CHAPTER 9

Stability in Ecological Communities

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Meanings of "Instability"

Both Elton (1958) and MacArthur (1955) argued forcefully that there might be a relationship between a population's dynamics and the intrinsic properties of the species, as well as those of the community to which it belongs. Both attributed instability to system simplicity. Elton argued that pest outbreaks were just one of many manifestations of instability and that they were more likely to occur in simple, agricultural systems than in complex, natural systems. He relayed a conversation with some tropical foresters that (perhaps mistakenly) led him to believe that pest outbreaks are a feature of simple, temperate forests but not of complex, tropical ones.

MacArthur developed his ideas somewhat more formally. He defined instability in these terms: "Suppose, for some reason, that one species has an abnormal abundance, then we shall say that the community is unstable if the other species change markedly in abundance as a result of the first. The less effect this abnormal abundance has on the other species, the more stable the community." MacArthur defined the correlate of stability, complexity, as "the amount of choice of the energy in going through the [food] web."

It is tempting to be highly critical of these early studies. Elton's arguments are heterogeneous and often based on scant evidence. Agricultural systems differ in many ways from natural ones, and there are some remarkably simple natural systems that are not devastated annually by insect herbivores. (Examples include the large stands of bracken fern, *Pteridium,* studied extensively by J. H. Lawton. Strong et al. 1984b, provide a review.) MacArthur's argument is fine as it stands, but is incomplete; it considers changes in abundance of species at the base of food chains. Changing abundances of top predators might (and indeed do) have the opposite effect: the more complex the web, the more widely disturbances may propagate. Yet we consider these early studies to be particularly important. They argue that examining the characteristics of a single species is not enough. We must look at the system to which it belongs.

From "Insect Outbreaks and Community Structure." In *Insect Outbreaks,* ed. Pedro Barbosa and Jack C. Schultz. New York: Academic Press, 1987, pp. 100–108.

They also point to a wide variety of possible meanings, not just of instability, but of community features that may correlate with instability.

Clearly, what we must do first is to look at the definitions of population stability. Then we must ask these questions: To what extent do the various kinds of instability correspond to pest outbreaks? How do these kinds of instability vary with the properties of the systems to which the species belong? Is there any evidence that outbreaks are more likely to occur in systems with certain trophic structures—simple ones, for example?

In reviewing the meanings of *stability,* we have recognized five major ideas: stability (in the strict, mathematical sense), resilience, persistence, resistance, and variability (Pimm 1984a).

Stability exists if and only if the species densities in a system tend to return to their equilibrium values following disturbances to the densities. In a variable, uncertain world, equilibrium levels may not be the population levels at which species remain; in such cases, equilibrium is better defined as the level below which the population tends to increase and above which the population tends to decrease (Tanner 1966; Pimm 1984b). Resilience is a measure of how fast a population returns to equilibrium. *Resilience* is measured in models by the characteristic return time—the time taken for the perturbation (equilibrium density minus the population density) to fall to $1/e$ (~37%) of its initial value. A resilient system has a short return time. *Persistence* measures the time a system lasts before it is changed to a different one—for example, how long a system may last before one equilibrium is replaced by another. *Resistance* is the tendency for a system to remain unchanged by a disturbance. *Variability* includes such measures as the variance, standard deviation, or coefficient of variation of population densities over time. . . .

The Stability-Complexity Question

Stability is well defined mathematically, and most theoretical studies examine it alone. Early studies (such as Gardner and Ashby 1970; May 1972) found that a smaller proportion of models of multispecies systems were stable when there were more species, when a greater proportion of those species interacted (high connectance), and when the species interacted more strongly. This seemed so contradictory to the notions of Elton and MacArthur that considerable efforts were made to evaluate the many unrealistic assumptions these early models required. The patterns of the interactions were made more realistic, as were the parameters and even the form of the equations.

Some reviews of this literature are given by May (1973a, 1979) and Pimm (1982, 1984a); to report them in detail here would be repetitious. The initial results, however, seem fairly robust. They can be reversed most easily by using models in which the predators have no effect on their prey's population growth rate (so-called donor-controlled models) (DeAngelis 1975). This can happen if predators take those prey that are most likely to die from other causes—starvation, for example. There is a large body of literature on removing predatory species from communities or, as in the case of biological control, introducing them. The vast majority of these studies show that predators do have an impact on the densities of their prey (Pimm 1980). For insects, this impact can be very large, with predators depressing prey populations to a fraction of 1% of the levels in the predator's absence (Beddington et al. 1978). In short, the donor-controlled assumption does not seem to be a good one, and so we are faced with the conclusion that more complex systems are less likely to have a stable equilibrium than simple ones.

