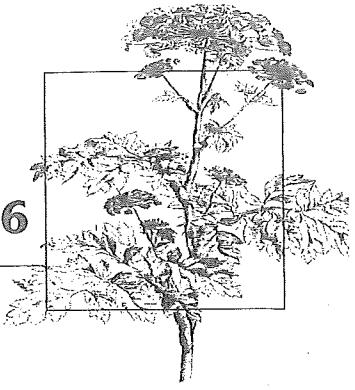


CHAPTER 6



Food Webs

OVERVIEW

This chapter introduces the basic attributes of food webs and reviews general patterns that arise from the examination of large collections of food webs. Simple predator-prey models introduced in the previous chapter are extended to make predictions about the dynamics of species in simple food webs with different structures. These models predict that some features of simple food chains, such as chain length and feeding on multiple trophic levels, may be associated with reduced stability. There are relatively few experimental tests of the predictions that food web theory makes about population dynamics. The available evidence suggests that food chain length may depend in a complex way on both productivity and constraints imposed by population dynamics, since increases or decreases in productivity both lead to decreases in food chain length. Other topics related to food chains and food webs, such as trophic cascades, are discussed in the context of indirect effects in Chapter 8.

FOOD WEB ATTRIBUTES

A **food web** describes the feeding relations among organisms in all or part of a community. Usually those feeding relations are described by a diagram linking the consumers and consumed with lines or arrows, as shown in the examples in Figure 6.1. **Links**, the lines, indicate a predator-prey interaction

between two **nodes**, which can correspond to a single species or groups of species. Because food webs focus on patterns of trophic interactions within communities, they describe communities



Food webs describe predator-prey relations in community. from the rather selective standpoint of predator-prey interactions. To the extent that competition among predators results

from the consumption of prey, food webs also outline a subset of the possible competitive interactions within communities. Other kinds of interspecific interactions, such as mutualisms, are not described by food webs. Consequently, food webs provide less than complete descriptions of interactions within communities, but they are probably no less complete than any other descriptive device, such as the niche.

Charles Elton (1927) emphasized the use of food webs and food chains as important summaries of community patterns. Figure 6.1 shows one of the earliest published food web diagrams (Summerhayes and Elton 1923), along with more recent, and disarmingly complex, computer-generated webs based on gut content analyses of tropical fish (Winemiller 1990). Elton posed questions about the limits of food chain length that continue to intrigue community ecologists. His original term for the food web, **food cycle**, referred to the collection of food chains within a community. Elton also emphasized the importance of basic patterns involving the sizes of organisms and their feeding relations in food chains. In general, typical predators are larger than their prey, and parasites are smaller than their hosts. This difference reflects obvious biomechanical constraints on the ways that some species feed on others, but these size differences, interacting with the sizes of habitats needed to sustain those predators, could ultimately impose limits on the length of food chains as well.

One pattern that emerges from the common inverse relation between trophic level and organism size noted by Elton is the **pyramid of numbers**, which is often referred to as an **Eltonian pyramid**. The basic idea is that small



organisms at the base of the food chain Eltonian pyramids of numbers, are more numerous than their larger biomass, and energy. predators, and so on up through the remainder of the food chain. There are, of

course, obvious exceptions to this generalization, especially where large primary producers (e.g., trees) are fed upon by much smaller and more numerous herbivores (e.g., aphids or other insects). Similar pyramids can be envisioned for biomass or productivity (measured in units of grams of carbon accumulating per unit area per unit time) for each trophic level. Inverted pyramids of numbers or biomass, where the abundance or biomass of a lower trophic level is less than in an adjacent higher trophic level, can also occur. This inversion can happen when primary producers are highly produc-

Before discussing the major patterns, it is important to first understand the terms and ideas used to describe aspects of the webs. Food webs are sometimes separated into three categories: **source webs**, **sink webs**, and **community webs** (Figure 6.2). Source webs describe the feeding relations among species that arise from a single initial food source, say a single plant species. Sink webs describe all of the feeding relations that lead to sets of species consumed by a single top predator, the sink. Community webs, at least in theory, describe the entire set of feeding relations in a particular community, although this ideal goal is never realized in practice because of the extraordinary complexity of most communities.

The following terms and concepts describe some rather abstract features



Important attributes of food webs.

of food webs that form the basis for most comparative studies. It is worth keeping in mind that these abstractions are simply a way of quantifying some of the fascinatingly complex interactions within large collections of predators and prey.

