COMPLEXITY, DIVERSITY, AND STABILITY: A RECONCILIATION OF THEORETICAL AND EMPIRICAL RESULTS

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Theoretical studies of the relationship between ecosystem complexity and stability usually conclude that systems with more species, more interspecific interactions per species (connectance), or stronger interactions are not as likely to be stable as systems with fewer of these attributes (Gardner and Ashby 1970; May 1972, 1974, 1979; DeAngelis 1975; Gilpin 1975; Pimm 1979a, 1979b, 1980). Yet, in one of the few empirical investigations of this problem, McNaughton (1977) concluded that increased complexity stabilized certain ecosystem properties; more precisely, that a large mammalian grazer changed total green plant biomass less in more diverse than in less diverse grassland plots. We try to resolve this apparent contradiction between theory and empiricism by investigating, in model grazing systems, the relationship between complexity and the lack of change in plant biomass (which we call biomass stability) following the removal of an herbivore.

We established a set of structured food web models composed of one herbivore and n plant species. The models were based on the familiar Lotka-Volterra equations, and we selected their parameters over intervals designed to be biologically sensible and also to reflect the pattern of interactions in the food web. Only those models with a locally stable equilibrium involving species with positive biomasses were retained for further analysis. From each model of this subset, the herbivore was removed and the resultant change in total plant biomass followed until a new stable equilibrium was achieved. Relative biomass stability was calculated from the relative change in the total plant biomasses of the two equilibria. Clearly, a ratio near unity indicates biomass stability, while a large ratio indicates that biomass has increased considerably, following removal of the herbivore. We modeled webs of varying complexity as measured by: (1) the number of species; (2) the number of competitive interactions between plant species; and (3) species diversity (a measure combining the number of species and their relative abundances), and related these features to biomass stability. Our conclusion is that increased complexity can enhance biomass stability, even

though the more complex systems are more likely to lose species (i.e., from a species composition view, be less stable) than simple systems (Pimm 1979a, 1980).

<center>METHODS</center>

Grazing system food webs of n species (fig. 1) were modeled using Lotka-Volterra equations of the form

$$\dot{X}_i = X_i \left(b_i + \sum_{j=1}^{n} a_{ij}X_j \right), \qquad i = 1, n \tag{1}$$

where X_i is the biomass and name of the ith species; $\dot{X}_i$ its time derivative; b_i is the rate of change of biomass of species X_i in the absence of prey and predators; and a_{ij} is the per unit effect of species j's biomass on the growth rate of species i's biomass. In Lotka-Volterra models the X_i's are usually considered to be densities, but exactly the same equation form is obtained when biomasses are used instead (see Kirkwood and Lawton 1981). Each model structure described by equation (1) involved choice of both the magnitude and sign of the elements b_i and a_{ij}. Their parameter values were set by the biological details implicit in the model. Although more extensive arguments concerning the selection of parameter values can be found elsewhere (Pimm and Lawton 1978; Pimm 1979b), we shall briefly outline the main arguments.

In all our models, species at the base of the web (basal species; Pimm 1979b) can be considered photosynthetic plants capable of increase when their herbivores are absent and experiencing shortages of resources which become progressively more severe with increasing plant density. With no loss of generality, our basal species might also be detritivores or the space-limited sessile species of intertidal communities (Paine 1966). For simplicity, we shall call our basal species "plants" throughout. The b_i's of all plant species were fixed as 1.0, and their a_{ii}'s distributed uniformly on the interval $(-1.000, -0.001)$. This scaled the system, since X_i's equilibrium biomass in the absence of herbivory (its carrying capacity K_i) is b_i/a_{ii}. Thus, the K_i were distributed on the interval (1.0, 1000). Values of a_{ij} representing competitive interactions between basal species were, depending on the simulation, either zero or else were uniformly distributed on the interval $(-0.500, 0.000)$. Interspecific competition was, therefore, usually less than the intraspecific competition modeled by the a_{ii} terms, implying that the plants partitioned resources to some extent.

The herbivores were limited only by the abundance of their prey (Lawton and Pimm 1978; Pimm and Lawton 1978; Pimm 1979b), and their a_{ii} terms were set to zero. Their b_i must be small in order to ensure feasibility (Pimm 1979a). Accordingly, the b_i's of herbivores were fixed as -0.2, reflecting a relatively slow rate of decrease in the absence of a food source.

