UPS}}$  for  $i = j + 1, \dots, n$ . Thus, for the more dominant species,

$$S_i^{\text{APS}} > S_i^{\text{UPS}}, \quad i = 1, \dots, j,$$

but for inferior species, the inequality reverses:

$$S_i^{\text{UPS}} > S_i^{\text{APS}}, \quad i = j + 1, \dots, n.$$

Competitive asymmetry dictates the species' rank,  $j$ , at which the reversal occurs: greater  $q$  leads to a lower  $j$  (to see reversal, cf. fig. 3B, 3D).

### Random Entry

In this second approach, a community of  $n$  species was comprised of a random subset of the  $N + 1$  possible species. Randomly assembled communities allowed us to separate (to some degree) the effects on community stability of species richness and species composition. This was accomplished by sampling different compositions, which have the same species richness, and then averaging the results to obtain a community stability estimate independent of a particular composition (Tilman 1999). Specifically, for each species richness,  $n = 1, \dots, N$ , the results from 5,000 trials were recorded on the basis of Dirichlet distributions for the three models described above (UPS, MPS, APS). For each trial,  $n$  species were chosen randomly without replacement from a total species pool of size  $N + 1$ , and their respective competitive abilities from the geometric decline were recorded,  $\{p_i\}$ . The parameters were the same for each model tested so that variation inherent in the model could be separated from variation due to sampling. Next, a species was designated as the unused resource according to the criteria of each model. After normalization to  $n + 1$  (see eq. [10]), this set became the parameters for the Dirichlet distribution.

For example, suppose when  $N = 20$  that  $n = 3$  species were chosen and sorted according to rank, resulting in the set  $\{3, 5, 15\}$ . In all three models, the corresponding parameters  $\{p_3, p_5, p_{15}\}$  derived from equation (9) represent the competitive abilities of the three species present in this sample community. We now consider the different broken-stick models.

For the UPS model, these three parameters were scaled such that the first three Dirichlet parameters summed to  $n = 3$ . Then the last Dirichlet parameter describing the unused resource was assigned the value of 1. For the MPS

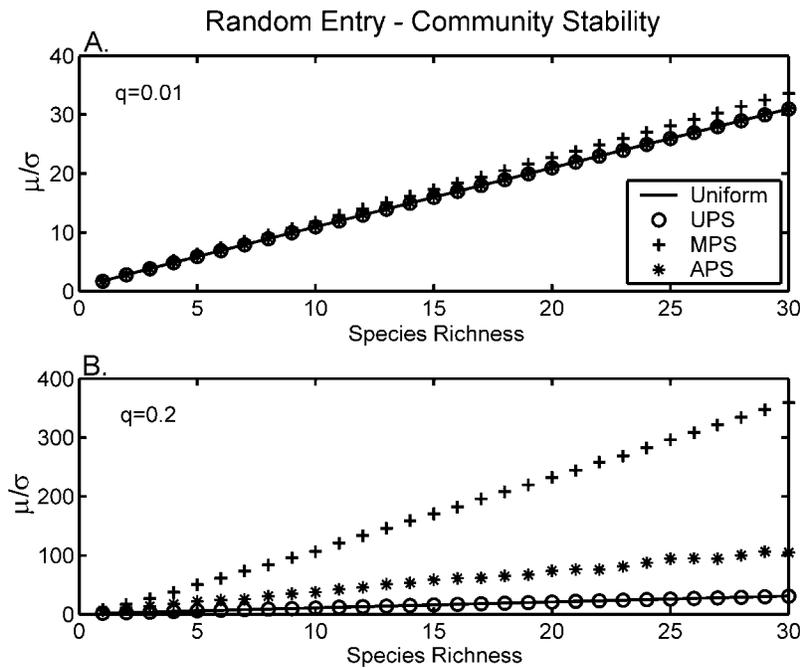
model, an additional species was chosen without replacement under the restriction that it must be competitively inferior to all species present, for example,  $p_{ur} = p_{18}$ . Then the set  $\{p_3, p_5, p_{15}, p_{18}\}$  was scaled to sum  $n + 1 = 4$ , and these normalized values became the Dirichlet parameters. The APS model is similar to MPS except that there was no restriction in choosing the additional species, for example,  $p_{ur} = p_6$ .

