

CHAPTER 6

INTERPLAY BETWEEN SCALE, RESOLUTION, LIFE HISTORY AND FOOD WEB PROPERTIES

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6.1 ABSTRACT

Perhaps the greatest challenge for ecologists is to predict population dynamics and ecological interactions of species-rich systems. In studying food webs of species-rich systems, ecologists necessarily sacrifice much resolution and complexity of the real world. Moreover, species life history strategies interact with environmental variation at multiple scales in space and time to yield variable degrees of density-independent population regulation. Is the quest for predictive food web models too daunting of a challenge? Peter Yodzis clearly recognized and articulated the principal obstacles and parameters of the problem. The indeterminacy of ecological dynamics in species-rich food webs is apparent,

even when species interactions are projected using relatively simple functions. Peter shed much light on the manner in which life history strategies, scale, and resolution in food webs influence population dynamics. Can the taxonomic and ecological diversity of nature be defined in units that permit prediction of population dynamics? This chapter reviews these issues, and briefly describes recent empirical field research in a tropical river designed to reveal food web structure and dynamics based on web modules. Evidence from recent field experiments suggests that, at appropriate scales of resolution, we may be able predict dynamics of some of the major elements of the system. To bridge the gap between food web theory and empirical research, several theoretical and, as importantly, practical issues will require greater attention than they have received in the past.

6.2 INTRODUCTION

The food web provides perhaps the most versatile model for dealing with ecological structures, dynamics, and functions at the community and ecosystem levels. Two fundamental challenges in food web research were clearly articulated by Peter Yodzis: the implications of how we model interaction strength for predicting dynamics in large complex systems, and the effects of scale and resolution on food web patterns and dynamics. According to Yodzis (1988) “the long-term outcomes of press perturbations [i.e., experiments that depress one or more populations to monitor responses by others] are highly indeterminate, in terms of both whether species densities increase or decrease and of which interactions have the largest effects.” In a press perturbation experiment, the effect of species i on species j is given by $dN_{ei}/dI_j = -(A - I)_{ij}$, where N_{ej} is the equilibrium density of species i , I_j is the rate of addition of species j , and A is the community matrix. Yodzis further maintained that “predicting those long-term effects not only requires data on the strengths of many interactions in the system, it requires very accurate data on many interaction strengths. This is a daunting prospect indeed.” The empirical estimation of variation in interaction strength assumes even greater importance when we consider an additional conclusion from Yodzis’s research: “There seems to be some indication, in the case of topological indeterminacy [i.e., inability to predict which species interactions will be present], that the indeterminacy is less severe in food webs that are more finely differentiated in the identification of trophospecies. . . . topological indeterminacy might be in part an artifact of aggregated models” (Yodzis 1988). One way that Yodzis addressed this dilemma was to simulate food web dynamics based on bioenergetics and allometric relationships (Yodzis and Innes 1992). Results from press perturbations simulations were examined as probability distributions of response variables that are skewed relative to expectations-based interactions between a single predator and prey (Yodzis 1998, 2000).

In addition to focusing on equilibrium solutions, the community matrix modeling approach assumes that every species can potentially influence every

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other species in the system via the network of interactions, both direct and indirect. This leads us to a very fundamental question: How are food webs structured? The answer is not derived only from the measurement of nature, but also depends on conceptualization of the model. Winemiller and Layman (2005) recently described four alternative concepts of food web structure. Their *spiderweb* model views the network of species trophic interactions as a complex network in which every species influences every other species via direct or indirect pathways. This view of food web dynamics is consistent with community matrix and network models that reveal the relative influence of indirect interactions. Effects from press perturbations might be expected to propagate through the network in a sort of quasiradial fashion in which the magnitude of change is a function of proximity to the source perturbation. Some have questioned the spiderweb model of food webs on the basis many or perhaps most species appear to be influenced by only a few species (Berryman 1993).

Their second model, the *Christmas tree*, views communities as having structural species that are essential in governing production dynamics, environmental conditions, etc., and that also support interstitial species. The latter may constitute a large fraction of species richness, but with relatively little effect on structural species or ecosystem dynamics. Their *onion* model views species' potential to affect other species and the ecosystem as a nested hierarchy in which a group of core species have strong effects on peripheral species. The peripheral species in the most distal layers of the onion would be strongly influenced by, but have the weakest effects on, species populations within interior layers. Their *Internet* model of food webs stresses the importance of network architecture in determining the relative influence of species (nodes) on other species. Species directly connected to highly connected nodes (hubs) have greater potential to influence large numbers of species than those lying at the ends of long chains containing single links. The answer to the question of how food webs are structured will be determined from empirical research.

