10
FOOD WEBS

Most of this book has been concerned with horizontal linkages in plant and animal assemblages. In other words, patterns of species richness (Chapter 8), diversity (Chapters 2 and 3), co-occurrence (Chapters 7 and 9), resource utilization (Chapters 4 and 5), and morphology (Chapter 6) of taxonomic or ecological guilds of species that potentially compete for resources and are thus at the same trophic level. Null models are an essential tool for delineating expected patterns in noninteractive assemblages of potential competitors.

A different perspective on community structure emphasizes the vertical linkages, that is, the identities and interactions of predators and their prey in an assemblage. Food web diagrams that depict binary interactions of "who eats whom" (Figure 10.1) have a long history in ecology, dating back to Shelford (1913). These diagrams have prompted a number of interesting ecological questions. What determines the number of links in a food web, and how is this related to the number of species in the web? Are certain web topologies more mathematically or biologically stable than others? What determines the maximum food chain length within a web? Does web structure vary systematically between terrestrial and aquatic habitats, or those with two- and three-dimensional structure?

Although the literature on food webs and on the ecological niche has developed somewhat independently, they are conceptually linked, because energetic constraints and prey availability are often the ultimate causes of niche divergence among competitors. For example, Hutchinson's (1959) seminal paper that suggested a constant size ratio between coexisting competitors (see Chapter 6) was primarily concerned with the way that energy flow ultimately constrains the total number of species in an assemblage. Assemblage patterns of qualitative niche overlap in diet can be directly equated with food web links. From food web diagrams, Cohen (1978) derived measures of niche overlap (and tested them against null models) that depicted the qualitative similarity in diet among a set of consumers at the same trophic level. Some of the detailed null models of food webs and biogeography are also similar. As an example,
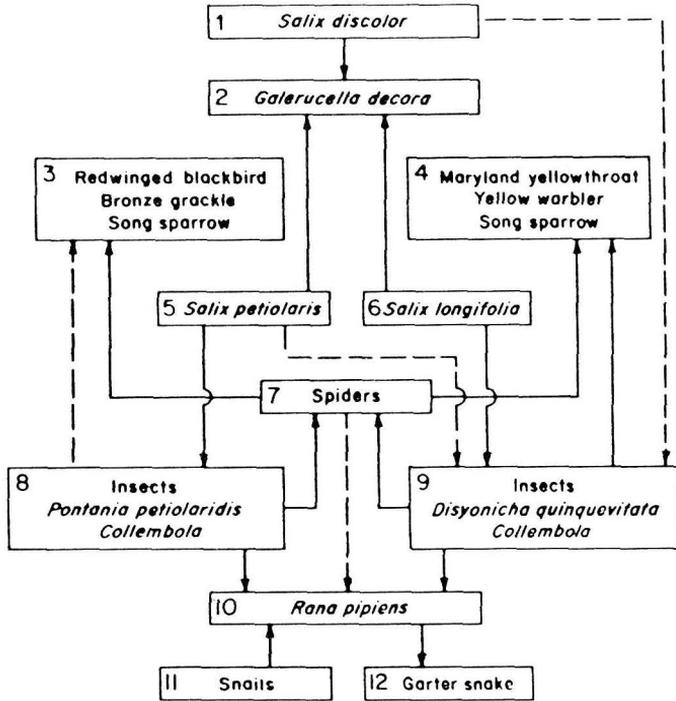
Figure 10.1. A simple food web for a willow forest (Bird 1930). Arrows are directed from prey to predator. Dashed lines are tentative linkages. Numbers indicate "kinds" of organisms used in food web analyses. Simplified food webs such as this have formed the basis for many analyses of web structure. From Cohen, J. E. *Food Webs and Niche Space*. Copyright © 1978 by Princeton University Press. Reprinted by permission of Princeton University Press.

Cohen's (1978) six randomization algorithms for food web matrices are very similar to some of Simberloff's (1978a) null model protocols for presence-absence matrices of co-occurring species.

In spite of these similarities, the influence of null models on niche and food web studies has differed. In niche analyses, null models arrived relatively late in the picture. By the time null models were used in niche overlap studies, theoretical principles were well established and explanations for assemblage patterns had often been uncritically accepted. Because null model tests often contradicted accepted interpretations of niche overlap patterns, they were highly controversial (see Chapters 4–7).

Null models also challenged conventional wisdom in food web studies, although their use has been less contentious, perhaps because they appeared so

early in the food web literature (Stuart L. Pimm, personal communication). In particular, early null models (Gardner and Ashby 1970; May 1972) failed to garner support for the popular contention that complexity of food webs leads to stability.

Null models were also essential to the early analyses of empirical patterns in the food web literature (Cohen 1978; Pimm 1980a, 1982). For example, many published food webs have only two or three trophic links. In contrast, webs of the same size that are randomly connected typically have more than three links (Pimm 1980a). Null model analyses led to a catalog of food web patterns that did not seem to be a simple consequence of the number of species in the sample. Several recent studies have called these patterns into question (Sprules and Bowerman 1988; Martinez 1991; Polis 1991). However, this controversy surrounds the quality of the original data (Paine 1988), not the null models that were used to establish the patterns.

This chapter provides a brief overview of the food web and stability literature, as it relates to null models. For more extensive coverage, see Pimm (1982) and Pimm et al. (1991). We first describe the use of null models in the development of food web theory. Next, we describe analyses of published food web data, and the empirical generalizations that emerged from these studies. We then consider null model analyses of community stability, as measured by the community matrix, and by temporal data on the rank abundances of species. Finally, we summarize some recent empirical controversies in the literature and suggest how null models might be applied in future food web studies.

STABILITY ANALYSES OF MODEL FOOD WEBS

Both Elton (1958) and MacArthur (1955) popularized the notion that complex ecological systems are more stable than simple systems. Elton (1958) summarized a diverse set of observations from mathematical, laboratory, and field studies to establish this idea. He noted that simple predator-prey models predicted fluctuating populations and concluded that more complex models would lead to stable populations. He also pointed to laboratory experiments, such as Gause's (1934), which demonstrated how difficult it was to achieve stable coexistence of predators and prey. Turning to field systems, Elton (1958) argued that invasions and outbreaks of pest species were much more common in agricultural systems that had been modified and simplified by human activity. He also suggested that insect outbreaks were characteristic of simple temperate forests but not of complex tropical forests (but see Wolda 1978).

Elton (1958) described several measures of "stability": (1) a tendency for populations to return to an equilibrium value when perturbed; (2) a small variance in population size; (3) the ability of an assemblage to resist invasion; and (4) the change in populations of an assemblage following an invasion. By "complexity," Elton (1958) meant both the number of species in the web and the number of links in the web (connectance). Much of the confusion over the relationship between stability and complexity arose because there are many ways that ecological and mathematical stability can be defined, and because the relationship between stability and complexity depends critically on how these definitions are constructed (Pimm 1984b).

MacArthur's (1955) approach was more mathematical and formal than Elton's (1958). By stability, MacArthur (1955) meant the degree to which species abundances changed when the abundance of one species in the web was greatly perturbed. His argument was that complex systems with many different pathways for energy flow were more stable than systems with few pathways. For example, if the population of a single prey species is reduced, a polyphagous predator can shift to alternative prey. Therefore, webs with polyphagous predators should be relatively stable. In contrast, webs with monophagous predators should be less stable, because perturbations in prey abundance will cause more violent fluctuations in predator abundance.

MacArthur (1955) proposed two hypotheses for community stability. First, biotic interactions among the species in the web can impart stability. This hypothesis underlies mathematical analyses of food web structure and provides a justification for the use of the Lotka-Volterra equations and the corresponding community matrix (Levins 1968). The Lotka-Volterra equations are the simplest first-order differential equations that describe pairwise interspecific interactions. Interactions such as predation, competition, and mutualism among species pairs can be modeled by setting interaction coefficients to positive or negative values. The community matrix contains all these interaction terms, plus terms for self-limitation of each species along the diagonal of the matrix.

