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# FOOD WEBS

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# Foreword

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## WHY REPRINT A TWENTY-YEAR-OLD SCIENCE BOOK?

Scientific knowledge accumulates so rapidly that papers just a few years old seem quaint in their assumptions and methods. *Food Webs*, published twenty years ago, is antediluvian by these standards, so why this reprint? One answer might be that it is a classic—something to be appreciated by those who study history and the origin of ideas—and that the lessons it teaches may yield insights into present science. To those who read this reprint with history in mind I wish only the best. It is not my reason for this reprint's existence.

In the twenty years since this book was published, we have added two billion humans to the planet, cleared about three million square kilometers of tropical forests, over-harvested a large number of fisheries, caused the warmest years in recorded history and witnessed countless other human actions have massive environmental impact. This is not the place to review these, nor justify my optimism that we can do what is required to protect our planet for countless future generations. I do so elsewhere (Pimm, 2001). Nor is this the place to outline the agenda of actions for that protection. In developing that agenda, a broad group of colleagues and I (Pimm et al., 2001) make an insistent and unanimous recommendation to train a new and much larger generation of professionals to tackle environmental problems. By “professionals” we mean those with skills far more wide ranging than just ecologists. Nonetheless, however much age teaches me that students must also speak law, politics, economics, and other languages foreign to scientists, ecology is a core skill. I still teach basic ecological concepts, including food webs, even as my students arrive from a class on international science policy and depart to another on economics. Importantly, many others are still teaching food web ideas too—something I know from those who photocopy chunks of this book and from the inquiries I have about reprinting it. Simply, at a time when our students learn even more skills and must do so with a keen sense of urgency, this book's material is a useful teaching resource. To protect Nature, we must have some understanding of her complexities, for which the food web is the basic description.

The justification of this reprint, then, is to provide, within this foreword and the original text, the materials to bring its reader up to speed with current ideas and controversies. Moreover, it must do so faster than simply reading the most current literature. There are some subjects where the current literature is far preferable to the old, which may be premature or conceptually muddy and confusing. Starting from the beginning—retelling a subject's history—need not be the only way. Yet,

I think it is for food webs. That's why *Food Webs* is being reprinted. It's also why this foreword has the structure it does.

*Food Webs* has four major themes:

- (i) The majority of communities consist of stable populations, that is, those showing a tendency to return to an equilibrium density when perturbed from it.
- (ii) The requirement of stability imposes constraints on the patterns of how species should be connected—that is, food web structure.
- (iii) Empirically, food webs are structured—they differ from what one would expect by chance and do so in ways anticipated by the theory.
- (iv) Food web structure affects community dynamics.

This book also introduces two broad methods—how to build multi-species models to investigate these topics and how to conduct field experiments to test them.

### THE NATURE OF POPULATION DYNAMICS

To develop a dynamical theory of food webs, I needed to show that stable populations were the norm (pp. 8–11). Ecologists have debated the nature of population change for decades, arguing the relative merits of density dependence—which is necessary if densities are to have some central tendency; density independence—for which populations vary without bounds; and density vagueness—by which populations vary wildly but are constrained at rarely encountered lower and upper limits. Whatever the merits of these explanations, my key concern was their generality. This requires the comparative study of populations.

The late Jim Tanner had attempted such a study and my addition to his results broadly followed his recipe. Statistical difficulties notwithstanding, fitting the parameters of the familiar  $r/K$  model— $r$  is the population's growth rate when well below its equilibrium level,  $K$ —is as simple an exercise as one could imagine. From Tanner's study and my analyses of British birds (pp. 10, 11), I concluded that the assumption of stability was a sensible one.

In the intervening two decades there have been three important advances.

*The Global Population Dynamics Database (GPDD)*. Accumulating population time series is a lengthy process, requiring ecologists to devote a lifetime to the same species at the same location. (Indeed, some of the longest series span several scientific generations.) The work is not only tedious but is notorious for not being financially rewarding. Not surprisingly then, there seemed to be few long-term studies. Yet as I searched the literature in the years following the publication of *Food Webs*, I realized there were far more than I had expected. My enlarged collection formed a resource for my next book *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities* (Pimm, 1991). John Lawton, of the Centre for Population Biology, Imperial College at Ascot, had also been compiling time series. We met in Tennessee in June 1994 and agreed to a joint effort to search the literature and make available as many series as we could

to the ecological community. The National Center for Ecological Analysis and Synthesis (University of California, Santa Barbara) soon joined that effort.

The NERC Centre for Population Biology built the GPDD, which now consists of more than 4,500 time series of population abundance, each longer than ten years. It encompasses over 1,800 animal species across many geographical locations. The GPDD is updated continuously with new information from published and unpublished sources. It is freely available and fully searchable: <http://cpbnts1.bio.ic.ac.uk/gpdd/>.

*Statistical modeling.* The techniques for modeling populations have improved spectacularly and now allow ecologists, inter alia, to dissect the time lags that lead to complex cycles, the interactions with other species, and the long-term impacts of climate events. Bjørnstad & Grenfell (2001) provide an excellent review of this progress. We now know that the complex bestiary of possible population dynamics anticipated by Fig. 1.2 is realized, plus there are many more possibilities than any of us dreamt of.

*The nature of population change revisited.* I found the idea of a species' equilibrium density embodied in the  $r/K$  equation to pose enormous problems when viewed in the context of the food web. This thing called  $K$ —the equilibrium density—is the integration of all the other species present in the community—predators, prey, competitors, mutualists, and diseases. Are all of these species expected to stand still politely, while our species of interest returns to its equilibrium? The food web view demands that we think of population change in a multi-species context. Change one species and, in time, all the others will change too. (That idea is at the heart of the explanation of why food chains are short, but I am getting ahead of the story.)

The idea that species depend on other species, which in turn depend on others, leads to the idea of dynamical effects imposed upon other dynamical effects, imposed upon yet others, and so on, throughout a complex of interactions that the food web describes. It suggests a model of dynamical change approximating “red noise”—where small, short-term changes are imposed on larger, longer-term changes, which are imposed on yet larger, longer changes, and so on. With that view, populations may appear to show some equilibrium in the short term, but that level will change over the longer term—and change more, the longer one looks at the population.

That idea prompted an analysis (Pimm & Redfearn, 1988) that showed that population variance increased over time—the “more time means more variation” as John Lawton put in his News and Views that accompanied the article in *Nature* (Lawton, 1988). John Halley told me that the analysis and particularly the explanation of it in the preceding paragraph “greatly angered” him when I presented the work at the CPB. He and Pablo Inchausti, armed with the GPDD, investigated the idea (Inchausti & Halley, 2001).

For the analysis, they used all annual series longer than 30 years. The GPDD contains 544 such series, representing 123 species. Their results confirm and

greatly extend my work (Pimm & Redfearn, 1988, Ariño & Pimm, 1995) and that of others that population variability increases with time series length. In over 95% of their series, there is an increase in population variability, but it decelerates with time series length. This deceleration need not imply convergence to an upper limit. For the majority of ecological series, variance fails to converge to any limit, at least over the time scales the data encompass.

Traditional models of density-dependent growth imply the existence of an equilibrium that confines the population abundances to a range of values about equilibrium. For such populations, the variance *should* converge to a clear limit. By contrast, density-independent dynamics, subject to the vagaries of environmental noise, show a random walk over time. For such dynamics, the variance grows linearly with time. Inchausti & Halley (2001) conclude—as did Arturo Ariño and I with our far fewer series—that the dynamics of animal populations typically lie somewhere between the two extremes.

It is possible to adopt a worldview of all populations undergoing a random walk. Steve Hubbell, in *The Unified Neutral Theory of Biodiversity and Biogeography*, has done just that (Hubbell, 2001). His predictions are numerous and compelling and, perhaps given the number of Inchausti and Halley's populations that appear close to (or indistinguishable from) random walks, we should not be surprised. Equally, the original assumption required to develop a theory of food webs survives intact, for most species dynamics are more bounded than random walks. A sensible assumption for community dynamics is of a multi-species equilibrium about which species are constantly attracted but which undergo a complex dance as environmental noise and a myriad of interspecific interactions drag them away from it.