On closer inspection, this conclusion does not contradict the ideas of MacArthur and Elton as much as it might superficially appear (Pimm 1982, 1984a). There is no difficulty with the idea that systems with stable equilibria are likely to persist. Those with unstable equilibria can have one of two initial fates: They can lose species and settle to a new stable equilibrium, or the populations may persist, oscillating probably in some complex manner. For many natural systems these two initial fates are really the same. Large-amplitude oscillations will eventually mean that populations will be driven to such low levels that they will not be able to recover. Thus, stable systems will persist, whereas unstable systems will tend to lose species and simplify to the point where they will contain a stable species assembly.

Although the quantitative results of stability analyses depend on the various assumptions made, there is a qualitative prediction that seems relatively robust: to retain stability, the product of two measures of community complexity, species number n and connectance C, should be smaller than a critical value (which depends on the strength of the species interactions). If the systems we observe in the real world are those that are stable, observed values of C and n should fall in a region *below* a hyperbolic function, as suggested by figure 8a. Data from a variety of communities, including the aphid-dominated systems shown in figure 8b, show this to be the case (Rejmanek and Stary 1979). What this reveals is straightforward: the systems we observe in nature are relatively simple ones. There is now considerable evidence that the patterns of trophic interactions we observe in nature are simpler, in a variety of ways, than we would expect by chance (Pimm 1982). There seems to be no reason to expect that simple crop ecosystems should not be stable.

Species Deletion Stability

Introduction and Model Results

What happens when we simplify a system, say by reducing the number of species present? How often are we likely to retain a stable system, and

