

1.2 | FOOD WEB SCIENCE: MOVING ON THE PATH FROM ABSTRACTION TO PREDICTION

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This chapter explores some basic issues in food web research, evaluates major obstacles impeding empirical research, and proposes a research approach aimed at improving predictive models through descriptive and experimental studies of modules within large, complex food webs. Challenges for development of predictive models of dynamics in ecosystems are formidable; nonetheless, much progress has been made during the three decades leading up to this third workshop volume. In many respects, food web theory has outpaced the empirical research needed to evaluate models. We argue that much greater investment in descriptive and experimental studies as well as exploration of new approaches are needed to close the gap.

The most fundamental questions in food web science are “How are food webs structured?” and “How does this structure influence population dynamics and ecosystem processes?” At least four basic models of food web structure can be proposed. One model could be called the “Christmas tree” model, in which production dynamics and ecosystem processes essentially are determined by a relatively small number of structural species. Most of the species’ richness in communities pertains to interstitial species that largely depend on the structural species for resources, and may be strongly influenced by predation from structural

species. Hence, interstitial species are like Christmas ornaments supported by a tree composed of structural species (Figure 1A). Structural species could include conspicuous species that dominate the biomass of the system, but also could be keystone species that may be uncommon but have disproportionately large effects on the food web and ecosystem (Power et al., 1996b; Hurlbert, 1997). In many ecosystems, certain plants and herbivores clearly support most of the consumer biomass, and certain consumers strongly influence biomass and production dynamics at lower levels. This pattern may be more apparent in relatively low-diversity communities, such as shortgrass prairies and kelp forests, in which relatively few species provide most of the production, consume most of the resources, or influence most of the habitat features.

A second alternative is the “onion” model in which core and peripheral species influence each other’s dynamics, with core species having a greater influence (i.e., magnitudes of pairwise species effects are not reciprocal). The core-peripheral structure is arranged in a nested hierarchy (Figure 1B). This model might pertain to high-diversity ecosystems such as tropical rainforests and coral reefs. Ecological specialization via co-evolution would result in interactions from peripheral species that may have strong effects on a few species, but weak effects on most of the community, and very weak effects on core species. In tropical rainforests, rare epiphytic plants and their co-evolved herbivores, pollinators, and seed dispersers depend upon the core assemblage of tree species, yet the converse is not true. Removal of a given pollinator species would yield a ripple effect within an interactive subset, or module, of the food web, but likely would not significantly affect core species of decomposers, plants, and animals.

A third food web structure could be called the “spider web” model in which every species affects every other species via the network of direct and indirect pathways (Figure 1C). This concept, in which everything affects everything, is explicit in network analysis (Fath and Patten, 1999), which gives rise to numerous emergent properties of networks (Ulanowicz, 1986). Signal strength, via direct or indirect propagation, may depend on proximity of nodes within the network. Propagation of indirect effects in food webs can yield counterintuitive results from press perturbations. For example, harvesting a competitor of a top predator can result in a decline rather than an increase of that predator (Yodzis, 1996; Wootton, 2001; Relyea and Yurewicz, 2002).

A fourth model of food web structure could be called the “internet” model. Following this concept, webs are networks having major and minor “hubs” in which their position within the network architecture

