

Notes and Comments

Diversity-Stability Relationships: Statistical Inevitability or Ecological Consequence?

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Elton's (1958) hypothesis that ecological stability should depend on biological diversity has stimulated many conceptual and empirical debates and advances (e.g., May 1973; Goodman 1975; McNaughton 1977, 1985, 1993; Pimm 1979, 1984; Frank and McNaughton 1991; Lawton and Brown 1993; Givnish 1994; Tilman and Downing 1994; Tilman 1996). A major, recent advance is provided by Doak et al. (1998), who use the mathematics of stochastic processes to explain some potential effects of diversity on stability. Their analogy between the effects of species diversity on ecological stability and the effects of the diversity of a portfolio of investments on the stability of its valuation is powerful. Indeed, there is a rigorous mathematical basis for this portfolio effect (e.g., Lee 1985; Brigham and Gapenski 1988; see also other textbook treatments of the capital asset pricing model [CAPM]).

Doak et al. (1998) put forward the novel and intriguing hypothesis that, even in the absence of ecological interactions, statistical effects can cause greater species diversity to lead to lower oscillations in community biomass. In exploring the applicability of their model to ecology, we have found fundamental differences between simple stochastic processes and ecological systems that mean that this effect, though of great ecological importance, is not statistically inevitable. For the Poisson and other abundance distributions, for some models of eco-

logical interactions, and for previous data (in Tilman 1996), the relationship between variance in species abundances and mean species abundances is such that there is little or no net effect of diversity on stability via statistical averaging. However, interspecific interactions, such as competition, that cause compensatory changes in the abundances of species can stabilize community biomass in these cases.

Inspection of their mathematics reveals that Doak et al. (1998) assumed that the variance in the abundance of each species increased as the square of its abundance—that is, that $\sigma_i^2 = cm_i^2$, where c is a constant, m_i is the mean abundance of species i , and σ_i^2 is the variance in its abundance. On the surface, this seems reasonable. After all, this is the mathematical relationship that occurs if an entity is subject to proportional rescaling. For instance, if x is a random variable with mean m and variance σ^2 , then $\text{var}(ax) = a^2\sigma^2$. This causes the coefficient of variation (CV, where $CV = 100\sigma/m$), which is the percentage variation around the mean, to be constant, independent of this rescaling. It is not in this mathematical relationship that a problem exists but in its applicability to ecological systems for which factors other than sampling determine population size. As shown later, this assumption controls the validity and generality of Doak et al.'s conclusions.

Proportional rescaling applies with mathematical exactness to changes in units of measure, such as from grams to kilograms, and with high precision to such statistical problems as sampling marbles in an urn or to purchases of various (small) quantities of stock, but does it apply to species abundances in natural communities? We might expect the abundance of an individual species living in a multispecies community to be less than its abundance in monoculture because of competitive inhibition in the multispecies community. Abundances of species in nature rise or fall not because of proportional rescaling but in response to the dynamics of interspecific interactions and to changing environmental variables. If the forces controlling an ecological system cause the

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mean abundance of a species to be cut in half, is there any guarantee that the variance in its abundance will be cut to a fourth, as Doak et al. assumed?

For a simple counterexample, consider the Poisson distribution. If species abundances follow a Poisson distribution, then the variance is equal to the mean, $\sigma_i^2 = m_i$. In this case, the variance will fall to half of its former value (not to one-quarter) when population size is cut in half. Thus, the statistical law $\text{var}(ax) = a^2 \text{var}(x)$, which applies so well to proportional rescaling, does not hold in this case. We are not proposing the Poisson as a population dynamic model. Rather, we mention it as a simple case that disproves the universality of the assumptions of Doak et al.