In grazing systems with, say, large mammalian herbivores and small annual plants, the herbivores' effect on the plants will probably be of much greater absolute value than the converse. Consequently, we chose the a_{ij}'s corresponding to the effect of herbivores on plant species on the interval $(-1.000, -0.001)$ and
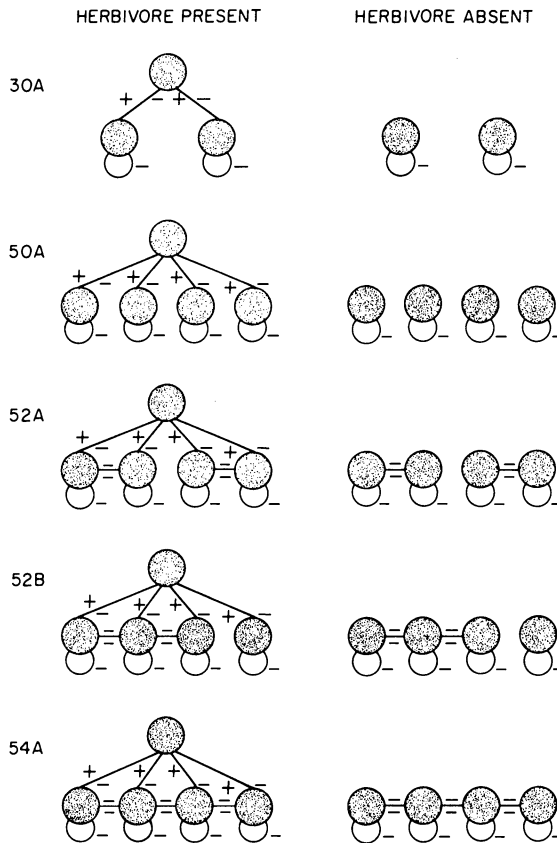
Fig. 1.—Examples of the models analyzed here. Stippled circles = species; lines = interactions between species; signs indicate the type of interactions: − + indicates predator-prey (herbivore-plant) interactions; − − indicates competitive interactions; − indicates resource limitation. Models all involve one herbivore but differ in the total number of species (first number) and the number of competitive interactions between plant species (second number); in some cases there are different possible arrangements of the competitive interactions (letter). We investigated 23 model structures.

those corresponding to the effect of plant species on herbivores on the interval (0.001, 0.100).

Are these models appropriate descriptions of grazing systems? The existence of both intra- and interspecific competition terms means that the systems' responses to grazing will be composites of individual plant responses and communitywide responses involving shifts in species composition. These features are in general agreement with experimental studies (reviewed by McNaughton 1979), although the details differ. McNaughton also recognized both species-specific and communitywide responses. The former involved a maximum plant productivity at intermediate levels of grazing: This occurs in our models at $K_i/2$. He also showed that plants remained productive despite very high levels of grazing. Our models do

not contain this refinement, and its effect on our overall results remains to be uncovered by subsequent analyses.

Given a model of an herbivore and the plants on which it feeds, we must first ensure that the equilibrium biomasses (X_i^*) of all species be positive: "feasible," in Roberts' (1974) terminology. These biomasses can be obtained as the solution to equation 1, subject to $\dot{X}_i = 0$; that is

$$b_i - \sum_{j=1}^{n} a_{ij} X_j^* = 0, \qquad i = 1, n. \tag{2}$$

The stability of the equilibrium of equation (1) is determined by the elements of a matrix, $\mathbf{M}$, called the Jacobian matrix, which evaluates the structure of a system described by equation (1) near equilibrium (Pimm 1979a). The typical element of $\mathbf{M}$ is

$$m_{ij} = a_{ij} X_i^*. \tag{3}$$

More specifically, the stability of the equilibrium depends on the sign of the largest eigenvalue of $\mathbf{M}$, and this was determined by numerical methods (details in Pimm 1979b).

From our set of random models we retained only those that were locally stable and feasible for further analysis. Depending on the food web structure under investigation, we found between 20 and 280 such models within the time constraints imposed by our computer program. The herbivore was deleted from each of these models and the new equilibrium biomasses of the plants obtained. This required numerical integration of the system of equations from the equilibrium involving the herbivore to a new equilibrium without it. Such simulations often yielded extinction for some of the plant species. Under this condition, there is often more than one stable equilibrium (Case and Gilpin 1974); which one is reached will depend upon the initial densities. This is why numerical integration, and not merely calculation of the new system's equilibrium, is necessary. The numerical technique was that of ORNL Routine ODE (see Shampine and Gordon 1975).

The relationship between biomass stability and system complexity was explored with three, not entirely independent, measures of complexity.