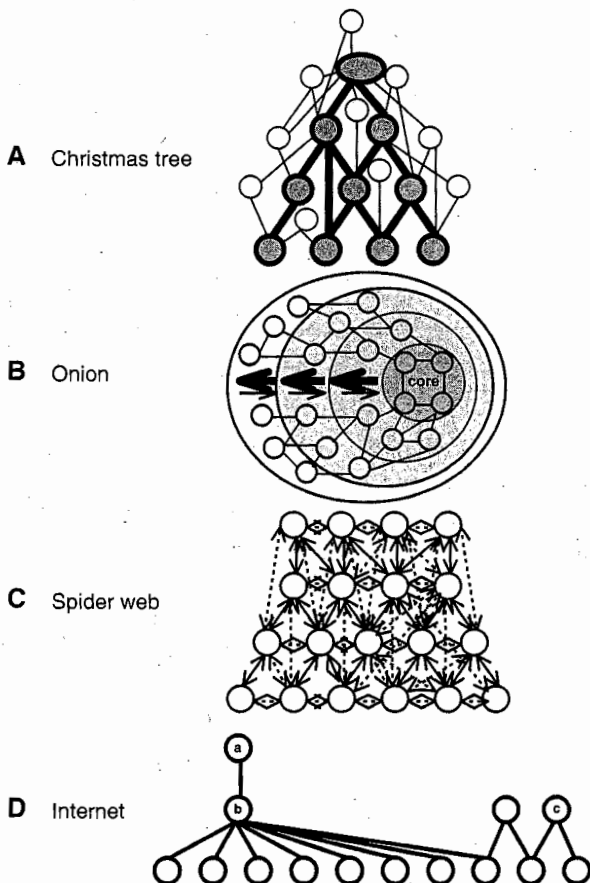


FIGURE 1 | Schematic illustrations of four models of food web structure: **A**, Christmas tree (structural and interstitial species); **B**, onion (hierarchy of core and peripheral species, the strength of effects is greater from the core outward); **C**, spider web (all species affect all others either directly or indirectly); and **D**, internet (network architecture yields disproportionate influence by hub species, which are not necessarily identified by the number of direct connections, that is, node a could actually have more influence on the system, via its control of node b, than node c).

determines the degree that a species can influence other species in the system (Figure 1D). Jordán and Scheuring (2002) reviewed the applicability of the internet model to food webs, and maintained that the density of connections to a node may be a poor indicator of the potential influence on web dynamics. For example, a highly influential species (e.g., top predator) could have only one or a few links connecting it to other species that in turn have numerous connections to other species in the system. Analysis of network features has become a popular pursuit in fields ranging from the social sciences to cell biology, but the

relevance of this approach for understanding food web dynamics is uncertain (Jordán and Scheuring, 2002).

How are food webs structured? The answer will necessarily rely on accumulated evidence from a large body of empirical research. We contend that available evidence is insufficient to state, with a degree of confidence, the general circumstances that yield one or another of these alternative models. Like any scientific endeavor, research on food webs advances on four interacting fronts: description (observation), theory (model formulation), model testing (experimentation), and evaluation. Evaluation invariably leads to theory revision and the loop begins again. After several trips around this loop, a model may begin to successfully predict observations, and we gain confidence for applications to solve practical problems. Important ecological challenges already have been addressed using the food web paradigm, including biocontrol of pests, fisheries management, biodiversity conservation, management of water quality in lakes, and ecotoxicology (Crowder et al., 1996). We believe, however, that the development of food web theories (models) and their applications is greatly outpacing advances in the descriptive and experimental arenas. Although this state of affairs is not unexpected in an immature scientific discipline, it results in inefficient development of understanding. Why have empirical components lagged behind theoretical developments? We propose that unresolved issues of resolution and scale have hindered empirical research. Resolution of four basic aspects of food webs is required: (1) the food web as an operational unit, (2) components of food webs, (3) the nature of food web links, and (4) drivers of temporal and spatial variation.

Food Webs as Units

First, the spatial and temporal boundaries of a community food web are always arbitrary, and it should be emphasized that any food web is a module or subnetwork embedded within a larger system (Cohen, 1978; Moore and Hunt, 1988; Winemiller, 1990; Polis, 1991; Hall and Raffaelli, 1993; Holt, 1997; and others). Food webs are almost always defined according to habitat units nested within, and interacting with larger systems (e.g., biotia living on a single plant, water-filled tree holes, soil, lakes, streams, estuaries, forests, islands). Hence, every empirical food web is a web module. Spatial and taxonomic limits of modules are essentially arbitrary. Thus, it probably makes little sense to speak of large versus small webs, for example. Web modules vary in their degree of correspondence to habitat boundaries. Although a lake has more discrete physical boundaries than a lowland river with flood pulses and

marginal wetlands, numerous links unite lake webs with surrounding terrestrial webs. Thus, broad comparative studies of food web properties necessarily deal with arbitrary units that may have little or no relationship to each other.