■ **Trophic position.** The nodes or species in the webs are distinguished by whether they are **basal species**, **intermediate species**, or **top predators**. Basal species feed on no other species, but are fed upon by others. Intermediate species feed on other species and are themselves the prey of other species. Top predators have no predators themselves, but prey on intermediate or basal species. These notions refer to the feeding relations drawn in the webs, rather than to strict biological reality. For instance, it is arguable whether true top predators really exist, since the species depicted as top predators in food web diagrams are in fact attacked by various parasites and pathogens that usually are not included in food web diagrams.

■ **Links** are simply the lines that link consumers and the consumed. **Undirected links** represent a binary (all or none) property of interactions between a pair of species. If a species occurs in the diet of a predator, they are joined by an undirected link in a food web diagram. **Directed links**

Continued

FIGURE 6.2. Source, sink, and community food webs. (A) Source web, based on the species known to feed on pine, from Richards (1926). (B) A sink food web, based on Paine's (1966) survey of feeding by Pisaster. (C) A community food web for Morgan's Creek, Kentucky, from Minshall (1967).

are usually represented by arrows, which describe the net effect of each species on the other. Ignoring intraspecific effects, each pair of species can be joined by up to two directed links. When quantitative data on diet composition are available, as in Winemiller (1990), it is possible to use different thresholds to establish linkage; for example, species are linked only if one constitutes greater than some fixed percentage of the diet of another.

- **Connectance** is a way of describing how many of the possible links in a food web are present. One formula for connectance, based on undirected links, is

$$c = L/[S(S-1)/2] \quad (6.1)$$

where L is the number of undirected links and S is the number of species (nodes). This formula is based on the notion that in a web consisting of S species there are $S(S - 1)/2$ possible undirected links, excluding any cannibalistic links. Highly connected systems contain many links for a given number of species. Another notion of directed connectance is the probability for any pair of species selected at random that a species will have a positive or negative effect on the other (May 1973).

- **Linkage density**, L/S , refers to the average number of feeding links per species. It is a function of connectance and the number of species in the web.
- **Compartmentation** refers to the extent to which a food web contains relatively isolated subwebs that are richly connected within subwebs but which have few connections between subwebs. One formula used as an index of compartmentation is

$$C_l = \frac{1}{s(s-1)} \cdot \sum_{i=1}^s \sum_{j=1}^s p_{ij} \quad (6.2)$$

for i not equal to j , where p_{ij} is the number of species that interact with both species i and species j divided by the number of species that interact with either species i or species j , and s is the number of species in the web (see Pimm and Lawton 1980; Winemiller 1990).

- **Trophic level** refers to the number of links + 1 between a basal species and the species of interest. For all but basal species, or species in linear food chains, the notion of a trophic level becomes rather uncertain because the number of links traced from a basal species to a species higher in the food web may vary with the path taken. One way of dealing with this problem is to represent the trophic level of a species as the

- **Cycles and loops** occur if species have reciprocal feeding relations. A cycle occurs if each of a pair of species eats the other. The top predators in the food web shown in Figure 6.2A are an example of a cycle, where wasps eat spiders, and spiders eat wasps. A loop occurs if species 1 eats species 2, species 2 eats species 3, and species 3 then eats species 1. Cycles and loops generally occur where species have a range of size or age classes and where large individuals of each species are capable of eating smaller individuals of the other.
- **Rigid circuit** properties have to do with the way that overlaps in the prey consumed by predators can be described. For any food web, one can draw a predator overlap graph such that predator species that have at least one prey in common are linked by a line segment (Figure 6.4). If every series of three predators completes a triangle of line segments, the predator overlap graph is said to have the rigid circuit property.
- **Intervality** is a property that is related to the rigid circuit nature of predator overlap graphs. If a food web is interval, overlaps between predators can be represented by a series of overlapping line segments, as indicated in Figure 6.4. If line segments cannot be so placed, such that a segment must be broken to represent prey overlaps, the web is not interval. This admittedly esoteric property of food web graphs has a possible link to the dimensionality of the niche space required to represent feeding overlaps among species. Cohen (1978) has argued that if food webs are interval, then the niche space required to represent overlapping feeding relations is unidimensional, for example, a series of overlapping line segments arranged along a line.