This chapter briefly reviews some of the fundamental challenges to the empirical study of food webs. Some of these challenges are logistical and, though potentially surmountable, will likely will be met only in studies of relatively small, low-diversity systems and perhaps in a very few systems for which major long-term funding permits detailed investigations of major ecosystem components. The more serious limitations are related to theoretical questions, such as how to define interaction operationally, or how to integrate life history variation or indirect interactions into models of food web dynamics. These kinds of challenges will be more difficult to address. This chapter also summarizes 10 years of research by the author and colleagues on the food web of the Cinaruco River in Venezuela. Highlighted are the many challenges of research on a species-rich system with strong abiotic temporal dynamics and high spatial heterogeneity. Although we are just beginning to understand the structure and dynamics of this tropical ecosystem, the study of web modules (subsets of co-occurring species and resources that interact and influence one

another) has enabled us to predict some patterns and dynamics of important food web elements.

6.3 EMPIRICAL FOOD WEB RESEARCH

Although the comparative study of food webs has generated tremendous interest among both theoreticians and empiricists, progress has been hindered by the quantity and quality of empirical data. To date, most results from comparative food web research have been confounded by biases in the fundamental units of comparison (Paine 1988, Winemiller 1990, Polis 1991). These biases are derived from issues of scale, especially differences in (1) definitions of food web boundaries, (2) definitions of species and feeding links, (3) methods of estimating consumption or species interaction, and (4) the manner in which food web data are reported the literature. Most food web patterns, such as constant connectance (Martinez 1992), seem to result from the different criteria and methodologies used by field investigators and data compilers rather than from ecological processes.

Sources of bias in food web analysis have been discussed in the literature, yet many of these critical points have been downplayed repeatedly, and when identified, their potential effects on food web trends have been assumed to be negligible (Sugihara et al. 1989, Cohen et al. 1990, Pimm et al. 1991, Williams and Martinez 2000, 2004). Comparative studies that have employed internally consistent methodologies have emphasized the serious limitations of datasets compiled from the literature and have yielded little or no corroboration of earlier "food web laws" (see also Hildrew et al. 1985, Winemiller 1989, 1990, Warren 1990, Martinez 1991, Polis 1991, Schoenly and Cohen 1991, Reagan and Waide 1996). The most essential elements of empirical food web research are highly sensitive to scale.

6.4 EVERY FOOD WEB IS A SUBWEB

Large variation in structural complexity is obvious among sets of community webs gathered from the ecological literature for comparative study (Cohen 1978, 1989, Pimm 1982, Briand 1983, Cohen and Newman 1985, Cohen et al. 1990, Williams and Martinez 2000). In most of the comparative food web literature, the fundamental unit for comparisons, the community, is a collection of taxa grouped together by arbitrary spatial and temporal criteria. Arbitrary variation among these units introduces bias into comparisons. Some community food webs simplify the complex network of feeding interactions within species-rich communities by reporting only those interactions perceived as being strong or important. Others have described feeding relationships in greater detail for a subset of species within a larger community. Polis (1991) described the challenges associated with compilation of a food web for the Coachella Valle, California. He identified a strong trade-off between taxonomic completeness and precision

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in estimating the presence or absence of species interactions. He estimated that complete accounting of all species within major taxa (plants, animals, parasites, and microorganisms) would total 10^3 – 10^5 in most cases.

Most reported food webs focus on a particular taxonomic group of special interest to the field investigator. For example, Martinez (1991) defined the Little Rock Lake community as all “organisms that spend virtually all the specified life stage at or below the lake’s surface.” His food web contained 6 fish species (4 species were divided into 2 life stages), 110 invertebrates, and 60 algae. The Little Rock Lake food web contains high taxonomic resolution (mostly to the level of species or genus), however this incurs a strong trade-off with the accuracy and precision of feeding interactions estimated from field studies or inferred from literature sources (based on studies at other locations) and expert opinions.