## BUILDING AND ANALYZING MULTI-SPECIES MODELS

Chapters 2, 3, and 4, (pp. 12–83), deal with mathematics that a friend in comments about *Food Webs* called “both dull and daunting”. He, like the rest of us, has to use them anyway and I presented them at some length because I found the alternative explanations just horrible. The analysis of systems of differential equations typically came toward the end of introductory textbooks on the subject and required substantial preparation in calculus. I found that undergraduate courses sometimes did not cover the topic at all in a first course. That meant that students had to sit through a couple of courses on calculus, then one on differential equations, and only then get into one that helped. I needed something to teach that was much more direct. Understanding how multi-species models behave and how best to characterize them is an essential skill in ecology. Two decades later, I'm still using these chapters and seeing them photocopied more than others. Yes, they require basic calculus and some algebra.

With those skills, it is then a matter of developing the intuition about how complex systems behave. The advent of personal computers has made modeling much easier, and there are excellent simulation packages. More importantly, one can do

so much using ubiquitous spreadsheet packages and, in doing so, check the intuitions the mathematics of these chapters provide.

For example, Chapter 6 asks: How quickly will an ecosystem recover when we subject it to transient shock? Suppose phytoplankton in a lake were shocked with a pulse of nutrients. The intuition is that the phytoplankton would first increase, then decrease as they use up the nutrients. Alone, they could probably recover normal levels quickly. If the lake also contained phytoplankton, zooplankton, and fish, the increased phytoplankton would cause the zooplankton to increase, and then the increased zooplankton would cause the number of fish to increase. Now, while the fish remain unusually abundant, their prey, the zooplankton will be rare. Consequently, their prey, the phytoplankton, will be unusually abundant.

Simply, no component of the system can return to equilibrium until all the others do so. To study only one component is to hear the plop of the stone in the pond, but not see the ripples spread. The recovery time is likely to depend on the length of the food chain. The longer the chain, the further those ripples have to travel. I lay out the requisite mathematics in Chapters 2, 3, 4, and 6, but the means to model the intuition is as close as your nearest spreadsheet.

The tinker toy models I used would first consider an equation for the phytoplankton limited by nutrients:

$$dX_1/dt = X_1(b_1 - a_{11}X_1). \quad (1)$$

The growth rate of the phytoplankton,  $dX_1/dt$ , depends on the size of its population,  $X_1$ , its intrinsic growth rate,  $b_1$ , and a limitation imposed by the shortage of nutrients,  $a_{11}$ . (This is the familiar “r and K” population model in a different guise. It is one that allows us to add other trophic levels more readily.) The population size approaches “K,” its equilibrium value  $b_1/a_{11}$  from any value of  $X_1$ . The question is how fast it will approach that value.

Now let’s add another trophic level, the zooplankton:

$$\begin{aligned} dX_1/dt &= X_1(b_1 - a_{11}X_1 - a_{12}X_2) \\ dX_2/dt &= X_2(-b_2 + a_{21}X_1). \end{aligned} \quad (2)$$

The phytoplankton now suffers predation from the zooplankton. The zooplankton die off if there are insufficient phytoplankton to support them, that is, when  $(-b_2 + a_{21}X_1) < 0$  or  $X_1 < b_2/a_{21}$ .

We can keep on adding levels—the three trophic level model is

$$\begin{aligned} dX_1/dt &= X_1(b_1 - a_{11}X_1 - a_{12}X_2) \\ dX_2/dt &= X_2(-b_2 + a_{21}X_1 - a_{23}X_3) \\ dX_3/dt &= X_3(-b_3 + a_{32}X_2). \end{aligned} \quad (3)$$

One way to explore the equations’ behavior is to simulate them. We can replace the differential equations with calculations using small but finite time steps,  $\Delta t$ .



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The smaller the step, the closer these finite difference equations will approximate the differential equations (that is  $\Delta X/\Delta t \approx dX/dt$  for small  $\Delta t$ ). The idea is that

$$X_{t+\Delta t} = X_t + \Delta X. \quad (4)$$

The finite difference approximation for equation (1) would be:

$$\Delta X_1 = \Delta t \cdot X_1(b_1 - a_{11} \cdot X_1) \quad (5)$$

As an example, I have investigated the three species system

$$\begin{aligned} dX_1/dt &= X_1(1.0 - 0.01X_1 - 0.1X_2) \\ dX_2/dt &= X_2(-1.0 + 0.02X_1 - 0.1X_3) \\ dX_3/dt &= X_3(-1.0 + 0.5X_2) \end{aligned} \quad (6)$$

using a time step,  $\Delta t = 0.1$ , and initial values of the three species of 50, 10, and 3.

You can do this at home (or wherever you keep your computer). Put these first three numbers into row 1 of a spreadsheet, into columns A, B, and C respectively, thus:

50	10	3
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Add three formulas into the three columns of the next row

Row 2, column A	=	A1+(0.1)*A1*[1-(0.01*A1)-(0.1*B1)]
Row 2, column B	=	B1+(0.1)*B1*[-1+(0.02*A1)-(0.1*C1)]
Row 2, column C	=	C1+(0.1)*C1*[-1+(0.5*B1)],

and ask the computer to calculate the new values, which are

47.5	9.7	4.2.
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Spreadsheets now have the convenient feature of allowing one to “fill down” the calculations as many rows as one wants. The next row will contain the formulas for A3, B3, and C3, and calculate them as

45.386	9.244	5.817
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and so on for 500 rows.

To simulate just the phytoplankton and the herbivore, set the first value of C to 0, and it will stay there. To simulate just the phytoplankton, set B = C = 0.

So, armed with only a spreadsheet, one can explore the section on the dynamical constrains of food chain length—and, for that matter, most of the other theories in the book. (The one warning is that the crude assumption of making  $\Delta t = 0.1$  will fail for some models and a smaller value will be necessary.)

*Do not bother reading the stuff on species deletion stability on pages 47–49 and 77–82—at least not just yet. It is not that it is wrong. My reasons for writing it were that I wanted to know the consequences of really bashing communities—taking out entire species—rather than just tweaking the densities of some popu-*

lations. The ideas this generated kept me busy for another decade. At issue is how *resistant* communities are to change. These were the topics of my next book (Pimm, 1991) and are something to which I shall return at the end of this foreword.

## HOW TO PARAMETERIZE MULTI-SPECIES MODELS

When *Food Webs* was first published, the best I could do was to guess parameter values and to assign values randomly over ecologically reasonable intervals. Figure 1.1 (p. 5) laid out the book's main argument: real communities are composed of species with dynamically stable populations. We can build food web models with different structures and with their parameters selected randomly over ecologically plausible intervals. We predict that those structures that rarely yield stable systems will not be common in nature.

Those with a more intimate knowledge of particular communities could go much further—and parameterize known food web structures with informed estimates of the parameters involved. A benchmark paper was de Ruiter et al. (1995). In discussing their work, Lisa Manne and I (1996) invoked the imagery of Rube Goldberg.

Recall a typical Rube Goldberg contraption with a long, complex, and vulnerable chain of processes to achieve some simple end. We do not meet objects like this in the real world and they obviously would not work. When one examines food webs such as the one presented by de Ruiter, we ask the same questions. Should we see objects like it in Nature? Will it work, and, if so, then why? The analysis by de Ruiter et al. shows that this and six other soil-based food webs do likely “work.” That is, these systems are likely to be dynamically stable. Unlike Goldberg contraptions that will fall apart, these food webs will not.

The structure of this web comes from the authors' knowledge of the system. But what about their interaction terms? These require several kinds of information. De Ruiter et al. took the biomass of a species to be the average annual population size of the species; call this  $X_i^*$ . The feeding rate,  $F_{ij}$ , of a predator of density  $X_j$  on a prey of density  $X_i$  is modeled using Lotka-Volterra dynamics. This assumption leads us to equate the feeding rate  $F_{ij}$  with  $c_{ij}X_i^*X_j^*$ , where  $c$  is a constant particular to the two species involved. De Ruiter et al. estimated each feeding rate directly, then estimated the per unit effect of predator  $X_j$  on prey  $X_i$  as  $F_{ij}/X_j$  or  $c_{ij}X_i^*$ .

