

CHAPTER 7



Predicting the Effects of Species Loss on Community Stability

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The question of how species richness and community organization may influence ecological stability has fostered a long-standing debate, recently revived through a spate of new field and microcosm studies (e.g., Tilman 1996; Naeem and Li 1997; McGrady-Steed et al. 1997) and modeling efforts (e.g., Doak et al. 1998; Hughes and Roughgarden 1998; Yachi and Loreau 1999). This new research has led to renewed claims regarding the importance of species diversity for various community and ecosystem functions as well as increasing efforts to develop simple principles to guide conservation policy and practice (e.g., Pimm 1991; Naeem 1998; Schwartz et al. 2000; Hector et al. 2001).

Nonetheless, the age of—and attention to—the stability-diversity question does not imply its resolution or direct application to questions of environmental management (McCann 2000; Schwartz et al. 2000; Hector et al. 2001). A particular problem with much of the ongo-

ing work is the neglect of details about species-specific life histories and ecological interactions. While the nuances of individual species are key in determining their community importance, most theoretical work on diversity effects glosses over such details.

Our goals in this chapter are twofold. First, we review recent work that has explored the relationship between species diversity and community stability, emphasizing modeling efforts (for reviews of more empirical work, see Loreau 2000; McCann 2000; and Schwartz et al. 2000). In addition to examining the consequences of species richness, we also ask whether it is possible to predict the consequences of losing *particular species* from a community. Although the problem of predicting single-species effects is far messier than that of arguing over more general stability-diversity patterns, it is also far more important for conservation.

Our approach comprises a Markov community model that addresses three general questions: (1) What aspects of life history or interactions with other species determine the importance of particular species for the stability of communities? (2) What features predispose a species to become dominant following the extinction of the original dominant species? And, most importantly, (3) can we accurately predict the importance of particular species removals in the absence of detailed field observations or experiments? Throughout this chapter, we gauge species importance in terms of its effects on the stability of aggregate community properties (e.g., total community abundance) or on community composition (May 1973; Power et al. 1996b; Tilman 1996).

Recent Studies of Stability-Diversity Patterns

The stage was set for the current crop of stability-diversity modeling by the historic mismatch between May's modeling results (1973) and the empirical work of McNaughton and others (Mellinger and McNaughton 1975; McNaughton 1977, 1985; Frank and McNaughton 1991). The models predicted declining stability with increasing species richness, whereas empirical observation generally suggested the opposite. Although there are numerous, competing ways of classifying the various mechanisms that contribute to stability-diversity patterns (e.g., Tilman 1999; Loreau 2000), we discuss them in terms of four simple categories:

- Simple sampling effects
- Niche complementarity and compensatory competition

- Averaging effects (a.k.a. portfolio effects)
- Addition of weakly interacting species

The first mechanism that can enhance community stability with increasing species number is a simple sampling effect: with a large number of species present, there is a greater chance that one or more of the species will be stable and dominant. In other words, the stability of more diverse communities may simply be due to the increased chance of a stable species being present. Although this simple sampling effect has more often been mentioned as a factor causing diversity-productivity relationships (Loreau 2000), it can also explain stability-diversity correlations.

The most common explanations of stability-diversity relationships are all somewhat more complicated versions of the sampling effect idea. These include niche complementarity and compensatory competition. The basic idea is that diverse groups of species are more stable because complementary species compensate for one another if one species suffers severe declines (e.g., Tilman 1996); with more species, there is an increased chance of complementary species being in the community. Naeem (1998 and this volume), using models from reliability engineering to describe ecosystem processes, has extended this basic idea to predict that more species-rich communities will be less affected by species losses. He argues that (1) as more functional groups are needed for proper ecosystem functioning, ecosystem reliability declines, simply because there are more ways for the system to fail, but (2) more species per functional group (higher species redundancy) increase the reliability of the ecosystem. Nijs and Impens (2000) use a careful, though abstract, probabilistic analysis to reach similar results. Essentially, redundancy within a functional group means that when one species is deleted from the community, another species with similar function will "step in" and fill the functional role of the deleted species.

Whereas the above ideas rely on the interactions of competing species, stability in aggregate measures (such as total productivity) is also expected to increase with species richness due to an averaging of random fluctuations in the growth of each species without any special competitive mechanisms. Using simple probability theory and simulations, Doak et al. (1998) demonstrated that as more independently varying species are added together, the sum of their abundances becomes more stable. However, the strength of this averaging effect depends on several factors (Doak et al. 1998; Tilman et al. 1998; Schwartz et al. 2000). First is correlation among the species' fluctuations, with more positive correlations leading to reduced averaging effects, and

negative correlations increasing the strength of these effects on stability. Second, the averaging effect is strongest when species are on average equal in abundance, and weakest when one species holds the lion's share of community biomass. Finally, the strength of averaging depends on the mean-variance relationships for individual species in the community. In the Doak et al. (1998) models, total community biomass was held constant and the variances of the biomass of individual species were assumed to scale with the square of the species' mean abundance (i.e., standard deviation scales linearly with mean abundance, and coefficients of variation are constant across species). In response to this study, Tilman et al. (1998) demonstrated that if per capita variability in numbers increases dramatically with decreasing mean abundance, the averaging effect can be eliminated or reversed.