To illustrate this point, we examine empirical food webs from three studies, all published in the journal *Nature*, that constructed models to predict statistical features of these webs (Williams and Martinez, 2000; Garlaschelli et al., 2003; Krause et al., 2003). Leaving aside issues related to web links and environmental drivers, let us examine the number of taxa within each habitat. For statistical comparisons, these taxa were subsequently aggregated into “trophospecies” (species that presumably eat all the same resources and also are eaten by all the same consumers). The number of taxa were reported as follows: Skipwith Pond, England (35); Bridge Brook Lake, New York (75); Little Rock Lake, Wisconsin (181); Ythan Estuary, Scotland (92); Chesapeake Bay, United States (33); Coachella Valley, California (30); and Isle of St. Martin, Caribbean (44). Thus, we are led to conclude that Skipwith Pond, a small ephemeral pond in England (Warren, 1989), contains more taxa than Ythan Estuary, Scotland (92) (Hall and Raffaelli, 1991), and Chesapeake Bay (33) (Baird and Ulanowicz, 1989), one of the world’s largest estuaries. These food webs were originally compiled based on different objectives and criteria. The Skipwith Pond food web reports no primary producer taxa, the Bridge Brook Lake web contains only pelagic taxa, the Chesapeake Bay web is an ecosystem model with a high degree of aggregation, and the Ythan Estuary web includes 27 bird taxa with most other groups highly aggregated. If we examine just the number of reported fish species, Skipwith Pond has none, Ythan Estuary has 17, and Chesapeake Bay is reported to have 12. In reality, Chesapeake Bay has at least 202 fish species (Hildebrand and Schroeder, 1972). These comparative studies analyzed features of Polis’s (1991) highly aggregated Coachella Valley web (30 taxa) even though that author clearly cautioned against it and indicated that the web contained, among other taxa, at least 138 vertebrate, 174 vascular plant, and an estimated 2,000–3,000 insect species. The Isle of St. Martin web was reported to have 44 taxa that include 10 bird and 2 lizard species plus 8 non-vertebrate aggregations (Goldwasser and Roughgarden, 1993).

Clearly, these empirical food webs represent an odd collection of woefully incomplete descriptions of community species richness and trophic interactions, and are unlikely to provide a basis for robust predictive models. Discrepancies are due to the fact that these webs were originally compiled based on different objectives and criteria. Objective methods for defining and quantifying nested modules are badly needed. At a minimum, consistent operational definitions for units and

standardized methodologies are required to make quantitative comparisons. For example, sink food webs (Cohen, 1978) can be defined based on the network of direct trophic links leading to a predator. Comparisons of different systems could be based on the sink webs associated with predators that are approximate ecological “equivalents”. Alternatively, food web comparisons can be based on the collection of sink webs leading to consumers of a given taxonomic group, such as fishes (Winemiller, 1990). Source webs (tracing the network trophic links derived from a taxon positioned low in the web) provide an operational unit for food web comparisons (e.g., grasses–herbivorous insects–parasitoids) (Martinez et al., 1999), but in most cases, as links radiate upward (to higher trophic positions), they would very rapidly project outward (to adjacent habitats) in a manner that would yield major logistical challenges for empirical study.

Components of Food Webs

Our second issue is the units comprising food webs. Entities comprising food webs have been invoked to serve different objectives that are rarely compatible. Consequently, great variation is observed among food web components, ranging from species life stages to functional groups containing diverse taxa. In most empirical studies, these components have been invoked *a posteriori* rather than *a priori*. We must decide *a priori* whether we wish to examine individuals (what we catch), species populations (what we want to model), “trophospecies” (what we invoke when taxa had been aggregated), functional groups (what we think might be relevant), or trophic levels (what we once thought was relevant). Yodzis and Winemiller (1999) examined multiple criteria and algorithms for aggregating consumers into trophospecies based on detailed abundance and dietary data. Taxa revealed little overlap in resource use and the extent to which predators were shared, and almost no taxa could be grouped according to a strict definition of shared resources and predators. A similar approach was developed by Luczkovich et al. (2003) in which graph theory and the criterion of structural equivalence were used to estimate degrees of trophic equivalency among taxa. Unlike trophospecies, structurally equivalent taxa do not necessarily feed on any of the same food resources or share even a single predator, but they do play functionally similar roles in the network. We contend that species populations are the only natural food web components, because populations are evolutionary units with dynamics that are largely independent from those of heterospecific members of a guild or functional group (Ehrlich and Raven, 1969).

