

FOOD WEBS

Integration of Patterns & Dynamics

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1996



KLUWER ACADEMIC PUBLISHERS
BOSTON/DORDRECHT/LONDON

Food Webs: What Can They Tell Us About the World?

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This book unites diverse approaches from theoretical ecology and empirical research in systems ranging from soil fauna to oceans. Major philosophical and methodological differences are expected from such a heterogeneous group of ecologists; indeed, one might be amazed by the establishment of a substantial common basis for discussion. Food webs provide this basis. Much recent ecological literature is cast within a food-web framework, including studies of: (1) Habitat heterogeneity and the regulation of community structure (e.g., Lubchenco (1983), Kareiva (1986), Moore and Hunt (1988), and Moore et al. (1989b)); (2) environmental change through time and community structure and function (Menge and Sutherland, 1976; Winemiller, 1990; Schoenly and Cohen, 1991); (3) productivity gradients and community structure (Oksanen et al., 1981; Persson et al., 1988, 1991); (4) direct and indirect cascading effects of predation on community structure (Paine, 1980; Power et al., 1985; Carpenter et al., 1987; Kerfoot, 1987; Yodzis, 1988; Schoener, 1989; Spiller and Schoener, 1990; Turner and Mittelbach, 1990); (5) intraguild predation (Polis et al., 1989; Oksanen, 1990; Polis and Holt, 1992); (6) indirect mutualism (Vandermeer et al., 1985); (7) apparent competition (Holt, 1984; Holt and Kotler, 1987); and (8) ecosystem stability and nutrient dynamics (DeAngelis, 1992). Some population interactions (e.g., competition, predation) cannot be fully evaluated outside of a food-web context because their outcomes can be modified by other members of the web. Aquatic ecologists have

achieved notable success by studying the interactions between top-down (consumption) and bottom-up (production) factors in the regulation of community structure (Carpenter, 1988; McQueen et al., 1989; Power, 1990a, 1990b; Vanni and Findlay, 1990; Vanni et al., 1990; Persson et al., this volume). Most food-web studies have viewed consumption exclusively within pathways derived from primary production, and only recently has the major role of detritus in ecosystem structure and function received much serious attention (Cousins, 1980; Rich, 1984; Coleman et al., 1988; Moore et al., 1989a; Polis and Hurd, this volume; Porter, this volume). There currently is little agreement on how to best characterize the role of detritus (itself a heterogeneous unit) in food webs (Rich, 1984; Cousins, 1985; Winemiller, 1990; Polis, 1991). In addition, food webs are the arenas for several major theoretical debates, such as paradigms associating complexity with stability (MacArthur, 1972; May, 1975, 1983; Pimm, 1982; Abrams and Taber, 1982) and hypotheses relating the effects of size-dependent predation to community structure (Brooks and Dodson, 1965; Warren and Lawton, 1987; Cohen and Newman, 1988).

The adoption of food web paradigms in applied research has yielded important insights. A number of problems in resource management (e.g., pest control, environmental contamination, fisheries management, bioremediation of lakes) require characterization of food web structure as an early step in formulating management solutions. The fundamental challenge of understanding the

regulation of populations and regional biodiversity usually requires basic knowledge of community structure and population interactions. For example, pest control in agroecosystems may be influenced by the response of predators to nontarget prey, or by predator-predator interference (Polis and Holt, 1992; Rosenheim et al., 1993; Ehler, this volume). Fisheries management requires predicting the responses of both predators and prey to harvest and other manipulations (Parsons, 1992). As demonstrated in several aforementioned aquatic studies, bioremediation of lakes may be either confounded or aided by the influence of indirect interactions in food webs. To a major extent, our current inability to predict responses of communities to exotic introductions is founded in poor understanding of food web dynamics (Lasenby et al., 1986; Spencer et al., 1991; Kaufman, 1992). The same is true of multispecies fisheries, especially in diverse marine and tropical communities.

Background

We define a food web as a network of consumer-resource interactions among a group of organisms, populations, or aggregate trophic units. Pimm (1982) broadened the definition for food webs as "diagrams depicting which species in a community interact," which allows the explicit inclusion of a variety of population interactions as food web components, e.g., horizontal (competitive) interactions and mutualisms. Cohen and Newman (1985) defined a food web as "a set of different kinds of organisms and a relation that shows the kinds of organisms, if any, that each kind of organism in the set eats." Although this latter definition is specific with regard to the class of biological interaction, the biological units are defined only vaguely as "kinds of organisms."

While the units and domain of a given food web can be debated, the acquisition of energy and matter plus the avoidance of death or damage by consumption are obviously vital for all organisms. With few exceptions (fossilization, mineralization), the ultimate fate of organisms is some form of consumption by and assimilation into tissues of other organisms, be they metazoans or microbes. The structure, dynamics, and spatial relationships

of the trophic networks derived from this basic observation are certain to affect the distribution and abundance of organisms in very fundamental ways.

Over 45 years ago, Hutchinson (1948) recognized the parallel development of two separate approaches for the study of trophic networks: the biogeochemical and the biodemographic. O'Neill et al., (1986) saw this dichotomy of approaches in the current process-functional and population-dynamic schools of ecosystem study. The food web is the basic unit of study for both schools. Credited with the first formal conceptualization and quantitative description of energetic processes within food webs, Lindeman (1942) paved the way for the development of systems ecology as a means to investigate higher-order biological processes. Systems ecology traditionally emphasized the currencies of natural economies (matter and energy) and tended to aggregate evolutionary units (organisms and populations), thus trading off the ability to study hierarchical interactions ranging from genetic to ecosystem levels (O'Neill et al., 1986; Allen and O'Neill, 1991).

By stressing the importance of physical principles, such as the laws of thermodynamics in relation to ecological efficiency, systems ecology tends to downplay the role of natural selection and stochastic environmental influences on population dynamics and community properties (Loehle and Pechmann, 1988; Oksanen, 1988). From the perspective of individual behavior, the evolution of predator foraging will increase ecological efficiency, while the evolution of prey escape tactics will lower ecological efficiency. Even in the short term, adaptive foraging greatly influences food web dynamics in Lotka-Volterra-based models (Abrams, this volume). Food web paradigms deal with network complexity in a holistic fashion, yet differ from the systems approach by retaining much potential for traditional demographic and evolutionary interpretations. Food webs also have emergent properties that are derived from, but not shared by, their constituent units (Hall and Raffaelli, 1993).