For a more concrete counterexample, consider a classic stochastic model of density-dependent population growth. May (1973) analytically determined the impact of random environmental noise, $\gamma(t)$, on the dynamics of a species growing according to the continuous logistic equation, using the following analytical formulation:

$$dN_{(t)}/dt = N_{(t)}(K_0 - \gamma_{(t)} - N_{(t)}),$$

where $N(t)$ represents the population density at time t , K_0 represents carrying capacity, and the equation has been rescaled to eliminate r (see May 1973). Algebraic manipulation of his analytical results shows that $\sigma_i^2 = \frac{1}{2}m_i$. We illustrate this via stochastic simulations of this equation (fig. 1A) from which we determined how the variance in population abundance depended on mean abundance. There was excellent agreement with the algebraic prediction; that is, variance scaled linearly with mean abundance (fig. 1B). Thus, a simple model of stochastic density-dependent population growth predicts a linear dependence of variance on abundance, not the squared dependence assumed by Doak et al. This simple but reasonable model proves that, when ecological dynamics are considered, variance need not increase with the square of mean abundance.

The fact that the relationship assumed by Doak et al. is not universally applicable in ecology raises several questions. First, what is the expected effect of diversity on stability for abundance distributions that give other dependencies of σ^2 on m ? If the relationship of Doak et al. is not general and inevitable, might there still be some other general effect of diversity on stability? Also, what is the actual dependence of σ^2 on m in ecological communities?

Stability and Diversity: The Theoretical Basis of the Portfolio Effect

Researchers have used the coefficient of variation in biomass to measure stability (May 1973; Tilman 1996; Doak

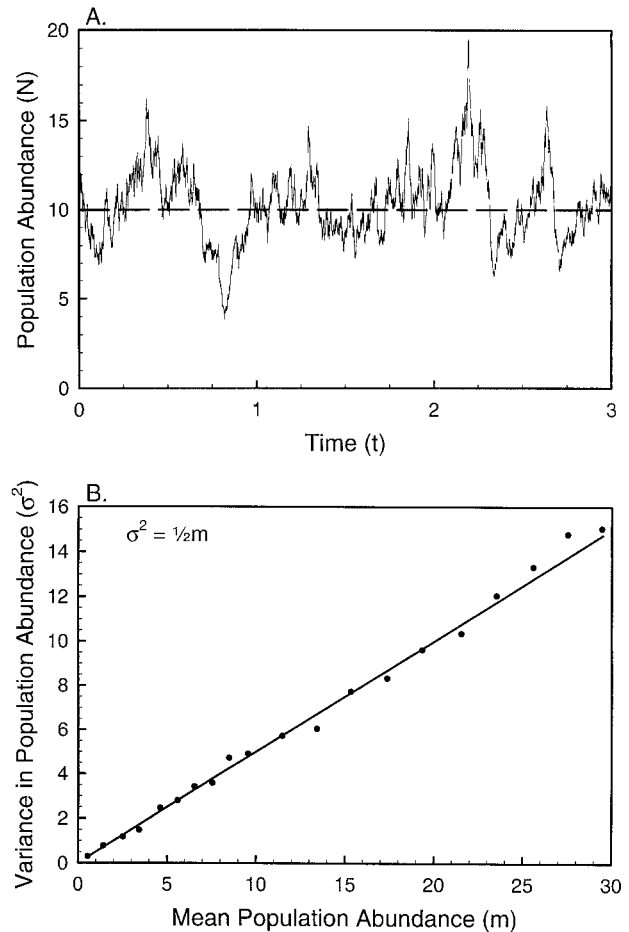


Figure 1: Simulated and theoretical results for the stochastic logistic equation with white environmental noise of Gaussian distribution with mean 0 and variance 1 (May 1973). *A*, Dynamics of a population with $K_0 = 10.5$ and $dt = 0.001$. The dashed line shows the analytically calculated mean population size. *B*, Variance increases linearly with the mean in these simulations (*data points*) and closely follows the analytically predicted relationship (*solid line*). The 20 dots represent 20 separate simulations, each with a different value of K_0 . As K_0 changes, the observed mean and variance also change. The position of each dot indicates the mean and variance observed over the first 100 time units in the corresponding simulation. The solid line represents the linear relationship analytically predicted by this model.

et al. 1998). Because it measures the percentage variation around the mean, greater CVs imply lower stability. Here we need to compare the stability of a single species living by itself with the stability of a community composed of k species and see how stability depends on diversity (i.e., on k). We first will consider two cases: the one proposed by Doak et al. in which $\sigma_i^2 = cm_i^2$ and an alternative in which $\sigma_i^2 = cm_i$, which occurs for the Poisson distribution and May's stochastic logistic equation. We then con-

sider a more general case in which $\sigma_i^2 = cm_i^z$, where c is a constant and z is any real number.