MacArthur's (1955) second hypothesis was that stability of the food web "can be intrinsic to the individual species." An assessment of this hypothesis ultimately requires knowledge of abiotic factors and physiological limitations to population growth of each species. MacArthur's (1955) second hypothesis acknowledges that food web stability may not be a biological property of interactions among species, but of the interaction of species with their physical environment.

In this view, food web patterns are an epiphenomenon, a secondary reflection of the habitat and abiotic factors that allow sets of species to persist together. Although this hypothesis does not deny the interaction of predators

and their prey, it does imply that trophic and competitive interactions do not determine the stability of the system. In fact, food webs for some real communities do seem to be mathematically unstable (Auerbach 1979). MacArthur (1955) did not develop his second hypothesis any further, but it stands as an excellent null hypothesis for the study of food webs.

Random Connectance: An Early Food Web Null Model

The hypothesis that stability begets complexity corresponds to the naturalist's intuition about the "balance of nature" (Pimm 1991). Perhaps for this reason, the stability-complexity hypothesis was accepted uncritically until the early 1970s, beginning with the publication of a brief, but important, paper by Gardner and Ashby (1970). They were concerned with the stability and organization of large, complex systems, such as airports, human brains, and urban slums. They began with a matrix of pairwise interaction coefficients for systems of four, seven, and 10 variables. For a noninteractive system, they first set all off-diagonal elements to zero, and then assigned a random negative number to the diagonals of the matrix. If the diagonal elements are negative, the system is locally stable to small perturbations because each component is self-limiting. This would correspond in a food web to a set of species that do not interact with one another but have stable, self-limiting populations.

Next, Gardner and Ashby (1970) defined connectance as the percentage of nonzero off-diagonal elements. For a given connectance, they filled the matrix with random numbers drawn uniformly from the range −1.0 to 1.0, constructing a system with arbitrary positive and negative linkages. For each such randomly constructed matrix, Gardner and Ashby (1970) calculated local stability, the tendency for populations to return to equilibrium values following a small perturbation in numbers. The proportion of randomly constructed matrices that were stable for a given matrix size was then plotted against connectance.

For all the matrix dimensions they investigated, stability decreased with increasing connectance, a direct contradiction of MacArthur (1955) and Elton (1958). Not only did stability decrease with connectance, but the larger the matrix, the steeper the decrease (Figure 10.2). For very large matrices, Gardner and Ashby (1970) suggested there may be some critical threshold of connectance, above which complex systems will be unstable.

May (1972, 1973) generalized their results and applied them specifically to ecological systems. He showed that as the number of species becomes large, there is indeed a critical limit to connectance, although that limit depends in part on α, the average interaction strength in the community matrix. The assemblage will usually be stable if

$$\alpha\sqrt{SC} < 1 \qquad\qquad\qquad (10.1)$$

where α is the average interaction strength, S is the number of species, and C is the connectance.

These early food web simulations do not conform strictly to the null model definition given in Chapter 1. For one thing, these were not stochastic food web models. Although the coefficients for the community matrix were assigned randomly, the criterion of stability was entirely deterministic. Moreover, the simulation results were never compared with empirical data. Nevertheless, the stability-complexity hypothesis was so thoroughly engrained in the ecological literature (Goodman 1975) that these simulations served as an important null hypothesis that described the behavior of systems with arbitrary linkages.

Constraints and Biological Realism

What was the response to the finding that model stability decreased with complexity? The common criticism was that the models were "too null." In other words, the simulations included communities that were not biologically
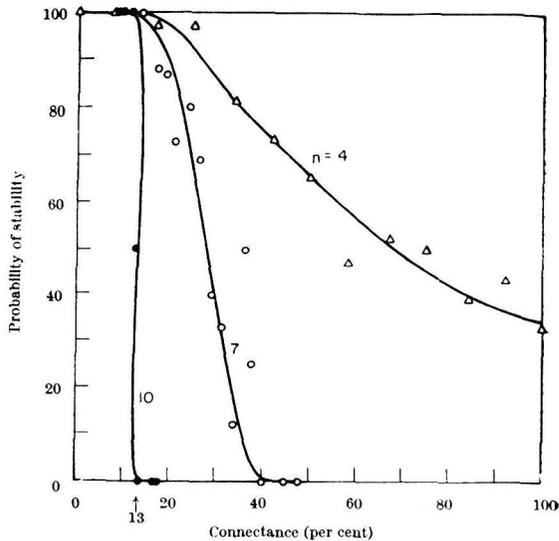

Figure 10.2. Relationship between the probability of stability and the connectance of a web of size 4, 7, or 10. Note that as connectance is randomly increased, stability decreases. This early null model contradicted conventional wisdom about stability-complexity relationships. From Gardner and Ashby (1970). Reprinted with permission from *Nature* 228:784, Figure 1. Copyright © 1970, Macmillan Magazines Limited.

reasonable. For example, if the community matrix is to represent a real community, the equilibrium population sizes must not only be stable, they must also be greater than zero. Gardner and Ashby (1970) did not impose this constraint of "feasibility" on their simulations. Roberts (1974) imposed the constraint, and his results suggest that feasible matrices tend to be stable, although his simulations did not directly vary connectance. However, Roberts's (1974) choice of parameters was restricted, and his results may not be general (Gilpin 1975; Goh and Jennings 1977).

A second criterion for a "biologically reasonable" simulation is that it obey basic principles of thermodynamics and energy transfer, which dictate that energy transfer from prey to predator is never 100% efficient. This restriction means that the magnitude of losses to the prey population must be greater than the corresponding gains to the predator population. DeAngelis (1975) built model food webs that incorporated energy transfer, imposed a hierarchical food web structure, and assumed that higher trophic levels were strongly self-damping. He also incorporated donor control, in which predators have only a limited ability to control their prey. These restrictions correspond to only a small subset of possible food web structures. When these constraints were imposed and coefficients were randomly assigned, stability sometimes increased with complexity.

Still another biologically reasonable constraint was that trophic loops not be allowed. In such a loop, species A eats species B, B eats C, and C eats A. The stability of models that forbid loops can increase with increasing species richness (Lawlor 1978). Although the early food web literature characterized these trophic loops as biologically unreasonable (Lawlor 1978; Pimm 1982), in fact they are quite common (Martinez 1991; Polis 1991), particularly for predators with size-structured populations or complex life histories (Polis et al. 1989). Thus, to some extent, modeling efforts were guided by preconceived ideas about the structure of food webs in nature.

Monte Carlo Modeling Strategies

Even in a simple food web, it is impossible to evaluate systematically all combinations of interaction coefficients. The Gardner and Ashby (1970) method has been used effectively to examine the general properties of other food web models. A common strategy has been to define the model and restrict either the sign or the range of values possible for the interaction coefficients. Within these constraints, the interaction coefficients are then chosen randomly and the mathematical stability of the resulting model is assessed. This process is repeated for a large set of community matrices. The result is an estimate of the

proportion of models that are stable for a small, but random, subset of possible coefficients.

These analyses have revealed a bewildering array of possible answers to the stability-complexity question, although a few generalizations are apparent (Pimm 1982). The key elements determining stability in community matrices are often the diagonal or self-limiting elements. Donor-control equations, which characterize many real food webs (Hawkins 1992), tend to be more stable than Lotka-Volterra equations (Pimm 1982). Different answers to the stability-complexity question also arise if one uses the criterion of global stability, local stability, or species deletion and addition stability (Pimm 1984b).

The early simulation work on food web structure also prompted a search for empirical patterns. In particular, May's (1972) simple equation (10.1) was seized upon as a new empirical rule for community structure. If interaction strength is constant, then the product of S and C should be constant in stable assemblages. Thus, if mathematical stability is important in determining food web structure in the real world, a graph of connectance versus species richness should form a hyperbola. However, the search for this pattern seems premature unless the relationship between S and C in assemblages that are not dynamically constrained has been studied. Later in this chapter, we examine null models of the relationship between connectance and species richness that do not impose dynamical constraints but nevertheless predict a hyperbolic relationship.