PATTERNS IN COLLECTIONS OF FOOD WEBS

Cohen (1977, 1978) was the first to suggest that even coarsely drawn diagrams of food webs yielded some repeatable, and therefore interesting, patterns.



Patterns emerge from comparisons of published food webs.

The ecological significance of these and other patterns remains controversial, since many ecologists have serious reservations about the accuracy and completeness of food web descriptions (Paine 1988). Many published descriptions of food webs are simply descriptive devices created to illustrate subsets of important interactions within communities and were never intended to serve as complete descriptions of trophic linkages. For example, Paine's (1966) *Pisaster* sink web only describes interactions between seven nodes, but the community contains at least 300 macroscopic species (Paine 1980)!

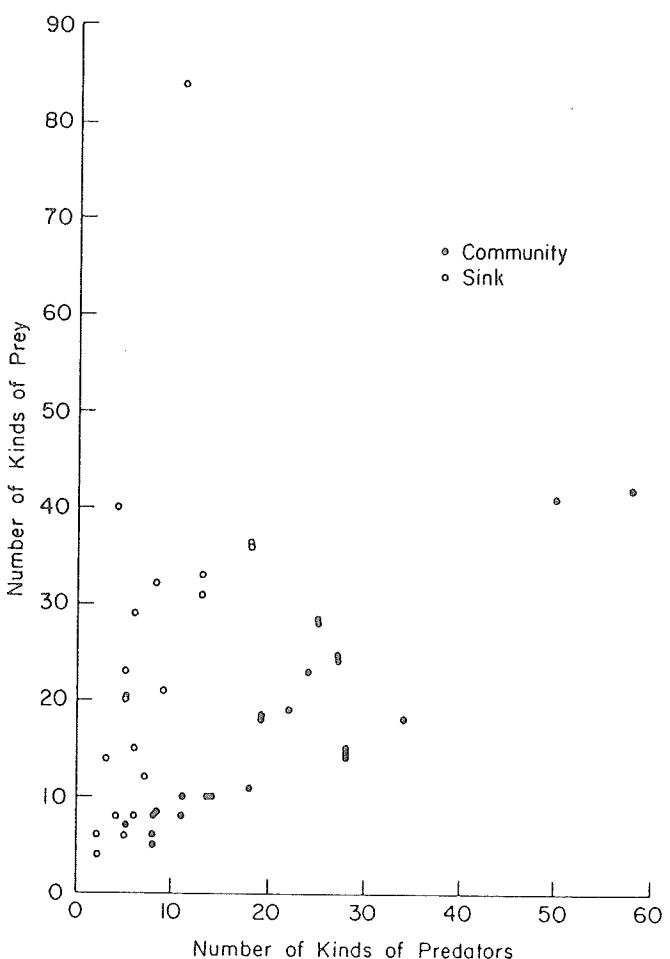


FIGURE 6.5. Relations between the numbers of predator nodes and prey nodes in collections of community food webs. The linear relation suggests a ratio of approximately four predator nodes to three prey nodes in the community webs shown by the filled circles. (From Cohen, 1978. © 1978 by Princeton University Press. Reprinted by permission of Princeton University Press.)

this seems odd, since it suggests that a larger number of predator species are being supported by a fewer number of prey species. It is less disconcerting when you consider that most prey “species” in this analysis are in fact highly aggregated collections of taxa—things like “insects” or “plants.” Later analyses extended the constancy of proportions to basal, intermediate, and top predators (Briand and Cohen 1984; Cohen and Briand 1984). Subsequent analyses of more detailed food webs have examined the effect that aggregating species into tropho-species has on food web patterns (Sugihara et al. 1989; Martinez 1991). Sugihara et al. found that additional aggregation of already aggregated webs did little to

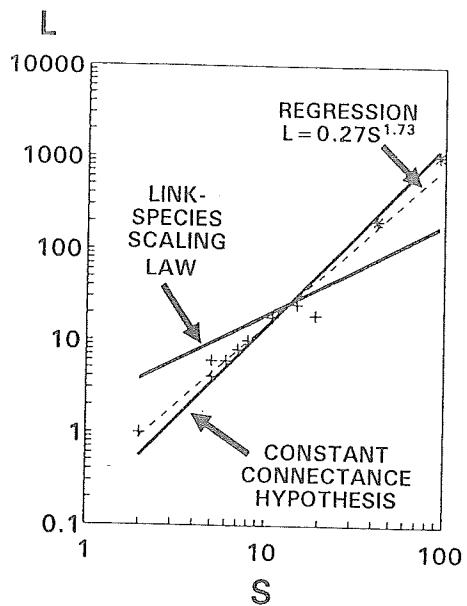


FIGURE 6.6. Alternate patterns suggested by the constant connectance hypothesis and constant links per species hypothesis. L and S refer to numbers of links and species per web. For highly resolved webs based on less-aggregated trophic nodes, the constant connectance hypothesis provides a better description. (Reprinted from Martinez, 1992, with permission of the University of Chicago Press.)

density and the constant proportions of species in basal, intermediate, and top positions.