Community stability was calculated from equation (11), and population stability was calculated from equation (12) for each species present in each trial. The community stabilities from the 5,000 trials were then averaged to eliminate the impact of composition and focus on the role of diversity on stability. Thus, there was an average community stability,  $S_{\text{com}}(n)$ , calculated for each species richness  $n = 1, \dots, N$ . Similarly, the population stabilities for species  $i$ ,  $S_i(n)$ , were averaged across all communities of the same species richness in which species  $i$  was present.

A comparison of simulation results for the models with a shape parameter of  $q = .01$  and  $q = .2$  (figs. 4, 5) permitted the following observations regarding the role of asymmetry in resource use on temporal stability in randomly assembled communities. First, community stability increased linearly with species richness for all models. Second, a collective increase in efficiency of resource use by species in the community, that is, a lower  $a_{n+1}$  parameter, resulted in an increase in predicted stability for a given level of species richness. This result was intensified as the degree of asymmetry increased from  $q = .01$  to  $q = .2$  (fig. 4). Thus, in communities for which resource competition is an important determinant of abundance (model MPS), enhanced community stability is predicted. Third, population stability for individual species was qualitatively similar for each model: each predicted an asymptotic decline to a constant as species richness increased (fig. 5). The UPS model for the dominant species was the one exception to this rule; the population stability of the best competitor actually increased, albeit to the same constant as the other models predicted. This asymptotic constant is dependent on the asymmetry,  $q$ , as well as the rank of the species,  $i$ . As expected, the stability of a dominant species is greater than the stability of an inferior competitor. Note again that the amount of asymmetry intensifies the results. Thus, greater dominance results in greater stability both of the community and of the dominant species but lower stability of the inferior species; moreover, greater asymmetry quickens the approach to the asymptotic constant in population stability.

### Threshold Requirements for Resource Use

Previous broken-stick models have assumed that species could survive on increasingly smaller levels of resources,