Types of Food Webs

Three basic approaches can be identified in the investigation of community trophic net-

works (Paine, 1980). A topological or descriptive web is a static description of feeding links, either observed or estimated, among species or guilds. A flow or bioenergetic web quantifies the transport of energy and matter, via predation, among species or guilds. An interaction or functional web identifies the species and feeding links that are most influential in the dynamics of community composition and structure.

Topological webs are static networks of feeding interactions recorded as either present or absent (binary links) in a matrix of $n \times n$ species that pairs potential predators (column entries) with potential prey (row entries). The community matrix of directed feeding interactions can be converted into a food web diagram containing vertices (nodes) connected by lines to indicate feeding links (Cohen, 1978).

The process-functional approach quantifies the flow of energy and matter through ecosystems and seeks to elucidate the biological processes that regulate these flows (Odum and Odum, 1976; Ulanowicz, 1986; DeAngelis, 1992). The flow of energy and matter, in turn, influences the dynamics of populations and communities (DeAngelis, 1992). Yet, flow webs are not sufficient to predict the dynamics of communities, because energy and biomass flow are themselves functions of interactions among populations with the food web. The dynamic importance of a particular species or feeding link cannot be inferred directly from measurements of energy transfer or diet composition (Paine, 1988, 1992; Polis, 1991, 1994; Polis and Strong, in press). This major limitation holds for both population-dynamic and process-functional food webs. Without experimentation, one cannot determine a priori which major feeding links exert strong demographic effects (Paine, 1980, 1988, 1992; Dayton, 1985; Polis et al., 1989). If some other factor limits population growth, then an apparent strong link (in terms of dietary biomass percentages, or kilocalories of energy transferred) might have little effect on population dynamics and community structure (Dayton, 1985; Hall et al., 1990; Polis and Strong, in press; Raffaelli and Hall, this volume).

Experimental manipulations of food webs can identify species and feeding links that most influence population and community

dynamics. These key species and strong links are joined together in an interaction web (Paine, 1992). The initial process of choosing species and interactions to experimentally manipulate is somewhat subjective and often based on imperfect knowledge of food web structure or function, ideally in the context of a keen appreciation of the natural history of the system. As researchers learn more, some community elements are deemed relatively unimportant and others are subjected to further experimentation (Paine, 1992; Raffaelli and Hall, 1992). Eventually, the community is condensed into an interaction web, a subset of species that most influence community biomass and diversity. For example, this approach has been adopted by experimental marine and aquatic ecologists to understand processes influencing community trophic cascades (Paine, 1980; Dayton, 1985; Power et al., 1985; Menge and Sutherland, 1987; Carpenter and Kitchell, 1988; Power, 1990a). Yet, even field experimentation is not without limitations: variables are often difficult to control, experimental timescales may be inappropriate, initial conditions and the spatial scale and methods of isolating systems for study influence outcomes, and indirect interactions can compromise the ability to infer causation from direct interactions (Bradley, 1983; Bender et al., 1984; Yodzis, 1988; Raffaelli and Hall, 1992; Bengtsson et al., this volume).

Generalizations From Topological Webs

This book contains little treatment of topological web comparisons. The comparison of static topological food webs has stimulated theory and empirical tests; these are summarized by Lawton (1989), Cohen et al. (1990), Pimm et al. (1991), Pimm (1992), and Hall and Raffaelli (1993) (but see Polis 1991). Such analyses have produced what has come to be known as food web theory, models that attempt to explain the general trends in web topology. Published webs were gathered by Cohen (1978), Pimm (1980, 1982), Briand (1983b), Sugihara et al. (1989), and Cohen et al. (1990) for quantitative analysis of their properties. Abstracted generalizations include: (1) Network linkage density does not vary with the number of species (Rejmanek and Sary, 1979; Pimm, 1980; Yodzis, 1980;

Auerbach, 1984; Briand and Cohen, 1984; Cohen et al., 1985); (2) food chains are usually limited to three or four trophic levels (Pimm, 1982; Cohen et al., 1986; Newman and Cohen, 1986; Briand and Cohen, 1987); (3) ratios of predator to prey species in food webs are roughly constant at about 0.8–1.0 (Briand and Cohen, 1984; Cohen et al., 1985; Jeffries and Lawton, 1985); (4) the fraction of species at the base, middle, and top of webs does not vary with species number (Briand and Cohen, 1984; Cohen and Briand, 1984; Cohen et al., 1990); and (5) the frequency of omnivory in nature is less than expected by chance (Pimm, 1982; Pimm and Kitching, 1987).

Although the analysis of topological webs has stimulated new areas of inquiry (Peters, 1988; Lawton, 1989; Pimm et al., 1991), there is major concern that the empirical data that are the foundations for generalizations are terribly inappropriate (Glasser, 1983; May, 1983; Paine, 1983, 1988; Taylor, 1984; Pimm and Kitching, 1988; Sprules and Bowerman, 1988; Lawton, 1989; Schoener, 1989; Winemiller, 1989, 1990; Cohen et al., 1990; Martinez, 1991a, 1991b; Pimm et al., 1991; Polis, 1991, 1994; Hall and Raffaelli, 1993; Yodzis, 1993). For example, early web diagrams contain far too few species, too few feeding links, too few omnivores, too few loops (A eats B, B eats C, C eats A), and too little cannibalism (Winemiller, 1990; Polis, 1991). Limitations of these traditional data sets stem from large variation in field methods, techniques of empirical analysis, definitions of operational units, and criteria for web construction. Some have argued that comparisons would be more valid among sets of webs constructed using the same criteria (Winemiller, 1990; Pimm et al., 1991; Martinez, 1991a, 1993; Goldwasser and Roughgarden, 1993). A handful of more detailed (yet vastly incomplete) webs have been described recently, and many results are inconsistent with earlier generalizations based on previous catalogs of topological webs (Hildrew et al., 1985; Warren, 1989; Winemiller, 1989, 1990; Hall and Raffaelli, 1991; Martinez, 1991a; Polis, 1991; Schoenly and Cohen, 1991; Goldwasser and Roughgarden, 1993).