Food Web Links

The third issue is how we estimate food web links. Too often in the past, food web architecture was treated as binary with links either present or absent (i.e., web topology with no magnitudes or dynamics). Motivated, in part, by the seminal theoretical work of May (1973), empirical studies attempt to determine the nature and magnitude of links (i.e., interaction strength) using field experiments in which one or more species are manipulated (Paine, 1992; Menge, 1995; Wootton, 1997; Raffaelli et al., 2003). Interaction strength determines system dynamics (Paine, 1980) and stability (Yodzis, 1981a; Pimm, 1982; McCann et al., 1998), as well as the manner in which we view the basic structure of the food web (Winemiller, 1990; de Ruiter et al., 1995). Weak links are associated with greatest variation in species effects (Berlow, 1999), and food webs seem to be dominated by these weak links. For example, food webs of tropical aquatic systems are strongly dominated by weak feeding pathways as estimated from volumetric analysis of fish stomach contents (Figure 2).

Despite the critical need to understand interaction strength and the manner in which it creates food web structure and drives dynamics, many theoretical and comparative studies that relied on empirical data have not considered species abundances and have portrayed food web links simply as binary. Why has this been the case? First, it is *difficult* to inventory species in natural communities (e.g., Janzen and Hallwachs, 1994). It is *more difficult* to estimate species' relative abundances, even for conspicuous sedentary species like trees (e.g., Hubbell and Foster, 1986; Terborgh et al., 1990). It is *even more difficult* to estimate the

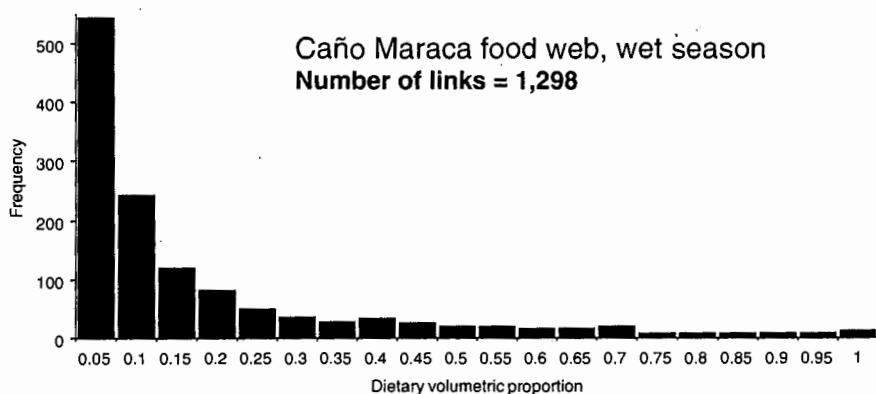


FIGURE 2 | Skewed distribution of feeding links of variable magnitudes (estimated as volumetric proportion of prey items in stomach contents) in a tropical wetland food web (Caño Maraca, Venezuela).

presence of feeding relationships (e.g., Thompson and Townsend, 1999). It is *yet more difficult* to estimate the magnitudes of feeding relationships (Winemiller, 1990; Tavares-Cromar and Williams, 1996). Finally, it is *exceedingly difficult* to estimate the strength of species interactions (Paine, 1992; Wootton, 1997).

Interaction strength can be inferred indirectly from quantitative dietary analysis, but this is extremely time consuming and requires a great degree of taxonomic and modeling expertise. The method is not viable for many consumer taxa, because most food items contained in the gut are degraded. Moreover, large samples are needed to estimate diet breadth (i.e., links) accurately and precisely and to reveal important spatial and temporal variation in feeding relationships (Winemiller, 1990). As sample size is increased from 1–20 individuals, the mean diet breadth of an omnivorous characid fish from Caño Maraca increases from 2.8–3.9, and the average number of feeding links increases from 3.7–22 (Figure 3). Similarly, sampling effort has been shown to affect food web properties associated with the number of nodes (Bersier et al.,