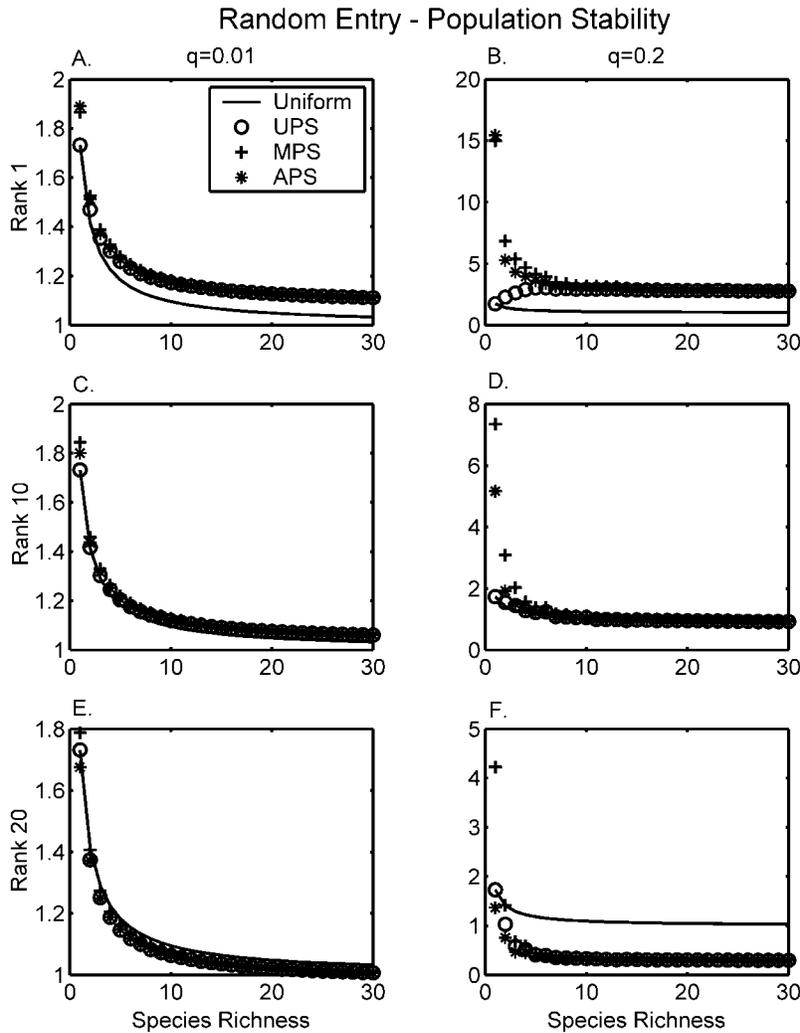


**Figure 4:** Predicted effects of asymmetric resource capture based on four versions of the broken-stick model with random entry; that is, species were added to the community randomly. Solid line represents a uniform distribution of resources among the species on the basis of uniform capture of resources by species (Lehman and Tilman 2000). Circles represent model UPS in which an average of  $1/(n+1)$  of resources are unused but species capture resources according to the geometric decline. Plus signs represent model MPS in which the least abundant species in the sample was chosen as the unused resource pseudospecies. Stars represent model APS in which the pseudospecies was chosen randomly from the sampled species. Community stability increased with species richness. This effect was heightened as asymmetry increased for both the MPS and APS models; however, the relationship remained linear.

resulting in the potential for an infinite number of species and an infinitesimally small unused component of the resource stick. We investigated whether introducing a minimal per capita resource requirement for survival influenced the relationship between diversity and stability. To address the effect of a threshold resource requirement, we assumed that all individuals in the community had identical, finite resource requirements. We then examined the stability of communities with fixed resources that could support maximum populations of 10, 25, 50, 100, 250, and 500 individuals. As before, we modeled unused resources as a pseudospecies.

Threshold requirements were incorporated in the following manner. The set  $\{p_i: i = 1, \dots, N+1\}$  derived from a geometric decline parameterized by  $q$  was normalized such that the sum equaled 10,000. Each normalized value was rounded up to the nearest whole number, which represented the number of individuals from each species. The total count represented the pool of individuals from which sample communities were drawn. By construction, this pool exhibited the same interspecific asymmetry in resource use as the geometric decline. A sample

community of size  $T \in \{10, 25, 50, 100, 250, 500\}$  was constructed by randomly selecting individuals without replacement from the pool. Once a sample had been drawn, one species found in the sample was randomly selected to serve as the unused resource (somewhat analogous to a finite version of the APS model). This procedure was used to produce 50,000 sample communities of size  $T$ . For a given  $T$ , sample communities were first grouped by species richness,  $n$ . All sample communities containing  $n$  species were then further subdivided into assemblages bearing the same species composition. Thus, an assemblage was defined as a collection of sample communities of the same size,  $T$ , which was composed of the same  $n$  species. Community stability was calculated for each assemblage containing at least four samples according to equation (4). These derived stabilities were then averaged across all assemblages having the same species richness (Lehman and Tilman 2000). We used this approach to obtain an estimate of community stability that was somewhat independent of species composition, in a manner analogous to our random-entry, broken-stick model. Simulations were con-