Despite the difficulties inherent in defining the boundaries of natural communities, large food webs can be divided into subwebs by objective criteria. A food web comprised of a single consumer species and all of its prey is a subweb within a larger interactive trophic 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). “Basal species” are those having predators but no prey “top species,” have prey but no predators, and “intermediate species” have at least one prey and one predator (Cohen and Briand 1984). Polis (1991) gave compelling arguments that top species that are entirely without enemies (i.e., predators, parasitoids, and parasites) do not exist in nature.

Since any community food web is actually a subweb within a larger open system (linked and nested within the biosphere), sink and source subwebs of various kinds might provide less biased units for comparisons. Because sink webs are subsets of larger, subjectively defined community webs, food web statistics might be expected to differ in comparisons between the two. Indeed, a number of quantitative measures varied greatly between community and sink webs in tropical aquatic webs (Winemiller 1989, 1990). The top predator in these sink webs was defined as the consumer with the highest trophic position within a community trophic continuum calculated from the bottom-up using volumetric dietary data. Yet in contrast to Cohen and Briand’s definition, top predators in these webs were sometimes consumed by species at lower trophic levels. Future empirical studies will need to do a better job of defining and standardizing food web boundaries, probably as subwebs defined by various objective criteria.

6.5 TROPHOSPECIES AND OTHER KINDS OF NODES

One could argue that all comparative food web analyses are confounded by large differences in levels and criteria for taxonomic aggregation (Paine 1988, Lawton 1989, Winemiller 1990, Polis 1991, Martinez 1994, Solow and Beet

1998, Yodzis and Winemiller 1999). Food web nodes are usually comprised of lumped species populations referred to as “trophospecies” (Yodzis 1988) or simply as “species” (Cohen 1978, Pimm 1980, 1982, Briand 1983, Auerbach 1984, Sugihara 1984, Cohen and Newman 1985). According to Pimm et al. (1991), trophospecies are sets of organisms with identical prey species and identical predators. If trophospecies share precisely the same set of predator and prey, it is highly unlikely that any biological species could be grouped in this manner.

Pimm (1982) observed that all published food webs appeared to involve some degree of lumping into functional trophospecies, particularly at lower trophic levels where plants and invertebrates predominate. He felt that most ecologists exhibit antipathy for plant and invertebrate taxonomy. More likely, the causal factors for this pattern are lack of taxonomic expertise for the species-rich invertebrates, logistical limitations, and a focus on questions regarding taxa at higher trophic levels. Most field investigators appear to have aggregated species by taxonomic rather than functional criteria when creating food web diagrams. Given that some taxonomic lumping must occur in all large food webs, a primary concern is that large variation in the degree of lumping among widely divergent studies may invalidate empirical food web comparisons. While this problem has been recognized previously (Glasser 1983, Paine 1983 1988, Winemiller 1990, Polis 1991, Cohen et al. 1993), many investigators have opted to proceed with their analysis with an apology that no other information is currently available, often followed by a plea for more precise information (Pimm 1982, Schoener 1989, Cohen et al. 1990, Pimm et al. 1991, Williams and Martinez 2000).

The pitfalls associated with comparisons of food webs from studies with different goals are illustrated by comparing species that occur both in Zaret and Paine’s (1973) Lake Gatún, Panama web and Winemiller’s (1990) Costa Rican stream webs. Zaret and Paine published their food web as “a generalized view of the trophic structure of Lake Gatún, based on information from stomach analyses and direct observations.” *Cichlasoma maculicauda* in the Lake Gatún food web had a single food resource, filamentous green algae. Based on stomach contents analysis, *C. maculicauda* in Caño Agua Fría Viejo, Costa Rica fed on more than 30 general prey categories in varying proportions that depended on season (32 items—wet season, 33 items—dry season, N stomachs examined = 155). Filamentous algae represented only 1 of 43 aggregate prey categories discovered in stomachs of *C. maculicauda* from Costa Rica. A similar contrast is seen in the diet of the piscivorous eleotrid *Gobiomorus dormitor*. Zaret and Paine listed a single fish species as the prey of *Gobiomorus*, whereas stomach contents data from Costa Rica (168 stomachs) yielded a conservative estimate of 12 prey categories. These large disparities are less influenced by environmental differences than methodological inconsistencies. The Panama study used a greater degree of prey lumping and intentionally omitted many prey items from the food web diagram, because those items were

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deemed unimportant for the primary objective of the report, documentation of the response of the lake community to an exotic predatory fish.

