

Food Webs As A Focus For Unifying Ecological Theory

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Abstract. A food web describes the feeding relations among plants and animals in some place over some time interval. Examples are given to show how food web structure connects with many other parts of ecology, including the species-area curve, the dynamics and stability of interacting populations, body size, species abundance, predator-prey allometry and the pyramids of numbers and of biomass. Different ecological patterns connect in meaningful ways. Food web models may prove to be useful instruments for making clear some of the connections.

INTRODUCTION

A food web describes the feeding relations among plants and animals in some place over some time interval (Camerano 1880; Elton 1927; Pimm 1982; DeAngelis, Post, Sugihara 1983; Pimm, Lawton, Cohen 1991). Detritus and decomposers are sometimes included. Large numbers of food webs have been collected in recent years (Cohen 1989). Though every food web is unique in detail, these collections have revealed previously unsuspected statistical regularities in food web structure (Lawton 1989; Schoener 1989). A simple stochastic model of random directed graphs, called the cascade model, explains many statistical regularities in food web structure (Cohen, Briand, Newman 1990).

Food web structure connects with many other parts of ecology. Here I will briefly describe some connections between food webs and (1) the species-area curve, (2) the dynamics and stability of interacting populations, and (3) body size, predator-prey allometry and species abundance. Details of these examples appear elsewhere. Further possible connections between food web structure and other aspects of ecological theory will be mentioned.

The point of the paper is that different ecological patterns can be connected in meaningful ways. Food web models such as the cascade model or improved successors to it may prove to be useful instruments for making clear some of the connections.

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ISLAND BIOGEOGRAPHY OF SPECIES DIVERSITY AND FOOD CHAIN LENGTH

The area of an island (or the volume of a habitat, or the equivalent) and the maximal or the mean food chain length on that island (or in that habitat) are related by very simple reasoning (Cohen and Newman, in press). What is meant by the maximal or the mean food chain length? A simple food chain is defined as a sequence of feeding links, all going from prey to predator in the same direction, that does not pass through any species more than once (no cycling), and that starts from a basal species and terminates at a top species. The length of a simple food chain is the number of links it contains. The maximal food chain length of a web, or the height H of the web, is the largest of all the chain lengths in the web. The mean or average food chain length μ is the average length of all the simple food chains in the web, weighting equally all possible simple food chains from any basal species to any top predator.

As the area A of an island increases, the number S of species of plants and animals on it usually increases. As the number S of species in the food web increases, the length of the longest food chain H and the length μ of the average food chain usually increase. Supposing that all the species of plants and animals on an island are involved in one food web, it follows that as the area A of an island increases, the lengths of the longest and average food chain are expected to increase. Moreover, if S increases slowly with A , and if H and μ increase very slowly with S , then H and μ increase extremely slowly with A .

These predictions may be made quantitative by combining three ingredients. First, quantitative species-area curves (log-species = $a + b \cdot \log$ -area [power function] or species = $a + b \cdot \text{area}$ [linear function]) determine the number of biological species as a function of the area. Second, theoretical or empirical arguments determine the number of trophic species in a food web as a function of the number of biological species. Third, the cascade model or related models determine the maximal and the mean food chain length as a function of the number of trophic species. Chaining these relations together, so to speak, gives various predicted food chain lengths as a function of island or habitat area.

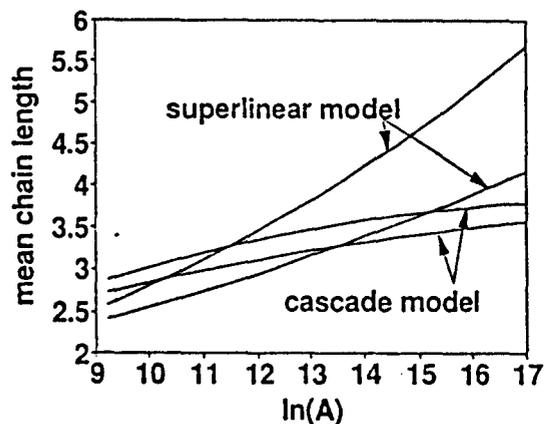


Figure 1. Mean chain length as a function of the natural logarithm of island area predicted by two models and the species-area power law. For each model, the upper curve assumes trophic species equal biological species, and the lower curve assumes trophic species = $1.7793 \cdot (\text{biological species})^{0.6805}$. In the cascade model, $E(L) = 2S$; in the superlinear model, $E(L) = 0.69S^{1.33}$, where $E(L)$ is the expected number of trophic links and S is the number of trophic species; in the species-area curve, biological species = $(\text{area})^{1/4}$.