While the prey species loses  $F_{ij}$  to the predator per year, the predator's gain is much smaller. (When a rabbit is running for its life, the fox chasing it is merely running for its supper.) The predator's gain must be reduced by the fraction of the prey's tissues that it can assimilate (the assimilation efficiency) and the fraction of the assimilated tissue that it can convert into new biomass (the production efficiency). These efficiencies are reasonably well known for many groups of species.

With these estimates in hand, the authors asked two questions. Where are the fragile linkages within each web? Are these real food webs special compared to imaginary webs that we might create using different assumptions?

To tackle the first question, de Ruiter et al. calculated the impact of each pair interactions on the stability of the food web, by varying their magnitude and then calculating the probability that the matrix will become unstable. They allow each of the pair of interaction strengths to take a random value in the range zero to twice the estimated strength of each particular interaction. They analyze the stability of the matrix of interaction strengths using the methods outlined in Chapters 2 and 3.

The impacts on web stability were not obviously correlated with the biomass of the species involved. Nor did the magnitude of the interaction strengths obviously correlate with impacts of stability: some of the sensitive interactions involved strong interactions and other weaker ones. Rather, it is the food web “patterning” that is crucial to stability. The highly interconnected trophic interactions among the bacteriophagous nematodes, fungivorous nematodes, predatory nematodes, nematophagous mites, predatory collembola, and predatory mites were crucial in terms of preserving stability. This result confirms Chapter 4’s general insight: it is the parts of the food web where the trophic connections are most complex that are important to its stability.

To address the second question, de Ruiter et al. compared the stability of four types of interaction matrices for each of the seven food webs, by doing 100 runs with different randomizations. The four types are “lifelike” matrices, using the estimated interaction strengths and observed patterns of trophic interaction (as already described); “disturbed” matrices, with the estimated interaction strengths, but where the patterns of trophic interactions were randomly permuted; and two different simulations where the observed trophic patterns were maintained but the interaction strengths were sampled randomly from different intervals.

The disturbed matrices were the poorest—they were less likely to be stable than any other alternatives. This result supports the conclusion that the patterns of trophic interactions are unusual in a statistical sense. The patterns we observe tend to be those consistent with stability: randomized patterns, even with the same interaction strengths, produce “contraptions”—systems much less likely to work.

The lifelike matrices were the “best buy”—they were the most likely to contain stable systems. This suggests that the parameter values are important too. The two sets of simulations with the same trophic patterns but different parameter values were less likely to be stable.

Together, the results point to a simple, but important, conclusion. Despite the inevitable uncertainties in producing the food web, the results are quite unusual. Certainly, some parts are more fragile than others. Perhaps they indicate the part of the system where we understand the dynamics the least. Overall, the structures have the parameter values and patterns of interaction that make them far more likely to work than we would expect by chance.

## THE COMPARATIVE STRUCTURE OF FOOD WEBS

Chapter 5 is short and starts with a discussion of empirical results about stability. I want to postpone the discussion of the first five pages, for they are again the subject of the consequences of food web structure—a subject to which I shall return. Pages 89–91 discuss the relationship of connectance to species number.

**Connectance and Linkage Density**

The simplest question one can ask of a food web is how connected it is. Connectance is the fraction of possible inter-specific links that realized. The reason to use connectance was a theoretical one—it played a role in May's famous result that stable systems would be those with a sufficiently small connectance (1972). As Chapter 5 explains, connectance depends on the number of species, which I called  $n$ . Joel Cohen and his colleagues (1990), more sensibly, have concentrated on the relationship between the number of species and the total number of trophic links,  $L$ . His original claim was that *linkage density*,  $d$ , was likely to be constant,

$$L = dn, \quad (7)$$

so that food webs were likely to “scale invariant” in this and other properties to be discussed presently. Were equation (1) to be the case, connectance would decline hyperbolically as Fig. 5.1 suggests.

By 1991, when Joel Cohen, John Lawton, and I joined to write a review about our combined efforts to elucidate food web structure (Pimm et al., 1991), we agreed that this was the pattern least likely to survive detailed scrutiny. Averaged over a much larger collection of food webs in the range from 3 to 48 species, the average number of linkages  $[E(L)]$  is roughly twice the number of species in any given web [i.e.  $E(L) = 2S$ ;  $d = 2$ ]. The original description of this pattern noticed that a power-law  $E(L) = kn^{1+\epsilon}$ , for some small positive  $\epsilon$ , was also a viable description of the data, and that future data on webs with large numbers of species would have to distinguish the alternatives. With the few larger webs in hand by 1991, a power law with  $\epsilon$  probably between 0.3 and 0.4 indeed seems reasonable. (Joel Cohen compiled the available food webs, has constantly undated the collection since, and they are available from him [Cohen, 1989a].)

Gary Polis and Neo Martinez were both sharply critical of low estimates linkage densities. Williams & Martinez (2000) discuss a sample of species-rich webs with 25 to 92 species, for which the linkage density ranges from 2.2 to 10.8. The highest linkage densities come from Martinez (1991) and Polis (1991). They may be right, but one of the difficulties with food web studies has been the problem of where to stop drawing connections. Yes, I eat rice, beans, potatoes, chicken, and occasionally seaweed wrapped around sushi and durian fruits (when I can get them). At what stage should I stop drawing trophic connections in my own personal food web? Martinez and Polis may be simply listing more connections than other workers.

The best solution is where one investigator compares two or more webs from his own work. The benchmark here was the work by Karl Havens who compared the food web connectance of different lakes (Havens, 1992). On page 89, I had supposed that “each species in a community feeds on a number of species of prey that is independent of the total number of species in the community” and called this the most “parsimonious assumption.” Havens both agreed and disagreed. Durians excepted, my diet doesn’t greatly expand when I move into a species-rich tropical forest, I still eat my usual rice and beans. So the addition of many species to a food web will not alter my feeding preferences. Species that select particular species of prey will surely follow suit and linkage density will remain constant and not increase as the size of the food web increases. On the other hand, filter feeders in lakes, for example, select prey based on their size. The more species of prey there are, the more that will be of the right size. Linkage density will then increase in direct proportion to the number of species present. Havens separated the species in his lakes into those expected to select prey species and those that should be indiscriminant. He found what he expected. This suggests that food web linkage density will be somewhere between being constant and increasing in proportion to the number of species.

### Other Features

Cohen’s first book on food webs preceded mine by three years (Cohen, 1978) and in the interval between its publication and our joint 1991 review, he noticed other features that were generally conserved across food webs. (Cohen et al. [1990] compiles those papers into one volume and adds additional material by way of added explanation.)

(i) Trophic cycles occur when species A eats species B and B eats species A, or A eats B, B eats C, and C eats A and so on. Such cycles are generally very rare (Cohen, 1978, p. 186).

My marine ecologist friends howled in pain whenever I said this quote during my seminars during the mid-1980s. In marine systems, it is quite common for fish to eat their way up a food chain as they grow, starting as planktivores when small and ending up eating fish that eat fish that eat zooplankton that eat phytoplankton. This doesn’t necessarily lead to trophic cycles. In some cases, a fish (call it species A) in the diet of this adult top-predator (species B) had a great liking to the eggs or early larval stages of the top-predator. In a special way A eats B and B eats A. So that I could show my face at marine meetings, I joined with Jake Rice to investigate the dynamics of this phenomenon (Pimm & Rice, 1987). Using the modeling methods of Chapters 2–4, we showed that eating one’s way up a food chain did not destabilize it as much as feeding on all lower trophic levels simultaneously (omnivory, to be discussed below) and that some of these life history cycles were dynamically feasible. Polis (1991) found complex trophic cycles in scorpions, but beyond this, the topic has not received much attention.

(ii) Cohen's work had shown that the average proportion of top-predators, intermediate species, and basal species remains roughly constant (but with high variance) in webs with widely differing numbers of species and from different habitats. The average proportion of trophic links that are between intermediate and intermediate species, intermediate species and top-predators, basal species and intermediate species, and basal species and top-predators remains constant (with large variance) in webs with widely differing numbers of species and from different habitats (Cohen et al., 1990).