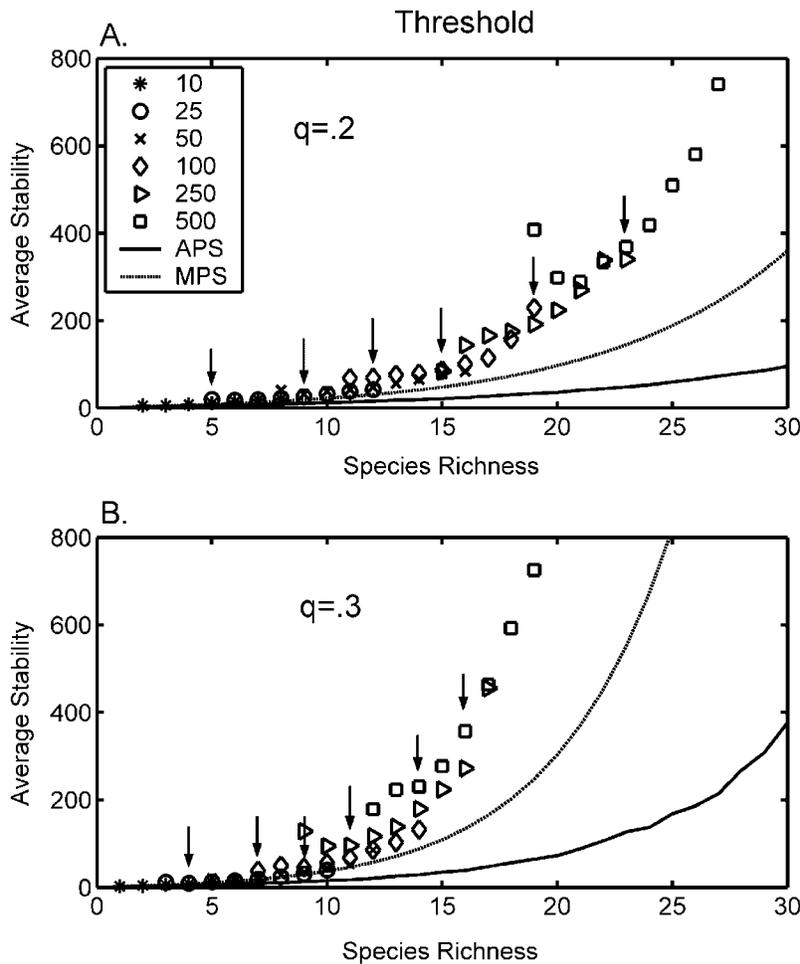


**Figure 5:** Predicted effects of asymmetric resource capture based on four versions of the broken-stick model with random entry; that is, species were added to the community randomly. The population stabilities of three different species for models UPS, MPS, and APS were qualitatively similar to each other and approached asymptotic constants rapidly. These asymptotic constants were above the values predicted under a uniform distribution of resources for rank 1 species, about the same for rank 10, and below for rank 20.

ducted from geometric declines parameterized by  $q = .01, .2, .3$ .

As expected, threshold resource requirements restricted species packing (fig. 6). Distributions associated with the range of species richness for each community size,  $T$ , were approximately normally distributed, and modal richness increased asymptotically with  $T$ . Greater asymmetry (greater  $q$ ) shifted the distributions to lower values and slightly decreased their variances. For example, consider a community size of 50 ( $T = 50$ ). When  $q = .2$ , all compositions containing at least four samples had a species richness that fell within the range of [8, 16], and the mode of the distribution was 12, whereas when  $q = .3$ , the range

shifted to [5, 12] with mode 9 (fig. 6). We attributed this shift to the inherent nestedness of this sampling scheme (i.e., passive sampling sensu Wright et al. 1998), in which superior competitors dominate assemblages. In fact, the shape of the diversity-stability curve was functionally similar to the broken-stick models MPS and APS that employed a systematic entry of species (fig. 6). In the absence of this nestedness, which occurs as  $q$  approaches 0, it was hard to get assemblages that had enough members from which to calculate community stability. In fact, most compositions were unique. Thus, the results for  $q = .01$  are not given because even with an increased sample size of 100,000 replicates for each value of  $T$ , we still had little



**Figure 6:** Predicted effects on community stability of imposing threshold requirements for individuals when  $q = .2$  (A) and  $q = .3$  (B). Communities were constructed for  $T = 10, 25, 50, 100, 250,$  and  $500$  individuals. Arrows point to the modal species richness for each  $T$  based on 10,000 trials. Predictions of the broken-stick models APS and MPS under systematic entry are depicted by a solid and dotted line, respectively.

confidence in the results.