(1) Richness, the number of species in the system. We explored the biomass stabilities of grazing models with 2, 3, 4, 5, 6, 8, and 12 species (see fig. 1).

(2) Number of competitive interactions between plants. The number of interactions (as the proportion of those possible) is connectance and is the most frequently used measure of complexity (May 1974; Pimm 1979a); see figure 1.

(3) Diversity. Diversity indices contain both a species richness component and an evenness component (called equitability) involving the species' relative abundances. We, like McNaughton (1977), calculated diversity from the plant biomasses using the corrected Shannon-Weaver formula ($H = \Sigma_{i=1}^{n} p_i \log_{10} p_i$, where p_i is the proportion of the ith species' biomass in the sample). We calculated these diversities both in the presence and absence of the herbivore using the biomasses generated by the simulations. Our use of H should not be taken as a defense of this index. Indeed, we shall presently point out one of its failings. We include it not
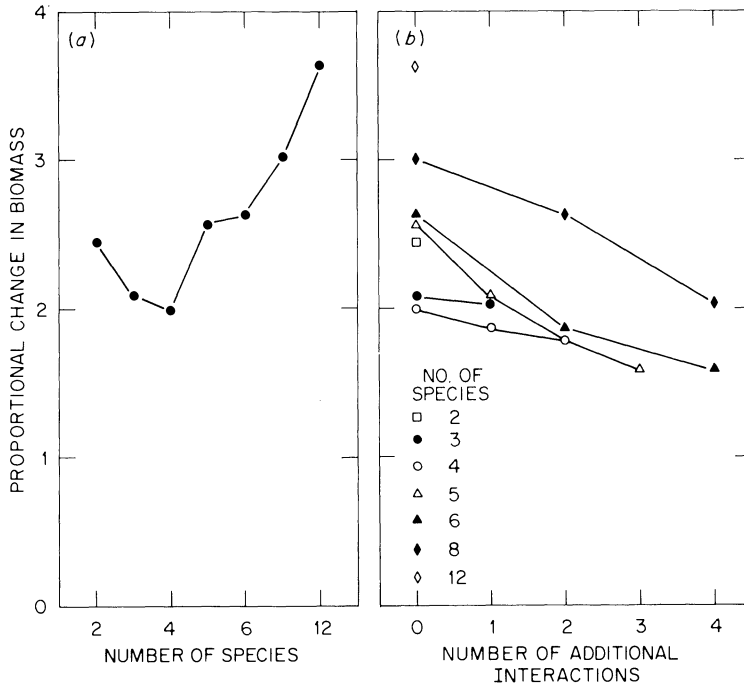
FIG. 2.—Geometric means of proportional changes in biomass (ratio of total plant biomass without herbivore divided by total plant biomass with herbivore) plotted against (*a*) total number of species in the system (models without competitive interactions between the plant species only) and (*b*) number of competitive interactions between the plant species.

only to indicate its problems but also to facilitate comparisons with McNaughton's (1977) results, and because there are many data on plant abundances summarized by this statistic.

RESULTS AND DISCUSSION

Our results are as follows: (1) Species richness. Figure 2*a* depicts the geometric means of the ratio of biomasses for models with different numbers of species and no interactions between plant species. An increase in the number of species from two to four was accompanied by an increase in biomass stability, but as the number of species increased beyond four there was a decided reduction in biomass stability. (We used geometric means because the biomass ratio is roughly lognormally distributed. Geometric means are less sensitive to occasional very high values than are arithmetic means.)

(2) Interaction between plant species. Increased connectance (obtained by adding competitive interactions between plant species) yielded increased biomass stability (fig. 2*b*).