Sugihara et al. (1989) recognized the lack of uniformity in the level of species aggregation among 113 food webs compiled for comparative analysis (Cohen 1989). Using an algorithm that collapsed species into aggregate trophospecies, they found that four of five food web properties were sensitive to aggregation beyond the level of trophically equivalent species (species having identical predators and prey). All five measures were robust against grouping of "trophic equivalents," and one measure (rigid circuitry) was robust even when lumping species beyond the level of trophic equivalents. Rigid circuitry is a property derived from graph theory that reflects guild structure in simple food web diagrams. It is not surprising that functional constraints on feeding or habitat utilization that produce guild structure yield similar community patterns when the most similar species are grouped into trophospecies. Sugihara et al. (1989) offered an overall assessment that food web regularities "may be legitimate despite understandable worries about the nonuniformity of trophic resolution in the data." Their optimism would only be warranted if one could demonstrate that widespread grouping of species into trophospecies in published food webs involves trophic equivalents in all instances. More often than not, species near the bottom of food webs have been aggregated on purely taxonomic grounds (e.g., beetles, ants, algae), because detailed feeding data are unavailable. In addition, the reported food web regularities (Briand and Cohen 1984, Cohen and Briand 1984, Cohen et al. 1990, Pimm et al. 1991) that involve scale invariance (value constancy with changing species richness) are actually more random (slope = 0 in association with low correlation among scattered points) than regular (slope = 0 for points lying on a straight line; Winemiller 1990).

Martinez (1991, 1993) examined the sensitivity of food web patterns to changes in resolution of nodes following hierarchical aggregation based on species' trophic similarities (Jaccard index) and the minimum-, maximum- and average-linkage clustering methods. His Little Rock Lake food web contained 182 species identified mostly to genus and species (Martinez 1991). The first aggregation grouped trophic equivalents (primarily algae species at the base of the food web) and reduced the number of nodes to 93; thereafter clustering reduced the number of nodes until a low of 9 functional groups was obtained. In each case, the influence of node aggregation on web metrics was major. Number of links per species, distribution of chain lengths, distribution of species trophic levels, the proportion of top species, and the proportion of links to top species were highly sensitive to aggregation. Connectance, the ratio of predators to prey, proportions of intermediate and basal species, and the proportion of links between intermediate and basal species also varied with node aggregation but were somewhat less sensitive. Martinez (1991) concluded that most of the early food webs from which "food web laws" were derived are equivalent to the highly aggregated versions of the Little Rock Lake food web.

Yodzis and Winemiller (1999) examined the performance of alternative methods for aggregating species into trophospecies. Using Winemiller's (1990) Caño Maraca, Venezuela, food web, they used an additive versus a multiplicative method to combine each species dual role as a resource and consumer. Similarity in feeding links was based on topological (presence/absence) and flow (volumetric) linkage patterns. For a given measure of similarity, 6 alternative algorithms were employed to derive 24 trophic hierarchies (dendrograms). In general, there was little correspondence between species overlap in resource use and the extent to which predators were shared. The additive method of combining species' resource and consumer roles performed better, and weak links had a large influence. Maximum and average clustering algorithms performed best, but it was unclear how to select a similarity criterion for assignment of trophospecies. Objective methods and criteria for creating trophospecies remain elusive (see also Solow and Beet 1998). Until this issue can be better resolved, empirical food web research is seriously hindered. Because differences in the level of taxonomic identification among trophic units influences food web properties, comparative studies require unambiguous criteria for defining trophic units and estimating predator-prey links.

6.6 VARIATION IN THE MAGNITUDE OF TROPHIC INTERACTIONS

MacArthur (1972) and Paine (1980) emphasized the fact that species interactions within trophic networks are extremely variable in magnitude and duration. Strong predator-prey interactions are likely to have greater influence on the local distribution and abundance of organisms than weak or spurious interactions (Paine 1980, 1983). However, the presence of many weak interactions may stabilize community dynamics (Yodzis 1981, McCann et al. 1998). Very few empirical food web studies have examined temporal variation in the strength and duration of predator-prey interactions (e.g., Winemiller 1990, Tavares-Cromar and Williams 1996). Most comparative studies have dichotomized consumption into a matrix of binary presence/absence elements (web topology). Discussions of the methods for estimating links and the level of confidence in the empirical datasets are rare in the literature.