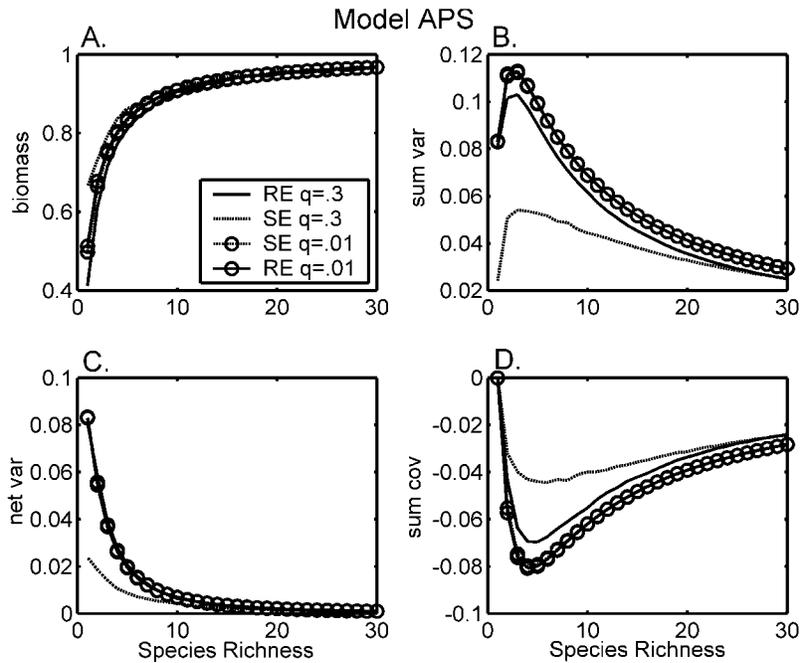
This model displayed an increasing, nonlinear relationship between community stability and species richness (fig. 6). Community stability increased with species richness, while community size was held constant. In addition, community stability increased with community size when species richness was held constant; that is, when the range of species richness overlapped for different community sizes, the stability increased according to community size.

### Discussion

Few communities consist of competing species that randomly partition resources, and no community can increase species richness indefinitely on a finite limiting resource. Because of this, we chose to investigate the diversity-

stability hypothesis with two models: first, a modified broken-stick model in which resource allocation was mediated through competition parameters derived from a geometric decline, and second, a model that imposed threshold resource requirements on individuals from distinct species competing for a finite resource under asymmetric competition.

Let us first consider the role of diversity (i.e., species richness) on the population stability of these simulated species. The literature provides no clearly defined relationship between population stability and species richness (Cottingham et al. 2001). Although recently some theoretical and empirical studies predict that population stability should decline with diversity (Tilman 1999; Lehman and Tilman 2000), others have found no relationship (McGrady-Steed and Morin 2000; Romanuk and Kolasa