(3) Diversity and evenness. The relationships between diversity, evenness, and biomass stability are not so simple as those discussed above. In figures 3*a* and 3*b*
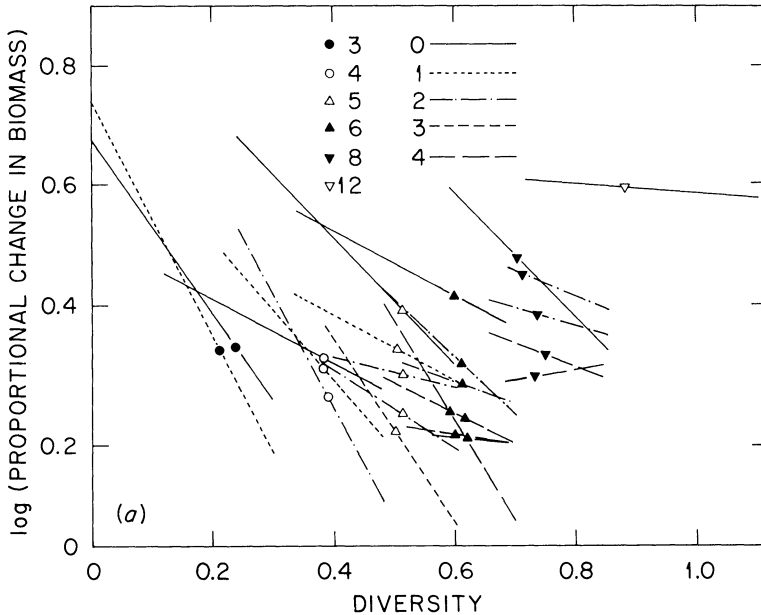
Fig. 3.—Regression lines of the logarithm of proportional changes in biomass, for each of the 23 models analyzed, against (a) plant biomass diversity (H, see text) with herbivore and (b) without herbivore. Length of lines = 95% of the range of values observed in simulations; symbols are positioned at the mean diversity values for each regression (Continued).

we plot the linear regression equations of the logarithms of the biomass ratios against the diversity of plant biomasses with (fig. 3a) and without (fig. 3b) the herbivore for each of the 23 food web structures analyzed. Examinations of the residual variation about these linear regression lines did not suggest that curvilinear models might describe the data more satisfactorily. For all but one of the 46 regression lines, greater diversity meant smaller change in biomass. The weakest relationships (and the only ones that were not significant at the 5% level) were between biomass stability and diversities in the presence of the herbivore when there were more than four plant species.

Within each model the number of plant species is fixed; thus these changes in biomass stability are related to the evenness component of diversity alone. Simply, the more even the plant biomasses, the greater the biomass stability.

These results are clear; the complications arise when we ask how biomass stability should be related to diversity over a wide range of systems. Diversity has two components—species richness and evenness; increases in the former cause greater changes in biomass (result 1 above), increases in the latter, exactly the opposite (result 3). How should biomass stability vary with an index whose two components are related in diametrically opposite ways? It will depend on how the index weights the two components and so the answer will probably vary from index to index. Moreover, the situation is further complicated by the relationship between possible values of diversity (H) and species richness (S). First, the
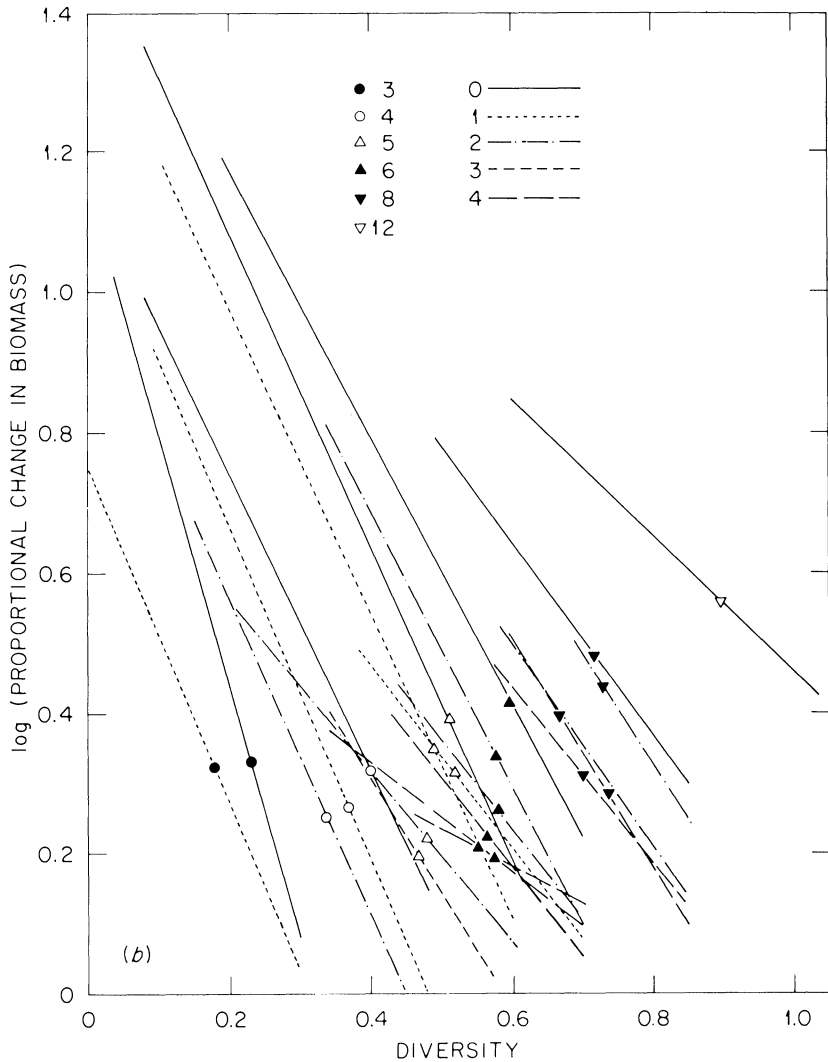
Fig. 3 (*Continued*).—Symbol type indicates number of species in the models (including the herbivore); line type indicates number of competitive interactions between plant species. Note that although the slopes are nearly always negative, the positions of the symbols yield an overall positive correlation.