Figure 1 illustrates some of the predictions for mean chain length. When the mean number of trophic links is twice the number of trophic species, as in 113 reported webs (Cohen 1990), then the theory predicts that the mean chain length approaches roughly 4.0 on arbitrarily large islands, while the ratio of maximal to mean chain length increases without limit. When the mean number of trophic links increases superlinearly with the number of trophic species (i.e., as a power of the number of species, where the power is greater than one [Schoener 1989; Cohen, Briand and Newman 1990, p. 131]), then for large number of species, the theory predicts that both the maximal and the mean chain length increase without upper bound as a power, less than one, of the area. Strangely enough, the ratio of the maximal to the mean chain length approaches e .

Unfortunately, most publications specify the area or volume of habitat represented by the reported food web only hazily, if at all. To the best of my knowledge, the data required to test these predictions have yet to be collected.

DYNAMICS AND STABILITY OF INTERACTING POPULATIONS

Perhaps the most widely studied model for the dynamics of populations of interacting species is the Lotka-Volterra model:

$$\frac{du_i}{dt} = u_i (e_i + \sum_{j=1}^n p_{ij} u_j), \quad u_i(0) > 0, \quad i = 1, \dots, n,$$

where μ_i is the abundance or biomass of the i th species, e_i is the intrinsic rate of natural increase of species i in the absence of other species, and the coefficient p_{ij} measures the effect per unit of species j on the growth rate of species i (e.g., Pimm 1982; Lawton 1989; Shigesada et al. 1989). A major problem in using the Lotka-Volterra equations is the need to specify the coefficients p_{ij} for all i and j . Food web models can provide some guidance on how to choose the coefficients p_{ij} .

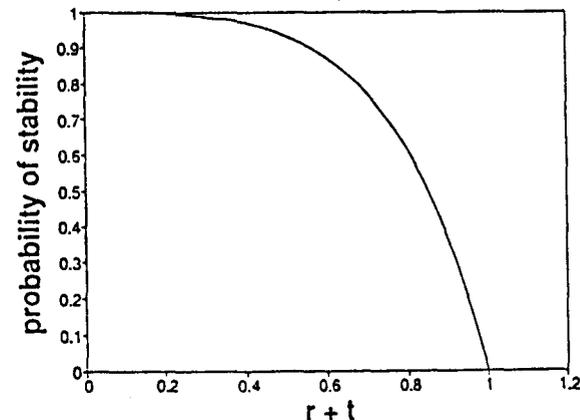


Figure 2. The probability of qualitative global asymptotic stability in the Lotka-Volterra cascade model, in the limit as the number S of species approaches ∞ , as a function of $r + t$, assuming $r = s$. (Here r , s , and t are the parameters of the LVCM, and have the following definitions: for $i < j$, $\text{Prob}\{p_{ii} = 0 \text{ and } p_{ij} < 0\} = r/S$, $\text{Prob}\{p_{ii} > 0 \text{ and } p_{ij} = 0\} = s/S$, $\text{Prob}\{p_{ij} > 0 \text{ and } p_{ii} < 0\} = t/S$, and $\text{Prob}\{p_{ii} = 0 \text{ and } p_{ij} = 0\} = 1 - (r + s + t)/S$.) Small values of $r + t$ assure a high probability of global asymptotic stability. For all values of $r + t = s + t > 1$, the probability is zero. The probability of stability is said to display a phase transition because the slope (or derivative) of the probability changes discontinuously at $r + t = 1$ from $-e^{1/2}$ to 0.