Doak et al.'s Case

Let us assume, as did Doak et al., that abundances of all species are random and independent, with all covariances being zero, that the total biomass of a community is m , that there are k species, and that all species are equally abundant (i.e., abundance of each is m/k). Let us further assume, as did Doak et al., that the variance in the abundance of species i scales as the square of its abundance, that is, that $\sigma_i^2 = cm_i^2$. Because $CV_{\text{community}} = 100(\text{var}_{\text{community}})^{1/2}/m$, it is necessary to determine how the variance in total community biomass depends on diversity for cases with 1, 2, . . . k species. This is done using the relationship that $\text{var}(a + b) = \text{var}(a) + \text{var}(b) + 2\text{cov}(a, b)$. Here we assume that $\text{cov}(a, b) = 0$. The variance in the biomass of a single species in monoculture is cm^2 , causing its coefficient of variation, $CV_{(1)}$, to be $CV_{(1)} = 100c^{1/2}$. For k species, each of abundance m/k , the variance for each species is cm^2/k^2 . This means that the variance of total community biomass is $k(cm^2/k^2)$ or cm^2/k , which gives

$$CV_{(k)} = 100(c/k)^{1/2}.$$

As Doak et al. show for this case, as diversity increases, CV declines as one over the square root of diversity, causing higher diversity to lead to greater stability. This important effect occurs even without interspecific competition (i.e., negative covariances), but, as shown later, it does not hold in other cases.

Poisson and Other Linearly Scaling Cases

Here we assume that $\sigma_i^2 = cm_i$, with $c = 1$ for the Poisson distribution. For a single species in monoculture,

$$CV_{(1)} = 100 \sigma/m = (c/m)^{1/2}.$$

Again assuming that covariances are 0, total community biomass is m , and species are equally abundant, then the variance in the abundance of each species, when there are k species, is cm/k . The variance in the total community biomass is thus $k(cm/k)$ or cm . This means that

$$CV_{(k)} = 100(cm)^{1/2}/m = 100(c/m)^{1/2}.$$

Note that k has canceled out, so that the coefficient of variation in total community biomass is constant, independent of diversity, k . This means that diversity has no effect on stability if species abundances follow any distribution for which variance increases linearly with mean abundance.

A More General Case

Let us now assume that the variance in the abundance of individual species depends on mean abundance as $\sigma_i^2 = cm_i^z$. The coefficient of variation for a community containing a single species would then be

$$CV_{(1)} = 100c^{1/2} m^{(z-2)/2}.$$

For a community of k species, with each species having an abundance of m/k and with covariances of 0, the variance in the abundance of each species would be cm^z/k^z . The variance in total community biomass would be $k(cm^z/k^z)$, which is $cm^z k^{1-z}$. Thus, the coefficient of variation in total community biomass for a community of k species is

$$CV_{(k)} = 100c^{1/2} m^{(z-2)/2} k^{(1-z)/2}.$$

To visualize the effect of diversity on community stability, it is easier to compare the stability of a community of k species with that of one with one species—that is, to look at the ratio of $CV_{(k)}/CV_{(1)}$, which becomes

$$CV_{(k)}/CV_{(1)} = k^{(1-z)/2}.$$

Lower values of $CV_{(k)}/CV_{(1)}$ imply greater stability (lower relative variation in community biomass). This equation shows that the effect of diversity on community stability depends on z (i.e., on the relationship between the mean and its variance) (fig. 2A).

The case derived by Doak et al. ($z = 2$) is but one of many possible effects of diversity on the stability of an ecological community. The critical determinant of stability, given the simplifying assumptions we have made, is z . If $z = 1$, diversity has no effect on the stability of total community biomass (fig. 2A). If $z > 1$, more diverse communities are more stable, which we call the portfolio effect. If $z < 1$, more diverse communities are less stable (fig. 2A). Thus, the tendency hypothesized by Doak et al. for stability to increase with diversity necessarily holds, given our assumptions (especially that of no covariances), only for $z > 1$.