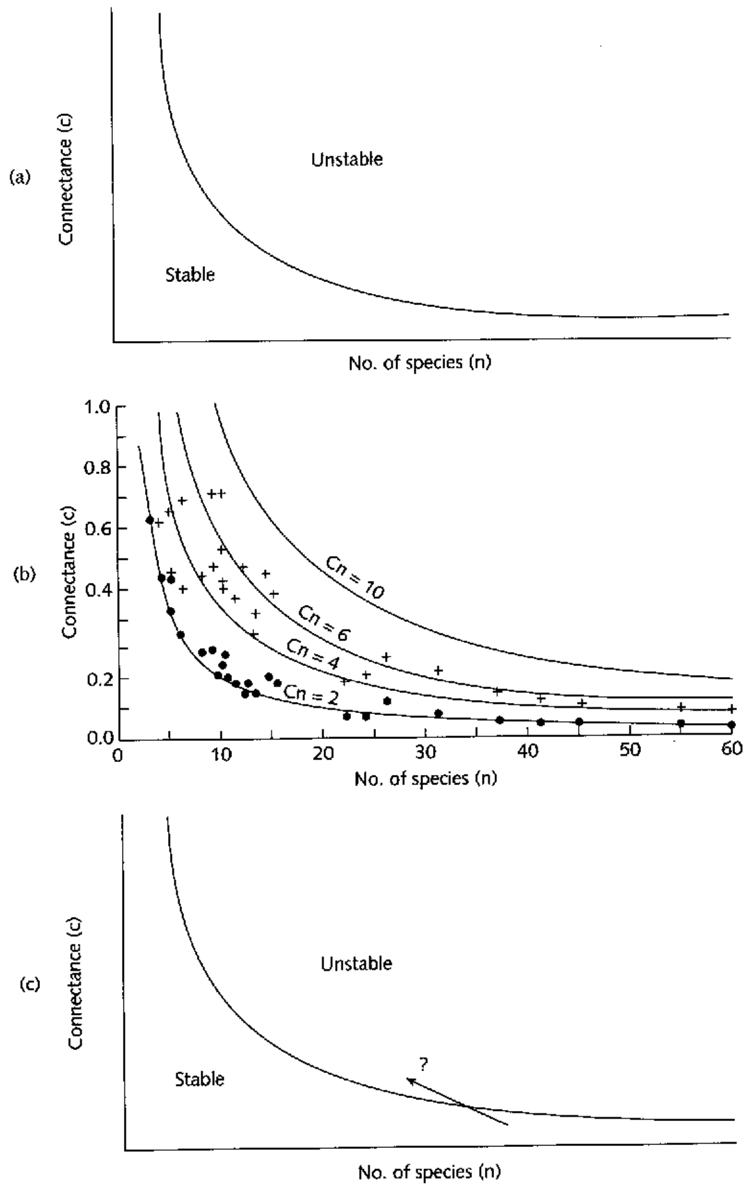

Figure 8. (a) Values of connectance C *and species number* n *that lead to stable and unstable systems in food web models. This result suggests that natural systems should have values of* C *and* n *bounded by a hyperbola. (b) Four hyperbolic approximations and the observed values of* C *and* n *for aphids, their plant hosts, and their parasitoids. Discovered trophic connectance (●) was calculated on the basis of only the discovered interactions, whereas potential total* C *(+) also includes all potential competitive interactions. (c) When species number is reduced, it is possible that the resultant system is unstable, even though, other things being equal, simple systems are more likely to be stable. (From Rejmanek and Stary 1979.)*

how often will the system become unstable (figure 8c)? Simple systems may often be stable, but there is no guarantee that we will produce stable systems from simplifying existing stable, complex ones. Answering these questions requires an examination of what we have called "species deletion stability" (Pimm 1979).

A system is deemed "species deletion stable" if, after the removal of a species, the remaining $n - 1$ species can coexist at a new, stable equilibrium (Pimm 1979, 1980). We can determine a system's species deletion stability repeatedly for the same species and the same model structure, but over ranges of interaction parameters designed to mimic those found in nature. This gives a probability of species deletion stability for that species' removal and for that particular web. These probabilities, averaged over all the species in a food web, vary in much the same way with connectance, species number, and interaction strength as does simple stability. The more complex the model community, the more likely it is that the loss of a species will cause further species losses. Most model systems with complexities anything near those observed in nature are not species deletion stable, nor are natural systems. The vast majority of natural systems cannot withstand species removals without changes in species composition (a review of this literature can be found in Pimm 1980).

From these studies it might seem that we have an explanation of pest outbreaks in accord with the view of Elton and MacArthur: instability is caused by simplification (rather than just by simplicity). This may be so, but on close inspection it is not anywhere near as clear-cut as it might seem. Species deletion stability varies markedly depending on which species are removed from a community (Pimm 1980). The reviews of species removals mentioned earlier tend to focus on the removals of predators or top predators. For these we expect, and find, further species losses. For plant removals, however, particularly those of plants fed on by generalized herbivores, models predict fewer losses. Moreover, these losses should become increasingly less likely with more complex systems. There is less evidence to support this result, but one cannot help notice the lack of an effect of removing chestnut, *Castanea dentata*, . . . from eastern North America. Chestnuts occupied more than 40% of the canopy in some areas in the early twentieth century and have now almost totally disappeared (Krebs 1978). Although the disappearance may have caused the loss of seven insect species that fed only on chestnuts, most insects that fed on chestnuts also fed on other tree species (Opler 1978). There do not seem to have been any losses of vertebrate species.

The simplification practiced in agriculture leads us to ask, How often does the removal of an unwanted plant species cause the crop species' load of insect herbivores to increase? Thus, in reducing the competitors of the plants we wish to harvest, do we make the crop species more vulnerable to attack by insects?

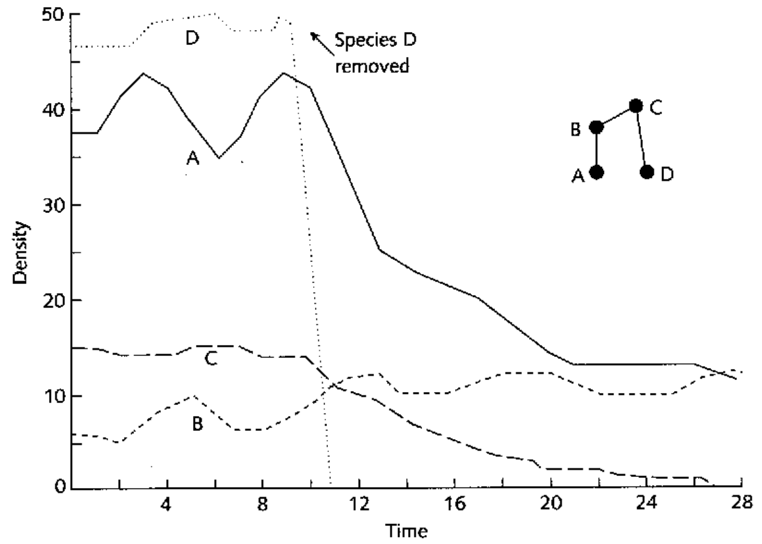

Figure 9. Effect of removing a plant species (D) on the densities of the species remaining in the system. Note that the other plant species (A) may end with a lower density because of the increased attention of its herbivore (B).