Specifically, the cascade model suggests that pairs of interaction coefficients (p_{ij} , p_{ji}) with symmetric locations in the matrix of interaction coefficients should differ from (0,0) with a probability that varies inversely as the number of species (Cohen, Luczak, Newman, and Zhou 1990). A new model, called the Lotka-Volterra cascade model (LVCM), assumes the nonlinear Lotka-Volterra dynamics between interacting species, when *which* species interact is determined by a refinement of the cascade model. The LVCM illustrates one possible way of relating population dynamics to trophic structure. In the LVCM, gradual changes in the probabilities of population-dynamical interactions related to feeding can have sharp effects on a community's qualitative global asymptotic stability (Figure 2). In particular, when the number of dynamical interactions exceeds a certain threshold, the probability of qualitative global asymptotic stability drops to 0; this happens when the dynamical interactions connect into closed cycles (see Cohen, Luczak, Newman, and Zhou 1990 for details). This analysis differs from the qualitative stability analysis of May (1973) in that the present analysis is global (not local) and nonlinear (not linear).

To test the assumptions of the LVCM and related models will require data on the population dynamical consequences of feeding in communities with large number of species. Many studies of food webs provide some, often extensive, data on the dynamical consequences of major feeding links (e.g., Menge et al. 1986; Carpenter 1988). I am not aware of any studies that demonstrate (rather than assume) the population dynamical consequences, if any, of all feeding links. In addition, testing the LVCM will require data on other non-tropic sources of population dynamical interactions, such as competition (Schoener 1983), mutualism (Kawanabe 1987), and symbiosis, to check whether significant dynamic effects have been omitted from the model.

BODY SIZE, PREDATOR-PREY ALLOMETRY, AND SPECIES ABUNDANCE

The relation between the size of a consumer species and the size of the species it eats has been studied in two ways. In one approach, the covariation in the weights of predator-prey pairs is reported as an allometric (or power-law) relation between predator weight and prey weight (e.g., Schoener 1968; Vézina 1985; Peters 1983, p. 277). There are at

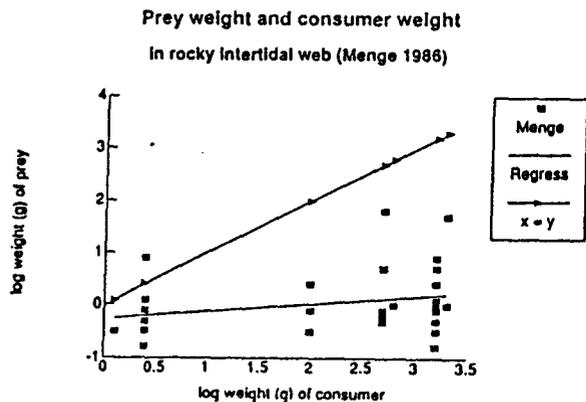


Figure 3. Prey weight and consumer weight in a rocky intertidal food web, according to data reported by Menge et al. (1986). Solid line with triangles: hypothetical case where prey weight equals consumer weight. Plain solid line: least-squares regression of log prey weight as a function of log consumer weight.

least two variations on this approach. Some studies combine data from different communities and ecosystems within taxonomically or functionally defined groups; others report the weights of all the predator-prey pairs in a particular community or ecosystem. To illustrate the latter variation, which appears to be rarely practiced, I plot in Figure 3 all the available pairs of (consumer, prey) weights reported by Menge et al. (1986) in a detailed study of a single rocky intertidal food web. In spite of considerable variation, a log-log linear regression between predator and prey weight is not a bad approximation to the data. With only one exception, prey weight is less than the corresponding predator weight.

A second approach considers the overall pattern of variation in the weights of predators and prey, not merely pairwise, but along the full length of a food chain or in an entire food web in a single community or ecosystem. Elton (1927) suggested that in some food chains (e.g., marine or aquatic grazers), body size generally increases with increasing remoteness from the green plants (for supporting data, see Sheldon, Prakash and Sutcliffe 1972 and Steele 1989); in others food chains (e.g., terrestrial herbivores), body size generally decreases. Exceptions to these generalizations come readily to mind, and it may be that the biomass of a pack of wolves is a more appropriate index of size than the biomass of an individual wolf. But the possibility of a general relation between body size and food web structure remains attractive.