Winemiller (1990) estimated volumetric consumption from stomach contents and calculated food web statistics at several threshold intervals for trophic links. A series of threshold intervals was used to successively exclude "weak" links defined by fractional volumetric consumption during various seasons of the year. Data were then log-transformed and link threshold was then treated as a covariate in comparisons of characteristics of different aquatic food webs. Although this method requires large amounts of dietary data, greater numbers of comparisons are possible among webs defined according to levels of weak link exclusion. Moreover, the shapes of the curves derived from plotting food web statistics versus link threshold reveal additional features of food web structure. For a given web, linkage density must decline as the link threshold

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increases, yet a large negative slope in the bivariate relationship reflects a food web dominated by many links of small magnitude. Other measures, like the average number of predators per prey node, need not decline at higher link thresholds, although this trend was predominant in tropical aquatic food webs.

Frequency of prey consumption is another measure of the magnitude of predator–prey interactions. Goldwasser and Roughgarden (1993) estimated the frequency of consumption for 44 terrestrial species in the cumulative food web of the Caribbean island of St. Martin. Diet data for lizards and birds were based on stomach contents reported in literature. Nematode parasites of lizards were revealed from dissections, and invertebrate diets were based on relative abundances of different taxa (most were aggregated into orders) in their environment. Estimates of frequency of consumption were reported as the number eaten per day (these units were directly estimated in one bird study). In order to scale highly disparate data into the same units of consumption frequency “more-or-less arbitrary decisions,” were required. For example, cannibalism and feeding loops were excluded based on Cohen’s (1978) finding that they are rare in the early food web diagrams. Arthropod diets were based on entomology texts, and frequencies of prey consumption (number/day) were weighted by the relative abundances of prey and multiplied by either 10 or 100 to account for the higher densities of these small species at lower trophic strata. Virtually all web characteristics deviated from expected values based on patterns in the EcoWeb dataset (Cohen 1989) and predictions of the cascade model of food web structure (Cohen and Newman 1985). Because the authors did not expect all of their estimates of feeding frequencies to reflect true consumption, they made no attempt to examine food web properties at different link thresholds based on variation in feeding frequencies. Despite highly arbitrary nature of the St. Martin food web, this attempt to estimate link strengths clearly highlights the challenges that arise in estimating food web structure by taking into account variation in the strength of pairwise interactions (see Bersier et al. 2002, Berlow et al. 1999, 2004). All predator–prey interactions are highly variable, both in time and space, and this variation must be estimated and incorporated into descriptive and comparative food web research.

6.7 ESTIMATION OF TROPHIC LINKS IS ALWAYS IMPERFECT

The empirical food web literature has been surprisingly uncritical toward estimates for trophic links. Caddy and Sharp (1986) reviewed the following techniques for estimating marine and aquatic trophic relationships: (1) direct observation, (2) experimental studies, (3) examination of morphological adaptations, and (4) stomach contents analysis. These methods also apply to terrestrial food webs. Stable isotope ratios in tissues also can be used to achieve crude estimates of trophic relationships (Lajtha and Michener 1994). In addition to ratios of naturally occurring isotopes, radioactive isotopes (H^3 , P^{32}) have been introduced into ecosystem components to quantify feeding rates (Odum and

Kuenzler 1963). Data from short-term observations can be used with individual-based simulation models (DeAngelis and Gross 1992) or aggregate food web models (Christensen and Pauly 1992) to estimate feeding dynamics over a longer time periods and across variable environmental conditions.

Indirect methods of feeding estimation (including radiotracers, isotopic ratios, and field experimentation) carry their own limitations. Teams of taxonomic specialists might reduce the margin of error in producing estimates of predation rates in natural systems. A complete description of a large food web would likely require a huge staff and budget. Given that ecologists are not likely to see this level of funding in the foreseeable future, we are faced with the unfortunate reality that progress must be made with imperfect knowledge of the true ecological relationships. Ecologists must proceed nonetheless, provided that they acknowledge methodological limitations and establish objective criteria for quantitative analyses.