Interspecific Competition and Stability

All of the prior discussion is based on the assumption that covariances in the abundances of species are 0, which is the case that Doak et al. explore. Quite different results occur if covariances are nonzero. For instance, interspecific competition can cause negative covariance. What effect would this have? In general, $\text{var}(a + b) = \text{var}(a) + \text{var}(b) + 2\text{cov}(a, b)$. If $\text{cov}(a, b)$ were negative, the variance of the two-species community would be less than the sum of individual variances, which would tend to stabilize the community.

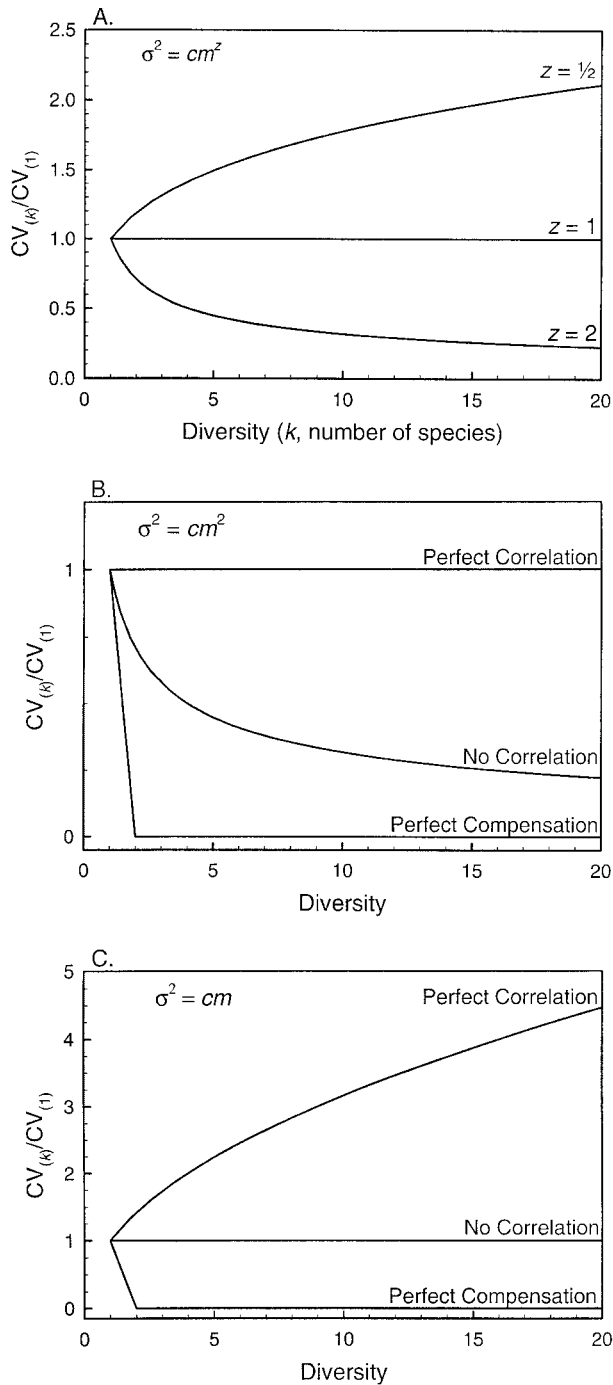


Figure 2: Coefficient of variation in community biomass for communities containing k species compared with those containing one species. Lower coefficient of variation ratios correspond with greater stability. *A*, When species abundances are random and independent with no covariance (no compensation or correlation), all species are equally abundant, and variance scales as the mean raised to the z power, the effect of diversity on stability depends on the value of z . Stability only increases with diversity if $z > 1$. *B*, Here variance scales with the square

Such compensatory changes in species abundances can cause stability to increase with diversity. For instance, when $z = 2$, $CV_{(k)}/CV_{(1)}$ declines to 0 and the community exhibits complete stability once two or more species are present if there is perfect competitive compensation (i.e., if declines in the biomasses of some species are completely compensated for by increases in the abundance of one or more other species) (fig. 2*B*). If all species increase and decrease in perfect unison (i.e., positive covariance), then, even with variance increasing with the square of the mean, stability would not increase with diversity (fig. 2*B*). If variance increases linearly with mean abundance, perfect correlation in species abundances would increasingly destabilize more diverse communities (fig. 2*C*). However, perfect competitive compensation would still completely stabilize the community.