In an artificial aquatic community with a relatively small number of species, Warren and Lawton (1987) found that, with few exceptions, bigger organisms ate smaller organisms. Warren and Lawton (1987) observed that the cascade model is compatible with patterns like those they and Elton observed. The cascade model assumes that species are numbered $1, \dots, S$ so that species i can be eaten only by those species j with $j > i$. If the numbering were assigned to species by increasing species size (where a species' size is measured by the geometric mean of individual sizes or in some other appropriate way), then the cascade model would predict that bigger organisms eat smaller organisms. If the numbering of species in the cascade model were assigned by decreasing body size, then the cascade model would predict that smaller organisms eat bigger organisms. Either way, body size is one natural interpretation of the ordering assumed in the cascade model.

I now show how a roughly linear relation between predator and prey weights on log-log coordinates can be derived from a progressive increase in size along food chains by using the cascade model as a theoretical link. This derivation calls on other known ecological patterns, such as species abundance distribution and the distribution of biomass across species size categories.

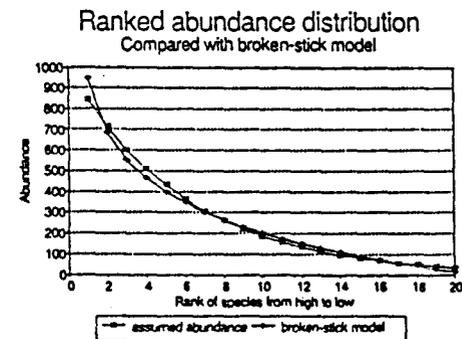


Figure 4. Hypothetical abundance (number of organisms) of $S = 20$ species according to $N_i = 1000(0.845)^i$, $i = 1, \dots, 20$, compared with the predicted abundance according to the broken-stick model.

Suppose the number N_i of individuals of species i , where i is the labelling or rank of the species in the cascade model, is an exponential function of i , $N_i = \alpha\beta^i$, $\alpha > 0$, $\beta > 0$. For $\beta = 0.845$, the ranked species abundance distribution given by this formula is practically indistinguishable from that predicted by the broken-stick model of MacArthur, a model which has some empirical and theoretical uses (e.g., Cohen 1966) (Figure 4). Thus this simple exponential model of abundance is not totally unrealistic.

Suppose further that the (geometric mean) weight of an individual of species i is $W_i = \gamma\delta^i$, $\gamma > 0$, $\delta > 0$. The common observation that bigger organisms (with the possible exception of *Homo sapiens*) are rarer than smaller organisms is expressed by assuming that $\beta < 1$ and $\delta < 1$, so that as i increases, abundance decreases and body size increases. Other combinations of parameter values could obviously be considered. These assumptions about abundance and weight make $\log N_i$ and $\log W_i$ linear in i ; that is, on a logarithmic scale, when ranked by abundance or by weight, each species constitutes an equal unit.

Many obvious alternative assumptions are equally simple and concrete, such as $N_i = \alpha i^a$, $W_i = \gamma i^b$. The choice of functional forms for N_i and W_i is best guided by actual data on abundance and body size, when such data become available in combination with a detailed food web.

It follows from the assumptions made that the biomass of species i is $B_i = N_i W_i = \alpha\gamma(\beta\delta)^i$. Peters (1983, p. 173) summarized several studies of the distribution of biomass in the open ocean as follows: "If the pelagic community is divided into logarithmic size classes, the amount of [living] matter in each class is approximately constant over the size range from bacteria to whales." Gaedke et al. (1990) supported this finding in a recent careful study of a pelagic lake community, but it seems to be an open question whether the generalization applies to terrestrial communities. For communities where this finding applies, it suggests the further assumption that $B_i = B$ for all i , since each species here constitutes a logarithmic size class. Under this assumption, $\delta = 1/\beta$ and $B = \alpha\gamma$. This completes a specification of abundance and weight. This specification implies that a plot of abundance as a function of weight on log-log coordinates has a slope of -1 , a value consistent with observed particle-size distributions in certain animal groups besides those found in the open ocean (see Peters 1983, pp. 294-295). Thus the assumed relation between abundance and body weight is also not totally unrealistic.