Regardless, Yachi and Loreau (1999) have demonstrated the same averaging effect of diversity under much less restrictive assumptions about the relationship between the mean and variance of species' biomasses. In their model, increasing the total number of species increases both the mean community productivity and the stability of community productivity with the dynamics of community biomass driven largely by the set of most abundant species. In particular, a species can contribute substantially to community stability only if its range of abundance overlaps with that of the most dominant species. In other words, the loss of species that are consistently rare is predicted to have little effect on either the productivity or the stability of the community as a whole. This is akin to Doak et al.'s (1998) result that stability-diversity relationships are weakened by highly skewed distributions of mean abundance.

The studies just cited rely largely on statistical descriptions of community fluctuations. Other studies, however, have more explicitly included the effects of competitive interactions into models of stochastic community dynamics. Hughes and Roughgarden (1998, 2000), Ives and his coworkers (1999), and Lehman and Tilman (2000) use several alternative stochastic, density-dependent Lotka-Volterra competition models to explore the stability of community biomass. Hughes and Roughgarden (1998) consider only two species at a time, and they assess the stability of these "communities" as a function of the strength of the competitive interaction (indicated by the magnitude of the competition coefficients) as well as the degree of asymmetry between the two species' competitive effects. They find that the stability of the aggregate, or community, biomass is relatively independent of the strength of the species' competitive effects, but that community biomass becomes less stable as the disparity between the two species'

competitive effects grows. Similar models of multispecies systems (Ives et al. 1999; Hughes and Roughgarden 2000) show more generally that positive stability-diversity relationships are usually predicted and appear to be robust over many alternative model structures (Lehman and Tilman 2000). Most surprisingly, the details of competitive interactions seem to have relatively little influence on the generation of stability-diversity relationships (Ives et al. 1999). Ives et al. (2000) show that multitrophic models also show similar stability-diversity relationships, considerably broadening the class of models that show these effects.

Finally, increases in diversity can enhance stability if the additional species have only weak interactions with the other members of the community. This possibility was first hinted at by Robert May's analyses of diversity-stability relationships (May 1971, 1973), in which a tight relationship between interaction strength and instability was documented. However, the exact mechanism was only recently worked out by McCann et al. (1998), using community matrix models much like May's, except with predator switching and nonequilibrium dynamics. Starting with simple food webs, McCann et al. added species while simultaneously titrating the interaction strengths of the new species. They found that diversity begets stability as long as the enhanced diversity comes in the form of species with weak interaction strengths. This pattern occurs because the addition of weakly interacting species dampens oscillations between strongly interacting species and thereby increases the stability of the overall community.

In sum, past modeling and empirical work indicates that the mechanisms driving stability-diversity correlations include averaging, competitive release, symmetry in competitive effects, and the addition of weak interactions to food webs. However, most of the diversity-stability models, like all models, suffer from a lack of realism of one form or another. First, all of the models to date assume a closed system and a constant suite of species. In reality, even intensively managed field studies cannot obtain precise control of species richness. The turnover of species is an integral feature of natural communities that is important to consider when linking model predictions to empirical data (Schwartz et al. 2000; Hector et al. 2001). Second, the use of stability-diversity models to make meaningful statements about the preservation and management of ecological communities is limited, since little or no attention has been given to what makes a *particular* species important to the community. Instead, models have sought to link total species number with community patterns, a relationship that may rarely be of importance

for practical management. Finally, even less attention has been given to whether readily available data would provide any insight regarding species importance. In other words, within the stability-diversity literature, there has been little progress toward recognizing the set of traits that might identify which species are the most dangerous to lose and hence most crucial to preserve. We investigate these last two questions using a simulation model of competing, space-occupying species.

Methods

Basic Model Structure

We developed a stochastic simulation model for a set of competing species that is a direct extension of a first-order Markov model of community replacement (succession) dynamics (Waggoner and Stephens 1970; Horn 1975). Markov community models best represent groups of sessile, competing species in which priority effects predominate (an individual must die before there is any chance of replacement by an individual of the same or a different species) and consumer-prey interactions are of reduced importance. This modeling approach has proven to be a highly robust way of quantifying community structure and dynamics for a variety of ecological communities, including termites (Usher 1979), coral reefs (Tanner et al. 1994, 1996), rocky intertidal systems (Wootton 2001), forests (Waggoner and Stephens 1970; Horn 1975; Runkle 1981; Barnes and Dibble 1988), and desert plants (McAuliffe 1988). These models are also capable of accurately predicting the effects of species removals for real communities (Wootton 2001). We chose to use this framework both because of its success in predicting real community patterns, and also because these models are able to incorporate various aspects of species' life histories and interaction types (McAuliffe 1988; Wootton 2001) while still having the virtue of minimal structural complexity.