NULL MODEL ANALYSES OF THE COMMUNITY MATRIX

The mathematical definition of local stability has been difficult to test in nature; small, controlled perturbations are difficult to achieve in field experiments and hard to recognize in time series of fluctuating populations. A more indirect approach is to take empirical community matrices and compare their properties with randomized matrices that are not subject to any dynamical constraints. The community matrix requires estimates of α_{ij}, the per capita effect on the growth rate of the population of species j caused by a small increase in the population of species i. In the absence of direct experimental manipulation, these coefficients can be estimated from resource utilization data (Levins 1968) or from multiple regression analyses in which the abundances of the component species are measured at different times (Schoener 1974d; Crowell and Pimm 1976).

Both methods have problems. As discussed in Chapter 4, overlap in resource use may or may not reflect competition (Sale 1974), and the estimates may be biased if the true niche overlaps are multidimensional (May 1975b). Regres-

sion estimates may also be biased and confounded by the presence of habitat heterogeneity (Rosenzweig et al. 1984; Rosenzweig and Abramsky 1985; Abramsky et al. 1986). Still, in the absence of experimental manipulation, these measures do provide some information about the nature of species interactions. Although the theory behind these concepts has been developed for predator-prey food webs, most of the data have come from studies of competitive interactions within a single trophic level, perhaps because overlaps within a single trophic level are easier to estimate quantitatively.

Lawlor (1980b) presented an ambitious null model analysis of the community matrix. His study asked two questions: first, is local (Lyapunov) stability important in real communities? If so, then the observed community matrix should be more stable than a corresponding set of randomized matrices. This is a different issue from that of simply establishing whether or not the observed matrix is stable. Second, if local stability is relevant to community structure, what makes observed communities more stable than analogous random communities?

Lawlor (1980b) analyzed 11 overlap matrices calculated by Cody (1974) for bird communities. The symmetric overlap matrices were based on observations of habitat, vertical foraging range, and feeding pattern. The stability of each matrix was measured as the minimum eigenvalue, which must be greater than zero for persistence. By this criterion, 9 of the 11 communities were stable. However, relative stability, as measured by the size of the eigenvalue, decreased with increasing species richness, in accord with May's (1972) result. Nevertheless, observed eigenvalues were always larger than eigenvalues for randomized communities (Figure 10.3). The interpretation of this result is a bit ambiguous, because some of the observed stability was a mathematical consequence of using a symmetric overlap index (May 1975b). On the other hand, this property was present in the randomized matrices as well.

A more powerful method is to directly randomize the resource utilization data, rather than rearrange the resulting competition coefficients. For this analysis, Lawlor (1980b) used the lizard resource utilization data of Pianka et al. (1979). He reshuffled the data with four randomization algorithms, all of which are discussed in Chapter 4. As in Cody's (1974) bird communities, observed stability decreased with increasing species richness, but was greater than expected stability generated by the null model. Average α (interaction terms) was also significantly lower than expected, and relative stability decreased with increasing average α and with increasing variance of α.

These patterns are important because Levins (1968) had suggested that coevolution should lead to a decrease in α variance. However, the observed α variances did not differ from expected except under RA1, the most liberal
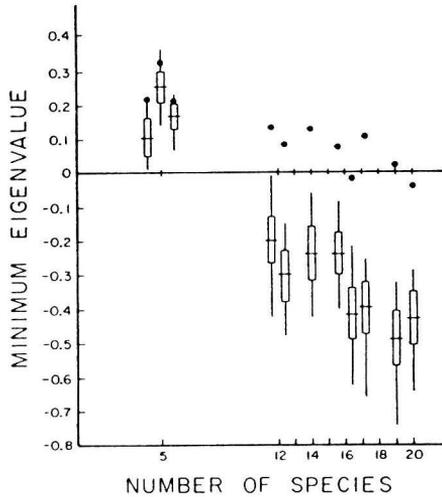
Figure 10.3. Relationship between species number and minimum eigenvalue of the community matrix, a measure of local stability. Solid circles indicate observed bird communities (Cody 1974). The mean, standard deviation, and range of the eigenvalue are also shown based on 100 randomizations of the observed community matrix. Communities with more species had lower stability, in accord with Gardner and Ashby's (1970) results. However, the observed community matrix was always more stable than randomized matrices of the same size. Reprinted by permission of the publisher from Lawlor, L. R. 1980. Structure and stability in natural and randomly constructed competitive communities. *American Naturalist* 116:394–408. Copyright © 1980 by The University of Chicago.

simulation routine. Lawlor (1980b) concluded that neighborhood stability was important in local community structure, and that competition had shaped communities by reducing the average overlap (though not the variance) between competitors.

Hallett (1991) used a similar analysis of community matrices for six small mammal communities for which interaction coefficients had been estimated by the regression method. He considered not only local stability, but also global stability (the tendency to return to equilibrium following a large perturbation) and resilience (the return time to equilibrium). He also measured the community covariance (Vandermeer 1972) and the presence of indirect pathways (Lawlor 1979). These pathways represent higher-order interactions that cannot be predicted on the basis of pairwise coefficients (Lawlor 1979; Holt 1984). For each matrix, he randomly interchanged two of the coefficients, recalculated the community metrics, and then repeated this procedure until all possible

distinct arrangements of the original matrix were produced. These matrices contained only three, four, or nine species, so it was not prohibitive to generate all of the matrix permutations. A second, more general set of randomizations filled the community matrix with elements chosen from segments of a random uniform distribution, representing strong or weak competitive effects. These simulations revealed the likelihood of finding indirect competitive pathways as a function of the number of species, the magnitude of competitive effects, and the structure of the matrix.

How did the observed mammal communities compare to these simulated assemblages? Both local and global stability were always significantly greater than expected, and return times were also unusually short compared to randomized matrices. Although total species number varied among the different assemblages, each community had only three or four competing species. Consequently, connectance fell as S was increased. However, the average interaction strength did not differ with S. This result implies that reduced connectance was a major factor that ensured stability of larger assemblages.

Community covariance was minimized for only one of Hallett's (1991) six assemblages. However, covariance seemed to be attributable to competitive structure: five of the six community covariances were negative and associated with asymmetrical competitive hierarchies. Finally, the observed matrices differed greatly from the simulated in the frequency of indirect pathways. The simulated and the randomized matrices had a high percentage of indirect pathways, and this percentage increased if the average interaction strength was higher. These pathways were relatively uncommon in two of the six real matrices and completely absent in the other four. Thus, observed assemblages tended to be relatively stable and resilient. They were also simple, with few or no indirect pathways, relatively few directly interacting species, and competitive hierarchies that usually were linear and asymmetrical (Figure 10.4).

The patterns revealed by the null model tests of Lawlor (1980b) and Hallett (1991) are intriguing, but it may be too great a leap of faith to assess community stability in terms of interaction coefficients, particularly when these are calculated from resource utilization data. Abrams (1981) questioned the use of resource utilization and the narrow criterion of neighborhood stability for analysis of the community matrix, although Hallet's (1991) results seem to be robust to the definition of stability. Abrams (1981) also suggested that the matrix rearrangements were biased toward revealing stability, and that some competitive structure would not be revealed by this method. We agree that in the absence of experimental manipulations of density, it may be difficult to say much about community stability. On the other hand, even nonexperimental overlap matrices contain a great deal of biological information, and the null