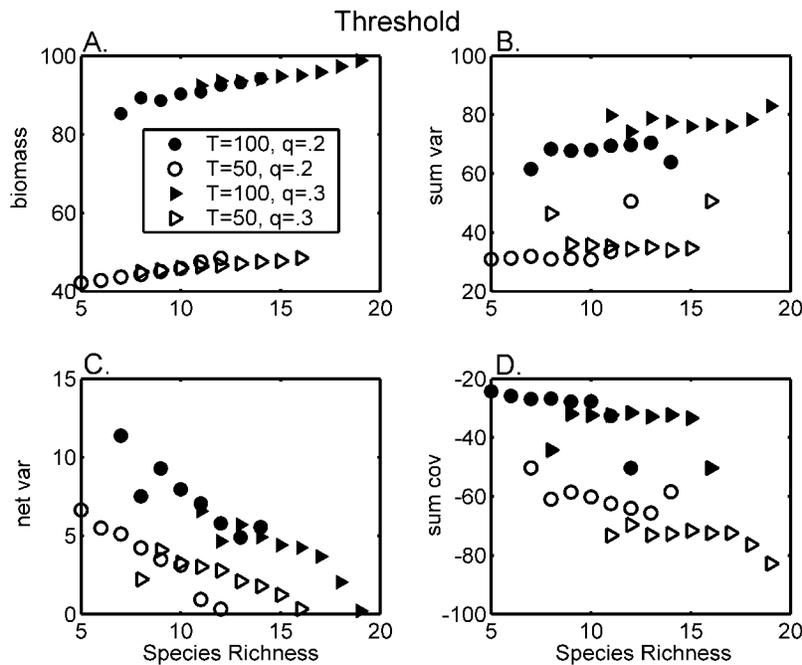


**Figure 7:** Comparative graph for model APS showing the influence of species richness on the following aggregate community properties: total biomass (A), summed variance (B), net variance (C), and summed covariance (D). Dotted lines resulted from systematic entry of species into the community according to rank, whereas solid lines resulted from a random entry of species. Lines marked with a circle correspond to  $q = .01$ , and lines with no markers correspond to  $q = .3$ . Other models (MPS, UPS) have similar results.

2002). Our broken-stick model suggests that the role of diversity is in part influenced by the organization of the community. In randomly assembled communities, population stability for all species generally declined with species richness; however, this relationship converged so quickly to a constant, especially in the presence of asymmetry, that it would be fair to say there is hardly any dependence on species richness once  $n$  exceeds 5 (fig. 5B, 5D, 5F). The results from a systematic entry of species into the community based on competitive ability stand in stark contrast to this result (fig. 3). Under this paradigm, the stability of each species will eventually increase without bound as long as additional species can pack into the community. Of course, it is hard to say whether species richness or composition is the driver of stability in this system. Regardless, it would be interesting to look at population stability in such highly structured ecosystems.

There is considerable evidence to support the idea that the temporal stability of the community is enhanced by species richness (Doak et al. 1998; Tilman 1999; Hughes and Roughgarden 2000; Lehman and Tilman 2000; Ives and Hughes 2002), and indeed, all of our results add to this support (figs. 2, 4, 6). But what mechanisms governed this relationship in our models? In a review article, Cottingham et al. (2001) noted that evenness, which measures

the degree of similarity in abundance or biomass of species, is a major factor in determining the strength of the diversity-stability relationship. Evenness is thought to enhance the diversity-stability relation (Doak et al. 1998; Hughes and Roughgarden 2000) through a process called statistical averaging (Doak et al. 1998; Tilman et al. 1998; Cottingham et al. 2001). This effect maintains that the variability of a sum of individual properties (e.g., total biomass) is dampened because the chance of individual fluctuations canceling each other increases with diversity. Evenness is thought to increase the likelihood of these cancellations and thus increase community stability (Doak et al. 1998). Evenness is the community attribute at the heart of the results we have presented. Indeed, the geometric parameter,  $q$ , which quantifies the degree of asymmetric competition, can be viewed as a measure of evenness where smaller values of  $q$  correspond to more evenness among the species and *visa versa*. However, higher levels of asymmetry among the species (larger  $q$ ) in the threshold model and all but one of the broken-stick models appeared to enhance both the level of community stability and the rate at which it increased (figs. 2, 4, 6). The model UPS was the one exception to this rule; this distinction was a result of community efficiency being independent of species composition.



**Figure 8:** Comparative graph for model threshold showing the influence of species richness on the following average community properties: total biomass (A), summed variance (B), net variance (C), and summed covariance (D). Open symbols correspond to a community constricted to  $T = 50$ , whereas closed symbols correspond to  $T = 100$ . Circles show results when  $q = .2$  and triangles when  $q = .3$ . Other community sizes showed similar results.

Recall that according to the definition (eqq. [2], [4]), the temporal stability of a community increases if either the mean of the sum of biomasses increases or the variance of the sum decreases. Recall further that the variance of a sum,  $\text{Var}(\sum X_i)$ , can be partitioned into the sum of the variances,  $\sum \text{Var}(X_i)$ , and the sum of the covariances,  $\sum_{i \neq j} \text{Cov}(X_i, X_j)$ . A decline in the variance of the sum can result from reductions in the individual variances, a statistical phenomenon termed the “portfolio effect” (Doak et al. 1998; Lehman and Tilman 2000). A decline in the variance of the sum also can result from reductions in the covariance between species, termed the “covariance effect” (Lehman and Tilman 2000). The covariance effect can be thought of as an ecological measurement of species interactions, with more intense competition leading to a more negative covariance (Lehman and Tilman 2000). Alternatively, covariance also measures the degree of similarity between species responses to their environment. A positive covariance (or correlation) reduces the role of statistical averaging (Doak et al. 1998; Yachi and Loreau 1999; Ives et al. 1999; Ives and Hughes 2002), whereas increasingly negative covariances support statistical averaging through the “insurance effect” (Ives et al. 1999, 2000; Yachi and Loreau 1999).