Many generalizations based on comparisons of simple webs culled from the literature

appear to have little or no biological basis (Winemiller, 1989, 1990; Polis, 1991, 1994). The statistical properties of these web diagrams may be functions more of human idiosyncracies than attributes of the natural world (Paine, 1983, 1988; Winemiller, 1989; Martinez, 1991a). When the primary objective was the description of general community feeding relationships, most illustrators drew fewer connections as diversity increased. In addition, illustrators tended to aggregate more species into each node in communities that contained more species. The early web diagrams were created to highlight the trophic roles of certain taxa, and biologists frequently lumped species into aggregate units to a greater degree near the base of web (Pimm, 1982; Paine, 1988; Polis, 1991).

Some of the metrics used in comparisons were confounded by attributes such as web size (defined as species richness). For example, Pimm's (1982) index of compartmentation is confounded by connectance (Winemiller, 1990), and comparisons of connectance between different systems can be confounded by web size (Bengtsson, 1994). The seemingly constant ratio of predators to prey in food webs (reported values between 0.76 and 1.1) has been shown to be an artifact of double counting species in food webs (Closs et al., 1993). Greater lumping of taxa into trophospecies at the bottom of reported webs tends to increase this ratio. In hindsight, this realization might have circumvented the search for the biological implications of constant P/P ratios (Jefferies and Lawton, 1985; Mithen and Lawton, 1985; Cohen and Newman, 1985; Warren and Lawton, 1987).

Scale Effects

Defining the limits of natural ecological communities is a difficult and, in practice, often subjective or arbitrary exercise. Various statistical methods have been employed to identify local communities as spatially segregated species assemblages (e.g., Gauch (1982) and Holling (1992)). Frequently, plants and animals are grouped into communities or species assemblages based on their patterns of co-occurrence on fairly broad scales of spatial

heterogeneity. In practice, this manner of grouping is largely subjective, although frequently rather obvious as for species assemblages confined by discrete habitat boundaries, like stream, lake, and sand dune communities. Cousins (this volume) suggests that community webs be delimited spatially by the home ranges or ambits of their top predators.

No community, not even one contained by discrete habitat boundaries, is entirely without interaction with, or influence from, adjacent habitats and species assemblages (Holt, 1993; Polis et al., this volume). For example, stream ecosystems are strongly influenced by adjacent terrestrial habitats (Mulholland et al., 1985; Junk et al., 1989). Even at fairly small spatial scales, terrestrial and fluvial systems interact, although many insights can be gained by focusing attention on either the terrestrial or aquatic unit separately. In many cases, knowledge of transport processes across habitat boundaries is essential for understanding the dynamics of local populations and communities (Lewin, 1986; Pulliam, 1988; Dunning et al., 1992; Robinson et al., 1992; Polis and Hurd, this volume; Polis et al., this volume). Consequently, no community web can be considered a discrete natural unit. This is not to imply that ecologists should not seek to define major interactive units by the most objective of the means at their disposal. Yet, the subjective definition of communities poses particularly acute problems for comparative numerical analyses of web features.

Despite the difficulties inherent in defining the boundaries of natural communities, large webs can be divided into subwebs in nonarbitrary ways. A web comprising a single consumer species and all its prey is actually a subweb within a larger network. Following Cohen (1978), a *sink subweb* consists of all the prey taken by a predator plus all prey consumed by the prey of this designated top predator, and so on. Alternatively, *source subwebs* include a set of one or more basal species (usually, but not necessarily, plants), their consumers, and predators of their consumers (Cohen, 1978).

Great variation also is seen in the definition of nodes. Polis (1991) discussed problems associated with such variation in published food webs. Nodes are usually composed of

lumped species populations referred to as *trophospecies* (Yodzis, 1988) or simply *species* (Cohen, 1978; Pimm, 1980, 1982; Briand, 1983a, 1983b; Auerbach, 1984; Cohen and Newman, 1985). According to Pimm et al. (1991), trophospecies are sets of organisms with identical prey species and identical predators, within the resolution limits of the study. Unless data are highly aggregated to begin with, it is highly unlikely that any biological species could be grouped in this manner. Indeed, the trophospecies concept ignores two decades of search for limiting similarity, *sensu* MacArthur and Levins (1967). To resolve trophic entities in a more specific way, Pimm and Rice (1987) and Martinez (1991a) proposed splitting biological species into separate web nodes based on distinct life cycle stages. This approach offers considerable potential to model the consequences of ontogenetic niche shifts for a target species within the context of community interactions, but makes the use of lumped trophospecies in other parts of the web even more problematic.

Temporal and Spatial Variation

Most ecological communities do not occur in stable environments, and some (perhaps most) only rarely or intermittently experience strong density dependence or exhibit equilibrium population dynamics (Wiens, 1977, 1984; Schoener, 1982; Strong, 1986; Dunson and Travis, 1991). Furthermore, few predators appear to eat prey in constant ratios over time during their entire life cycles. Aquatic organisms, in particular, reveal much ontogenetic, size-dependent predation (Brooks and Dodson, 1965; Werner and Gilliam, 1984). Diet often shifts in response to seasonal changes in the availability of preferred food resources. For example in the Venezuelan llanos, loricariid catfishes consume aquatic primary production mostly as living algae during the wet season and as dead macrophyte tissues (detritus) during the dry season (Winemiller, 1990, this volume). Such seasonal variation in fish diet is more the norm than the exception (Werner and Gilliam, 1984), even at less seasonal locations in the tropics (McKaye and Marsh, 1983; Winemiller, 1990). Similar changes also

characterize terrestrial consumers (Polis 1991). Price (1992) discussed the effects of alternative resources at the base of webs on the structure of plant-herbivore-parasitoid webs. He noted that "even a small difference between plant resources can have an enormous impact on food web structure."

Despite widespread recognition of the transitory nature of natural habitats and trophic interactions (Thompson, 1988), surprisingly little attention has been given to variation in the time intervals used to estimate food web structure. A web based on large amounts of data collected over an annual cycle (a cumulative web) is more complex than a web describing the same system based on data collected during a short interval, say a week or several months (Kitching, 1987; Warren, 1989, 1990; Winemiller, 1990; Schoenly and Cohen, 1991). The cumulative web is a more complete and accurate portrayal of the sum of all trophic interactions in the network, yet it may not be the most appropriate unit for analysis. Because trophic interactions always exhibit some degree of temporal dynamics, webs estimated over shorter time intervals could provide a basis to evaluate within-system temporal changes in web properties (Winemiller, 1990; Schoenly and Cohen, 1991). In practice, however, large samples are needed to minimize omissions of feeding links due to the hazards of sampling error for data collected over relatively short time intervals. For some communities, the sampling design and effort will require compromise between the many benefits associated with a large sample size and the negative impact that collecting without replacement might exert on normal ecosystem performance.