### Food Chain Length

Chapter 6 deals with food chain lengths. I still find it to be a useful introduction, but there is one important argument that I overlooked. Area must play an important role in limiting food chain lengths. In the limit, very small islands simply cannot have the production base to support top-predators. This is an important—and testable—extension of the energy flow argument developed on pages 104–10. Those pages cast doubt on the energy flow argument for short food chains because systems with low primary production do not obviously have shorter food chains than those with high production. In the former, the top-predators simply feed over larger areas. The area-limitation hypothesis simply asks what happens when area runs out! While per area production varies only over a couple of orders of magnitude, it's possible to compare the trophic levels of islands that span just a few square meters to those of more than 100,000 square kilometers. Not surprisingly, small islands have shorter food chain lengths (Schoener, 1989).

The argument that long food chains produce species with long recovery times (pp. 115–20) received support from an experimental study by Steven Carpenter and his colleagues. Carpenter et al. (1992) chose a small (area, 1.2ha), steep-sided (depth, 18.5m) experimental lake in Wisconsin and estimated both the flows and the stocks of phosphorous. Phosphorous is often a limiting nutrient in lakes. They aggregated the phosphorous in the web into six compartments: dissolved phosphorous, seston (mainly algae, but also the associated bacteria and protozoa), herbivorous zooplankton, *Chaoborus* (a predatory midge that feeds on the herbivores), planktivorous fish (that also feed on herbivores and also on the *Chaoborus*), and piscivorous fish. In 1984, planktivorous minnows were at the top of the food web. During 1985, over 50kg of minnows were removed and replaced by a similar mass of piscivorous largemouth bass. This re-configured the food web, adding an extra trophic level without significantly changing the total amount of phosphorous.

The team estimated the flows of phosphorous between compartments from the consumption of one by another. Other inputs to compartments include the emergence of eggs from benthic sediments. In both years, a major input was from the fish feeding in the lake's small but important littoral zone. There were flows of phosphorous back into the water column and losses, mainly to the benthic sediments. When all the numbers were in, neither year looks very much like the theo-

retical food webs (Fig. F.1). (In doing all this, there are obvious parallels to the de Ruiter et al. study discussed earlier; food web ecologists can now estimate the parameters of their systems.)

The final step was to use these numbers to calculate both the resilience and rate of nutrient recycling in each year. In 1986, the recycling was slightly tighter than in 1984. The addition of the extra level increased the return time from an estimated twenty-eight days in 1984 to over 200 days in 1986. Adding the extra trophic level alters the distribution of the phosphorous. Freed from predation from planktivores, *Chaoborus* increases dramatically, and its prey, the herbivorous zooplankton, decrease. The major phosphorous stocks moved to higher trophic levels (piscivores, *Chaoborus*) in 1986, and these species have slower turnovers than the zooplankton and seston.

The predicted values are interesting for reasons other than their confirmation of theoretical predictions. There are at least two reasons for the increase in return time with trophic levels. First, the number of levels itself may matter. More levels must often slow the transit of nutrients through the system, even if the converse is possible. Second, species at higher trophic levels are larger and longer-lived in aquatic ecosystems. In this lake, shifting stocks from algae (which live days) to fish (which live years) slows the nutrient transfers. If this second mechanism is by far the more important, then these results may not apply to terrestrial ecosystems.

Terrestrial ecosystems often show a marked pyramid of biomasses. Terrestrial plants outweigh their herbivores often by factors of ten. The herbivores outweigh their predators similarly. Adding an extra trophic level moves the distribution of biomass upwards only very slightly. In contrast, Fig. F.1 shows that the stocks of phosphorous (which reflect biomass and vice versa) can be greater at higher rather than lower levels in aquatic systems.

The dynamically slower compartments need not always be at higher trophic levels—as they are in many pelagic aquatic webs. The relative life spans of species at different levels differ from system to system. Trees live longer than the insects they house, which have shorter life spans than the birds and mammals that eat them. In other terrestrial ecosystems, long-lived birds and mammals may eat insects that typically live for a year and feed on annual plants. The lake results are stacked in favor of finding an increase in return times with increasing levels. Other systems may behave differently.

Why should we care? Systems with very long recovery times may never come close to their equilibria if the shocks are too frequent. Some systems may spend almost all of the time recovering from some historic shock. The practical consequences of this may not always be severe. Adding a trophic level to the lake means that the phosphorous can be “parked” at higher trophic levels. This improves the water quality, which equates with low algal biomass. There is an added benefit. A pulse of phosphorous would quickly pass through the algae into the higher trophic levels. There it receives only a temporary parking permit—but it is a permit with a 200-day return time.

The section in this book on the dynamics of food chain lengths includes a

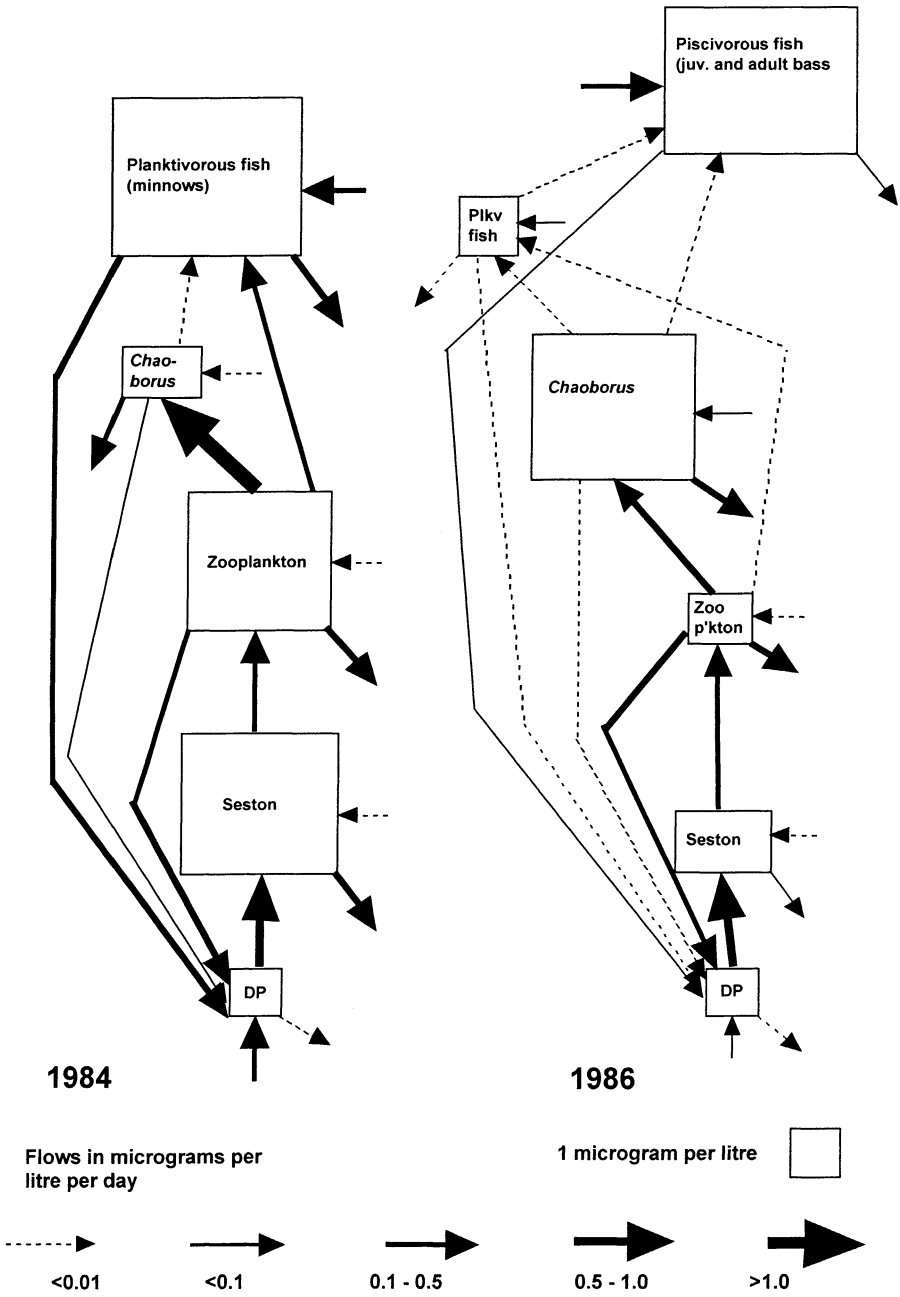


Figure E1. The biomasses and the flows of phosphorous in a lake food web before and after an experimental addition of the top-trophic level.



couple of pages about tree-hole communities and the work of Roger Kitching. From that small start, Kitching developed a major research program that included both exhaustive comparative studies and a very active experimentation on food webs. Tree-holes and container habitats such as the fauna of *Nepenthes* pitcher plants are very suitable subjects for this work. Kitching's book *Food Webs and Container Habitats* (2000) develops the subject in far more ways than I can easily summarize here. I will return to these comparative studies later.