To assess the mechanisms governing the relationship

between diversity and community stability in our models, consider figures 7 and 8. Both broken-stick and threshold models were characterized by statistical averaging, that is, a decline in net variance with increasing species richness (figs. 7C, 8C). In the broken-stick model APS, the summed covariances for each value of  $q$  decreased until four species were present and then increased with increasing species richness, implying that the insurance effect was not present (fig. 7D). Note that when asymmetry increased (increase in  $q$ , i.e., decline in evenness), the level of covariance also increased, an effect that was more pronounced with systematic entry. Increased covariance alone depresses statistical averaging; however, this effect was countered by the portfolio effect, which reduced the variances with increasing species richness. Thus, the net variances of the broken-stick models were dominated by the portfolio effect, which was actually enhanced by dominance. However, the threshold models exhibited increasingly negative covariances as species richness increased (within a fixed community size or regardless of community size; fig. 8D). The role of statistical averaging thus was increased through the insurance effect (Yachi and Loreau 1999), which explains the elevated community stability of the threshold model at a given species richness over the APS model (fig. 6).

All of our models were characterized to some degree by

overyielding (Naeem et al. 1995); that is, average abundance increased with diversity. In our threshold model, overyielding occurred but was highly constrained by fixing the size,  $T$ , of a community (fig. 8A). However, overyielding was prominent in all the broken-stick models (e.g., fig. 7A). Indeed, this process is actually built into the model a priori by normalizing the Dirichlet parameters to  $n + 1$ . Recent empirical evidence lends support to the qualitative nature of this assumption. Bullock et al. (2001) observed overyielding in hay meadow restoration experiments in southern Britain. Tilman et al. (2001) compared biomass production in experimental grasslands and found that productivity increased with species richness. Increased asymmetry decreased overyielding (albeit only slightly) with model APS under random entry yet increased overyielding under systematic entry (fig. 7A).

The degree of competition among species and their composition also plays a role in the diversity-stability debate. Resource capture and hence predicted productivity were greater for MPS models than for APS models, suggesting that species composition can also be an important determinant. Competitively structured communities near equilibrium should outperform equally diverse but non-equilibrium communities in which the effects of competition are ameliorated by stochastic events (figs. 2, 4). Our results support the notion that tightly coevolved species associations can lead to enhanced community stability, whereas reduced effects of species richness on stability are predicted for communities consisting of more opportunistic, less efficient species. A logical extension of our work would be to assess the stability of real communities that have experienced varying levels of disturbance. Experimental microcosms may be most appropriate for these studies because of the greater level of control provided, although longitudinal data sets on natural plant or vertebrate communities may also be appropriate in some instances (e.g., Heske et al. 1994; Brown et al. 2001).

From a conservation perspective, our findings highlight potential implications associated with reserve design. In one sense, community stability increases with community size and thus bolsters an argument for larger reserves. However, community size alone may be insufficient to counteract the effects of asymmetric resource capture among species. For example, if two reserves with identical resource levels are available, results from our threshold model predict that the reserve characterized by a more competitively structured community will exhibit lower species richness, despite its greater community stability (fig. 6).

In conclusion, our statistical models showed an increase in community stability with species richness. This effect was actually enhanced with increased asymmetry among species. However, the relationship among population sta-

bilities and species richness could not be generalized and was further confounded by how a community was assembled.

### Acknowledgments

We are grateful to A. DeWoody, S. Knapp, J. Moore, R. Russell, and G. Shao for providing helpful comments on the manuscript. We also thank our reviewers for their thoughtful suggestions. This work was supported by the National Science Foundation under grant SES-0119908 to R.K.S. and B.A.C. and by the John S. Wright Fund, Purdue University.