Web Structure and Population Dynamics

What are some potential implications of variance in densities of species components on food web structure and function? Consider a species whose diet consists of large fractions of several other species in the community. If the species is extremely rare, its overall effect on the system may be trivial. Conversely, a functionally significant prey species could appear rare if it is kept in check by strong interactions with predators (Paine, 1980).

Whether or not the rare species is involved in significant food web interactions may depend on whether the perspective is by predators from above, or by prey from below (Polis, 1991). Furthermore, a superabundant species exhibiting numerous weak interactions could be important in food web dynamics. There are few means to determine *a priori* which rare species might be excluded from analyses, and probably only experiments, be they manipulative or natural, can tell us this for certain.

Web structure depends upon current densities of predators and prey, which, in turn, are derived from rates of biomass accumulation, population growth rates, and predation rates during preceding intervals. In discussing the implications of population dynamics on web properties, Power (1990b) noted how the ecological significance of an observed link is largely determined by the functional and numerical responses of predators to prey. Models of ratio-dependent predation (where the functional response depends on the ratio of predator to prey rather than prey density) yield dynamics quite different from simulations based on the familiar Holling (1959, 1966) predation model (Arditi and Ginzburg, 1989; Arditi and Saïah, 1992; Arditi and Michalski, this volume). Berryman (1992) concluded that the behavior of Lotka-Volterra predation models, with either logistic modifications to predator and prey or with ratio-dependent functional responses, have greater biological realism than models with classical functional responses. To achieve even modest coupling of food web structure with dynamics requires not only knowledge of species composition and population interactions (i.e., topology and flow), but also population densities and growth dynamics (Bengtsson et al., this volume).

Food Webs in Relation to Abiotic Factors

Biotic factors in the form of predator/prey interactions are explicit in food webs. Much theoretical and empirical work documents the influence of predation on demographics, behavior, and evolution of both consumers and prey (e.g., Hespenheide (1975), Zaret (1980), Werner et al. (1983), Ryan (1985),

Feder and Lauder (1986), Kerfoot and Sih (1987), Polis et al. (1989), and Turner and Mittelbach (1990)). Yet, not all populations or communities are regulated solely by the dynamics of observed predator/prey or competitive interactions (Menge and Sutherland, 1987; Dunning and Travis, 1991; Pimm, 1991; Hunter and Price, 1992; Price, 1992; Power et al., this volume). Paine (1980, 1983) provided convincing arguments and empirical evidence against an emphasis on the configuration of trophic links (network connectance) at the expense of other factors. Static topological webs can be misleading in light of results from experimental manipulations (Paine 1980, 1983) and natural experiments (Schoener, 1989). To make the situation more difficult, experimental manipulations can yield wrong interpretations given the complicated dynamics of multispecies interactive networks (Bender et al., 1984; Yodzis, 1988; Abrams, this volume).

Abiotic factors such as the availability of nest sites or refuges, density-independent mortality due to climatic factors, and nutrient availability can limit populations under appropriate circumstances. How does one recognize when such factors periodically override density-dependent dynamics within food webs? Can we recognize a web structured by a hurricane or fire, and how would it differ from the web of a mature community structured by density-dependent biotic interactions? Several features of aquatic webs are derived, either directly or indirectly, from seasonal changes in the physical environment (Winemiller, 1990, this volume; Power et al., this volume; Rosemond, this volume). Despite considerable theoretical interest in the relationship between web structure and community stability (May, 1975; DeAngelis, 1975; Pimm, 1979; Yodzis, 1981a; King and Pimm, 1983; Post and Pimm, 1983; Hastings, 1988), the direct effect of abiotic factors on food webs remains relatively unexplored. Menge and Sutherland (1987) obtained experimental evidence from marine intertidal communities that supports the view that abiotic environmental factors and predation suppress competition and thereby regulate populations to varying degrees depending on their relative position within the trophic continuum. This problem takes on

even greater importance when anthropogenic disturbances are added to the list of natural ecosystem perturbations (Crowder et al., this volume). Ulanowicz's (this volume) flow model suggests that dynamic food web properties change in response to stress.

Early discussions of community diversity and stability assumed cybernetic control. As previously noted, frequently this assumption is undoubtedly false. The intermediate disturbance model predicts highest species diversity for communities that experience intermediate levels of disturbance (Connell, 1978; Huston, 1979; Petraitis et al., 1989). Biotic factors, some of which may not be directly related to trophic interactions, can also violate the assumption of density-dependent feedback in food webs. Consider, for example, species that pollinate (Gilbert, 1977). If the web is depicted as a network of direct trophic interactions, then pollinators exert a direct negative influence on their host plants in terms of their consumption of energy and matter that might otherwise have been channeled to other physiological functions. Yet clearly, pollinating vectors represent a net positive effect on their hosts. In this specific case, some links within the trophic network would portray a direct effect that is opposite in sign to the real effect. The same argument could be made for the roles of seed dispensers and some other kinds of mutualists. Strong mutualistic interactions (e.g., Mullerian mimicry, habitat or refuge facilitation) could override the net negative effect of direct trophic links.

In any large web, some feeding relationships will exert disproportionately great impact on ecosystems. Consider, for example, the major role that African elephants or beavers play as architects of their habitats. In contrast, consider the food chain of leaf cutter ants (*Atta* sp.)-fungi-vegetation (= three nodes, two links). Fungi are a crucial food web element in terms of the physiological ecology of leaf cutter ants. By itself, *Atta* cannot extract nutrition from plants, and therefore depend upon its association with fungi. If leaf cutters were suddenly to evolve their own biochemical capacity to digest and assimilate plants directly, how would the elimination of the fungus (one node, one link) affect the overall food web? The idiosyncratic influence of species on web structure and

function is highlighted by Morin and Lawlor, Power et al., Rosemond, and Strong et al. in this volume.