6. Food chains are relatively short, usually containing no more than five or six species (Elton 1927; Hutchinson 1959; Pimm and Lawton 1977; Pimm 1982). This pattern is partly due to the low taxonomic resolution of many webs, as food chains tend to increase in length in more detailed webs (Martinez 1991). Both energetic (Lindeman 1942; Slobodkin 1960) and population dynamic (Pimm and Lawton 1977) hypotheses have been proposed to account for this pattern. These ideas are described in greater detail below.
7. Omnivory appears to be relatively infrequent in some systems (Pimm and Lawton 1978), but this may be a consequence of inadequate description rather than biological reality. In more recent detailed descriptions of some food webs (Sprules and Bowerman 1988; Polis 1991; Martinez 1992), omnivory is common. Omnivory also seems common in webs rich in insects and parasitoids, or in decomposers.
8. Connectance and estimated interaction strength appear to vary between webs in relatively constant and variable environments (Briand 1983).

 Possible causes of some food web patterns.

models, and static models, such as the cascade model of Cohen et al. (1985), that make no specific reference between population dynamics and food web patterns.

Dynamic models attempt to explain food web patterns on the basis of food web configurations that promote stable equilibrium population dynamics, which presumably allow populations to persist for long periods of time, as opposed to configurations that are unstable and that presumably fail to persist for very long. The models used to predict these patterns are based on relatively simple Lotka-Volterra models that have been extended to include more than two species (May 1973; Pimm and Lawton 1977, 1978).

For a system of n species, the differential equation for the dynamics of species i looks like

$$dX_i/dt = X_i(b_i + \sum a_{i,j}X_j) = F_i \quad (6.3)$$

where b_i is the per capita population growth rate of species i , $a_{i,j}$ is the per capita effect of species j on species i , including intraspecific effects when $i=j$, and X_i is the abundance of the species i , in a system of n species. The stability of these systems depends on the properties of the Jacobian matrix (see the appendix), which consists of the matrix of partial derivatives $\partial F_i/\partial X_j$ evaluated at the equilibrium densities of the n species, the X_i^* . Models of simple food chains can be constructed by choosing the elements of the Jacobian matrix from an appropriate range of values. Different food chain configurations can be modeled by setting entries to zero, positive, or negative values, as shown in Figure 6.8. The return time of the system, which is approximately the time required for the system to return to equilibrium following a perturbation, is roughly $1/\lambda_{\max}$, the reciprocal of the largest negative eigenvalue of the Jacobian matrix. This approach allows comparisons of the stability and return times for simple-model food webs of different configurations.

Stuart Pimm and John Lawton (1977) used this approach to assess the dynamics of systems of four “species” arranged in food chains of different

 Models suggest that long food chains may be unstable.

length. The assumptions included were that basal species were self-limiting (negative a_{ii} 's for basal species), whereas other

species were limited only by their food supply and their predators. For each food chain configuration, numerical entries in the appropriate Jacobian matrix were selected at random from a uniform distribution of values of the appropriate sign and magnitude. This process was repeated 2000 times, a process called Monte Carlo simulation, to produce frequency distributions of return times and to estimate the frequency of stable and unstable webs. One result, shown in Figure 6.9, is that all of the food chains consisting of four