According to the cascade model and certain generalizations of it, each species $j > 1$ has a probability of eating any of the species i with a lower numbering $i < j$ that is the same for all such i (while species number 1 has no prey). If it is assumed that species with a higher label j are bigger, i.e., $\delta > 1$, then an immediate consequence of the cascade model is that bigger consumers should eat a wider range of prey size than smaller consumers. This prediction is consistent with the trends in the data assembled by Wilson (1975, pp. 772-773; I thank T. W. Schoener for pointing out these data).

Beyond such qualitative consequences, it is possible to derive quantitative predictions from the cascade model. I now calculate the mean weight of prey eaten by predators of a given weight. When a predator species does eat a prey species, as determined by the cascade model, how much of that prey does it eat? We shall consider two alternative simple behavioral assumptions: first, that the predator consumes a particular prey in proportion to its numerical abundance (number of individuals); second, that the predator consumes a particular prey in proportion to its biomass. Under the first assumption, the number-weighted mean weight of prey of consumer $j = 2, \dots, S$ is defined as

$$\left(\sum_{i=1}^{j-1} N_i W_i \right) / \left(\sum_{i=1}^{j-1} N_i \right)$$

If the biomass is constant in every species, then the number-weighted mean weight of prey of consumer $j = 2, \dots, S$ simplifies to

$$(j-1)B / \left(\sum_{i=1}^{j-1} N_i \right),$$

and from the exponential formula for species abundance, this simplifies further to $(j-1)\gamma(1-B)/[B(1-B^{j-1})]$. Under the second assumption, the biomass-weighted mean weight of prey of consumer $j = 2, \dots, S$ is defined as

$$\left(\sum_{i=1}^{j-1} B_i W_i \right) / \left(\sum_{i=1}^{j-1} B_i \right).$$

If the biomass is constant for every species, then the biomass-weighted mean weight of prey of consumer $j = 2, \dots, S$ simplifies to

$$\left(\sum_{i=1}^{j-1} W_i \right) / (j-1),$$

and from the exponential formula for the weight of a species, this simplifies further to $\gamma\delta(1-\delta^{j-1})/[(j-1)(1-\delta)]$.

These formulas assume that the probability that a predator eats a particular prey is the same for all the prey which that predator can eat. The formulas are therefore independent of that probability, even if that probability is different from one predator to another. Thus the formulas are valid for all generalizations of the cascade model where the predation probability is determined by the predator, including all the so-called "predator-dominant" and the superlinear homogeneous models considered by Cohen (1990).

Recall that the parameter β is the ratio of the abundance of one species to the abundance of the next more abundant species. As β approaches 1, the species become more nearly equal in abundance and weight, and the number-weighted mean weight of prey of consumer j becomes indistinguishable from the biomass-weighted mean weight of prey of consumer j . At the other extreme, as β approaches 0, the number-weighted mean weight of prey of consumer j approaches a constant, nearly independent of j , as almost all the number-weight is given to the first, or first few, species; by contrast, the biomass-weighted mean weight of prey of consumer j approaches a constant multiple of the weight of the consumer (i.e., on log-log coordinates, a line parallel to the diagonal line where prey weight

Mean prey weight and consumer weight
Cascade model, constant biomass/species

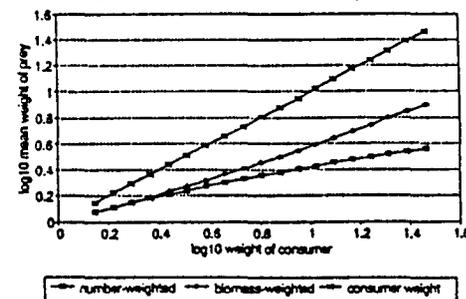


Figure 5. Predicted mean prey weight as a function of consumer weight according to the cascade model with $S = 20$ species, assuming constant biomass per species, with the parameter values $N_i = 1000(0.845)^i$ and $W_i = (0.845)^{-i}$.

equals predator weight), as almost all the biomass-weight is given to the species number $j - 1$, the weight of which (by assumption) is a constant multiple of the weight of consumer j . Clearly it would be easiest to distinguish empirically between number-weighted predation and biomass-weighted predation by examining the relation between predator and prey weights in communities with a very wide range of abundances and sizes (corresponding to a value of β near 0).