A. CG ⟶ PM ⟶ MP

B. ON ⟶ TS ⟶ PL

C. MP ⟶ ZH ⟶ PL ⟶ MM

D. RM ⟶ OCO ⟶ OCA

E. ST
           ↘
      MP ⟶ PM
         ↗
  ZH

F.   PP
           ↗
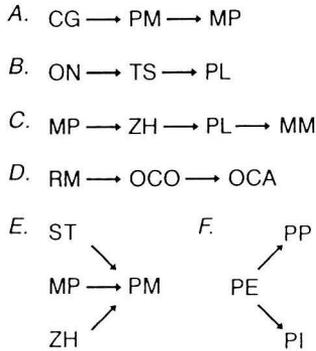   PE
           ↘
             PI

Figure 10.4. Competitive hierarchies in mammal communities. These linear (A–D) and branched (E–F) hierarchies are significantly smaller and more linear than predicted by null models. (**A**) Maine coastal island; (**B**) Tennessee temperate forest; (**C**) Maryland barrier island; (**D**) Venezuelan premontane humid forest; (**E**) North Dakota grassland; (**F**) Chihuahuan Desert. CG = *Clethrionomys gapperi;* PM = *Peromyscus maniculatus;* MP = *Microtus pennsylvanicus;* ON = *Ochrotomys nuttalli;* TS = *Tamias striatus;* PL = *Peromyscus leucopus;* ZH = *Zapus hudsonius;* MM = *Mus musculus;* RM = *Rhipidomys mastacalis;* OCO = *Oryzomys concolor;* OCA = *Oryzomys capito;* ST = *Spermophilus tridecemlineatus;* PE = *Peromyscus eremicus;* PP = *Perognathus penicillatus;* PI = *Perognathus intermedius.* From Hallett, J. G. 1988. The structure and stability of small mammal faunas. *Oecologia* 88:383–393, Figure 1. Copyright © 1988 by Springer-Verlag GmbH & Co. KG.

model tests can at least establish emergent patterns in the data that are relevant to discussions of stability.

Plant ecologists have been able to make more progress in experimentally measuring species effects on one another. The classic tool for studying species interactions in plant assemblages is the de Wit (1960) replacement series. In these experiments, seeds from a pair of species are planted in different ratios at constant density. Short-term measurements of output (growth, biomass, or seed production) are compared for species grown at a constant total density in monoculture and in various proportions in a two-species mixture. The ratio of growth in a mixed-species planting to growth in a monoculture has been interpreted as a measure of the Lotka-Volterra competition coefficients (Harper 1977).

There are some problems with this approach. The ratio diagrams address frequency, not density of competitors (Inouye and Schaffer 1980). They do not indicate the temporal dynamics of species interactions (Connolly et al. 1990), and they may exaggerate the competitive abilities of large plants, particularly in short-term experiments (Grace et al. 1992). Nevertheless, pairwise studies of

competitive interactions are the most powerful approach to the study of community structure and stability, particularly when all the species in an assemblage have been experimentally tested in pairs.

Shipley (1993) used a simple null model to examine structure in competitive matrices that are derived from de Wit output experiments. In these binary competition matrices, the effect of species A on species B is assigned a one if species A grows better in mixture than in monoculture. A zero is assigned otherwise. Thus, for any given species pair, the two interaction coefficients specify four possible outcomes, corresponding to the four theoretical possibilities of the two-species Lotka-Volterra competition equations (species A wins, species B wins, stable coexistence, unstable coexistence). Shipley (1993) looked for the presence of "completely transitive" pathways in such matrices. In a completely transitive pathway, the species can be arranged in a strict hierarchy of competitive relationships, such that species A outcompetes species B, B outcompetes C, and A outcompetes C. If C could outcompete A, the path would be intransitive. The ecological significance of completely transitive pathways is that all species in such a pathway can be competitively excluded except for the single competitive dominant.

For his null model, Shipley (1993) randomly filled the competition matrix with ones and zeros, based on their frequency of occurrence in the original matrix. For a given frequency of "winning" interactions, the state of each coefficient was independent of the state of any other coefficient. The null model generated the expected number of pathways of a given length for an assemblage with randomly structured competitive hierarchies.

Shipley (1993) applied this test for transitive pathways to 10 published plant competition matrices that were based on de Wit plantings. The results were clear-cut: all but one matrix had significantly more transitive pathways than predicted by the null model. The finding that competitive interactions between species are often organized in linear hierarchies is very similar to Hallett's (1991) results for mammal assemblages, even though the null models and metrics used were rather different.

In summary, null model analyses of community matrices have generated consistent results for diverse assemblages of plants, mammals, lizards, and birds. Most of these matrices are more mathematically stable than predicted by chance. Compared to the universe of possible species interactions, those that are observed tend to be simple linear hierarchies involving only a small subset of species. Interestingly, these patterns are qualitatively in line with the original stability-complexity models of Gardner and Ashby (1970) and May (1972).

How these stability properties relate to the persistence of assemblages in nature is another matter entirely. For example, Rabinowitz et al. (1984) used de

Wit plantings to estimate the competitive abilities of sparse and common prairie grasses. Contrary to their expectations, the uncommon species were superior, not inferior, competitors. Thus, these grass species were rare in nature in spite of, not because of, their competitive abilities. At least in this assemblage, factors other than species interactions, and hence community stability, were responsible for relative abundance.

PERSISTENCE STABILITY AND THE CONCORDANCE OF SPECIES RANKS THROUGH TIME

Although mathematical stability has been difficult to address with field data, many empirical studies have explored the idea of community persistence (Pimm 1984b)—the tendency for species composition and rank abundances of species to remain constant through time. Empirical tests of community persistence have not relied on mathematical stability analyses, but they have been interpreted in a consistent theoretical framework. Assemblages for which species rank abundances remain constant through time have been described as equilibrial, deterministic, and controlled by strong biotic interactions, whereas assemblages in which rank abundances repeatedly change are nonequilibrial, stochastic, and not controlled by species interactions (Grossman 1982; Wiens 1984). In hindsight, these conclusions about underlying forces controlling community structure are premature. In particular, a pattern of rank concordances does not necessarily imply deterministic, biotic interactions (Yant et al. 1984; Ebeling et al. 1990). Early on, MacArthur (1955) pointed out that autecological factors independently stabilizing the abundance of each species can generate assemblage stability. However, the temporal pattern of abundances is important in that it can at least give insight into whether or not assemblages are at an equilibrium state.

Grossman (1982) popularized the analysis of species ranks in a study of California tidepool fishes. Tidepools were repeatedly defaunated and sampled over a 29-month period. Grossman (1982) found that despite repeated defaunation, the assemblage returned to a characteristic species composition and relative abundance (Figure 10.5). From this pattern, he concluded that the intertidal fish assemblage was both resilient and persistent. In contrast, 12 years of samples of stream fishes from a single site in Indiana showed no concordance of rank abundances through time (Figure 10.6), and Grossman et al. (1982) concluded that this assemblage was probably regulated by stochastic factors.

Perhaps because the nonequilibrium conclusion was unpopular, the second, but not the first, of Grossman's studies provoked a series of rebuttals. Critics
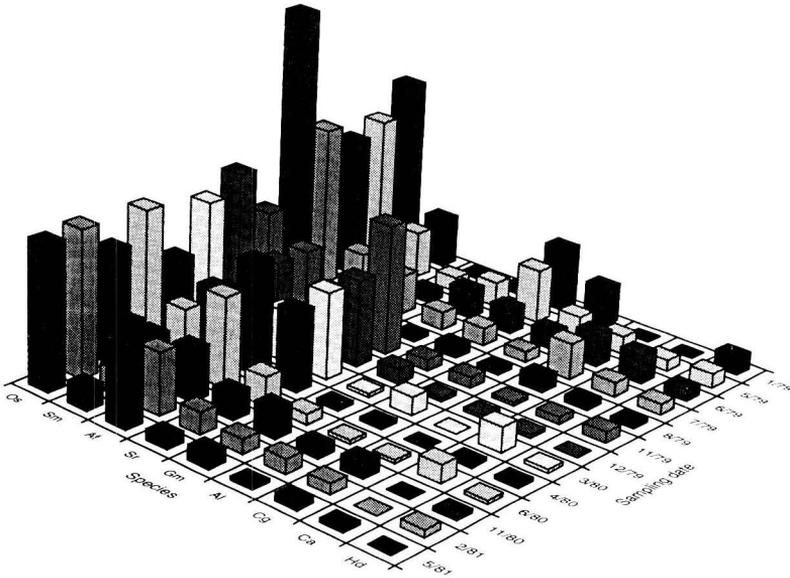
Figure 10.5. Relative abundance of resident coastal tidepool fishes. The height of each bar is proportional to the relative abundance of a species collected on a particular sampling date. By Kendall's W, the abundance rankings of the species were significantly concordant among censuses. Os = *Oligocottus snyderi;* Sm = *Scorpaenichthys marmoratus;* Af = *Apodichthys flavidus;* Sr = *Sebastes rastrelliger;* Gm = *Gibbsonia metzi;* Al = *Artedius lateralis;* Cg = *Clinocottus globiceps;* Ca = *Clinocottus analis;* Hd = *Hexagrammos decagrammos.* Data from Table 3 of Grossman (1982).

complained that guild designations (Herbold 1984) and choice of site, season, and sampling methods (Rahel et al. 1984; Yant et al. 1984) exaggerated the patterns of variability in this assemblage. The sampling issues raised by these critics are probably typical of any study that spans a 12-year period, and Grossman et al. (1985) responded effectively to many of the criticisms.