We first present the deterministic form of the model, then describe stochastic simulations based on this framework. Our model is represented as an $(S+1) \times (S+1)$ matrix for S species (the "+1" is because we also keep track of empty space). By repeatedly multiplying the community transition matrix, C , by a vector, N_t , of the amount of space occupied by each species (or empty) at time t , we can project changes in the abundance of each species, n_i , as well as of the total community, $CB = \sum_{i=1}^S n_i$ through time:

$$\begin{bmatrix} n_1 \\ n_2 \\ \dots \\ n_S \\ E \end{bmatrix}_{t+1} = \begin{bmatrix} s_1 + a_{1,1}(1 - s_1) & a_{1,2}(1 - s_2) & \dots \\ a_{2,1}(1 - s_1) & s_2 + a_{2,2}(1 - s_2) & \dots \\ \dots & \dots & \dots \\ a_{S,1}(1 - s_1) & a_{S,2}(1 - s_2) & \dots \\ 1 - \left[s_1 + \left(a_{1,1} + a_{2,1} + \dots + a_{S,1} \right) (1 - s_1) \right] & 1 - \left[s_2 + \left(a_{1,2} + a_{2,2} + \dots + a_{S,2} \right) (1 - s_2) \right] & \dots \end{bmatrix} \times \begin{bmatrix} n_1 \\ n_2 \\ \dots \\ n_S \\ E \end{bmatrix}_t$$

In the matrix, C , c_{ij} is the probability that an individual of species j is replaced by an individual of species i in a single time step. For transitions between individuals of the same species ($i = j$), $c_{ij} = s_j + (1 - s_j)a_{ij}$, where s_j is the survival probability for an individual of species j , and a_{ij} is the probability that an area vacated by species j is immediately colonized by new individuals of the same species. For transitions between species ($i \neq j$), $c_{ij} = (1 - s_j)a_{ij}$, where a_{ij} is the probability that an area vacated by species j is immediately colonized by new individuals of species i .

The final ($S + 1$) row of C includes transitions to unoccupied space. The total amount of space remains constant through time due to the constraints that $\sum_{i=1}^S a_{ij} \leq 1$ and that all vacated space not immediately colonized becomes "empty." The final ($S + 1$) column of C includes the probabilities that empty space is colonized by a species i , a_{iE} , or remains unoccupied. This model structure implicitly assumes that annual sampling of the community occurs just after the major recruitment season for most members of the community—if sampling occurs at some other season, or if recruitment is highly asynchronous, the transition probabilities cannot be divided so cleanly between survival (s_j) and conditional replacement probabilities (a_{ij}).

Although simple, this model allows a substantial amount of ecological reality. For example, the species-specific survival terms allow one to incorporate variable life spans, and the probabilities of transition between each pair of species allow the implicit inclusion of factors such as shared habitat requirements and preferential colonization by some species of space already occupied by others (McAuliffe 1988). However, this model is still quite limited in the types of communities

that it can portray accurately. These are largely communities in which adult survival precludes the establishment of new individuals, and in which the abundance of recruits is not limited by the local abundance of adults.

Stochastic Simulations

We used the basic model structure just described to conduct stochastic simulations, picking new values for each s_j and a_{ij} in each year based on predefined means and variances for each parameter. The basic model represents a community using $4S + 2S^2$ parameters: the mean and variance for the annual survival of each species and for the conditional probabilities that determine how vacated space is reallocated among all combinations of species and unoccupied space.

To simulate the dynamics of a broad range of randomly constructed species and community types, we first had to specify the rules that govern the behavior of each community matrix. To create a community (limited to 10 or fewer species in this paper), we randomly picked means for all s_j values from a uniform distribution between the limits of $\{0,1\}$, $\{0,0.5\}$, $\{0.5,1\}$, $\{0.25,0.75\}$, or $\{0.5\}$, and means for a_{ij} values from a uniform distribution such that all lay between $\{0,1\}$ and $\sum_{i=1}^S \bar{a}_{ij} \leq 1$. We also randomly assigned variances to each parameter, selecting values from a uniform distribution bounded by 0.001 and either 10% or 50% of the maximum possible variance given a parameter's mean (cf. Doak et al. 1994). In these models, annual variation in a_{ij} and s_j values was simulated by beta-binomial variables with no correlation or autocorrelation.

In all, we used 10 sets of parameter value restrictions (5 sets of bounds on s_j and 2 bounds on maximum variation) and created a minimum of 20 different random communities for each combination of rules. For a given set of parameter values, we simulated the dynamics of the entire community for 110 years. We recorded no information for the first 10 years (transient dynamics for a deterministic version of the model generally settled within 10 years) and then recorded the abundance of each species and of the entire community for each of the remaining 100 years. The total amount of space in a simulation always remained constant at $100(S + 1)$ spaces. The model was initiated with space divided evenly among the number of species + 1. For example, in a community with 10 species, each species initially occupied 100 spaces with the remaining 100 spaces empty.

Over the 100 years of data collection for each simulation, we recorded the mean and variability in the abundance of each species. To measure community stability (or, really, instability) we used the coefficient of variation in total numbers, or community biomass, over the 100-year sampling period, CV_{CB} .

We used the model in two ways. First, to examine the overall relationship between species diversity and community stability, we created communities that varied in the total number of species ($S = 2$ to 10) and recorded CV_{CB} over 100 years. Here, we allowed annual survivorships with means of $\{0,1\}$ and with standard deviations up to 50% of the maximum. We simulated 40 replicate communities per level of species richness.