For $\beta = 0.845$, Figure 5 compares the predicted mean weight of prey as a function of the predator weight for number-weighted and biomass-weighted predation. The similarity between Figure 5 and Figure 3 (disregarding the arbitrary scales of the axes in Figure 5) is encouraging.

Pyramids. This integrated model of a food web, species abundance distribution, and body size distribution has many testable implications beyond predicting the mean weight of prey as a function of the predator weight. To illustrate, I calculate the pyramid of biomass and the pyramid of numbers (Elton 1927) when species are categorized as top, intermediate and basal species, that is, the expected biomass and the expected numbers of individuals in these three categories of trophic species.

The expected biomass of top species is the sum, over all species, of the probability that a species is a top species times the biomass of that species. Since all species have the same biomass, the expected biomass of top species is simply the expected number of top species times the biomass of any one species. Similarly, the expected biomass of the other categories of species (e.g., nonisolated, proper top, intermediate, basal, or proper basal) is just the expected number of those species times the biomass of any one species. (A proper top species is a nonisolated top species, i.e., a top species that has at least one prey species; a proper basal species has at least one consumer.) Formulas for the expected number of each of these kinds of species have already been calculated for the cascade model (Cohen, Briand, Newman 1990, pp. 84-85) and for many generalizations of it (Cohen 1990, pp. 82-83). Hence the fraction of expected biomass in each category of species is precisely the fraction of expected species in that category. If the ratio of trophic links to trophic species is precisely 2.0 (the best estimate from data is that the ratio is 1.99), then it follows from the cascade model that the fraction of expected biomass in proper top, intermediate, and proper basal species is 0.231, 0.537, and 0.231 (Cohen 1990, p. 56). This distribution of biomass is more barrel-shaped than pyramidal.

The pyramid of numbers is calculated similarly, using the previously calculated formulas (Cohen, Briand, Newman 1990, pp. 85-86) for the probabilities that species i is a proper top, intermediate, proper basal, or nonisolated species. (These probabilities are $q^s - i - q^{s-1}$, $1 - q^{s-1} - q^{s-i} + q^{s-1}$, $q^{s-1} - q^{s-1}$, and $1 - q^{s-1}$, respectively, where $q = 1 - p$ and p is the probability of a trophic link from species i to species j) i . These probabilities hold for any p , whether determined by the cascade model, the superlinear homogeneous model, or otherwise.) Thus

$$E(\text{abundance of nonisolated species}) = (1 - q^{s-1}) \sum_{i=1}^s N_i = (1 - q^{s-1}) \alpha \beta \frac{(1 - \beta^s)}{1 - \beta}$$

$$E(\text{abundance of proper top species}) = \alpha \beta \frac{q^s - \beta^s}{q - \beta} - \alpha \beta q^{s-1} \frac{(1 - \beta^s)}{1 - \beta}$$

$E(\text{abundance of intermediate species}) =$

$$\alpha \beta \frac{1 - \beta^s}{1 - \beta} - \alpha \beta \frac{1 - (q\beta)^s}{1 - q\beta} - \alpha \beta \frac{q^s - \beta^s}{q - \beta} + \alpha \beta q^{s-1} \frac{(1 - \beta^s)}{1 - \beta}$$

$$E(\text{abundance of proper basal species}) = \alpha \beta \frac{1 - (q\beta)^s}{1 - q\beta} - \alpha \beta q^{s-1} \frac{(1 - \beta^s)}{1 - \beta}$$

where it is assumed that $q = \beta$, $q = 1/\beta$, $\beta = 1$. (The derivation of these formulas is straight-forward. For example, $E(\text{abundance of proper basal species}) = \sum_{i=1}^s (1 - q^{s-i}) \alpha \beta q^{s-1} \beta^i$ (probability that species i is a proper basal species) \times (abundance of species i) =

$$\sum_{i=1}^s (q^{i-1} - q^{s-1}) \times \alpha \beta^i = \alpha \beta \sum_{i=1}^{s-1} (q\beta)^i - \alpha \beta q^{s-1} \sum_{i=1}^{s-1} \beta^i,$$

which gives the stated formula.)