Important statistical issues were raised as well. Grossman (1982; Grossman et al. 1982) used Kendall's W as a statistical test of rank concordance. For this test, the null hypothesis is that different orderings of species rank abundances are equally probable from one year to the next. The alternative hypothesis is that ranks are unusually concordant among years. One problem with applying Kendall's W to assemblage data is that the test is sensitive to sample size (Rahel et al. 1984). In particular, if many rare species are included in the analysis, the test will often reveal concordance, even though there may be important shifts in rank abundance of the more common species. This is not necessarily an artifact. Indeed, one of the critical questions in studies of community stability is why
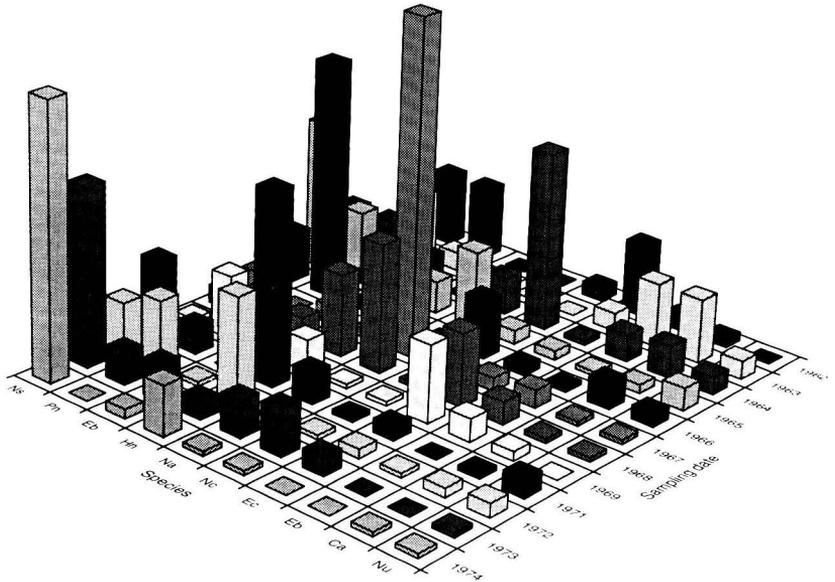
Figure 10.6. Relative abundance of common Indiana stream fishes. The height of each bar is proportional to the relative abundance of a species collected on a particular sampling date. By Kendall's W, the abundance rankings of the species were not significantly concordant among censuses. Ns = *Notropis spilopterus*; Pn = *Pimephales notatus*; Eb = *Etheostoma blennoides*; Hn = *Hybognathus nuchalis*; Na = *Notropis atherinoides*; Nc = *Notropis chrysocephalus*; Ec = *Etheostoma caeruleum*; Eb = *Ericymba buccata*; Ca = *Campostoma anomalum*; Nu = *Notropis umbratilus*. Data from Table 4 of Grossman et al. (1982).

rare species never become widespread and abundant. If assemblages are carefully defined a priori, and sample-size effects are examined, rare species need not bias the test.

A second difficulty with Kendall's W is that the test results are sensitive to the underlying species abundance distribution (Jumars 1980). For this reason, Jumars (1980) recommended testing the data against an appropriate sampling model that treats fluctuations in relative abundance as sampling error. The test is a simple chi-squared analysis of a species × time table, in which each entry is the number of individuals sampled of a particular species. The null hypothesis is that all the samples are drawn from the same species abundance distribution. The alternative hypothesis is that the samples come from different distributions, causing relative abundances to change through time. The test may be problematic because individuals are rarely sampled independently of one another in field studies. Pooling collections and treating the data as in-
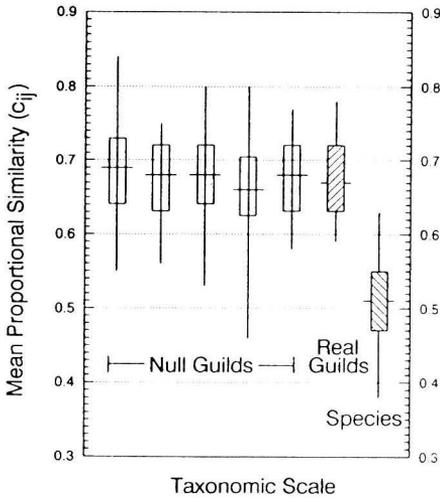
Figure 10.7. Proportional similarity between censuses of coral reef fishes. Similarity is higher when species are organized into guilds (right hatching) than when they are counted individually (left hatching), but this is a sampling effect found in random guild assignments. Horizontal lines are means, vertical lines are ranges, and vertical bars are standard errors. From Sale, P. F., and J. A. Guy. 1992. Persistence of community structure: what happens when you change taxonomic scale? *Coral Reefs* 11:147–154, Figure 1. Copyright © 1992 by Springer-Verlag GmbH & Co. KG.

dependent may greatly inflate the Type I error (Kramer and Schmidhammer 1992), making the test overly sensitive to minor fluctuations in abundance.

Other null models have been used to examine temporal changes in assemblage structure. For example, Sale and Douglas (1984) found that the species composition of Australian coral reef fish assemblages varied greatly through time, so that similarity indices between consecutive samples were usually low. In comparison with a null model, species associations changed substantially from census to census (Sale and Steel 1989). Sale and Guy (1992) explored the possibility that assemblage structure was obscured by a dilution effect, and postulated that species classified into ecological feeding guilds might reveal more temporal concordance in composition. Similarity indices at the guild level were indeed higher than for the total set of species. However, this appears to be entirely an artifact of sample size, because random assignment of species to pseudoguilds yielded comparable similarity indices (Figure 10.7).

Ebeling et al. (1990) built several null models that directly evaluated the behavior of Kendall's *W*. Their data consisted of annual estimates of abundance for a guild of five species of surfperches that inhabited rocky subtidal reefs off

the California coast. Kendall's W indicated a high degree of concordance in rank abundances, with one species (*Embiotoca jacksoni*) retaining first rank in 12 different censuses. Random census data were constructed by generating artificial population tracks for each species. Each species abundance was allowed to change according to a proportion drawn uniformly from a −1.0 to 1.0 range, subject to constraints in four different null models.

Models 1 and 2, which retained autecological population limits for each species, typically generated large, statistically significant values of W, and there was a substantial probability (0.21 and 0.35, respectively) of always finding the same species in the first rank. Models 3 and 4, which permitted more violent fluctuations in species abundance, had substantially lower values of Kendall's W. The analyses of Ebeling et al. (1990) demonstrate that deterministic species interactions need not be invoked for assemblages in which species rank abundances are strongly concordant through time.

Finally, Evans (1988) took a multivariate approach to analyzing changes in community structure through time. Grasshopper assemblages in six tallgrass prairie sites were sampled by sweep net from 1982 to 1986. Evans (1988) used a detrended correspondence analysis to ordinate the relative abundances of species at each site. In this analysis, assemblage structure appeared as a set of six connected vectors when plotted on the first two axes of the ordination. Next, Evans (1988) adapted a null model by Kareiva and Shigesada (1983), which was originally used to describe insect movement as a random walk in two-dimensional space. Observed vector lengths and angular displacements were randomly sampled to construct a correlated random walk in two-dimensional space. The squared displacement from an initial position increased with time in this null model. In contrast, the observed vectors for the grasshopper assemblages were steady or slightly decreasing across years (Figure 10.8). The results suggest that changes in the frequencies of different species were less than expected by chance. However, the patterns are difficult to interpret, because the detrended correspondence analysis obscures the pattern of change for individual species and because the null model of random change in community structure is not based directly on changes in abundance of individual species.