Kitching and I used the organisms that inhabit natural water-filled tree-holes in subtropical rainforest ecosystems in Australia to test the ideas on food chain length. Energy enters tree-holes in the form of plant and animal detritus that falls into habitat units from the rainforest canopy. To circumvent any problem associated with the physical variability in natural tree-holes, we used plastic containers as analogues of natural habitat units. The first experiment conducted in subtropical rainforest in southeastern Queensland showed that the majority of species that inhabit natural tree-holes colonized water-filled plastic containers into which a quantity of leaf litter had been added as a source of energy (Pimm & Kitching, 1987). We varied productivity by using half to four times the natural rates of leaf litter input in their experiment.

This magnitude of difference in productivity did not affect food chain length significantly. However, the establishment of the containers did. It took much longer for the predators to colonize than the detritivores. We argued that, under natural circumstances where environmental vagaries might often eliminate species from natural tree-holes, the lower resilience of the longer food chains might be the principal factor in limiting their length.

In the extreme, energy must limit food chain length—for if there is no energy there can be no species. Nonetheless, this does not mean that the magnitude of energy flow is the best predictor of food chain lengths over the range of energy flows observed in nature. In a second experiment, Burt Jenkins, R. L. Kitching, and I used a far larger range of productivities than is likely to ever be encountered by natural tree-holes (Jenkins et al., 1992).

The 'high' energy treatment consisted of an initial loading of 6 grams of crushed leaf litter per container. This treatment also involved the input of subsequent installments of 0.6 grams of litter every six weeks. This is close to the average amount that we expected to enter a container over such a period if the container received only natural leaf litter falls. The 'medium' energy treatment consisted of an initial loading of 0.6 grams and an installment of 0.06 grams every six weeks which is an order of magnitude less than the amount of leaf litter added to containers in the 'high' energy treatment. The 'low' energy treatment had only an initial input of 0.06 grams of litter per container, an amount two orders of magnitude less than the 'high' energy treatment and ten times less than the 'medium' energy treatment. We added no further installments to the low energy containers.

We collected samples at weeks 6, 12, 24, 36, and 48 and observed food webs with the highest number of species, trophic links, and the longest chains in the twenty-fourth week. The lower the energy input, the fewer the trophic links, food

chain lengths, and species were in the containers. There was also a decline in species numbers and food chain length in the thirty-sixth week as a result of dry conditions in the forest during which natural tree-holes in the vicinity of the experiment dried out. The effect on food chain length was most marked in the most productive system. We concluded that while relatively long food chains were possible only in the most productive systems, these systems were especially vulnerable to external perturbations.

### **A Null Hypothesis for Food Webs and Cohen's Cascade Model**

Pages 124–30 deal with what I called the null hypothesis for food webs. It was an attempt to explore what food web features one might expect by chance, given the necessary constraints on an observed food web—its numbers of species of top-predators, of species that are both predators and prey, of species that are only prey, and the number of trophic interactions between them. I further constrained the webs so that there could be no trophic cycles (see above). Cohen's cascade model is very similar to this—a close cousin—and I shall return to his model soon.

### **Omnivory**

Chapters 7, 8, and the first parts of Chapter 9 (pp. 131–76) deal with a variety of statistics that completed the set of patterns that one can derive from the food web itself. Of these, only omnivory has caused much controversy in the intervening years. I claimed that it was rarer than it should be, but there were a list of exceptions. These included webs dominated by parasitoids, detritivores that feed on the dead, and, after *Food Webs* was published, the species that feed their way up the food chain as they become larger. All of these are permissible exceptions in light of the unifying theory that nature abhors a food web that is likely to be unstable.

Over the two decades since these claims there have been many who have presented their webs, claiming them to show an abundance of omnivores. (See for example Williams & Martinez [2000] and the references therein.) Not once have I been convinced. *Food Webs* does not claim that there is “little omnivory” but simply that omnivores were rarer than expected by chance. “Read the instructions!” I often felt like writing. To my knowledge, no one has yet applied a food web null hypothesis (as I did) and shown that omnivores are as common (or more common) than one would expect. That doing this might be extremely difficult computationally for a web as complex as the one for Little Rock Lake (Martinez, 1991) is not an excuse for assuming the results are already in hand.

Nor have I ever understood why this pattern proved to be so contentious. Most ecologists routinely accept the idea that competition restricts the coexistence of two species, A and B. If A and B share a prey species, C, then they likely compete. So, if B makes A's life miserable by eating C, how much more so than if B also eats A! Simply, being both the prey and the competitor of another species is a tough option in a constantly changing world.

As a side note, feeding on different trophic levels in different food chains does not impose such dynamical constraints. The models do not exclude my eating potatoes and beef, since cows eat grass and not potatoes. *Food Webs* makes a clear distinction between within-chain omnivory (previous paragraph) and between-chain omnivory (this paragraph). Similarly, species that feed on carrion do not affect the abundance of their now-dead prey. Finally, species that eat their way up food chains may appear to feed on several trophic levels, but it is their individual life stages that feed on particular levels.

### **Compartments**

The issue of compartments has a murky history. May (1973) suggested trophic interactions should be clumped, but his numerical argument was flawed (p. 144). Perhaps more importantly, he absorbed the conventional wisdom of ecologists of the day. Lawton and I only found evidence of compartments across broad divisions of habitats—as between the land and the sea, for example.

Even that barrier might not be what it seems. Gary Polis berated his fellow ecologists as they blithely assumed an ability to draw distinct boundaries around their systems. His studies of islands in the Sea of Cortez show that many of these islands received large amounts of energy and nutrients from the seas around them in the forms of bird droppings and washed-up carcasses. Islands, Michael Rose and he argued, need not be insular (Rose & Polis, 2000).

### **Predator–Prey Ratios**

The topic of the ratios of predators to prey species in food webs was first raised by Cohen (1978). I criticized his specific ratio because the data available to Cohen were severely prejudiced against plants and invertebrates (p. 168). The top-predators of many food webs are described as species by the ecologists who reported them, but the lowest trophic level is often described as “plants,” “detritus,” or “phytoplankton.” Jeffries & Lawton (1985) addressed the criticisms with a new data set of almost one hundred studies of freshwater habitats assembled with special care taken to address the taxonomic difficulties. They found a predator–prey ratio that varied from 1:2 in communities with few predators and prey species to 1:3.5 in communities with many predators and prey species. They found no differences in the ratio among communities in streams, rivers, or lakes, though across a wide range of communities the ratio is likely to vary. It is not the value of the ratio itself that is perhaps so interesting but its constancy within any broadly defined habitat.

### **Features of the predator overlap graphs**

The final section of Chapter 9 (following p. 176) reviews the Cohen’s book (1978). There is a distinction here that I did not emphasize as clearly as I would

like to now. Food webs are a kind of graph, in the mathematical sense of that word. That is, a graph shows the relationships between objects. The objects in a food web are the species, and the relationship is a trophic one: A eats B. The food web is the basic graph, but one can derive other graphs from it.