This can certainly happen theoretically. A simulation is shown in figure 9, where the removal of a plant causes the loss of a generalist predator on a specialist herbivore; the remaining plant species goes to a lower equilibrium than before. However, the models do not tell us the frequency of this occurrence in practice; it is certainly not inevitable, and it may be unlikely. Common sense dictates the conditions under which it will be a likely event—when we remove plant species essential to the survival of generalist predators that have a controlling effect on the herbivores feeding on the crop (just as in figure 9). Moreover, the loss due to these herbivores must be greater than the gain obtained from competitive release.

In short, taking an existing system and simplifying it by removing species will usually cause further species losses. It is far from certain, however, whether removing one plant species will cause a decrease in the other remaining plant species by increasing their vulnerability to insect herbivores. How do these results match our observations and intuition about the real world?

Some Field Studies

The kinds of studies that have tested the ideas about simplification have asked, How do a crop's insect numbers differ if that crop is grown singly or in a multispecies planting? Root's (1973) work is an early example of such a study. *Brassica* were grown in a single-species planting and also among many other plant species. In multispecies plantings, more species of insects were present throughout the planting, and on the *Brassica* itself, insect herbivores did not reach such high levels. From this, we might conclude that simplification caused a pest outbreak. But how general is this result, and exactly what is being simplified?

Answering these questions requires many other studies. More than 150 such studies have been compiled in a timely and important review by Risch et al. (1983). In a highly significant proportion of cases, insect herbivores were more likely to reach high densities in single-species plantings, but there were some important patterns of variation. Risch et al. argued that increased density in single-species plantings might occur for one of two reasons. First, reduced predator diversity and impact might make herbivore outbreaks more likely. Second, on the basis of the phenomenon described in the "resource concentration" hypothesis (Root 1973), the plants associated with the crop in a multispecies planting might have a direct effect on the ability of insects to find and utilize the crop. They argued that these associated plants might mask the herbivore's host-finding stimuli, generally reduce movement between individual plants, or in various other ways lower herbivore colonization rates.

The two hypotheses make different predictions about the effects of plant diversification on monophagous and polyphagous herbivores. Both groups might be expected to suffer from the increased attention of predators in multispecies plantings, if this is the cause of the reduced densities. Monophagous species, however, should decline far more than polyphagous species, if the "resource concentration" hypothesis is correct, because for polyphages the multispecies plantings will not represent such a dilution of resources.

The data support the "resource concentration" hypothesis. For monophagous species, 61% of studies showed a decrease in density with multispecies plantings, 10% showed an increase, and the rest were equivocal. For polyphagous species, 27% of the studies showed a decrease and 44% an increase. The differences were highly significant.

Risch et al. (1983) went on to consider the differences between herbivores on annual and perennial plant species. They argued that annual species might rely more heavily on escape in time from their herbivores, whereas perennials might rely on chemical defenses to slow herbivore growth. In the latter case, herbivores would be subject to longer periods of exposure to predation. If the reduced numbers in multispecies plantings were due to the effects of predators, we might expect differences between annuals and perennials. Risch et al. were unable to detect such an effect. Thus, monophagous herbivores were less abundant in diversified plantings of annuals in 58% of the cases and in 67% of the cases for perennials. For polyphagous species, the corresponding figures were 27 and 28%, respectively.

In short, Risch et al. (1983) make a persuasive case that complexity reduces herbivore densities, but the complexity is that of the plant species and the physical effects spacing plants might have. It seems to have little to do with the trophic structure of the insect communities.

Summary

Early studies suggested that pest outbreaks in agricultural systems might be due to simplification of the system. Later theoretical studies suggested that there is nothing inherently unstable about simple systems. Indeed, it is the sufficiently complex systems that should be unstable. We might expect such systems to become simplified through species losses. The result should be that the systems we observe in nature are relatively simple compared with what chance dictates (figure 8a). This seems to be the case.

Models show that the actual process of simplifying a system by removal of species from it can be expected to cause further species losses and changes in the densities of the remaining species. Removal of plant species can lead to increased herbivore levels on some of the remaining plant species, but this is not inevitable. There is now a large collection of studies that show the effects on insect herbivores of simplifying a system by removing plant species. The insect herbivores are generally more abundant on plant species grown in monoculture, but this seems to have far more to do with the difficulty of getting from host plant to host plant in the multispecies planting than to any trophic interactions.