The proportions of the total expected abundance of nonisolated species constituted by the expected abundance of proper top, intermediate, and proper basal species are independent of α . For $q = 1 - c/S = 1 - 4.0/20 = 0.8$ and $\beta = 0.845$, these proportions are, respectively, approximately 0.068, 0.444, and 0.488. Fewer than one individual in 14 is predicted to be a top predator.

To repeat: the point illustrated here is that different ecological patterns are not independent. A relation between predator body size and the average body size of its prey is not independent of the proportions in the pyramids of numbers and biomass. Both follow from the structure of food webs, species abundance and the distribution of body size. The particular assumptions in the model just described are likely to be wrong; the point of the model is to display concretely the connectedness of the phenomena it describes. Empirical observations of both predator-prey size relations and pyramids of biomass and numbers can help to check underlying assumptions about the structure of food webs, species abundance and the distribution of body size. Some steps in this direction are under way (Cohen, Pimm, Yodzis, in preparation).

FURTHER POSSIBILITIES

Many possibilities remain for using food webs and food web models to interpret and connect known ecological patterns and to predict new ones. The previous and following examples suggest that food webs can provide a central focus for efforts to unify qualitative and quantitative theory in community ecology.

1. **Ecological allometry.** Coupling food webs to abundance and body size (as in section 4) creates the possibility of exploiting the several thousand reported regression relations between body size and other physiological and ecological variables (e.g., Peters 1983; Calder 1984). By means of the intermediary of body size, each of these physiological and ecological variables can be correlated with rank (the assigned label) in the cascade model. Since the probability of being a basal, intermediate, or top species is known for each rank in the cascade model and many of its generalizations (Cohen 1990), all of these physiological and ecological variables can also be correlated with measures of trophic position such as being basal, intermediate, or top.

2. **Dynamics.** Food web models that incorporate abundance and body size (section 4) can be combined with population-dynamic models (section 3), even though the LVCM admittedly has many unrealistic features (Cohen, Luczak, Newman, and Zhou 1990). The higher the label in the cascade model, the bigger the species (section 4), so the lower the population growth rate and the greater the generation time (e.g., May and Rubenstein 1985). Thus the intrinsic rates of natural increase e_i in the Lotka-Volterra cascade model should systematically decrease with increasing i . It would be worthwhile trying to relate the nonzero interaction coefficients p_{ij} to body size as well. A descendant of the LVCM model in which the coefficients e_i and p_{ij} were related to body size and food web structure might make it possible to predict, in a mildly believable way, how different perturbations of population sizes (those of top species vs. those of basal species, for example) or invading predators (cf. Shigesada et al. 1989) might affect different communities or ecosystems (those with increasing vs. those with decreasing body sizes along food chains, for example.)

3. **Predation and competition.** Alternative hypotheses about the roles of predation and competition (e.g., Schoener 1982; Menge et al. 1986; Hixon and Menge 1991) as a function of trophic position can be interpreted and evaluated in the framework of food web models. For example, Menge and Sutherland (1976) proposed that the further a species is from being or depending directly on green plants, the less the role of predation in regulating its population size. If we interpret distance from the green plants as increasing with the label assigned to a species in the cascade model, then it is immediate that the expected number of species that prey on species i is proportional to $S - i$, which is linearly decreasing with increasing i as Menge and Sutherland proposed. Under the additional assumptions about abundance and biomass made in section 4, the expected biomass of predatory species on species i is also linearly decreasing with increasing i , since all species have the same biomass. The expected number of predatory individuals of all species that eat species i decreases much more rapidly than linearly with increasing i . Similar interpretations and analyses of competition in relation to trophic position will be presented elsewhere.