One of these is the *predator overlap graph*—the objects are now the predators and the relationship involves the question of whether they share prey species, or henceforth, whether the predators overlap in their diet. To produce these graphs, we draw lines connecting each pair of predators that share one or more species of prey. These graphs show dietary overlap and dietary overlap indicates the potential for indirect (i.e., exploitive) competition.

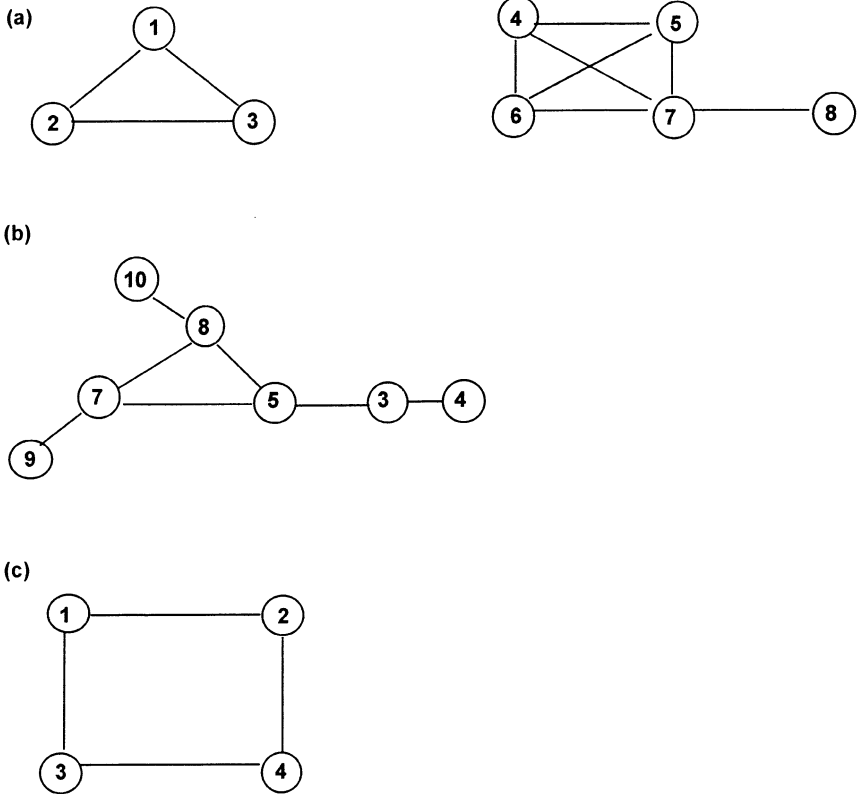
In nature, predator overlap graphs show surprising regularities (Fig. F.2). Consider an approximate physical analogy. Make a physical model of the predator overlap graph with spheres to represent the predators and rods to connect those predators that share prey. The physical model of Fig. F.2(a) would be rigid, not flexible, because when there are connections around four or more predators these connections are triangulated. This would not be the case for the overlap graph in Fig. F.2(c). Also notice that species 8 in Fig. F.2(a) does not violate this condition because it is not part of a circuit around four or more species. The two unconnected parts of the graph (species 1–3 and 4–8) do not violate the condition for the same reason. If the connections from species 4–7 and 5–6 were missing, then the graph would not be triangulated. Technically, this property of being triangulated is called a *rigid circuit*. The predator overlap graphs of real food webs contain an overwhelming preponderance of rigid circuits compared to sets of computer-generated model food webs (Sugihara, 1984).

The pattern discussed by Cohen (and so in my Chapter 9, p. 176 and following) also comes from considering the overlap in the predators' use of their prey species. Cohen deemed a food web to be *interval* if the overlaps in the predators' use of prey species can be expressed as possibly overlapping segments of a line (Cohen, 1978).

For many arrangements of predator overlap graphs, the rigid circuit property ensures that the overlaps will have an interval representation. Yet the rigid circuit property does not *guarantee* that food webs are interval. It is possible to draw a non-interval, rigid circuit predator overlap graph, and Fig. F.2(b) is an example. The graph is a rigid circuit because there are no circuits around four or more points, yet it is still not possible to express the overlaps as overlapping segments of a line. For obvious reasons, this pattern is called *asteroidal*. If the overlap graph is not asteroidal and it is rigid circuit, it will be interval (Sugihara, 1984). Indeed, when real food webs are non-interval, it is because they are asteroidal.

### Assembling the Prey Overlap Graphs

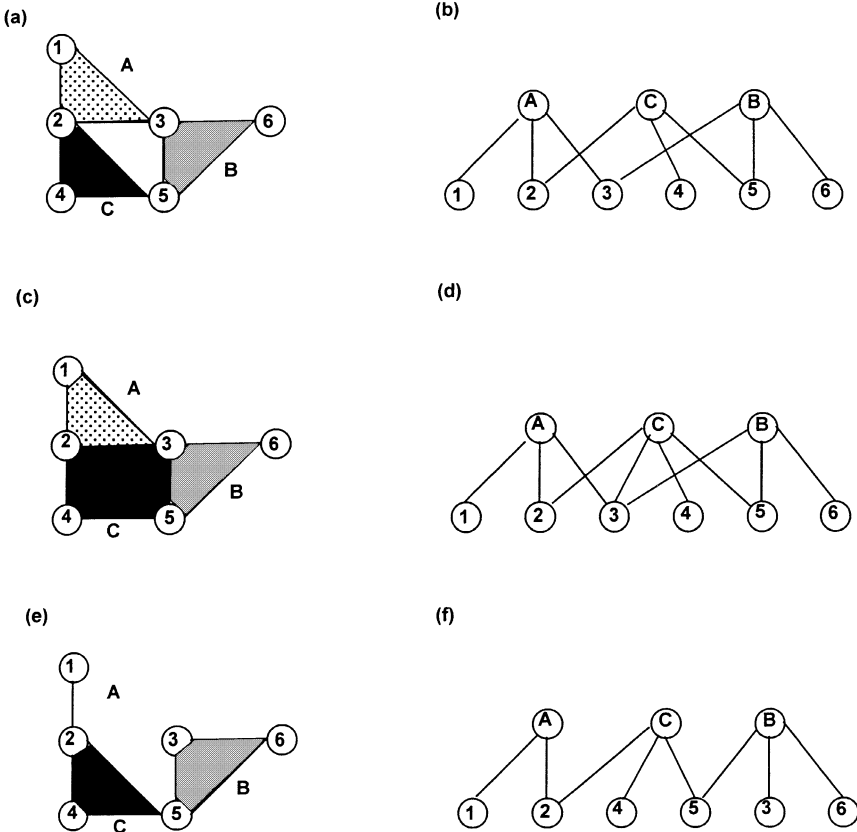
Another graph one can produce from the food web lets us combine information on both predators and their prey. One forms this graph by connecting prey species sharing a particular predator. Two prey species sharing a particular predator



*Figure F2.* Predator overlap graphs connect predators that share one or more prey species. Both (a) and (b) are rigid circuit, (c) is not. Only the predator overlap graph for (a) has an interval representation, as (b) is asteroidal (see text for definitions). Key: (a) is from Bird's (1930) study of a Canadian willow forest. 1, a fungus, 2, insects, 3, another group of insects, 4, three species of birds, 5, another three species of bird, 6, spiders, 7, a frog, 8, garter snake. (b) is from Kohn's (1959) study of predatory gastropods of the genus *Conus* on the sub-tidal reefs of Hawaii. All are species of *Conus*; 3 *ebraeus*, 4 *chaldeus*, 5 *miles*, 6 *rat-tus*, 7 *distans*, 8 *vexillum*, 9 *vitulinus*, 10 *imperialis*. (c) This pattern is so rare in nature that I have no example: this graph is hypothetical. (Pimm, 1991).

would form a line, three a triangular plane, four a tetrahedron, and so on. The graphs formed in this way are the *prey overlap graphs*.