A General Effect of Diversity on Stability

The most interesting feature of the effect pointed out by Doak et al. is the greater stability of more diverse communities that occurs, even without negative covariances, when $z > 1$. This comes from statistical averaging, as Doak et al. stress, and is analogous to the portfolio effect of economics. The essential feature of this statistical averaging is not that greater diversity inevitably leads to greater stability (it does not if $z \leq 1$) but that the coefficient of variation of a group of species is necessarily less than the average coefficient of variation of the individual species, given the simplifying assumptions made earlier. To see this, consider a case in which there are k species, each with an abundance of m/k , with the abundance of each species having a variance of σ^2 , and covariances of 0. In this case, the coefficient of variation of the biomass of a single species is

$$CV_{(\text{single species})} = 100\sigma k/m.$$

The variance in total community biomass is $k\sigma^2$, and total community biomass is m , giving

$$CV_{(k)} = 100k^{1/2}\sigma/m.$$

The ratio of the coefficient of variation of the total community biomass, $CV_{(k)}$, to the coefficient of variation of

of the mean. Stability increases with diversity (CV ratio declines) for cases with interspecific compensation, but it is independent of diversity for perfectly correlated changes in species abundances. *C*, Here variance scales linearly with the mean. Perfect correlation is destabilizing, and perfect compensation is stabilizing.

the biomass of an individual species in this community is then

$$CV_{(k)}/CV_{(\text{single species})} = 1/k^{1/2}.$$

Given our simplifying assumptions, this means that a community is necessarily more stable than the individual species that it contains and that the magnitude of this effect increases with diversity. This effect holds for all values of z . This effect, which has guided financial investment strategies for decades, contributes to the dependence of community stability on diversity, but the total effect also depends on the relationship between the variance and mean of population abundances. However, it does not necessarily imply that a more diverse community is more stable than a less diverse one. Given our simplifying assumptions, this only occurs if $z > 1$ (fig. 2A) or if there is interspecific compensation (fig. 2B, C).

An important question, then, is what value of z occurs in ecological communities. Because Doak et al. use the results in one particular study (Tilman 1996) as their prime example, we will address this issue using these data, and we urge others to explore it using their data.

Diversity-Stability in Nature

It has been shown (Tilman 1996) that the CV for biomass of individual species tended to increase significantly, but weakly, with diversity at Cedar Creek but that the CV for total community biomass decreased significantly with diversity. To determine whether the greater stability of more diverse communities might be explained by the Doak et al. hypothesis, we determined the dependence of the variance in the biomass of each species on its mean abundance for each plant species present in the experiment. For each species in a plot, we calculated the variance in its year-to-year abundances using data collected annually from 1984 through 1996 in that plot. We also calculated its mean abundance in that plot across the period from 1984 through 1996. The best fit to this entire data set was provided by $\sigma^2 = 34.5 m^{1.22}$ ($r^2 = 0.510$, $n = 5,248$, $P < .0001$; fig. 3A). By comparison, the same data when fit to a linear relationship ($\sigma^2 = 104 m^{1.0}$) had $r^2 = 0.500$ and to a squared relationship ($\sigma^2 = 0.49 m^2$) had $r^2 = 0.438$. If we restrict the analysis to the subset consisting of the eight most abundant species, the best fit was provided by $\sigma^2 = 13.1 m^{1.37}$ ($r^2 = 0.588$, $n = 915$, $P < .0001$; fig. 3B). The data for the eight most abundant species, when fit to the linear or squared relationship, had r^2 values of 0.552 and 0.525, respectively. Our data do not support $\sigma^2 = cm^2$. Rather, it seems more reasonable to assume for our community that $\sigma^2 = cm^z$ where $1.2 \leq z \leq 1.4$.