In summary, a variety of statistical tests and null model procedures reveal a substantial amount of concordance in assemblage structure through time. Some of this concordance may simply reflect the lifespans of the component species (Connell and Sousa 1983), but most studies have been long enough for substantial population turnover to occur. Lawton and Gaston (1989) argued that most assemblages of organisms show this pattern; Eric R. Pianka (personal communication in Pimm 1984b) suggested that, with the exception of successional
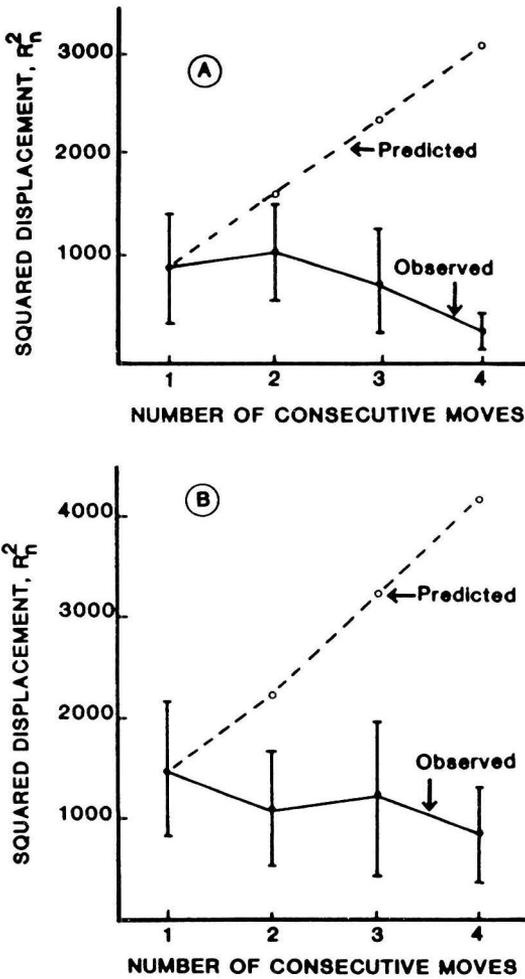
Figure 10.8. Temporal change in community structure of prairie grasshoppers compared with a null model of random change. The *x* axis is the number of consecutive "moves" or changes in ordination after 1 to 4 years. The *y* axis is the squared displacement vector of ordinated community structure. The null model of a random walk predicts increasing change in community structure, whereas the observed assemblages showed little change from their initial structure. Vertical lines indicate 95% confidence intervals. Dashed line is the predicted value from the null model of Kareiva and Shigesada (1983). Analyses are shown with (**A**) and without (**B**) *Phoetaliotes nebrascensis,* the numerical dominant in the assemblage. From Evans (1988), with permission.

systems, most assemblages of organisms will be stable during the lifetime of an ecologist. Yet, there is a growing literature suggesting that many assemblages may not be in an equilibrium state (Rotenberry and Wiens 1980; Sale and Douglas 1984; Boecklen and Price 1991).

In many communities, certain species are persistent but chronically rare, and it remains an important challenge to understand why this is so (Rabinowitz 1981). Larger-scale null models of species composition that incorporate regional source pools and colonization potential (Cornell and Lawton 1992) may be necessary to complement small-scale null models of population change for an understanding of temporal constancy of species assemblages.

PATTERNS OF FOOD WEB STRUCTURE

Null models have been frequently used to quantify and describe general food web patterns. These analyses have used a large database of published webs, initially compiled by Cohen (1978) and expanded by Briand (1983) and by Briand and Cohen (1987). This compendium of published webs is important because it forms the basis for the conventional wisdom of how food webs are organized in nature (Figure 10.9).

However, the compiled webs suffer from some serious, perhaps debilitating, distortions. The major problem with the compiled webs is that they often lump taxa into "trophic groups." This lumping may represent an attempt to depict only the important interactions in the food web, but it may also reflect artistic convenience (Paine 1988) and taxonomic biases against invertebrates and small-bodied organisms (Pimm 1982). Lumping in published food webs is not random and is almost always concentrated near the base of the food chain. This introduces a systematic bias into the webs that may distort basic food web patterns. For example, Cohen (1977) found that the ratio of the number of prey species to the number of predator species in webs was often 3:4. Such ratios arise from stable Lotka-Volterra food webs with apparent competition between prey species via shared enemies (Mithen and Lawton 1986; see Chapter 7 for tests of the related hypothesis that predator and prey *abundances* are relatively constant). But the ratio may simply represent differential lumping of prey categories (Pimm 1982), and is not predicted by other simple theories of community development (Glasser 1983).

For now, we accept the food web data "as is" and show how null models have been used to elucidate nonrandom patterns in the webs. We review null model tests of three food web patterns: trophic chain length, interval webs, and
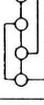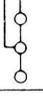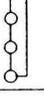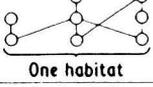
Figure 10.9. A catalog of features typically observed in published food webs. Features "not usually observed" often represent comparisons with null models. From Pimm (1982), with permission.

connectance. We conclude by summarizing recent controversies over the reality of these patterns and new directions in food web analysis.

Is There a Limit to the Number of Trophic Links in an Assemblage?

Considerations of the ecological pyramid of numbers (Elton 1927) and the inefficient transfer of energy from one trophic level to the next (Lindemann 1942) suggest that energetic constraints may limit the number of trophic levels in a web. Alternatively, food chain length may be limited by body size and design constraints on predators (Pimm 1982, 1984a). Optimal foraging principles also predict that species should forage low in the food web (Hastings and Conrad 1979), which would lead to short food chains. Finally, short food chains

may be more stable than long ones and reflect dynamic constraints of the sort predicted by Gardner and Ashby (1970).

But a simpler (null) explanation is that there is no biological or mathematical significance to observed chain lengths and they simply follow the expected pattern for a set of randomly linked species. Before we can decide whether observed food chains—which typically have two or three links (Pimm et al. 1991)—are unusually short, they must be compared to an appropriate null model.

Pimm (1980a) constructed random food webs subject to some simple constraints. His webs retained predator and prey numbers, ensured that every predator consumed at least one prey species (and that each prey species had at least one predator), and did not allow for loops within the same trophic level. By retaining observed trophic levels, the null model may have incorporated some important structure it was trying to detect. This would cause the simulated webs to be more similar in appearance to the observed webs, and in that sense the test for food chain length was conservative.

For a set of 14 published webs, Pimm (1980a) found that observed chain lengths were typically shorter than expected. The patterns for any single web often could have arisen by chance, but the consistent result across the set of 14 webs was highly improbable. These tests also revealed that omnivory (feeding on more than one trophic level) was relatively uncommon and that when it did occur, it was usually between adjacent trophic levels.

These conclusions were limited to the data in hand; for example, observed levels of omnivory may be considerably higher in zooplankton food webs (Sprules and Bowerman 1988). Other sorts of data are needed to distinguish among the alternative mechanisms that have been proposed to account for short chain lengths (Pimm 1982), but these null model tests did suggest that chain lengths in published webs were unusually short.

Do Food Webs Exhibit Internal Structure?

Cohen (1978) noted an interesting property of predators at the same trophic level in a food web. If the predators are ordered on the basis of the prey species they consume, the overlaps in diet among the set of predators can sometimes be represented in a one-dimensional graph. These "interval food webs" correspond to a set of predators that partition prey species in a simple fashion. Cohen (1978) suggested that this nonrandom pattern indicated niche differentiation among the predators and that the major axis of ecological differentiation was one-dimensional.