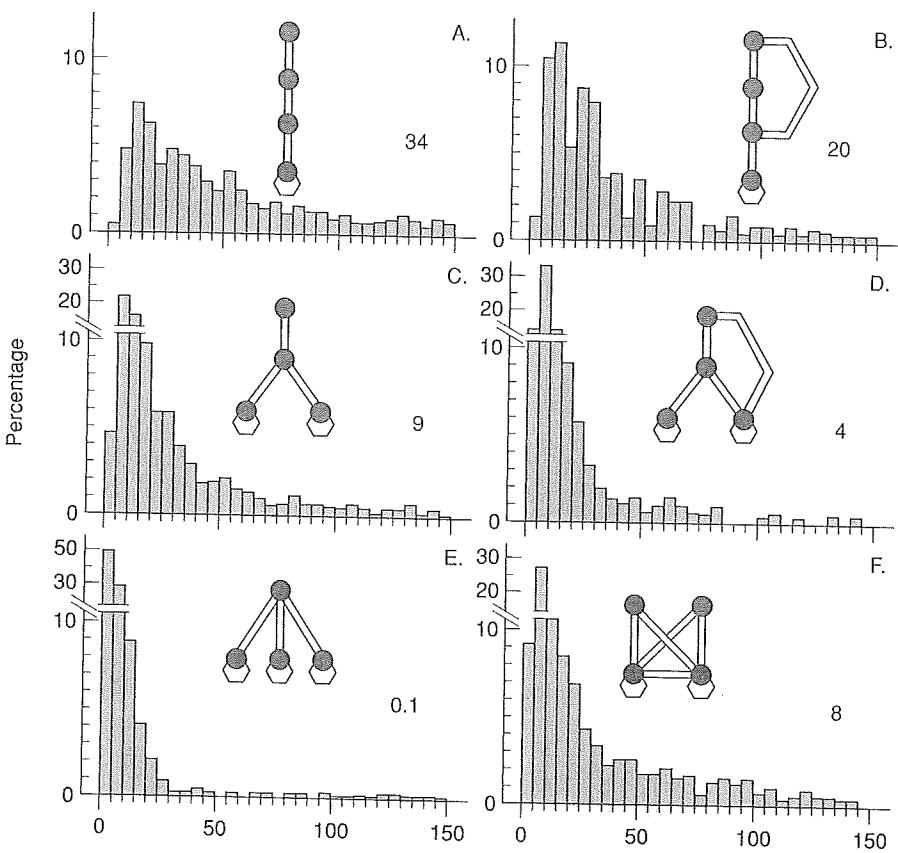


FIGURE 6.9. Frequency distributions of return times (horizontal axis) for the model food chains described in Figure 6.8. Longer food chains, shown in panel A, have a greater frequency of long return times than the shorter chains in panels C and E. (Adapted with permission from *Nature* 268: 329–331, S. L. Pimm and J. H. Lawton. © 1977 Macmillan Magazines Limited.)

species arranged without omnivorous feeding links were locally stable, but return times were substantially longer in longer chains. Longer return times suggest that populations in longer chains would require longer periods of time to return to equilibrium values following a perturbation. Pimm and Lawton equated these prolonged return times in longer chains with reduced stability, in the sense that they would recover more slowly after perturbation. An example of that property is shown for a pair of two-level food chains in Figure 6.10, which are contrived to differ in their return times. If perturbations are large or frequent, populations in systems with long return times might be more prone to extinction.

Recent work suggests that the greater stability of the shorter food chains

ity may have been a consequence of a greater frequency of density-dependent self-regulation and not of food chain length per se.

The second aspect of food chain architecture considered by Pimm and Lawton (1978) was the effect of same-chain omnivory on population dynamics within these relatively simple four-species food chains. As before,



Omnivory may also destabilize food chains.

omnivory could be modeled by including appropriate entries in the Jacobian matrix and then evaluating the eigenvalues of the Jacobian. Omnivory had an even more

striking effect on dynamics than did food chain length. Fully 78% of the longer chains with an omnivorous link were unstable. Of the remaining 22% that were stable, return times were on average shorter than in comparable food chains without omnivores. The conclusion was that omnivorous systems should be rare, given the unstable behavior of their dynamics. However, those relatively few stable systems that contained omnivores should be more stable (in the sense of having shorter return times) than comparable food chains without omnivores.