Whether or not they elect to deal with it analytically, most ecologists are keenly aware of the role that historical biogeography plays in setting the stage for contemporary ecological interactions. Yet few methodologies have been developed to identify or adjust for the influence of historical constraints (Endler, 1982; Ricklefs, 1987). The influence of historical factors (invasions, local extinctions, succession, assembly rules) on food web features has been investigated from both theoretically and experimentally (Yodzis, 1981b, 1984; Post and Pimm, 1983; Drake, 1990, 1991; Holt, this volume), but only superficially based on natural communities (Beaver, 1983; Kitching, 1983, 1987; Winemiller, 1990). Priority effects in community assembly can greatly influence community dynamics and structure (Drake, 1991; Holt, this volume). Moreover, the influence of alternative life-history strategies on food web structure and function has scarcely been addressed (Schoenly and Cohen, 1991; Winemiller, this volume). For example, the relative impact of a strong feeding link on an opportunistic (*r*-selected) prey population is certainly less than the same level of interaction with a relatively *K*-selected prey with a low intrinsic rate of natural increase.

Indirect Interactions Implied From Direct Predator-Prey Interactions

Although food webs are composed of direct predator-prey interactions, their structure provides opportunities to study population and nutrient dynamics across multiple indirect pathways. Quantitative analysis of web properties and dynamics is facilitated by the fact that web diagrams and resource matrices are directly interchangeable. Several methods have already been employed, including loop analysis (Lane and Levins, 1977; Lane, 1986), network analysis (Patten, 1982, 1991; Higashi and Burns, 1991; Gaedke et al., this volume; Ulanowicz, this volume), and stability analysis of model webs (Pimm, 1980; Yodzis, 1981a, 1988; Pimm and Rice, 1987; DeRuiter et al., this volume; Yodzis, this

volume). Coincident with the development network analysis has been the advancement of models based solely on direct population interactions. Hastings' (this volume; Hastings and Powell, 1991; McCann and Yodzis, 1994) model of chaos based on direct food web interactions among just three species suggests that dynamics of real food webs may be considerably more difficult to predict than was believed based on results from analyses of complex networks.

A growing body of empirical evidence demonstrates a variety of indirect effects mediated through networks of direct trophic interactions (reviewed by Abrams et al. and Persson et al. in this volume). With as few as three species arranged in three discrete trophic levels, direct predator-prey interactions give rise to indirect vertical interactions among species at nonadjacent levels. Indirect horizontal (competitive) interactions can arise in a simple web consisting of two predators that share two prey. Miller and Kerfoot (1987) distinguished three types of indirect effects: trophic linkage effects (e.g., species A affects C via direct effect on B), behavioral effects (species A affects the behavior of C due to the presence of B), and chemical effects (species A chemically affects C due to influence of B). Apparent competition (Holt, 1977, 1985; Abrams, 1987) and indirect mutualism (Addicott, 1984; Dungan, 1987) are other kinds of potential indirect interactions. Prospects and implications of increased understanding of indirect effects within trophic networks excite theoreticians and holistically oriented empiricists (Vandemeer, 1980; Pianka, 1987) and, to some degree, frustrate experimentalists seeking predictable responses from units embedded within complex networks (Bender et al., 1984; Yodzis, 1988). If indirect effects prove to be of universal importance, will it imply that field ecologists, whether comparative or experimental, must evaluate population phenomena always within the context of the entire community matrix (Bender et al., 1984; Tilman, 1987; Berryman, 1993)? Some experimental results have shown that populations respond to only a single factor, despite the complexity of the webs in which they are embedded (e.g., Morris (1992)).

Exploitation competition is by definition

an indirect interaction mediated by resource depression due to consumption. Cohen (1978) illustrated the potential to study resource overlap in food webs composed solely of predator-prey links. Sugihara (1983, 1984) also used a graphical analysis to explore patterns of species packing in food webs. The limitations of the early food web data compiled from the literature were already discussed. Given that competition and guild structure have been examined more directly with greater precision by other means for a number of years, the utility of these exercises seems questionable. Many have proposed using guilds, rather than food webs, as the focal units for detailed studies of competition. Studies of community guild structure can, but need not, involve most of the community web in the numerical analysis (Winemiller and Pianka, 1990). Trade-offs between quantitative precision, spatiotemporal scale, and taxonomic inclusiveness will determine the extent that data for guild analysis and data from corresponding food webs will overlap. The primary utility of a holistic food web approach is the generation of novel insights from information that integrates with other kinds of information gained from lower or higher levels of biological organization. We suggest that food webs not be used to reinvent phenomena that are fairly well understood, or more approachable, from other levels of organization.

These observations might suggest to some that any holistic approach to multispecies interactions must incorporate the net effects of each species on every other species in the system (i.e., the community matrix concept, Levins (1968)), as opposed to modeling only trophic relationships. Ultimately, the theoretical constructs of community ecology must be approachable operationally and amenable to empirical tests (Peters, 1988). In practice, it will never be possible to estimate the net effect of all forms of species interactions simultaneously for every element of a community matrix. In effect, an idealized community matrix could be considered one of the major goals of community ecology as a predictive science (Patten, 1991). Currently, the food web probably comes as close as anything to a holistic description of community interactions.