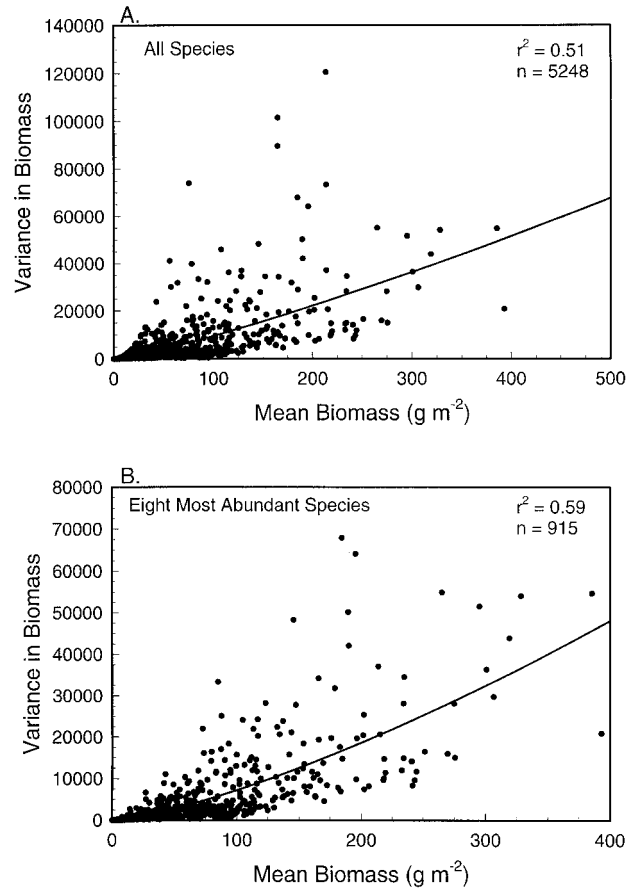


Figure 3: A, Year-to-year variance in biomasses of individual species in each plot, graphed against the mean biomass of each species in that plot, using data from 1984 to 1996 for all plant species. Data for the nitrogen addition biodiversity experiment (described in Tilman 1996) reveal that variance increases as abundance rose to the 1.22 power. B, Similar data, but only for the eight most abundant species (*Agropyron repens*, *Poa pratensis*, *Schizachyrium scoparium*, *Artemesia ludoviciana*, *Sorghastrum nutans*, *Carex* sp., *Lathyrus venosus*, and *Rubus* sp.). Here variance increases as abundance rose to the 1.38 power.

Because these z values are greater than 1, statistical averaging (the portfolio effect) did contribute to stability, but to a lesser extent than Doak et al. propose. More detailed analyses will be required to determine the relative importance of the portfolio effect versus interspecific compensatory effects. The analyses of earlier work (Tilman 1996) and of figure 3B suggest that both may have played a role in causing stability to increase with diversity in our grasslands.

Statistical averaging effects and negative covariance effects are two separate mechanisms that cause stability to depend on diversity. Both are of ecological importance, and both depend on biotic interactions. The strength and form of biotic interactions influence how variance scales

with mean abundance and determine the covariances in species abundances. However, the importance of the statistical averaging effect and the negative covariance effect as ecological principles relating stability to diversity comes not from whether they have a biotic or statistical origin but from their very existence. Greater stability of more diverse ecosystems is just as real, and just as important, whether it is caused by interspecific competition or statistical averaging. There is no need to invent null models against which actual results would be compared to determine whether they were more stable than would "inevitably" occur, because such an occurrence is not inevitable.

Further analyses are needed to determine how general the statistical averaging effect is. It may be that most mechanisms of interspecific interaction cause z to be greater than 1. Similarly, empirical studies (e.g., Taylor and Woiwod 1980) may show that z is greater than 1. If so, then statistical averaging could be an important mechanism causing more diverse ecosystems to be more stable, elevating the portfolio effect to the level of a principle as applicable in ecology as it is in economics. Similarly, further empirical and theoretical work is needed on the effects of interspecific interactions on covariances in species abundances. Interspecific competition is a prevalent force (Connell 1983*b*; Schoener 1983), especially in communities of sessile organisms such as plants and intertidal invertebrates, but indirect effects could cause positive covariances (Connell 1983*a*). Finally, statistical averaging and negative covariance need to be considered simultaneously. If, on average, variance tends to scale at least slightly more than linearly with mean abundance, and if competitive interactions tend to cause many species to be negatively correlated, then many other ecosystems would have stability depend on diversity as it does at Cedar Creek.

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