Cohen (1978) tested for the presence of interval food webs with a set of six null models based on the randomization of the food web matrix. These models

placed fixed or probabilistic constraints on either the row, column, or total sums of the food web matrix. Cohen's (1978) models were more "null" than Pimm's (1980a) because they allowed for loops and may even have included predators with no prey and prey with no predators. There were usually more observed interval food webs than expected by chance for all six of the models, perhaps providing support for simple models of niche overlap.

However, other null models of food webs do not give this same result. Yodzis (1982) tested for the presence of "cliques," a form of ecosystem compartmentalization that is similar to the interval graph. Each species pair in a clique has at least one prey species in common, and the dominant clique is one that contains no other clique. Cliques in a food web correspond roughly to trophic guilds, although they tend to contain more species than the typical guild.

Yodzis's (1981) null model for testing for cliques was more restrictive and complex than Cohen's (1978) models. Yodzis (1981) established the parameters n (the number of primary producer species), p (production per primary producer), and e (ecological efficiency of consumers). Beginning with the set of n primary producers, consumers were added sequentially to the community. Each consumer was assigned to a random set of producer species and removed a randomly chosen fraction of the remaining production, reminiscent of the mechanics of MacArthur's (1957) broken-stick model (see Chapter 3). This process was repeated for higher trophic levels until energetic constraints forbade the addition of more species. For each real web, constants were fitted so that the null web could plausibly be viewed as having been chosen at random from the universe of all possible webs with the parameters $n, p,$ and e.

Compared to these null webs, real food webs had very few dominant cliques, even though other properties, such as predator/prey ratios and number of trophic links, were well fit by this model (Yodzis 1981). These constraints on the number of dominant cliques in turn seemed to account for the presence of interval graphs detected by Cohen (1978). Perhaps these elements of internal structure represent "small, functionally coevolved guilds or component communities," which Colwell (1979) suggested as the focus of study in community ecology. But neither Yodzis (1981) nor Cohen (1978) provided satisfying biological explanations for these units of organization that are inspired by graph theory.

What Is the Relationship Between Species Richness and Connectance?

Dynamical constraints (Gardner and Ashby 1970; Rejmánek and Starý 1979) suggest that connectance should decline with increasing species richness, per-
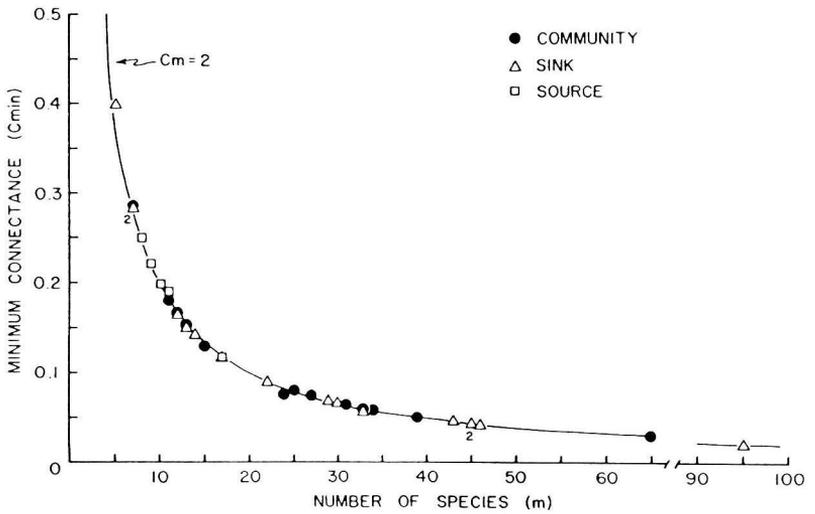
Figure 10.10. Relationship between minimum possible connectance and the number of species in a community. The curve represents the hyperbolic function $Cm = 2$. "Community webs" were defined as sets of organisms selected from a habitat without regard to their trophic relationships. "Sink webs" were constructed by selecting a set of predators and tracing the connections to their prey. "Source webs" were constructed by selecting a set of prey and tracing the connections to their predators. From Auerbach, M. J. Stability, probability, and the topology of food webs. In: *Ecological Communities: Conceptual Issues and the Evidence*. D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds). Copyright © 1984 by Princeton University Press. Reprinted by permission of Princeton University Press.

haps in hyperbolic fashion if interaction strength is held constant (May 1972). The pattern is certainly common in published food webs (Rejmánek and Starý 1979; Pimm et al. 1991; but see Winemiller 1989). But connectance could also decrease if each species fed upon the same number of prey species, regardless of web size (Pimm 1980b), which seems biologically reasonable.

Auerbach (1984) noted that for a web of m species, a minimum connectance of $2/m$ is necessary to maintain at least one link for each species in the web; this constraint by itself can generate a hyperbolic relationship between species richness and connectance. A similar bound on maximum connectance arises if predator identities are maintained and looping is forbidden, as in Pimm's (1980a) null models. Published food webs nicely fit these constraining curves (Figure 10.10).

Kenny and Loehle (1991) calculated the expected connectance for a web with S species and k links. The only constraint on this expectation was that all
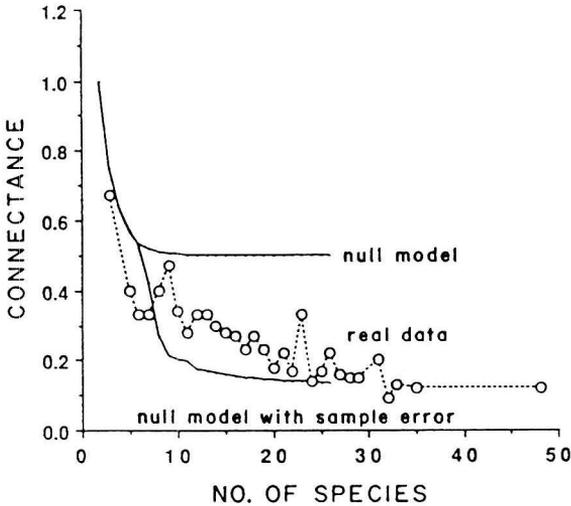
Figure 10.11. Relationship between connectance and species number for several aquatic ecosystems. The null model is the expected connectance for a randomly connected web of a given number of species. The null model with sampling error assumes that links in the observed web are sampled in proportion to their relative strength. From Kenny and Loehle (1991), with permission.

species had at least one link; loops were not disallowed. Connectance decreased with increasing S in this model, but the observed connectances in Briand and Cohen's (1987) compiled webs were too low to be fit by this model.

However, this comparison is valid only if the entire web is known. In reality, the published webs represent a small and probably nonrandom subset of the true web structure. Thus, a null model for connectance needs to incorporate not only the observed numbers of species and links, but also some element of sampling error. Such a model is difficult to formulate, because the links that are missing from an observed food web are not random. Missing food web links do not simply represent rare species, either, because most top predators are rare, but they are usually well represented in food webs.

Instead, Kenny and Loehle (1991) argued that the "missing links" in published food webs probably represent very small energy transfers, corresponding to prey items that rarely occur in a predator's diet. Kenny and Loehle (1991) explored the use of energy transfer in food web sampling by analyzing food webs for several large aquatic systems that had been compiled by Robert E. Ulanowicz specifically for the purpose of quantifying energy transfers. The plot of ranked link sizes (biomass or carbon transfer) was well fit by a geometric series, in which each link is some constant fraction of the size of link before

it. This fraction ranged from 0.75 to 0.95 in the observed data sets. Randomly sampling from this distribution yielded an expected connectance for a web that has been constructed with sampling error. The connectance in these truncated webs provided a good match to the observed values (Figure 10.11). This null model effectively accounted for observed connectance by assuming only that the underlying linkage strengths followed a log series and that observed web links were randomly sampled in proportion to link strength. The quantitative linkages were important only in determining sampling biases, not in influencing web stability. These findings suggest that linkage strength is a key to understanding both the biological (Paine 1992) and the statistical (Ulanowicz and Wolff 1991) properties of food webs.