Community Stability and Complexity

Although they now appear in several introductory ecology texts (e.g., Kikkawa (1986), Begon et al. (1990), Ricklefs (1990), and Smith (1992)), some food web generalizations have created controversy. At the center of one controversy is May's (1971, 1972, 1975) formula for Lyapunov stability in parameter space for community matrices, $b(SC)^{1/2} < 1$ (where b is the average magnitude of interspecific interactions, S is species richness, and C is network connectance). May proposed that network connectance should decrease as the number of species in real community increases (but see methodological objections raised by DeAngelis (1975), Lawlor (1978), Newman and Cohen (1984), Law and Blackford (1992), and Haydon (1994)). This resulted in the quest to describe the relationship CS in nature (reviewed by Cohen et al. (1990)). Rejmanek and Stry (1979) were among the first to propose that S and C exhibit a hyperbolic inverse relationship ($CS = \text{constant}$) based on examination of real food webs. Later comparisons based on compiled web diagrams corroborated the claim (Yodzis, 1980; Pimm, 1982). Meanwhile, some ecologists argued for greater examination of b , since at any given moment S and C are fixed for natural systems. Yet, many have proposed that CS constancy is an artifact of systematic biases in published web illustrations (Auerbach, 1984; Paine, 1988; Winemiller, 1989; Warren, 1990; Martinez, 1991b), and CS constancy has not been supported by analyses of new webs containing greater taxonomic resolution and more objective identification of trophic links (Hildrew et al., 1985; Warren, 1990; Winemiller, 1989, 1990; Martinez, 1991a, 1991b). Generalizations based on comparative analyses of published webs have been reviewed and promoted, often with apologies for the limitations of empirical data gathered by others (e.g., Sugihara et al. (1989), Cohen et al. (1990), and Pimm et al. (1991)). Great caution is urged in the acceptance of results based on comparisons of highly heterogeneous, simplified, and unevenly aggregated food webs culled from the literature (Paine, 1983, 1988; Winemiller, 1990; Polis, 1991).

Among the numerous food web properties, network linkage density and connectance have received the most attention. In terms of its potential for unique contributions from a holistic ecological macrodescriptor, connectance is perhaps among the least relevant of web features (Paine, 1983). In essence, network connectance is equivalent to a highly aggregate measure of average diet breadth among community members (Warren, 1990; Winemiller, 1990). The evolution of niche width is an exciting but fairly old topic, and one that might be pursued more profitably at lower levels of organization that can be characterized more completely (e.g., populations or guilds with detailed estimates of consumption and ratios of supply and demand). At the very least, framing the problem of niche width within a holistic food web context requires a dynamic model in one form or another (Pimm, 1992; Cohen and Newman, 1988; Burns et al., 1991; Patten, 1991).

Determinants of Web Structure

Lawton (1989) identified at least six kinds of models used to explain patterns observed in empirical webs: (1) Energetic constraints (Odum, 1969); (2) dynamic predator-prey models (Cohen and Newman, 1988); (3) dynamic donor-control models (Pimm, 1982); (4) static assembly models (Yodzis, 1981b, 1984); (5) the static cascade model (Cohen and Newman, 1985); and (6) natural history constraints (Warren and Lawton, 1987). Hybrid approaches that combine two of the above models exist, including a dynamic predator-prey cascade model (Cohen et al., 1990) and a dynamic assembly model (Law and Blackford, 1992). Warren and Lawton (1987) and Warren (1990) offered mechanistic explanations of food web patterns based on morphological and functional constraints of body size and feeding mechanisms (see also Hairston and Hairston (1993)). Cousins (1985, 1987) contrasted historical developments of size-based versus energetics-based interpretations of community trophic structure. Currently, neither the empirical database nor actual knowledge of dynamical ramifications of these alternative models appear sufficient to permit a synthesis relating cause to effect at the level of whole communities

(Lawton, 1989). A systematic evaluation of alternative hypothesis of causation for observed food web properties might begin with natural history constraints (involving body size, foraging behavior, life history, etc.) and work up the hierarchy of organization and abstraction toward mechanisms such as ecosystem energetics.

Food Web Research a Decade Later: A Comparison of Two Workshops

One decade elapsed between the first workshop on food webs and the gathering that led to this book. The U.S. Department of Energy sponsored a food web workshop organized by the Oak Ridge National Laboratory and held in Fontana Village, North Carolina in October 1982 (DeAngelis et al., 1983). This workshop was an important event in the early development of food web theory. A number of influential papers subsequently published in the open literature were born of ideas and analyses presented at this workshop (e.g., a special series of papers in *Ecology*, Vol. 69(6), 1988). Perhaps because it was the first such gathering of researchers dealing with an emerging discipline, the Fontana Village workshop generated a relatively mild controversy regarding the interpretation of food web connectance (e.g., Paine (1983, 1988)), one that has only recently subsided. It is important to acknowledge that the first workshop was instrumental in stimulating a decade of vigorous research that has resulted in the redirection of inquiries and the emergence of new questions.

During the decade that followed, the body of published food web research has grown exponentially and the discipline has matured considerably. A food web symposium was organized by Joel Cohen and Don DeAngelis and held at the 1990 INTECOL meetings in Yokohama, Japan. Even though this second meeting was much smaller than the first (eight vs. 42 participants), it generated vigorous debate among attendees involved in empirical versus theoretical aspects of food web research (e.g., Cohen (1991), and Polis (1991, 1994)). Most recently, a second major workshop convened in September 1993 at Colorado State University's Pingree Park Conference Center in the Rocky Mountains (this

volume). The Pingree Park symposium brought together more participants (72) and a wider spectrum of views and approaches than ever before, with the objective to assess where the discipline stands and to facilitate future research. Eight participants (but only five speakers) were present at both the 1982 and 1993 workshops, and representation by female ecologists was markedly greater at the second workshop (24% vs. 0% of first authors, and 17% vs. 5% of total participants).

One can infer much about the development of the discipline by comparing the areas emphasized by the two workshops. Nineteen oral papers were presented at Fontana Village and 30 oral papers presented at Pingree Park. The oral papers presented at Gatlinburg and Pingree Park workshops are broken down by subject matter and ecosystem. Three differences are apparent. The 1993 workshop had: (1) More empirical emphasis relative to pure theory; (2) relatively little focus on patterns based on topological webs; and (3) at least some presentation of food web applications to resource management and environmental problems. The 1993 workshop also had a more even distribution among aquatic and terrestrial studies, but soil/microbial studies remained underrepresented.

| | 1982 | 1993 |
|--------------------------|------|------|
| Theory/models | 84% | 27% |
| Patterns in web topology | 21% | 7% |
| Empirical/experimental | 16% | 73% |
| Applied | 0% | 17% |
| Aquatic/marine | 10% | 33% |
| Terrestrial | 5% | 40% |
| Soil/protozoa | 5% | 13% |

Some of the main issues discussed at the Gatlinburg meeting were: (1) Intervals of web digraphs; (2) patterns generated by dynamic food web models; (3) relationships between observed and model web topology with predictions from May's (1972, 1975) stability-complexity model; (4) energetic and biological constraints on omnivory, food chain length, and looping; (5) relationship between connectivity and interaction webs; (6) assembly rules; (7) species packing in topological webs; and (8) ecosystem cycling. Primary topics discussed at the Pingree Park work-

shop included: (1) Trophic cascades and the interaction between production and consumption; (2) temporal/spatial variability in food webs, scale effects, and transport across boundaries; (3) relationships between direct and indirect interactions; (4) effect of disturbance in structuring food webs; (5) the role of key species; (6) the influence of life history on web dynamics; (7) effect of adaptive foraging on food webs; (8) predicting effects of anthropogenic disturbances on food webs; and (9) application of empirical data and food web models to agricultural pests and fisheries management. In summary, comparison of the two workshops reveals movement toward more detailed empirical analyses, less focus on static descriptions, greater integration between patterns and ecological processes, greater reflection on the role of operational units and scale, and the emergence of applications of food-web knowledge to natural resource problems.