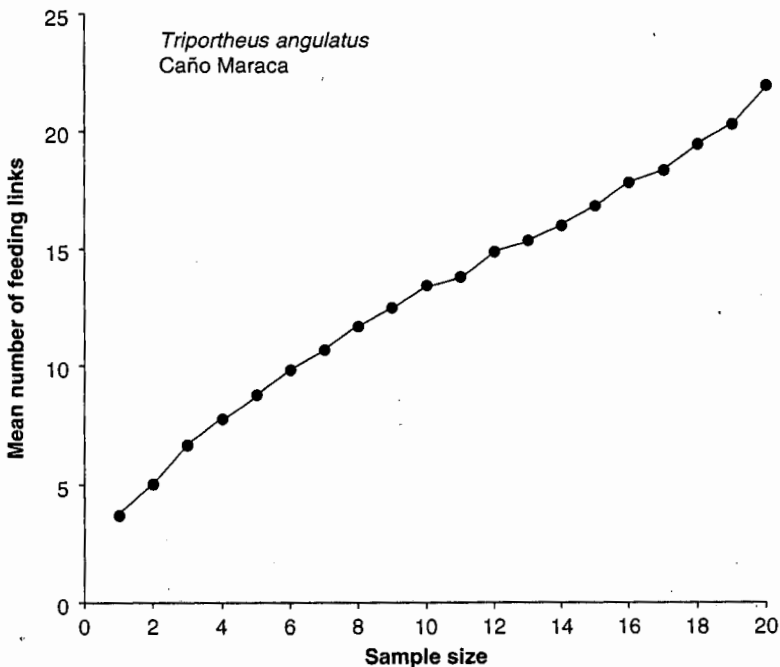


FIGURE 3 | Plot illustrating increases in mean number of feeding links (estimated from stomach contents analysis) with increasing sample size for an omnivorous characid fish, *Triportheus angulatus*, from Caño Maraca, Venezuela.

1999). Quantitative estimates of diet composition must be converted to consumption rates for use in dynamic food web models (see Koen-Alonso and Yodzis, Chapter 7.3).

Interaction strength can be directly estimated via field experiments, but this method is beset with its own set of challenges (Berlow et al., 2004). A major problem is the quantitative measure used to quantify interaction strength. Several indices have been employed (reviewed by Berlow et al., 1999), including a raw difference measure $(N-D)/Y$; Paine's index $(N-D)/DY$; community importance $(N-D)/Np_t$; and a dynamic index $(\ln(N/D))/Y_t$, in which N = prey abundance with predator present, D = prey abundance with predator absent, Y = predator abundance, p = predator proportional abundance, and t = time. Different indices computed from the same set of experimental data can yield very different conclusions (Berlow et al., 1999).

Even if we could agree on a single empirical measure of interaction strength, we would still face serious challenges in estimating community dynamics with this information (Berlow et al., 2004). That is because species interactions typically are nonlinear, which implies that single estimates of interaction strength will be unlikely to assist in building dynamic community models (Abrams, 2001). According to Abrams, "Measuring interactions should mean determining the functional form of per capita growth rate functions, not trying to encapsulate those complicated relationships by a single number." Application of simple models to predict features and dynamics of complex systems would be justified if these models could, *a priori*, yield successful predictions. Clearly, considerable theoretical and empirical research remains to be done on the crucial issue of interaction strength.

An additional consideration is that food web links are usually assumed to be consumer resource; however, other kinds of species interactions, such as mutualism and other forms of facilitation, can be critical (Bruno et al., 2003; Berlow et al., 2004). Describing the functional forms of these relationships could be even more challenging. Some of the most important community interactions are not determined by resource consumption. Gilbert (1980) described ecological relationships in a food web module within a Costa Rican rainforest. This module is delimited by 36 plant species in 6 higher taxa inhabiting 3 habitat types. Each plant species has a set of generalist and specialist herbivores, pollinators, and seed dispersers, some of which are shared with other plants within the module and, in some cases, plants outside the module. In this food web, some of the most critical interactions determining species' abundances and distributions are mutualisms.

Drivers of Temporal and Spatial Variation

The fourth critical issue is the influence of environmental and life history variation on food web structure, species interactions, and population dynamics. Do food web dynamics drive species abundance patterns, or do species abundance patterns drive food web dynamics? Species' relative abundances determine functional responses, adaptive foraging, predator switching, and their effects on numerical responses. Does food web structure determine relative abundance patterns, or are other factors equally or more important?

Interaction strength varies in space and time, sometimes as a function of behavior, but sometimes as a function of environmental variation and species life histories that affect abundance patterns (Polis et al., 1996a). Species with different life histories and ecophysiological adaptations respond differently to environmental variation (Winemiller, 1989a). Species with short generation times and rapid life cycles respond faster to environmental variation (including resource availability) than species with slower life cycles that often reveal large variation in recruitment dynamics and demographic storage effects (Polis et al., 1996a; Scharler et al., Chapter 8.3). Empirical studies have demonstrated how species' abundances and web links change in response to environmental drivers. Rainfall and leaf litter deposition determine food web patterns in tree holes in tropical Australia (Kitching, 1987). Temporal dynamics in rocky intertidal webs are influenced by local disturbances (Menge and Sutherland, 1987) and coastal currents (Menge et al., 2003). Food webs of streams and rivers vary in relation to seasonal changes in photoperiod and temperature (Thompson and Townsend, 1999) and hydrology (Winemiller, 1990; Marks et al., 2000).