Second, to explore the consequences of removing particular species, we compared the stability of communities before versus after an extinction event. We began by simulating each full community to establish baseline dynamics and then explored the consequences of removing each of the original species one at a time. For $S = 5$, for example, we ran a simulation with all 5 species, and then 5 additional simulations, each with 1 species removed and the other 4 remaining. For communities with 5 species, we ran 40 replicates, whereas for communities with 10 species we ran 20 replicates. Following a species removal, we reallocated the share of vacated space that would have been colonized by the removed species, by assigning the removed species' share of space to all remaining species proportional to their mean a_{ij} values. For example, if species 1 were removed, the new replacement values (a'_{ij}) for species i and $j = 2$ through 5 would be recalculated as:

$$a'_{ij} = a_{ij} + a_{ij} * a_{1j} / \sum_{i=2}^5 a_{ij}.$$

To compare the effect of each species' removal on community stability, we used the percentage change in CV_{CB} between the full model and each of the models with one species missing:

$$PCV_{CB} = 100 \left(\frac{CV_{CB,removal} - CV_{CB,full}}{CV_{CB,full}} \right),$$

where $CV_{CB,removal}$ is the coefficient of variation in community numbers after a species removal, and $CV_{CB,full}$ is the coefficient of variation for the full community.

Using this measure of community importance, we asked how easy is it to predict the effects of a species' loss with limited information (e.g., previous abundance, longevity, or ability to colonize unoccupied space). In addition, for the subset of simulations in which the dominant species was removed, we used discriminant function analysis to identify attributes that predispose a species to become the new community dominant. We also ran analyses using a measure of community compositional change after a species removal. In particular, to quantify shifts in the abundances of the remaining species after a removal, we calculated the multidimensional Euclidean distance between abundances in the full community and those after a removal for all species but the one removed (Collins 2000; Collins et al. 2000):

$$ED = \sqrt{\sum (n_{i,full} - n_{i,removal})^2}.$$

Results

Before turning to patterns of stability (or instability), it is important to note that the distribution of abundances among species in our model communities was altered dramatically by changing the extent to which survival rates varied among species and through time. The abundance of species in the simulated communities ranged from highly skewed to very even (fig. 7.1). The range of mean survival rates was far more important in generating these differences than was the maximum temporal variability in s_j and a_{ij} values (data not shown). As expected, the more variable survival was among species, the more highly skewed was the distribution of abundances among species. Many of the results regarding patterns of stability and model details likely follow from changes in species abundance patterns such as those depicted in figure 7.1.

First, like almost all other diversity-stability models, we found the typical, asymptotically declining relationship between community instability (CV_{CB}) and species number (fig. 7.2). In other words, according to our model, the removal of species usually results in more temporal variation in community biomass, with the destabilizing effects of extinction being more pronounced in species-poor communities. However, despite the overall decrease in mean CV_{CB} with increasing species number across communities, removing a particular species from a particular community can generate a wide range of effects on the percentage change in community variability, PCV_{CB} (fig. 7.3). For example, 43% of removals from 5-species communities and 31% from 10-species communities actually increased stability (negative values

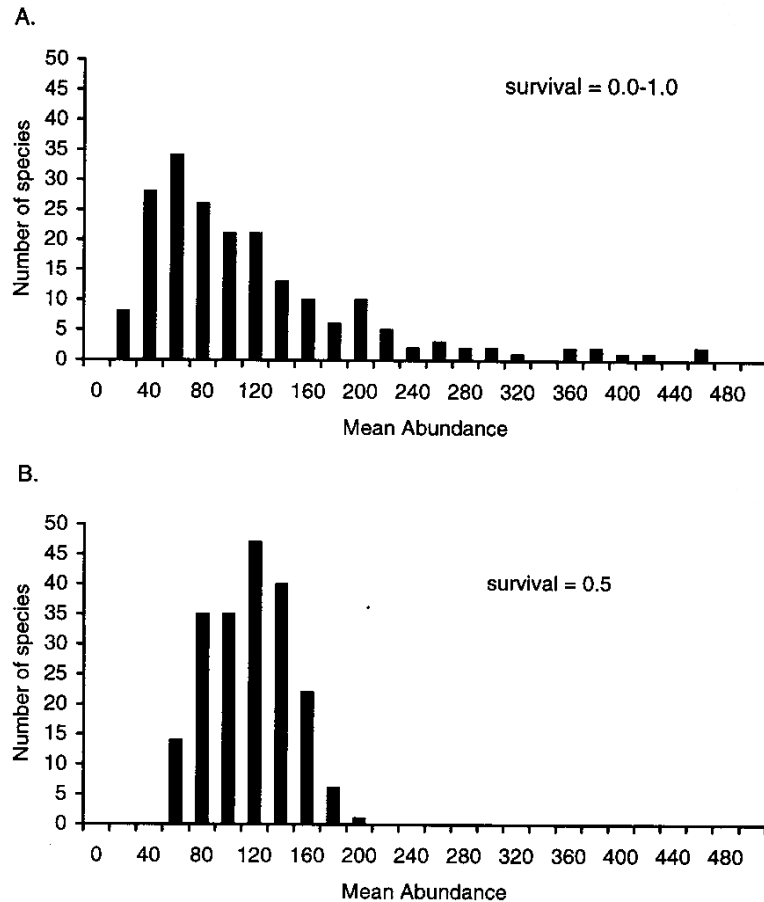


Figure 7.1 Distributions of species abundance for two community rules. The ten different community rules resulted in species distributions ranging from (A) highly skewed (survival rates 0.0–1.0) to (B) quite even (all survival rates = 0.5). Results are shown for communities in which $S = 5$ and annual variability in species' survival rates ranged up to 50% of their maximum.