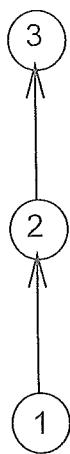
Robert May (1972, 1973) used a similar approach to compare the stability of webs differing in species richness, connectance, and the intensity of interactions between species. Rather than using webs of a particular predetermined structure, May constructed randomly connected food webs consisting of s model species. Each of the species was assumed to display intraspecific density-dependent regulation, which is modeled by placing -1's down the diagonal of the Jacobian matrix from upper left to lower right. Interactions between species are modeled by selecting off-diagonal elements of the Jacobian matrix at random and then filling the entries with positive or negative values from a normal distribution with a mean of zero and variance i . The larger the value of i , the larger a nonzero value describing the strength of an interaction is likely to be. In this model, connectance, c , is the probability that an off-diagonal element will be nonzero. May explored the relative contribu-



tions of s , species richness, c , connectance, and i , which he termed interaction strength, to the stability of these model systems. His main result was that as s

becomes arbitrarily large, to a reasonable approximation, the system will be stable if $i(sc)^{1/2} < 1$. This means that increases in i , s , or c will tend to be destabilizing in randomly connected model food webs. Counter to the conventional wisdom of most field ecologists, (e.g., Elton 1958), increases in the complexity of a system involving increases in either the number of species (n) or the richness of trophic connections (c) should create greater instability in that system. One reason for this is that in increas-

A.



B.

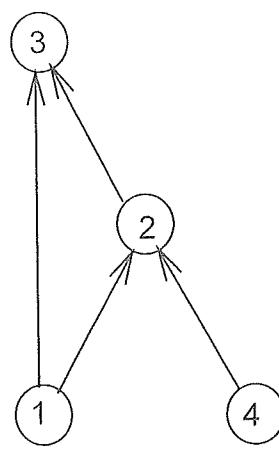


FIGURE 6.11. Examples of single and multiple trophic pathways in specialized and generalized predators. (A) In the simple food chain, extinction of either species 1 or 2 will lead to the extinction of species 3. (B) In the more complex chain, alternate pathways of energy flow exist, such that some energy will reach species 3 if species 1 is lost and 2 remains, or vice versa.

EXPERIMENTAL TESTS OF FOOD WEB THEORY

Causes of Food Chain Length

Most explorations of the possible causes of patterns in food webs rely heavily on models because the dynamics of species in natural food webs are difficult to study. Long-lived species require equally long-term studies to separate apparent dynamics from artifacts imposed by life history traits (Frank 1968; Connell and Sousa 1983). For example, very long-lived organisms, such as trees, might appear to be stable simply because their dynamics occur on a different timescale than do those of shorter-lived organisms, such as bacteria. To avoid such artifacts, temporal changes in population sizes must be scaled against the generation time of the organisms in question. It is also very difficult to collect information about the dynamics of complex multispecies systems in which species operate on very different timescales. Consequently, experimental studies of links between food web attributes and the population dynamics of their component species tend to focus on simple systems containing organisms with short generation times. There is also the nontrivial problem of actually determining the feeding relations in a natural food web. Determining the major feeding links in a single food web can consume years of dedicated effort (e.g., see Polis 1991; Winemiller 1990), even without

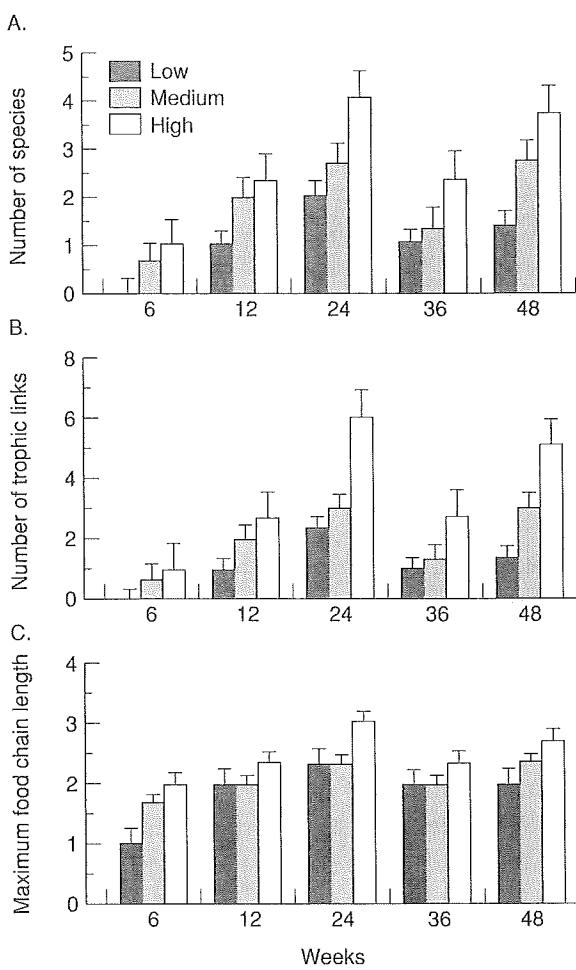


FIGURE 6.12. Number of species, number of links, and food chain length in tree-hole communities subjected to different levels of nutrient inputs for 48 weeks. Different levels of productivity, denoted high, medium, and low, correspond to 1 times, 0.1 times, and 0.01 times normal levels. (Adapted from Jenkins et al., 1992, with permission from Oikos).