index, H, has a maximum value of $\log_{10}(S)$. Second, although the theoretical minimum is always zero, most values will cluster toward the upper end of the range because extremely uneven biomasses are required to make the index small. For example, for two species the maximum diversity is 0.30 when the two species are equally abundant; but H is still 80% of this value when one species is three times as common as the other.

Combined, these two results mean that S and H are closely correlated. In figure

3 we plot the regression lines only over the approximate ranges for the data in our simulations. We also indicate the mean values for the diversities by the placement of the symbols. Now, suppose we were to collect field data on biomass changes for a variety of systems comparable to those we have modeled. The diversity values would tend to cluster around the mean values. As can be seen from the figures, the greater the mean diversities the greater the mean change in biomass to be expected. We would conclude that increased diversity was associated with decreased biomass stability, even though within a fixed species richness just the opposite is true. In sum, there is a decrease in biomass stability with increasing richness but the opposite with increasing evenness. There is also a strong, positive relationship between richness and the diversity index, H, and this can overwhelm the positive relation between stability and evenness. While the relationships of evenness and richness to biomass stability should be clear, that of diversity to biomass stability will probably be confusing.

(4) Changes in diversity and evenness. The greatest changes in biomass were associated with increases in evenness with the addition of herbivory (fig. 4). Biomasses changed less (the systems were more stable) when the addition of the herbivore caused a reduction in plant evenness. This result matches that of McNaughton (1977). He found a decrease in diversity after the introduction of an herbivore accompanied by a smaller change in biomass; where diversity increased with grazing, it was accompanied by the larger change in biomass.

As before, the changes in diversity in figure 4 reflect only changes in evenness within each model because within each model species richness is constant. But these data do not produce the problems inherent in those of figure 3. There is no relationship between the change in diversity and species richness. So, the overall relationship between biomass change and diversity change follows the same trend as within models. Unlike the data of figure 3, the data in figure 4 show no positive correlation of mean changes in biomass and mean changes in diversity.

SUMMARY AND CONCLUSIONS

These results suggest a resolution to the apparent contradiction between theory and observation of ecosystem complexity-stability relations pointed out by McNaughton (1977). In model grazing systems, we have examined the relationship between complexity and the lack of change in total plant biomass (i.e., biomass stability) following the removal of an herbivore. The results show that various facets of complexity can enhance plant biomass stability in model grazing systems. Certainly, systems with relatively few plant species are expected to be more stable than systems with more (but also fewer) plants per herbivore. But systems with more competing plant species are more biomass stable than those with few, if any, interactions between plants. Moreover, increased evenness in plant abundances also enhances biomass stability. We also find that, with the removal of the herbivore, increases in evenness are associated with smaller changes in biomass.