of PCV_{CB}). For most species, removal has little effect on community stability, but for a few species, removal greatly destabilizes the community (see fig. 7.3). These results are consistent across both 5- and 10-species communities; for convenience, we present further results only for 5-species communities.

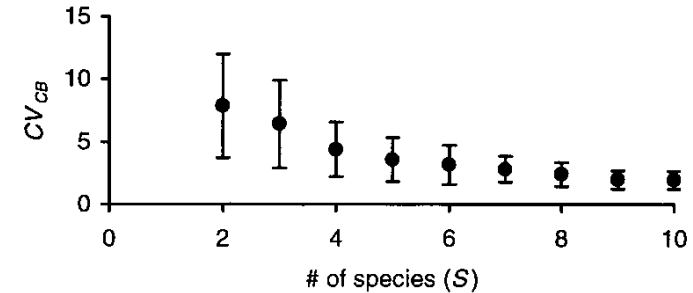


Figure 7.2 Relationship between community stability and species richness (# of species, S). CV_{CB} , the coefficient of variation in community biomass, is used as a measure of instability. Here, mean annual survivorships range from 0 to 1, with standard deviations up to 50% of maximum possible. Means ± 1 s.e. are plotted for 40 replicate simulations at each diversity level.

The primary determinant of a species' effect on community stability, when removed, was its abundance (or dominance) prior to its removal (fig. 7.4). For the most part, the species with very high PCV_{CB} were those that were highly abundant in the original community (see fig. 7.4). Roughly speaking, if a species constituted 50% or more of the original community's biomass, its removal nearly always destabilized the community to some extent. To ask more rigorously how well the magnitude of these effects could be predicted, we ran a suite of general linear models (GLM), using PCV_{CB} values as the response variable. When running these analyses, we always included the set of community rules as a categorical variable. As potential predictor variables, we focused on the attributes of species from intact communities (i.e., prior to any extinction) that might be readily available. For example, perhaps the easiest information to collect on a species is the mean and variability of its abundance. For our communities, mean abundance alone could predict about 31% of the variability in species-removal effects. (Including the coefficient of variation for abundance did not increase this model's predictive power: table 7.1). Running GLMs with more detailed species information gave negligible gains in predictive power. For example, the mean and temporal variance in survival rates, the probabilities of taking over space from other species, and the probabilities of colonizing empty space together predict only 22% of the variation in PCV_{CB} (see table 7.1). Finally, taking all this information together allowed prediction of about 44% of the variation in PCV_{CB} . The message seems to be that abundance alone

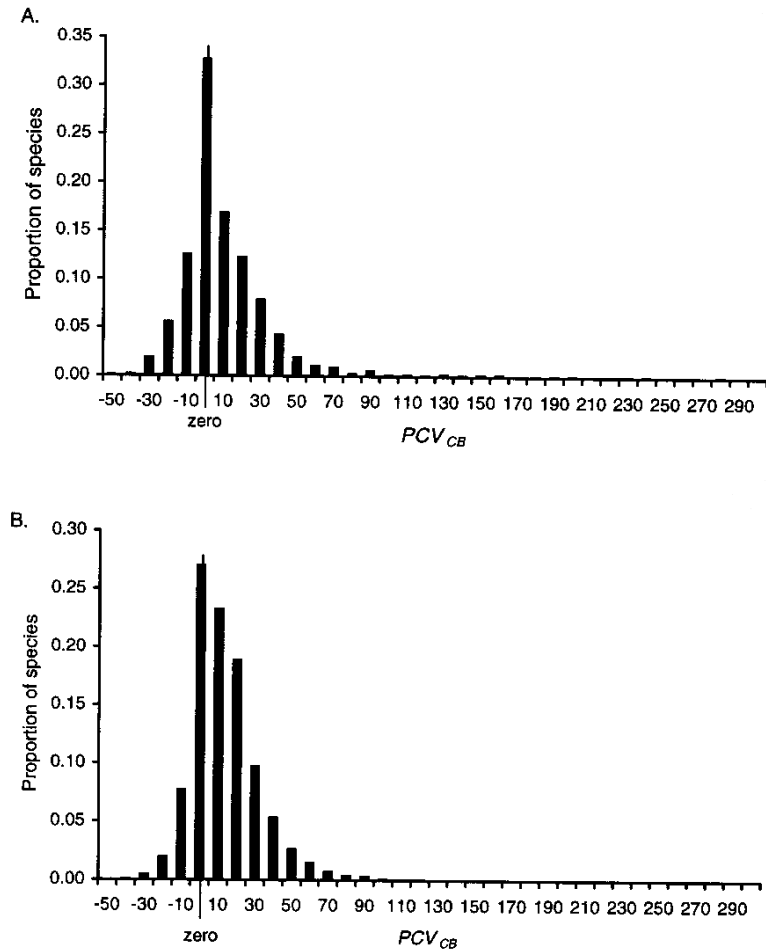


Figure 7.3 Histograms of % change in instability (PCV_{CB}) following individual species removals. A. Removals from all simulations of 5 species communities. B. Removals from all simulations of 10 species communities. Many removals produce little change in stability, whereas only a small number produce a large decrease in stability (large positive values).