entering the system was reduced. Luckinbill manipulated food input by adding increasingly dilute suspensions of bacteria, which served as food for *Paramecium*. At the highest food concentration used, 6 ml bacteria per 350 ml total, abundances of *Paramecium* and *Didinium* go through a single strong oscillation that results in extinction after about 6 days. Dilution to 2.0 ml bacteria per 350 ml total yields about five repeated oscillations and persistence for 34 days (Figure 6.13). The relation between persistence and food supply appears nonlinear, with a threshold of greatly enhanced persistence occurring between 4.5 ml bacteria per 350 ml total and 2.5 ml bacteria per 350 ml total.

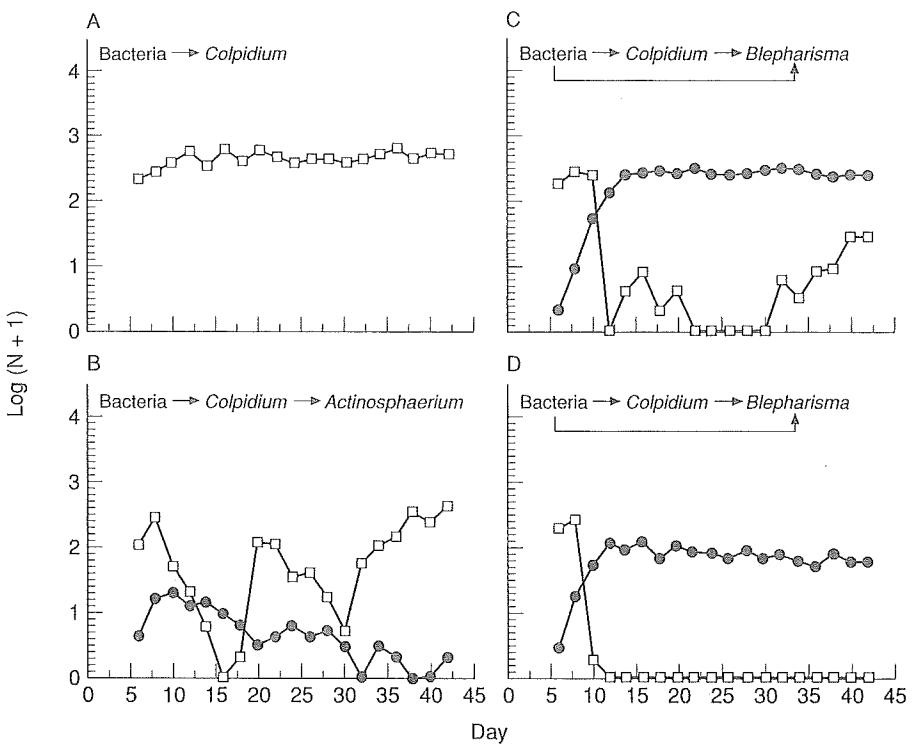


FIGURE 6.14. Increased temporal variation in population dynamics that accompanies an increase in food chain length by one trophic level. Populations of the same species, *Colpidium*, in long food chains (B, C, D; open squares) exhibit greater fluctuations in abundance over time compared with their dynamics in shorter food chains (A). (Adapted from Lawler and Morin, 1993b, with permission of the University of Chicago Press.)

that the population dynamics of protists in simple laboratory food chains become less stable with modest increases in food chain length. They compared the temporal variability of populations of the same bacterivorous protists in short food chains in which bacterivores were the top predators and in slightly longer food chains in which the bacterivores were intermediate species preyed on by another predatory protist. In the majority of cases, an increase in food chain length caused increased temporal variation in abundance (Figure 6.14). Increased temporal variation in abundance would be consistent with longer return times in longer food chains, as in Figure 6.10.

These somewhat conflicting results suggest that productivity influences the length of food chains, but in a curvilinear way (Figure 6.15). Below natural levels of productivity, there is insufficient energy to sustain higher trophic levels, and species may be lost. Above natural productivity levels,

than one prey are less likely to fluctuate greatly in abundance when one of their prey fluctuates in abundance.