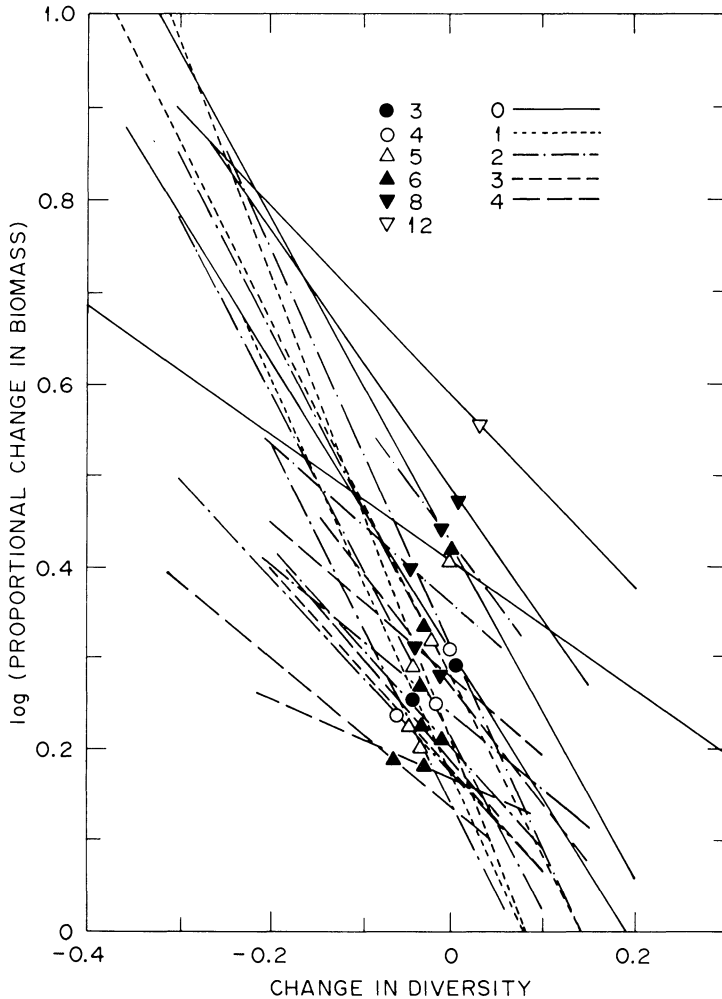Elsewhere, we shall consider in more detail the mechanisms behind our results

Fig. 4.—Regressions of logarithm of proportional biomass change against change in diversity (without the herbivore minus with the herbivore) for each of the 23 models analyzed. Lines and symbols as in fig. 3.

and the factors that modify the relationships presented here. It remains for us to discuss two points.

(1) Given this history of theoretical and field approaches tending to opposite conclusions about stability and complexity, we find it encouraging that our results and those of McNaughton (1977) generally coincide. When there is even apparent conflict between theory and experiment, it is easy to reject either, depending on one's predilections. Theoretical results are based on special, inevitably simplified assumptions, but experimental results are also special; they are obtained for a very limited range of conditions. When both models and experiments agree, there is the chance that the phenomenon is general and readily observable. We are currently assembling data to see if this is so.

The models' real utility, however, is not based on their ability to duplicate field results, even if this duplication were unexpected. The models suggest a number of testable predictions, perhaps more emphatically than field experiments (e.g., the effects of evenness, and not diversity, on biomass stability). Moreover, the models' simplicity suggests further analysis incorporating more realistic effects for plant growth and herbivore foraging. As an example, we suggest the incorporation of a plant's ability to grow even under intense grazing (discussed above). If such a phenomenon alters our results it would suggest perhaps testable predictions about differences between systems with long histories of heavy grazing (like the Serengeti studies by McNaughton) and others where large mammalian herbivores are more recent.

(2) We find that one aspect of ecosystem stability, biomass stability, is enhanced by some features of complexity. Yet our model systems are identical in both the equations, and the parameters used in these equations, to previous studies which concluded that more complex systems are less likely to be stable than simple ones. Indeed, previous results on models involving the deletion of species from a system (Pimm 1979a, 1980) showed that species composition rarely remained unchanged (''species deletion stability'') following a deletion. Moreover, increased richness and connectance greatly reduced the chances of species deletion stability. There is no paradox here: Our study addresses a different question than previous studies. It may be surprising—but it is certainly not impossible—that more connected systems are both more likely to change in composition yet less likely to change in total biomass following the removal of a species from the system. We believe, however, that our results say something more than that one obtains different answers to different specific questions about complexity and stability. The question posed by this study differs in two fundamental respects from previous theoretical studies. First, the property under investigation, total biomass, is different in kind from those approached by previous theoretical studies that focus on the abundances of individual species. Second, many theoretical studies cannot indicate whether, among observed systems, more complex systems are more or less stable. This is because the systems we observe in nature are, by the studies' definitions of stability, unlikely to be anything other than stable (Pimm 1982). These studies imply comparisons of existing communities with hypothetical ones. In contrast, this study suggests comparisons within existing communities (for example, whether plant community A is more or less biomass stable than plant community B, in response to varying levels of herbivory). The two kinds of system comparisons: existing with hypothetical, existing with existing, are both biologically interesting, but need not, of course, yield similar answers. The idea of systems possessing different kinds of stability and each changing differently with complexity has also been made by Armstrong (1982) using a very different modeling approach.

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