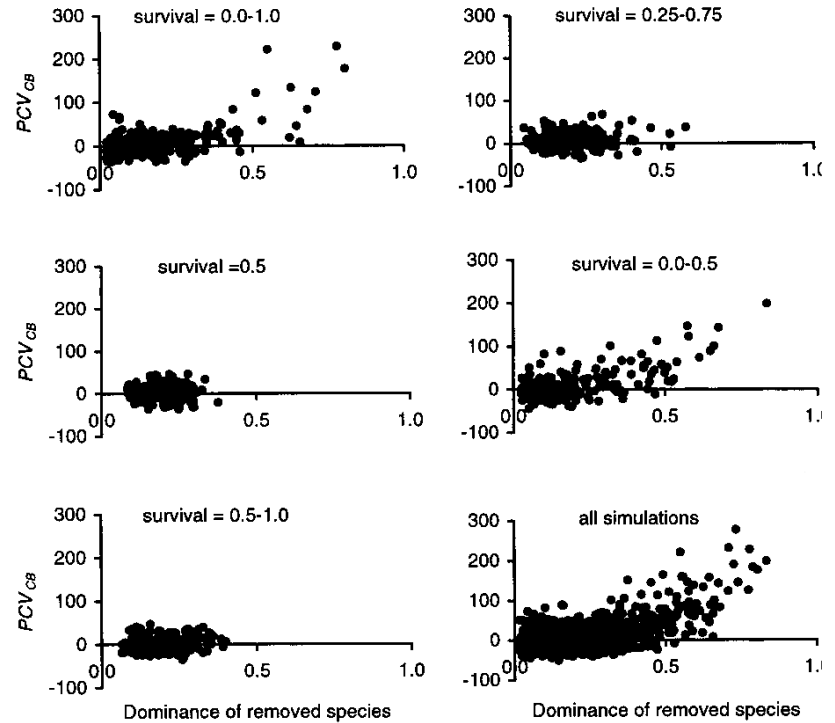


Figure 7.4 Relationships between change in community stability (PCV_{CB}) and the dominance of the removed species. All communities shown consist of 5 species. Dominance is calculated as the mean proportion of total community biomass prior to a species' removal. For our communities, abundance and dominance are basically interchangeable, with correlation coefficients ranging from 0.990 to 0.999 for different community rules. Results are shown for communities constructed with 5 different ranges of species survival rates (all with standard deviations up to 50% of maximum possible) and for all 10 sets of simulations combined.

is a reasonably good predictor of the effect of a species' extinction. On the other hand, that predictive power is so poor that one could never guarantee that rarer species, if they were to go extinct, would have minor effects on stability.

Because it is natural to overlook species of lesser abundance, it is worth focusing on those species alone. We found that the removal of species with lower dominance values could either stabilize or de-

TABLE 7.1

Ability to predict the importance of species removals with prior information

Different general linear models (GLM) were run on output from the five species community simulations. Either PCV_{CB} or ED was used as the dependent variable in each GLM, while information on the characteristics of the species prior to removal were used as independent variables. In all GLMs, the rules used to formulate the community were included as a 10 level categorical variable. The percentage of variance explained (r^2) is used to gauge explanatory power.

Model	Models Predicting PCV_{CB}	Models Predicting ED
	r^2	r^2
Mean abundance	0.311	0.747
Mean and CV of abundance	0.311	0.747
Mean and CV of survival, mean a_{ij} , and a_{iE}	0.223	0.543
Mean abundance and mean survival	0.324	0.747
Mean and CV of abundance, survival, mean a_{ij} , and a_{iE}	0.435	0.762

stabilize the community (see fig. 7.4). Clearly, it would be useful to be able to predict the effects of losing a rare species a priori. To address this issue, we selected the subset of species that contributed less than 30% of total community biomass (dominance < 0.3). We then used discriminant function analysis to examine how well we could classify species as stabilizing (defined as $PCV_{CB} > 40\%$) versus destabilizing ($PCV_{CB} < -30\%$), given different limitations on the availability of data. We found that several single variables provided equally poor predictions; abundance, survival, and colonization abilities (a_{ij} and a_{iE}) each led to correct classification of 55% of cases. Of these, mean abundance is by far the easiest to estimate in the field. We also found that very little predictive power is gained from embellishing the model (table 7.2). For example, when we included six predictor attributes (mean and cv of survival, a_{ij} , and a_{iE}), we correctly classified only 66% of the cases, in comparison with 55% of cases with but one attribute.