Some prey species will feed more than one predator and this allows us to connect the individual graphs. Figure F.3(a) shows a combination of the graphs for three predators and how they exploit six species of prey. Figure F.3(b) is the food web from which I produce the prey overlap graph. Generally, I have used three prey species in the diet of each predator because planes are easier to draw than a multi-sided solid and so the examples are easier to visualize. Again, consider a



*Figure F.3.* Parts (a), (c), and (e) are the assembled prey overlap graphs, formed by connecting prey species that share a predator and parts (b), (d), and (f) are the food webs from which these graphs are derived. In (a) prey species 1, 2, and 3 are connected because predator A feeds on all three species. Species 1 and 4 are not connected because they have no predator in common. Prey connected in this way form “solids”. (These are planes in all cases except the tetrahedron connecting 2, 3, 4, and 5 in (c) and the line connecting 1 and 2 in (e).) This recipe of connecting species forms a hole between 2, 3, and 5 in (b). I discuss the significance of the different figures in the text. (Pimm, 1991.)

physical analogy of the overlap graph. The planes or the multi-sided objects formed by connecting the various prey species that share a particular predator are solid in the physical analogy. Continuing the physical analogy, observe that there is a hole between prey species 2, 3, and 5; no predator species feeds on this set of prey species. For another example, consider the web in Fig. F.3(c). Predator C now feeds on prey species 3 and so there is no longer a hole. These topological holes are rare in real food webs (Sugihara, 1984).

Why do these patterns predominate in Nature? Discussing them a decade later (Pimm, 1991), I argued that they are a reflection of an important view of how species select resources. The most familiar view of niche geometry is represented in a caricature that imagines species strung along a resource axis. (A overlaps with B, B with C, C with D, etc. where the relative positions might represent some environmental gradient, prey size, or a more abstract ranking of the prey's characteristics.) There might be more than one dimension, but the overall idea is the same. Such a view is the basis of many of the models of species packing, resource partitioning, limiting similarity, and many other ideas. I suggest a better caricature of niche geometry, the *flower petal model*. Here we imagine the niches drawn, as a Venn diagram, to show the extensive predator overlap formed by species exploiting some common prey species and the resource partitioning which tends to give each species a slightly different, though idiosyncratic, set of resources.

Why should the niches of the predators be arranged like flower petals? Some prey species are much more abundant in the diet of predators than others. (These prey species may be actually more abundant, more available, relatively more nutritious, etc. I shall talk about "abundance" for simplicity.) These abundant prey species will be the ones selected by the first predators to invade the community. Unless the predator's influence in the community is already so great that it depresses the common prey species below the abundance of the rare prey species in a community, predators will not create "donut-shaped" holes in prey species abundances. Only if they did so would they force the later predators to enter the community by taking a selection of rare prey species. Predators may enter a community by taking rare species of prey, but they also take the common ones. Predators thus give the impression of entering the community and overlapping with others predators where there are more species competing for the resources, rather than where there are few species sharing those resources. In short, it is the range of prey abundances that impose a ranking on the prey species so that the predators appear to avoid the ends of resource axes. I argue that this results in the topological regularities we have been discussing.

### Small Worlds

That some species form the key centers for the action in the food web—those that are the cause of many species overlapping in the "flower petal" model just discussed—brings up my final topic about food web structure. First, a short preamble.

From the very start of my interest in food webs, it was obvious that many other things vaguely looked like food webs, and we could represent yet others as webs and the other graphs derived from them. As Steven Strogatz put it in his review of complex networks:

The study of networks pervades all of science, from neurobiology to statistical physics. The most basic issues are structural: how does one characterize the

wiring diagram of a food web or the Internet or the metabolic network of the bacterium *Escherichia coli*? Are there any unifying principles underlying their topology? (2001)

He continues by noticing empirical studies of food webs, electrical power grids, cellular and metabolic networks, the World Wide Web, the neural network of the nematode *Caenorhabditis elegans*, the citation networks of scientists, and the ‘old-boy’ network—the overlapping boards of directors of the largest companies. The Internet now makes it possible to search these and many other networks in a way that we could not have twenty years ago. (I just love the fact that he always mentions food webs first.)

His particular interest is an extension of the notion of “six degrees of separation”—that your friends’ (1) friends’ (2) friends’ (3) friends’ (4) friends’ (5) friends’ (6) encompass all 6 billion of us on the planet. You only need to have twenty-six friends, each one of whom has to know twenty-five other friends, and so on. The catch is that those twenty-five other friends must not include your twenty-five friends. While one can design networks with this property (and Strogatz shows how), the usual way to connect everyone is for there to be some broad power law to the number of connections. Many nodes have few “friends,” fewer

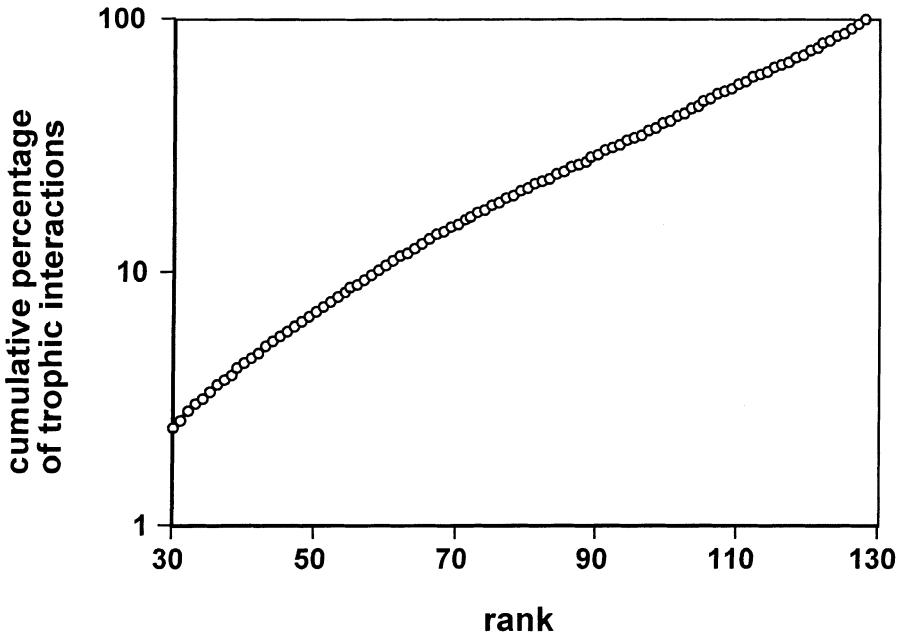


Figure F4. The logarithm of the cumulative number of  $\sim 1500$  trophic interactions against the rank for 128 species of predators in the rainforest food web of Reagan and Waide (1996). Rank is defined so the most trophically specialized species have rank 1 and the most trophically generalized species has rank 128.



have some, and the occasional one has very many. So yes, you can connect the hermit in his cave to absolutely everyone provided the cave is in a congressional district where the currently serving member is running a tight race—and so wants to be friends with everyone, including the hermit.

How does the frequency of connections scale in real food webs? I don't know in general, though I do know the place to look—the species-rich webs described by Baird & Ulanowicz (1989), Goldwasser & Roughgarden (1993), Hall & Raffaelli (1991), Havens (1992), Martinez (1991), Polis (1991) Reagan & Waide (1996), and Warren (1989). Using the penultimate reference, Fig. F.4 shows the cumulative percentage of about 1,500 trophic interactions between 128 species of predators and their prey. The twenty-three most specialized species have only one prey species, seven more have only two prey species and these thirty species combined account for only about 2% of the trophic interactions. Thereafter the relationship accelerates. The twenty-two most generalized predators account for over half of all the trophic interactions. As in other networks, a few (nodes, people, internet web sites) are well connected, but most are not. How this scaling affects the propagation of disturbances through a food web has not yet been determined.

## THE CAUSES OF FOOD WEB PATTERNS

Chapter 10 summarizes the list of food web patterns—a list to which Joel Cohen, John Lawton, Gary Polis, George Sugihara, and others greatly extended and for which Cohen, Lawton, and I were able to review in our 1991 paper (Pimm et al., 1991).

We asked: Are food web patterns artifacts? There were good reasons for concern about the quality of data in published webs. Communities often contain thousands of species. Because published webs include only tens of trophic species, they are either highly aggregated or represent only a tiny part of the entire system. Aggregation is rife in many published webs; moreover, aggregation varies in extent from web to web and at different positions in the same web. Even when webs are detailed enough for most of their elements to be single biological species, the linkages are less often based on experimental evidence than on casual observations. While accepting these problems, we also concluded that the evidence overwhelmingly rejected the patterns being artifactual.