### Literature Cited

- Brown, J. H., E. S. K. Morgan, J. M. Parody, and J. P. Haskell. 2001. Regulation of diversity: maintenance of species richness in fluctuating environments. *Oecologia* (Berlin) 126:321–332.
- Bullock, J. M., R. F. Pywell, M. J. W. Burke, and K. J. Walker. 2001. Restoration of biodiversity enhances agricultural production. *Ecology Letters* 4:185–189.
- Buss, L. W. 1980. Competitive intransitivity and size-frequency distributions of interacting populations. *Proceedings of the National Academy of Sciences of the USA* 77:5355–5359.
- Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters* 4:72–85.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist* 151:264–276.
- Heske, E. J., J. H. Brown, and M. Shahroukh. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. *Ecology* 75:438–445.
- . 2000. Species diversity and biomass stability. *American Naturalist* 155:618–627.
- Huston, M. A. 1994. *Biological diversity*. Cambridge University Press, Cambridge.
- Ives, A. R., and J. B. Hughes. 2002. General relationships between species diversity and stability in competitive systems. *American Naturalist* 159:388–395.
- Ives, A. R., K. Gross, and J. L. Klug. 1999. Stability and variability in competitive communities. *Science* 286:542–544.
- Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. *American Naturalist* 156:536–552.
- MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–536.

- . 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the USA* 43:293–295.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, N.J.
- May, R. M. 1972. Stability and complexity in model ecosystems. Princeton University Press, Princeton, N.J.
- . 1973. Stability in randomly fluctuating versus deterministic environments. *American Naturalist* 107: 621–650.
- . 1975. Patterns of species abundance and diversity. Pages 81–120 *in* M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Mass.
- McCann, K. S. 2000. The diversity-stability debate. *Nature* 405:228–233.
- McGrady-Steed, J., and P. J. Morin. 2000. Biodiversity, density compensation, and the dynamics of populations and functional groups. *Ecology* 81:361–373.
- McNaughton, J. S. 1993. Biodiversity and function of grazing ecosystems. Pages 361–383 *in* E.-D. Schulze and H. A. Mooney, eds. *Biodiversity and ecosystem function*. Springer, Berlin.
- Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Bjornstad, G. L. Eckert, J. M. Fischer, T. H. Keitt, B. E. Kendall, J. L. Klug, and J. A. Rusak. 1999. The dual nature of community variability. *Oikos* 85:161–169.
- Mikkelsen, G. M. 1997. Methods and metaphors in community ecology: the problem of defining stability. *Perspectives on Science* 5:481–498.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 347:249–262.
- Odum, E. P. 1953. *Fundamentals of ecology*. Saunders, Philadelphia.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the USA* 71:2141–2145.
- Pielou, E. C. 1981. The broken-stick model: a common misunderstanding. *American Naturalist* 117:609–610.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307:321–326.
- Romanuk, T. N., and J. Kolasa. 2002. Environmental variability alters the relationship between richness and variability of community abundances in aquatic rock pool microcosms. *Ecoscience* 9:55–62.
- Roxburgh, S. H., and W. J. Bastow. 2000. Stability and coexistence in a lawn community: mathematical prediction of stability using a community matrix with parameters derived from competition experiments. *Oikos* 88:395–408.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- . 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363.
- . 1997. Distinguishing between the effects of species diversity and species composition. *Oikos* 80:185.
- . 1999. The ecological consequences of biodiversity: a search for general principles. *Ecology* 80:1455–1474.
- Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the USA* 94:1857–1861.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? *American Naturalist* 151: 277–282.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
- Wilks, S. S. 1962. *Mathematical statistics*. Wiley, New York.
- Wootton, J. T. 2001. Causes of species diversity differences: a comparative analysis of Markov models. *Ecology Letters* 4:46–56.
- Wright, D. H., B. D. Patterson, G. M. Mikkelsen, A. Cutler, and W. Atmar. 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia (Berlin)* 113:1–20.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the USA* 96:1463–1469.