Of course, stability is not the only thing one is interested in when examining the effects of species removals. An additional way of measuring change entails the Euclidean distance between communities before and after an extinction. In contrast to our findings on the effects of extinctions on stability, the effects of extinction in terms of altered community composition responded in a much more predict-

TABLE 7.2

Predicting the importance of rare species for community stability

For the subset of species with dominance < 0.3, discriminant function analysis was used to classify species as strongly stabilizing ($PCV_{CB} > 40\%$) vs. strongly destabilizing ($PCV_{CB} < -30\%$). Rare species with intermediate effects on community stability were excluded from the analysis.

Model	% Correctly Classified
Mean abundance	54.7
Mean and CV of abundance	49.5
Mean and CV of survival, mean a_{ij} , and a_{iE}	67.4
Mean abundance and mean survival	56.8
Mean and CV of abundance, survival, mean a_{ij} , and a_{iE}	66.3

able manner. In particular, we ran a second suite of GLMs, similar to those described above, to predict the change in community composition, measured as ED (see table 7.1). Mean abundance before removal was by far the most important factor predicting ED , and accounted for 75% of the variance in removal effects on community composition. Adding other information did little to increase predictive power, with the full model (that included means and variability in abundance and per capita rates) predicting only 76% of the variation in ED (see table 7.1). While ED and PCV_{CB} showed a modest correlation (fig. 7.5; Pearson $r = 0.39$), this was driven almost entirely by a very few, extremely abundant species that were important for both measures.

The importance of abundance in predicting the community consequences of species removal seems to be due in part to its integration of the effects of survival rates and colonization ability. GLMs show that survival rates alone do a poor job of predicting a species' abundance, whereas adding the mean probability of taking over space from other species and the probability of occupying empty space allows prediction of 62% of the variance in abundance (table 7.3). In particular, high abundance and the resulting strong effects of removing an abundant species depend on high survivorship (fig. 7.6A) and strong colonization abilities (fig. 7.6B).

Finally, we asked whether we could predict which species would become dominant following the extinction of the original community dominant. To address this, we selected a subset of simulations in which the single most dominant species was removed, then used discriminant function analysis to classify the remaining species accord-

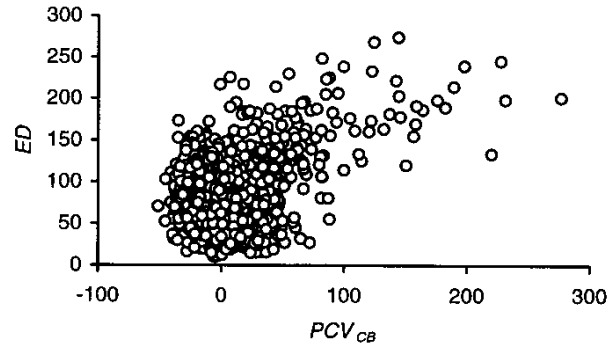


Figure 7.5 Relationship between the effects of species removals on community composition (ED) and on temporal variability in community biomass (PCV_{CB}).

ing to whether they became the new community dominant. Mean abundance in the intact community was the single most important variable; 76% of species could be classified correctly on the basis of abundance alone. In fact, in 287 out of 400 cases, the species that was the second most abundant in the original community became the new dominant after the original dominant was removed. In contrast, knowledge of those variables that are more difficult to measure (e.g., survival, replacement rates and colonization abilities) together allowed for correct classification of only 70% of species.

TABLE 7.3

Individual rates explaining mean species abundance

Different general linear models (GLM) were run on output from the 5 species community simulations. Mean abundance is the dependent variable in all analyses. In all GLMs, the rules used to formulate the community were included as a 10 level categorical variable. The percentage of variance explained (r^2) is used to gauge explanatory power. Mean a_{ij} is the average amount of vacated space freed by other species that the removed species occupied, and a_{iE} is the mean probability of colonized previously empty space.

Model	r^2
Mean survival	0.386
Mean and CV of survival	0.390
Mean of survival, mean a_{ij} , and a_{iE}	0.610
Mean and CV of survival, mean a_{ij} , and a_{iE}	0.617