Andrew Redfearn and Stuart Pimm (1988) used the comparative method to test MacArthur's hypothesis. They surveyed published accounts of the population dynamics of herbivorous insects that were known to feed on many versus few species of plants. Their results provide some qualified support for MacArthur's hypothesis, in that less-specialized species tend to show reduced fluctuations in population dynamics over time when compared with more-specialized insects that feed on relatively few species.

Sharon Lawler (1993b) also used studies of protists in laboratory microcosms to explore whether more complex food webs were less stable than simple ones. Her simplest systems consisted of four different three-level food chains containing different species of bacterivores and top predators but



Increasing complexity can decrease food web stability.

similar bacteria. Each of these four food chains was known to be stable. These chains were then paired and combined to form eight different communities con-

taining four protist species, or one community containing all eight protist species (Figure 6.16). The main result was that webs containing increasing numbers of species, and increasing possibilities for kinds of predator-prey interactions, exhibited significant increases in the frequency of extinctions of component species. This finding is in general agreement with May's (1972, 1973) original suggestion that increasing complexity in food webs may decrease rather than increase the stability of the system as a whole.

Interaction Strength

Paine (1992) has suggested another empirical approach to studies of interactions in natural food webs. His approach focuses on the experimental measurement of interaction strengths for an assortment of predators and their prey. The approach is labor intensive, since it involves measuring how prey respond to replicated removals of various predator species. Paine's operational measure of interaction strength is an index, I , that is calculated using the following expression:

$$I = (D_p - D_0)/(D_p)P \quad (6.4)$$

where D_p is the density of the prey with a known density of predators, P is the known density of predators, and D_0 is the prey density when predators are removed. Negative values indicate negative per capita effects of predators on prey, but positive effects are possible if predators facilitate certain prey by removing others, as in Paine (1966).

use of known trophic links, rather than interaction strengths, may badly overestimate the frequency of important trophic connections in real food webs. It is also important to point out that Paine's measure of interaction strength is very different from the one used by May (1973). Paine's measure potentially includes both direct and indirect effects (see Bender et al. 1984; Yodzis 1988). May's interaction strength involves only direct effects, since it is the value of a partial derivative evaluated at equilibrium for a particular pair of species. The various measures of interaction strength that have been used by ecologists are described and compared in an important paper by Laska and Wootton (1998).

SOME FINAL QUALIFICATIONS CONCERNING EMPIRICAL PATTERNS

Food web research is an active, dynamic, and rapidly changing field. As more and better descriptions of food webs accumulate, some of the original generalizations about food web patterns have become problematic (see Lawton 1989; Pimm et al. 1991). Examples of two current concerns are whether some of the original major patterns seen in collections of food webs are independent of the scale of taxonomic resolution used in depicting the web (termed **scale independence**) and whether the patterns within webs vary significantly within communities over relatively short—seasonal or annual—timescales.

Scale independence refers to whether basic patterns, such as connectance, linkage density, food chain length, or ratios of numbers of taxa in different trophic categories, depend critically on the level of taxonomic resolution employed. The first studies that compared differences involving relatively coarse levels of taxonomic resolution suggested scale invariance (e.g., Briand and Cohen 1984; Sugihara et al. 1989). More recent studies of the effects of aggregating highly resolved webs, in which most nodes in the web correspond to real species or genera, suggest that aggregation may distort some patterns (Martinez 1991, 1992; Polis 1991). Webs with greater taxonomic resolution tend to have greater numbers of omnivores, longer food chains, and roughly constant connectance when compared with webs in which nodes are highly aggregated collections of many biological species.

A second question concerns the degree of temporal variation in food web patterns. Most published food web diagrams depict interactions that are pos-

ible, but may include interactions that are infrequent or interactions among seasonally fluctuating species that are seldom simultaneously active in the same community.

 Food web patterns vary over time.

They are collages, rather than single snapshots, of the interactions

CONCLUSIONS

Even if many of the early generalizations about food web patterns eventually fail to survive the careful scrutiny of increasingly detailed data sets, food webs will retain an important role in community ecology. Food webs can identify pathways of potentially important interactions, including indirect effects (Wootton 1994b), and they emphasize that communities are far more complex entities than arbitrary collections of pairwise interactions among species. Experimental tests of food web theory are rare (see Morin and Lawler 1995), and much important work remains to be done in this area.