Theories, Tests, and Applications

So where are we now? Theory and attempts at application of theory seem to have outpaced observation and model testing. There is little agreement and consistency regarding use of operational units, methods for quantifying links, indices of interaction strength, etc. Use of confidence intervals is virtually non-existent in empirical food web research. This state of affairs is perhaps a natural consequence of an "immature" scientific discipline (i.e., abstract concepts, lack of consensus and empirical rigor). Nonetheless, society demands that ecological science address current problems. Currently, food web models have low predictive power and certainly lack the precision and accuracy of physical models that allow engineers to put a spaceship on the moon or build a sturdy suspension bridge. Food web models currently used for natural resource

management are highly aggregated and employ crude quantitative estimates of production dynamics and species interactions. Output from these models can be considered educated guesses, yet, currently, we have no other options. It is unreasonable to expect individual investigators or labs to achieve predictive food web models, yet few are lobbying for empirical food web research on a grand scale. This state of affairs may be an unfortunate legacy of the IBP (International Biological Program, supported in the 1960–1970s by large sums of national and international science funding aimed at understanding major ecosystems of the planet).

Were past efforts to describe large food webs misguided? Nearly 20 years ago, the first author attempted to describe food webs of tropical streams in a standardized manner based on intensive sampling (Winemiller, 1989b, 1990, 1996). Two continuous years of field research yielded over 60,000 fish specimens and countless invertebrates. Two additional years of lab research (19,290 stomachs analyzed) produced data that supported analyses that have been ongoing for 17 years. These quantitative food webs have provided insights into how environmental variation driven by seasonal hydrology affects population dynamics and interactions. Yet, as descriptions of community food webs, these webs suffer from the same limitations that plague other webs. The many issues, both conceptual and methodological, requiring resolution in order to make meaningful comparisons of web patterns ended up being a major discussion topic (Winemiller, 1989b, 1990).

Is there a better way? We advocate a multi-faceted empirical approach for field studies as a means to advance understanding of food webs. Researchers investigating large, complex systems would be better served to investigate food web modules in a hierarchical fashion. Long-term research mindful of environmental drivers is extremely valuable in this context. Research that blends together description and experimentation will yield models that can then be tested within relevant domains (Werner, 1998). This approach obviously will require research teams with specialists that collectively provide a range of methodological and taxonomic expertise. Several groups around the world have already adopted this long-term, team research approach to investigate food webs of ecosystems ranging from estuaries (Raffaelli and Hall, 1992) to rainforests (Reagan and Waide, 1996).

We have attempted this hierarchical modular approach in our research on the Cinaruco River, a floodplain river in the Llanos region of Venezuela. Our group is describing nutrient dynamics, primary production, community structure, habitat associations, and feeding interactions in channel and aquatic floodplain habitats during various phases of the annual hydrological cycle in this diverse food web (see Layman

et al., Chapter 7.4). Population abundance and distribution patterns are assessed from field surveys (Jepsen et al., 1997; Arrington and Winemiller, 2003; Hoeinghaus et al., 2003a; Layman and Winemiller, 2004), and feeding links are investigated using dietary and stable isotope analyses (Jepsen et al., 1997; Jepsen and Winemiller, 2002; Winemiller and Jepsen, 2004; see Layman et al., Chapter 7.4). We also are investigating three food web modules (Figure 4): (1) benthivorous fishes, benthic biota, detritus, and nutrients; (2) herbivorous fishes interacting with terrestrial and aquatic vegetation; and (3) piscivores and their diverse prey (see Layman et al., Chapter 7.4). Field experiments (enclosures, exclosures, and artificial habitats) have been conducted over variable spatial scales in different seasons and habitats to examine species effects on prey assemblages (Layman and Winemiller, 2004) and benthic primary production and particulate organic matter (Winemiller et al., 2006). In virtually all experiments designed to test for top-down effects, one or a small number of fish species (including large detritivores and piscivores) reveal strong and disproportionate effects in this species-rich food web (more than 260 fish species documented).