Much has changed in the last decade as with numerous studies paying particular attention to the problems we raised. Some of these involve complex food webs, such as the linkages in food webs centered on gall wasps and, in particular, how alien species fit into new communities (Schönrogge & Crawley, 2001). Douglas Reagan and Robert Waide tackle perhaps one of the most complex food webs of all—that of a tropical rain forest (Reagan & Waide, 1996).

If food webs are patterned, then how many independent web patterns are there? Which patterns are the consequences of others? What causes the patterns? Of the various ideas put forward, two require particular comments—the cascade model and web dynamics.

Cohen's cascade model focused on the static patterns of trophic interaction and assigns linkages at random that are subject to two constraints (Cohen et al., 1990). First, the model assumed that we can arrange the species a priori into a cascade or hierarchy such that a given species can feed on only species below it, and itself can be fed on only by species above it in the hierarchy. This ordering automatically precludes trophic cycles and decomposer loops. It does not specify whether any particular species must be top, intermediate, or basal (except the lowest and highest species in the cascade). Second, the model requires two parameters obtained empirically: the number of species and the linkage density. By assumption, connectance declines hyperbolically.

By assigning linkages randomly within these constraints, the cascade model generates quantitative predictions that we can compare rigorously with observed patterns. It correctly predicts the average and variance of the fractions of all species that are basal, intermediate, and top-predators; the average fractions of linkages that are basal-intermediate, basal-top, intermediate-intermediate, and intermediate-top; the modal length of chains from basal to top species; and the decline in the frequencies of interval and rigid-circuit predator overlap graphs as webs get larger.

The cascade model was not used to explore some features of webs such as omnivory, compartments, and the ratios of how many prey species a species exploits to how many predatory species that species suffers. It also gets some of the fine details wrong though, again, problems in the quality of the data may be partly responsible for the discrepancy. For example, the predicted frequencies of very short and very long food chains within a given web are too high. The assumption of constant linkage density is challenged by data on species-rich webs (see above).

The original formulation of the cascade model offered no explanation for the postulated trophic cascade. Body size is the likely candidate because predators are typically larger than their prey and parasites are smaller (Cohen et al., 1993). The success of the cascade model is that it shows that many food web patterns are the consequence of a few simple underlying assumptions. It begs important questions.

What determines the linkage density? Quantitative theory is used to explain why the average species apparently utilizes, and is utilized by, a predictable and fairly small number of other species, and it is crucial to a deeper understanding and ultimate testing of the model. One explanation is the dynamics of the webs. Most webs are static descriptions, but the communities they describe are not static—as *Food Webs* asserts from start to finish.

With a decade of hindsight, I chose to reformulate the explanations of dynamics in terms of food web assembly. Some species are successful at invading a community while others are not, and the successes may or may not cause extinctions of former residents. This process of assembly and disintegration may explain many of the empirical web patterns (Pimm, 1991, Chapter 10). Some food web structures are hard to invade—they will persist. Others are easy to invade—they

will not persist. In yet others, their instability means that some species will make quick exits.

In short, web dynamics is not an explanation incompatible with the cascade model. Rather, it suggests general mechanisms that limit linkage density and species richness and makes specific predictions about the details of web patterns.

## THE RISE OF COMPARATIVE AND EXPERIMENTAL FOOD WEB ECOLOGY

Perhaps the most surprising fact found in *Food Webs* is how far one can take simple food web models and the empirical data on food webs (so often collected for every purpose but comparison) and blend them into a cohesive whole. The explanation is not that the models are sophisticated and the data excellent, but that the processes are basic and powerful and the patterns obvious and ubiquitous. Nonetheless, further progress would require far better data and careful, well-documented studies that compared food webs over time and space. Crucially, there would need to be thoughtful experiments to confirm the insights of these comparisons.

In the last twenty years, there have been many experiments on particular systems: the 1992 Carpenter et al. study is one. Bob Paine's long experience with inter-tidal communities suggested another approach—documenting the strengths of the interactions between species. Such strengths are so conspicuously absent from most representations of food webs! Paine (1992) found that most interactions were quite weak ones interspersed with a few strong ones.

It was obvious even when *Food Webs* first appeared that container habitats—tree-holes, the contents of pitcher plants, and so on—would allow both comparative and experimental studies of food web structure. Small, self-contained, highly replicated, and technically simple—the preferred tool for sampling them is a turkey baster—these *phytotelmata* were ideally suited to the task.

If I can be permitted one personal recollection, it would be of sitting in a undergraduate lab at Oxford in a white lab coat sorting horribly messy tree-hole samples from Wytham Wood for a practical led by Roger Kitching, then a graduate student. I recall Charles Elton coming in. I think he said something to the effect of “ecologists don't wear lab coats” though perhaps this is just part of the legend. Certainly, I have never worn one since, nor do I allow them in my lab. (The offending article still hangs in a wardrobe in my parents' house.) So, yes, I remembered Roger when I met him a decade later at a conference.

In a few paragraphs, I cannot do justice to his excellent new book *Food Webs and Container Habitats: The Natural History and Ecology of Phytotelmata* (Kitching, 2000). It is a superb natural history of these communities—Elton would be proud of his former graduate student—and a 100 pages are devoted to describing “the phytotelm bestiary.” Almost another 100 pages describe the different kinds of container habitats and their environments. Thus armed, Kitching neatly overcomes most of the uncertainties of previous food web studies.

Better than any other study, Kitching demonstrates how gradually increasing spatial scale alters the explanations for food web structure. One of the best insights is offered by a figure that shows the local food web template—all the species and their potential trophic interactions at the location. A particular tree-hole’s food web is “ghosted” onto this. A particular tree-hole will only have a subset of the species (and so their interactions), though this subset will change both seasonally and capriciously. The local food web itself is constrained by what species are present regionally. Particularly, for the food webs inside the pitcher plants of the genus *Nepenthes*, the Old World tropical distribution of species centered on Malaysia affects the number of coexisting species. That number also affects the number of species that might be found within an individual pitcher. In short, there are progressively larger scales that set the possible food webs that may be present in individual holes, in a food, or in a region, and there are factors—of the kind discussed here—that effect whether the full web will be realized.

### CONSEQUENCES OF WEB PATTERNS

If food webs have structure, then so what? “Why is network anatomy so important to characterize?” Strogatz asks. “Because structure always affects function,” he answers. That answer lies in *Food Webs*, and I lifted it from Charles Elton (1958).

Earlier in this foreword, I asked you to skip parts of *Food Webs*. In writing those parts, I struggled to define “stability” in some operational way. In addition to local dynamical stability, I suggested “species deletion stability,” and I mentioned various experiments. None of this was at all satisfactory. Even less so were those couple of pages in Elton (1958) where he asserted that more complex systems would be more stable—all on the basis of a few completely unrelated anecdotes. The answer, of course, was that the recipe of stability outlined in *Food Webs* separated systems that would likely persist in Nature from those that would not. It was silent about how we might compare natural systems. The answer came from the recognition that “stability” also meant other things—resilience, variability, persistence, and resistance—and that these measures could be applied to different variables—species abundances, total biomass, species composition. Elton’s anecdotes were perceptive, but very incomplete. It wasn’t until I understood the full range of meanings of stability that I could appreciate the connections he was trying to draw. It took me a decade before I could present the larger case that food web structure affects population and community dynamics in my next book *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities* (Pimm, 1991). The arguments presented there are still hotly debated—the role of species numbers in affecting how resistant species are to change being the most recently controversial. (The papers of Tilman et al., 1997, Hector et al., 1999, and Huston et al., 2000 are sufficient to give the flavor of this debate.) And that’s just on the number of species.

How connected food webs are, how long their food chains are—and so on

down the list—are all factors that likely affect how natural communities change and respond to changes. In a world where we are changing so much so quickly, understanding natural complexity—what it means, how we are simplifying it, and what will be the consequences—is a manifestly important task.

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