Some Promising Areas for Inquiry

Following four days of discussion, participants at the Pingree Park workshop charted areas likely to produce significant advances in food web knowledge and its application to other areas of basic ecology and resource management. We briefly outline topics from closing summaries by D. Strong, B. Menge, and L. Persson. Greater integration is needed between population dynamics and the flow of energy, biomass, and nutrients in food webs (i.e., better coupling of the biodemographic (species interactions) with the biogeophysical (energy/nutrient cycling) paradigm). Analysis of stable isotope ratios will become more prevalent as a means for documenting flow (Peterson and Fry, 1987; Duggins et al., 1989; Kling et al., 1992). What is the relationship between flow web and interaction web for a given system? How do we demonstrate interaction strength empirically, and how can this be achieved in the study of large or complex systems? Greater insights into the relationship between web structure and dynamics will be achieved from greater examination of the effects of spatial and temporal scale, habitat boundaries, and transport (e.g., the relative incidence of habitat donor control versus feedbacks between habitats).

In this vein, community gradient studies could be integrated with food web research. The role of detritus and material cycling deserves greater attention, and greater coupling between traditional producer-grazer webs and detrital webs is needed.

Given the importance of ontogenetic niche shifts for many species, what are the effects of size structure on food web structure and function? Perhaps the more fundamental question is What is the influence of life history variation on web structure/function? Given the transient behavior derived from simple food web models, how do we predict long-term dynamics? Even reliable prediction of short-term dynamics may be a daunting task in speciose systems. We need to identify those phenomena that are species-specific (key species) versus those dependent only on functional groups. Greater integration of evolutionary biology with food web ecology likely would strengthen both fields. Finally, the application of food web approaches to problems such as bioaccumulation, contaminant fates, exploited populations, habitat alteration, and global climate change will feed back to basic research and improve existing paradigms that are only now in their infancy.

Food Webs in Altered Ecosystems

It would be inappropriate to end this introductory chapter without mentioning one of the most dominant factors currently influencing food webs. Humans, and not just the natural ecological factors discussed throughout this book, play a major role in the distribution and abundance of species and the structure and dynamics of food webs. Anthropogenic influences range from the extirpation of top predators and the harvesting of dominant or key species, to the wholesale introduction of exotic species. As biologists interested in theory and unifying principles, we often seek to discern natural processes and patterns, ideally within pristine systems. Consequently, we tend to pay comparatively little heed to artificial phenomena caused by human alteration of natural systems. As Crowder et al. and Parsons (this volume) demonstrate so well, such a worldview is myopic and serves

to inhibit our understanding of the structure and dynamics of the ecosystems we now study. Surely, it will be difficult to understand food web biology when many key players are absent or decimated, when biodiversity has been reduced to varying and unknown degrees, or when exotic species become important system components. It is uncertain how the structure of natural systems and those altered by humans correspond to one another; we are unsure to what extent knowledge gained in one system applies to the other.

The two principal effects of humans have been, first, to reduce the diversity of communities and food webs, and, second, to homogenize similar biomes via species introductions. Diversity continues to be reduced by the elimination of species that compete with or threaten humans, the overharvest and depletion of species that serve as commodities, the replacement of natural habitats with agrosystems or urban areas, the reduction of species sensitive to chemical or thermal pollution, and the loss of species from habitat fragmentation (Ehrlich and Ehrlich, 1981). Large top predators, from mammalian carnivores to birds and fish, have been decimated and now exist at a fraction of their former abundances and distributions (Estes, in press). The same is true for many species exploited for food or fiber: marine mammals (e.g., the great whales, fur seals, sea otters), certain fish stocks (e.g., salmon, tuna, totoaba), birds (e.g., passenger pigeon, dodo), herbivorous mammals (e.g., rhinoceros, bison and other components of North America's pleistocene megafauna), and many trees from tropical hardwood and temperate old growth forests. Likewise, species that historically occupied habitats now used as crop- and rangelands are extinct or greatly endangered (e.g., black-footed ferret, San Joaquin kit fox, teosinte grass). Lost or decimated species, many of which were dominant components of local communities, exist at all levels of the trophic spectrum.

We can imagine that many of these species were key community interactors, and their reduction has had major effects on remaining biotas. Potential effects occur both within the context of food web interactions (e.g., changes in consumer-resource interactions,

competition, apparent competition) and outside (e.g., symbioses, habitat facilitation, biotic disturbance, translocation of nutrients or organic matter). Analyses of several human-influenced systems illustrate the magnitude and types of changes that may accompany the reduction of dominant species. Although our database and knowledge of such systems is highly variable, there is strong indication that many effects of species alteration are mediated through the food web. In these cases, changes in the abundance of focal species are often accompanied by changes in the abundance of species linked both directly via consumer-resource interactions, and indirectly via competition and trophic cascades. In general, populations of resources and competitors tend to increase, and populations of predators decrease, with declines in formerly dominant species. Removal of top predators often allows intermediate-level predators to increase, due both to the relaxation of competition and intraguild predation (Polis et al., 1989; Polis and Holt, 1992).