Are Food Webs Real?

In a special feature section of *Ecology,* Paine (1988) provocatively questioned the biological reality of published food webs. He argued that most webs have been so overly simplified or "sanitized" that it is premature to make any claims about general food web patterns in nature. He also emphasized that only a direct study of interaction strengths (Paine 1992) will reveal the forces that organize assemblages, and that qualitative depictions of interaction sign (+ or −) will not uncover critical linkages such as keystone species (Paine 1966).

Perhaps in response to his criticisms, several authors have recently published very detailed food webs and compared the patterns in those webs to the generalizations derived from previous web catalogs. The new webs are complex and do not conform to previous generalizations. They provide strong support for Paine's (1988) contention that published catalogs are inadequate and do not represent true web structure.

For example, Polis (1991) described a complex, species-rich food web for a desert community. This web included 174 species of vascular plants, 138 species of vertebrates, over 55 species of arachnids, and an estimated 2,000–3,000 species of other invertebrates and microorganisms. Even using a highly simplified subweb, Polis (1991) found an average of seven trophic links (Figure 10.12), compared to the "expected" two or three links in published webs. Although omnivory is claimed to be uncommon in food webs, 78% of the species in the desert web were omnivorous. Polis (1991) argued that lumping and deletion of biological species, inadequate dietary information, and a failure to recognize the presence of age structure and looping compromise the quality of most published webs.

Martinez (1991) found similar patterns for a well-resolved aquatic food web. For the 93 trophic taxa (most of which were resolved to the species or genus
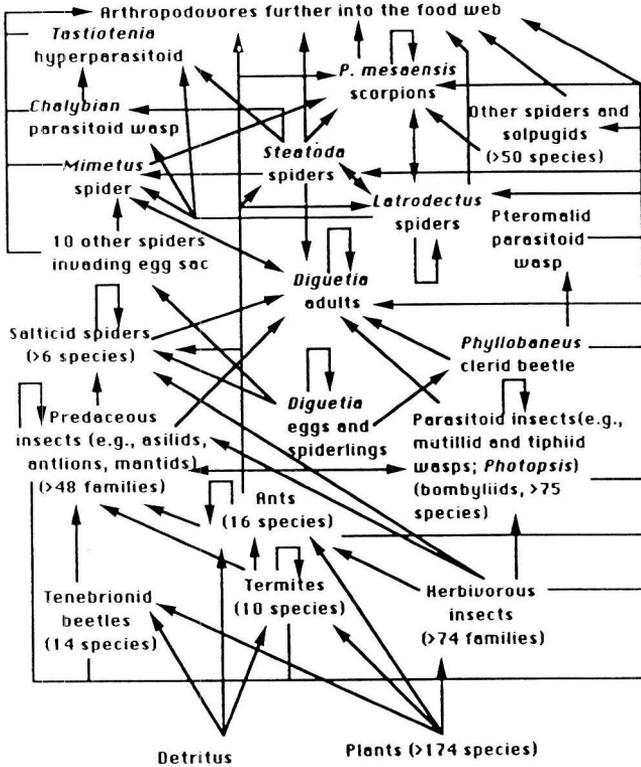
Figure 10.12. Trophic interactions of a few predaceous arthropods in a desert food web. This subweb represents a small fraction of all interactions. An arrow returning to a taxon indicates cannibalism. Reprinted by permission of the publisher from Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* 138:123–155. Copyright © 1991 by The University of Chicago.

level) of a Wisconsin lake, there were an average of more than 10 trophic links, with more links per species and more species at higher trophic levels than in other published webs. Other species-rich assemblages that show "atypical" trophic links and high levels of omnivory include estuarine (Hall and Raffaelli 1991) and tropical (Winemiller 1989) aquatic food webs. Even the celebrated hyperbola of connectance and species richness may not be valid (Martinez 1992). For at least one large food web (Winemiller 1989), connectance actually increased with increasing species richness (Figure 10.13).

Proponents of food web theory have acknowledged the limitations of published food webs (e.g., Pimm and Kitching 1988; Pimm et al. 1991; Schoenly
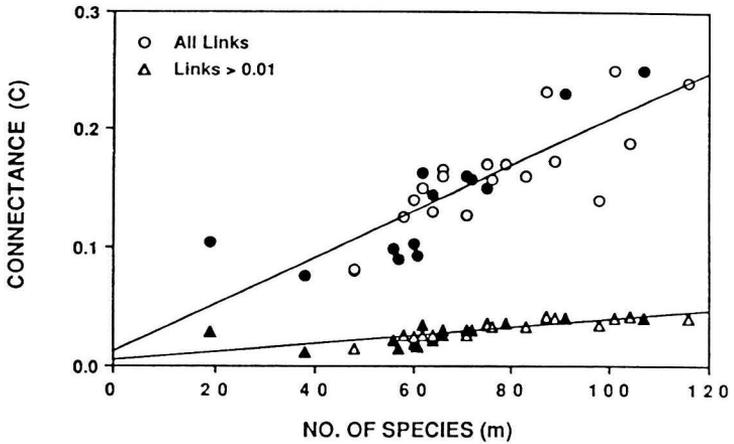
Figure 10.13. An increasing relationship between connectance and species richness for 34 food webs derived from four tropical fish study systems. Circles represent all links, and triangles represent strong links. Solid symbols are top-predator sink webs. Reprinted by permission of the publishers from Winemiller, K. O. 1989. Must connectance decrease with species richness? *American Naturalist* 134:960–968. Copyright © 1989 by The University of Chicago.

and Cohen 1991) but have suggested that the revealed patterns still tell us something important about how communities are assembled. One strategy to deal with poorly resolved food webs is to aggregate the data and then examine scale-invariant properties of the resulting webs (Sugihara et al. 1989; Havens 1992). Some food web properties do not change with aggregation, suggesting they are not sampling artifacts. However, because links are not randomly deleted from food webs initially, this aggregation does not remove biases that are inherent in simplified food webs (Kenny and Loehle 1991). On closer analysis, many of the web statistics do seem to be sensitive to aggregation (Martinez 1993a, b).

We think the arguments over scale-invariant properties of food webs are uninformative without comparison with a null model. Other constant metrics in community ecology, such as body size ratios of 1.3 (Chapter 6) and species-area slopes of 0.26 (Chapter 8), frequently appear but in no way imply a single, underlying cause. On the other hand, the fact that many web metrics are correlated with the number of species does not mean that the patterns are purely sampling phenomena. Only by comparison with a null model can we decide if a certain web metric is unusually large or small.

Along these lines, it will be especially interesting to compare food web properties of these new species-rich webs with null models. It might still be the

case that the chain lengths in Polis's (1991) and Martinez's (1991) webs are unusually short, given the number of species they contain. Simplification of a food web is not necessarily a bad thing, particularly if the reduced web is the one that contains the strong linkages. But this aggregation can only be made when all links are thoroughly investigated and their strengths quantified. Perhaps when this is done, the resulting webs will appear like the ones in the current literature catalog, and we will have come full circle on the issue. But in the meantime, we agree with Paine (1988) that it is premature to say much about the underlying patterns of food web structure until we develop a large catalog of more detailed webs. It may be difficult to apply null models to such webs, however, because of constraints on computing time.

In summary, null models have had a long history in food web analysis and have revealed important nonrandom patterns. But, as Sale (1984) has pointed out, our vertebrate sensory systems predispose us to organize and simplify patterns in nature. It may turn out that the existing catalog of food webs is more a reflection of past perceptions of nature than an indicator of true structure.

RECOMMENDATIONS

In contrast to other areas of community ecology, null models have figured prominently in food web analysis, both in formulation of theoretical expectations and in testing existing food web patterns. Many food web patterns cannot be explained simply by the number of species or links in the collection. However, recent critical reviews suggest that the set of existing food web data is empirically flawed; null model tests are needed for new species-rich webs that more accurately reflect the links and interaction strengths in nature. When such data are available, the null models of Pimm (1980a) and Kenny and Loehle (1991) are appropriate for detecting pattern.