The descriptive research elements have led to creation of models that predict effects of abiotic ecosystem drivers (the most fundamental being seasonal hydrology) and aspects of species life histories (e.g., seasonal migration by a dominant benthivorous species) on food web dynamics and ecosystem processes. For example, the relative influence of top-down and bottom-up processes on benthic primary production, benthic particulate organic matter, and meiofauna diversity is a function of the seasonal cycle of hydrology, habitat volume, allochthonous nutrient inputs, migration by the dominant benthivorous fish, and changing densities of resident benthivorous fishes as a function of habitat volume. Experiments have been conducted to estimate the magnitude of treatment effects that reveal the relative influence of bottom-up (nutrient limitation and sedimentation) and top-down (grazing) effects on standing stocks of algae and fine particulate organic matter (Winemiller et al., 2006). A separate series of experiments examined effects of predators on prey fish densities and habitat use (Layman and Winemiller, 2004). The relative influence of dominant piscivores on littoral zone fish assemblages is strongly dependent on body size relationships (see Layman et al., Chapter 7.4) and habitat features which in turn are influenced by seasonal hydrology. In short, almost no aspect of this river food web could be understood without examining the direct and indirect effects of the annual hydrological cycle.

Guided by our descriptions of the overall food web, the predictive models developed for modules are being joined together based on elements

of overlap. The degree to which predictions of module dynamics will agree with predictions from a model that incorporates all elements remains to be investigated. Nonetheless, it seems more rational to begin at smaller scales and work incrementally toward a model of the larger system, rather than the reverse approach. Many of the contributions in this book describe similar small-to-large approaches employing multiple lines of empirical evidence to test model predictions. Several research groups have reported results from long-term research that blends description, experimentation, and modeling—for example, temperate lakes (Carpenter and Kitchell, 1993a; Tittel et al., 2003), soils (de Ruiter et al., 1995; Moore et al., 2003), coastal systems (Menge et al., 2003; Raffaelli et al., 2003), rivers and streams (Marks et al., 2000; Nakano and Murakami, 2001; Flecker et al., 2002), ponds (Downing and Leibold, 2002), and fields (Schmitz, 2003). It is still too early to generalize about food web structure, and perhaps some systems conform to the onion model whereas others function according to the internet model, and so on. Given the disproportionate effects of a few dominant species demonstrated by field experiments in the Cinaruco River, the “Christmas tree” and “internet” models seem to be candidates for that species-rich system.

Discussion and Conclusions

Empirical food web research lags behind theoretical research. We agree with Englund and Moen's (2003) assertion “that it is vital for progress in ecology that more models are experimentally tested, and the main question is how to promote and speed up the process.” They continue: “By testing a model, we mean the act of comparing model predictions with relevant empirical data.” Another basic challenge identified by these authors is the critical need to determine whether or not an experimental system lies within the theoretical domain of the model being tested. In too many cases, models and tests were mismatched from the start (e.g., invalid assumptions of linear or equilibrium dynamics or inappropriate spatial scales).

Empirical food web studies must carefully consider the dynamical consequences of definitions for operational units and scale, resolution, and sample variability. Obviously, it is impossible to quantify every species and interaction in even the smallest food web modules. Even if this were possible, it is unlikely that most trophic interactions have a strong effect on system properties such as nutrient cycling and production of dominant biomass elements (e.g., the “Christmas tree” and “internet” models). Thus, it is crucial that we determine, to the extent possible, the degree of resolution needed to make successful predictions, and

then, for the sake of efficiency, not seek to achieve high levels of detail for their own sake.

We advocate a focus on a hierarchy of nested food web modules and measures of interaction strength that hold potential to yield successful predictions of population dynamics and other ecosystem features. Descriptive and experimental research should be combined in long-term studies of field sites (see also Schmitz, 2001). Such efforts require consistent funding and collaborations among scientists with different expertise. In many countries, these sorts of projects are difficult to fund and provide fewer individual rewards than short-term projects addressing specific mechanisms in small-scale ecological systems. Yet many of our most vexing ecological problems require a large-scale food web perspective. Despite the fact that a deficient empirical knowledge base is the main hurdle to scientific advancement, pressing natural resource problems require application of existing models. In many respects food web research is basic yet complicated—esoteric yet essential for natural resource management. The urgent need for application of the food web paradigm for solving natural resource problems motivates us to walk faster down the path from abstraction to prediction.

ACKNOWLEDGMENTS

A portion of this work was funded by National Science Foundation grants DEB 0107456 and DEB 0089834.