We mention a few of many possible systems in which dominant species have been extirpated or their populations greatly reduced: overfishing of marine stocks with changes in the populations of associated resources, competitors, and intermediate-level consumers (Parsons and Crowder et al., this volume); decimation of the great whales in the southern oceans with increases in krill and competitor populations (e.g., penguins, seals, and smaller whales; Laws (1985) and Brownell et al. (1989)); systemwide changes from overfishing of Peruvian anchovetta, including reduction of seabirds that eat these fish, greater prey (phytoplankton) abundance, and greater detrital input (and possible secondary production) to benthic communities (Murphy, 1972; Rowe, 1981); extirpation of sea otters with major changes in prey (e.g., urchins and abalone), the resources of these prey (kelp and other algae), and the consequent structure of entire subtidal (and intertidal) systems (Simenstad et al., 1978; Duggins et al., 1989); systemwide changes in the productivity and abundance of taxa throughout the trophic spectrum with the overharvest of oysters (Ulanowicz and Tuttle, 1992); changes in species abundances and the composition of native mammal communi-

ties upon the arrival of sheep and the decimation of predators in the Great Basin of North American (Berger and Wehausen, 1991); and cascading effects of the Pleistocene extinction of the North American megafauna due to overhunting (Janzen, 1986).

The other major alteration associated with humans is exotic species introductions, both deliberate (e.g., crop plants, domesticated animals, stocked game fish) and accidental (i.e., weedy plants and animals, pathogens). Changes on impacted ecosystems are often obvious and all-encompassing: e.g., the near-wholesale replacement of entire biomes (e.g., prairies) and their associated fauna with a few species of agrosystem plants and their associated pest fauna; the trend toward homogenization of tropical lowlands caused by introductions of trees and weedy plants that provide commodities; decimation of the rich native fish assemblage of Lake Victoria by exotic Nile perch (Kaufman, 1992); massive reductions of salmonid fishes in lakes following introduction of *Mysis relicta* shrimp (Lasenby et al., 1986) with indirect effects on nearby terrestrial communities (e.g., decreased densities of bears and eagles) (Spencer et al., 1991); changes in North American forests following introduction of chestnut blight and reduction of chestnut (Hill, 1994); the loss of systemwide productivity from desertification of large parts of the world wrought by human activities and overgrazing by introduced herbivores (e.g., the Sahiel, southwestern North America) (LeHouerou and Gillet, 1986); the destruction of temperate forests by exotic insect herbivores (e.g., gypsy moth) (Stephens, 1971); the alteration of plant-pollinator communities by exotic honeybee strains (Roubik, 1978; Seely, 1985); and the degradation of entire communities with the introduction of particularly noxious species (e.g., fire ants and zebra mussels in North America). In many northern temperate freshwater ecosystems, fish stockings and other management practices determine much of the food web structure. Introduced species can carry pathogens and parasites that infect native species via apparent competition (e.g., malaria carried by exotic birds decimating the native Hawaiian avifauna, which, in turn, caused native plants, dependent on native pollinators, to

decrease) (Holt and Lawton, 1994). Overall, introductions and the ecological success of dominant exotic species tend to homogenize the community structure of entire biomes in different biogeographic areas.

It should be obvious that humans influence food web structure and dynamics in ecosystems worldwide. Although much of the book does not directly address such anthropogenic influences (but see section introduced by Crowder et al., this volume), it is our hope that it contributes to our ability to deal with these changes by advancing basic understanding. For example, the chapters on spatial components of food webs convey a clear message to conservation biologists. Allochthonous input via the flow of energy, material, and organisms across boundaries is often a key process in web dynamics and the functioning of ecosystems. Nature preserves are likely not isolated trophically from surrounding ecosystems. The spatial dynamics of trophic interactions must be considered in order to foster ecosystem integrity and biodiversity. Similarly, the recognition that indirect effects are often important and that the productivity of particular species may depend on taxa positioned several links away in a food chain might suggest that entire communities should be managed in order to conserve rare species. Nearly every page of this book provides pieces to a puzzle that, when assembled, potentially will provide a great deal of useful information as we attempt to maintain at least a semblance of the natural world.

Acknowledgments

Many people were instrumental in the organization of the food web workshop and the production of this book. In particular, John Moore handled many of the details involved with putting 80 people from all over the globe together in one room. We thank John sincerely for his work at the conference and for his many editorial contributions. Mike Vanni was another key player throughout the process. We thank Mike for help in writing the National Science Foundation proposal, chairing part of the program, and excellent and timely editorial work. Janne Bengtsson has our sincerest gratitude for his assistance at

the workshop, and especially for his skillful editorial service. Other people that helped us to compile the final list of authors, set the workshop itinerary, and saw to its successful completion include Don DeAngelis, Peter DeRuiter, Diana Freckman, Bob Holt, Bruce Menge, Lennart Persson, and Mary Power—a sincere thanks to them for their time, energy, encouragement, and goodwill throughout the long process. Editorial chores for the book were shared by a number of participants. In particular, Janne Bengtsson, Don DeAngelis, Peter DeRuiter, Bob Holt, John Moore, and Lennart Persson were outstanding and provided helpful comments on science and grammar. Almost every author in this book reviewed one or more chapters. To each of these fine people, we offer a sincere and heartfelt thanks for their generous and conscientious assistance.

The conference and the production of this book was greatly facilitated by a grant from the National Science Foundation (DEB 9310619). We are particularly grateful to Laurel Fox and Scott Collins for their encouragement and support. Additional support was provided by the Vanderbilt Research Council (Gary Polis). We also thank the staff at Pingree Park Conference Center, Colorado State University, for providing such a wonderful atmosphere for our workshop—truly first rate. Important editorial and clerical work was performed by Kim Snyder and Pomma Phothimat, and we gratefully acknowledge the assistance and patience of Greg Payne, editor at Chapman & Hall.

We thank the many people in our personal lives that facilitated this book and made our existence productive and happy. We are infinitely grateful to our wives (Sharon Lee Polis and Leslie Kelso Winemiller) and families (Evan Polis and Megan and Brent Winemiller) for their understanding and patience during the long process. Gary Polis also thanks Bob Bednarek, Steve Hurd, Steve Polis, Dan Polis, and Larry Pomeroy for help and friendship and extends his warm and sincere thanks to Kirk Winemiller for his dedication, generosity, humor, perseverance, diplomacy, and friendship during the long and heartfelt process of editing. Kirk Winemiller offers sincerest thanks to Gary Polis for his foresight and initiative in organizing the Pingree Park workshop and his

collaborative efforts in editing this volume. Finally, this book would not have been possible without the support of the scientists that served as workshop participants, authors, referees, and editors. Their work made this enterprise both productive and pleasant

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