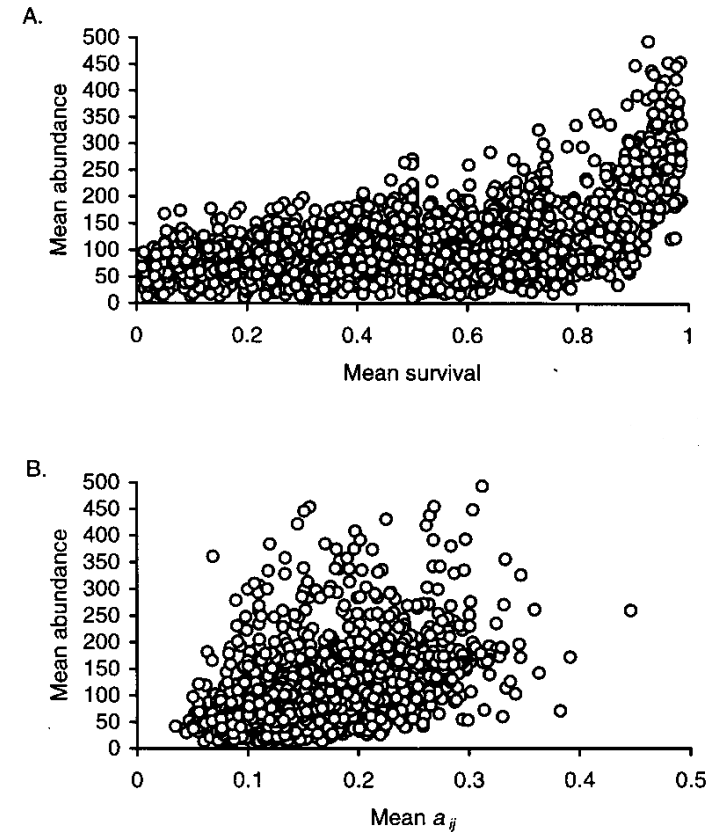


Figure 7.6 Relationship between mean abundance of species and (A) mean survival rate and (B) mean a_{ij} (the average amount of space vacated by other species that a species takes over).

Discussion

Current rates of species extinction are alarming—both in and of themselves, and because it seems clear that at some point so many extinctions may accrue that natural ecosystems will become irreparably damaged. A growing body of theoretical work has focused on the question of how many extinctions are “too many”—or, put differently, how many species we can afford to lose before permanent damage is done. These efforts have focused on the relationship between

species richness and either ecosystem function or ecosystem stability (McCann 2000). Although these questions are of theoretical interest, their relevance to the real world is probably limited (Schwartz et al. 2000). In particular, it appears that in real communities each extinction does not result in an incremental increase (or even a nonlinear or "threshold"-type increase) in damage at the community and ecosystem levels. Rather, the effects of extinctions are highly species- and context-specific (Power et al. 1996b; Soulé and Terborgh 1999). For example, some real-life extinctions have resulted in minimal consequences for communities and ecosystems (Simberloff this volume). On the other hand, it is now widely appreciated that certain keystone species exert effects on communities or ecosystems that are disproportionately large relative to the species' abundance (Paine 1966, 1969a, 1974, 1988, 1992, Power et al. 1996b). Thus, in some cases, real communities are strongly altered by the loss of a single species, but in other cases not; and the magnitude of the effects appears to depend on the specific traits of the deleted species or on the nuances of how the deleted species interacted with others in the community, rather than on the changes in the number of species per se.

Here, we have addressed how the community-level effects of single-species extinctions vary on the basis of some easily measured (and some not-so-easily measured) species traits. In our models, the removal of more abundant, or dominant, species exerts the strongest effects on community stability and composition. However, even for these simple, space-limited communities, moving much beyond this broad generalization is difficult. The power to predict the effects of extinction on community stability is depressingly low, given the data that are usually available. We find that even for a very simple set of model assumptions, and even knowing all the rules of the game, the importance of removing particular species is difficult to predict. This result parallels that of models for specific communities, in which the sensitivity of damping ratios or community composition to specific rates is not easily related to species abundances or other species traits (Tanner et al. 1994; Wootton 2001). However, we reiterate the caveat that our models have only considered competing species; models that include trophic diversity may suggest worse, or better, predictive power regarding species importance.

More positively, some aspects of community dynamics were highly predictable for our models. For example, easily obtained information such as rank abundance prior to an extinction was very useful in predicting which species would "take over" after the extinction of a community dominant. Also encouraging was the finding that mean abundance is a better predictor of species importance than more diffi-

cult-to-collect per capita rates or variability in abundance. Thus, to the extent that prediction of removal effects can be gauged ahead of time, information that is most easily gathered may be as useful as much more labor-intensive information.

As with any model, our results are driven by our assumptions. Although our results do not apply directly to any particular natural community, they do provide a clear set of hypotheses to test about the factors that direct the importance of species losses in competitively structured systems. Specifically, relative abundance alone is a reasonable surrogate measure for a wide variety of effects (e.g., changes in stability, shifts in community composition, and which species will take over for the lost taxa). However, there are notable exceptions to the overall abundance-importance correlation. When we turn to the real world, we find that although abundant species are a good place to look for large effects of extinction, several extremely abundant species have been lost with no dramatic effects recorded (Simberloff this volume).

The challenge that this work suggests for conservation is how to prioritize species-management efforts when clear rankings of species by community importance are not easy to make a priori. We hope that our general modeling approach will encourage the development of models that can be linked more accurately to data from real communities. In particular, models that take per capita rates for different species as a starting point are clearer and more understandable than are less "mechanistic" models or more complex frameworks (Wootton 2001). In addition, there is a clear need to incorporate trophic interactions into stability-diversity models.

Like most others pursuing community stability ideas, we have taken the easy road here, explicitly considering only competitors (but see McCann et al. 1998; Ives et al. 2000). Given the striking importance that R. T. Paine and his long line of students and collaborators have shown for trophic interactions in determining average community structure, better modeling of such effects for community stability is clearly needed. Hopefully, such models can be developed hand in hand with manipulative field experiments to carefully test and expand assertions of community stability patterns in real-world communities. Such testing is needed both for the science of ecology and for clarification on how best to pursue pressing conservation goals.

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