4. **Succession.** Most published food webs are static and cumulative: they depict information gathered over many occasions, which are often reported hazily or not at all. A web observed over a single, relatively short time period is time-specific. Kitching and Beaver (1990) illustrate spatial and temporal variation in web structure, and Schoenly and Cohen (in press) analyze the relation between cumulative and time-specific webs in 16 published cases. These studies provide empirical background for integrating the study of food webs with the study of succession. It remains to extend the cascade model or its relatives to describe temporal changes in food web structure.

5. **Biogeography.** I have determined the approximate latitude and longitude of most of the 113 webs in the Briand-Cohen collection (Cohen, Briand, Newman 1990, Chap. 4). These data will make it possible to examine whether and how food web structure varies with geographical coordinates. The patterns, if any, in food web structure can then be related to known geographical patterns in species diversity, body size, and other variables. For example, in many taxonomic groups, species diversity increases from the poles to the tropics. Analysis of food webs in relation to their latitude will show whether and how this increasing species diversity affects web structure.

6. **Cycling.** Ecosystem networks are linear compartment models for ecological flows of materials and energy. Some studies of ecosystem networks have emphasized the importance of cycling of energy among living compartments in addition to cycling through decomposers. For example, Patten, Higashi and Burns (1990) analyze cycling in a 6-compartment model of energy flow in an oyster reef. They contrast the importance of cycling in this example with the acyclic food chains emphasized by "traditional Lindeman-Hutchinson trophic dynamics" (Patten, Higashi, Burns 1990, p. 1).

The emphasis by Lindeman, Hutchinson and many others on acyclic chains is not a mere theoretical predisposition. After suppressing cannibalism (cycles of length 1) and cycles due to decomposers, both of which were unreliably reported in published food webs, Cohen, Briand and Newman (1990, pp. 75, 130) found cycles of length 2 or more in only three of 113 community food webs; each of these three webs had only a single cycle of length 2. How can the cycling in ecosystem energy networks be reconciled with the relative rarity of cycling in community food webs?

A complete answer may be complex, but part of the answer may be simple: the frequency of cycles in a description of real organisms depends heavily on the units used to categorize organisms, i.e., on the scale of description. Suppose individual organism A is eaten by individual organism B, and then individual organism B is eaten by individual organism C. If A and B are, respectively, an egg and an adult of the same biological species of fish, then a description in terms of biological species will report cannibalism, i.e., cycling, while a description in terms of trophic species must distinguish A and B

as belonging to different trophic species (assuming the eggs and the adults have different diets) and will not report cycling. If A, B and C belong to different biological species, but the species of A and C are considered to belong to one broad category from which the species of B is excluded, then a cycle of length 2 will be reported as energy flows first from A to B, and then back to C which is categorized with A. However, a description in terms of biological species would report no cycling.

Whereas the best food webs of the Briand-Cohen collection use trophic species, as defined by Briand and Cohen (1984; see Cohen, Briand, Newman 1990, p. 28), as units of analysis, the ecosystem energy model of Patten, Higashi and Burns (1990) uses highly aggregated units such as "filter feeders," "predators," "deposited detritus," "deposit feeders," "meiofauna," and so on. It seems possible that some portion of the difference in the frequency of cycling between that found in the Briand-Cohen webs and that found in ecosystem models may be explained by different degrees of aggregation in the units of analysis. It remains to formulate a quantitative model of how the trophic species in the cascade model might be aggregated to construct an ecosystem model and to verify whether the aggregation accounts for the increased appearance of cycling.

In addition to aggregation, food webs often ignore detritus and decomposers, unlike ecosystem models, and this difference could also contribute to the differing prevalence of cycles.

Empirical testing of the new models and predictions that relate food webs to other parts of ecology will require new field data. If there is a single message for field ecologists in all this theory, it is that the traditional food web is no longer enough (Cohen et al., submitted). Future reports of food webs should specify more exactly than most previous reports the boundaries of the location and time covered and the sampling effort expended, should include measures of numerical abundance and body size (preferably a full distribution, not just a mean) for each trophic species, and, to the extent possible, should experimentally establish the population dynamic consequences for both predator and prey species of each trophic link. This is a tall order, and may require more resources for field work than field ecologists have customarily had at their disposal.

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