Cohen and Newman (1985) attempted to account for observer bias in empirical food web structure using a model of imperfect observation. Their model assumed that the probability of correctly recording a feeding link between two species involved in a predator–prey interaction is inversely related to the size of the food web. As webs accrue more species, the fraction of real predator–prey interactions reported declines according to the function $P(C_1 S_T)$, where C_1 is web connectance, and S_T is the number of trophospecies. Based on comparisons of empirical webs, C_1 was assumed to be approximately 2. By running simulations that combined the observer bias model with a model of food web dynamics at the edge of linear local stability, Cohen and Newman estimated that just 10% or fewer of the actual dynamic interactions among species are recorded for communities containing 50 or more species. The authors pointed out that both models are based on many untested assumptions, yet they “would not be surprised if the qualitative behavior derived from the collection of assumptions corresponds well with what would be predicted from vastly more realistic models.” The risk in this approach is that patterns can sometimes mask the processes that created them, even when we possess complete knowledge of the system (Neill and Gallaway 1989).

Taxonomic resolution incurs a negative trade-off with resolution of feeding interactions in food webs. Hildrew et al. (1985) used stomach contents analysis to estimate invertebrate feeding interactions in a small acidic stream. Because some chironomid larvae (Diptera) were known to regurgitate stomach contents during preservation, no attempt was made to quantify feeding rates. Their topological food web contained only 24 species but 96 feeding links. Martinez (1991) claimed to have “directly documented” trophic interactions in the Little Rock Lake community by interviewing ecologists involved in studies of various higher taxa and by reviewing literature. The Little Rock Lake food web is a composite topological web that combines diverse sources of information without regard for temporal or spatial variation and contains no estimates of interaction strengths. Whereas the focus of Martinez’s analysis, the level of

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taxonomic resolution, was shown to have large effects on several food web properties, feeding links were crudely estimated. The average number of links per species was 11 in an aggregated food web containing 93 “trophospecies.” In the fully resolved Little Rock Lake food web, largemouth bass fed on 95 taxa (including all of the fish and zooplankton species in the lake, 2 of 18 benthic microcrustaceans, 46 of 52 aquatic insects, a worm, a leech, a triclad, and one amphipod). Strangely, bass ate only one of the four species of dragonfly nymphs, yet they consumed the full complement of other aquatic insects. Other predators were more specialized. Triclad ate only harpacticoid copepods. The amphipod *Crangonyx gracilis* specialized on filamentous algae (notably, it consumed the entire assemblage of 25 filamentous algae genera). Given large uncertainties associated with estimation of trophic links, the question of taxonomic scale seems almost moot.

Havens (1992) analyzed features of “nonaggregated natural webs sampled consistently and constructed from identical linkage criteria.” Data for his 50 food webs of small lakes and ponds were derived from cumulative lists of species from sampling performed by the Adirondack Biota Project. Feeding links were assigned based on diet information in Martinez (1991), Scott and Crossman’s (1973) *Freshwater Fishes of Canada*, Sprules and Bowerman (1988), and two other literature sources for invertebrates. Because little detailed information on fish diets appears in Scott and Crossman’s book, one can only assume that Martinez’s assumptions regarding food web interactions were replicated in Havens’ webs. Similarly, Sprules and Bowerman (1988) obtained knowledge of feeding links between invertebrates and their prey “from the extensive literature available and from the collective experience of people in our laboratory.” Whenever literature reports provide the basis for the estimation of feeding links, no spatial or temporal variation in predator–prey interactions is possible. Most comparative food web studies have been derived mainly from faunal surveys and therefore could not estimate variation in feeding interactions.

Accurate estimates of feeding behavior by all species of even a small community obviously pose a daunting task. Practical problems of prey identification were discussed by Paine (1988), Winemiller (1990), and Polis (1991). Ultimately, some imprecision and inaccuracy will be associated with the identification of food web links and the estimation of their magnitudes. Species with broad diets require larger samples for quantitative diet estimation than relatively specialized feeders. As in any form of measurement, reported estimates for the strength of predator–prey interactions are imperfect. Most biological parameters are reported in the scientific literature using measures of central tendency with associated error statistics. Unfortunately, this convention is seldom possible for food web units. In the case of diet estimation through stomach contents analysis, individual consumers usually contribute only one estimate of their feeding behavior (i.e., they are usually euthanized). Given the fact that food web data are exceedingly difficult to gather and impossible to replicate, investigators must provide an assessment of the reliability of their observations or

measurements. A lucid account of methodology and sample sizes would provide a modest beginning. In this manner the suitability of data for meta-analysis could be evaluated.

6.8 SPATIAL AND TEMPORAL VARIABILITY

A large body of literature indicates that most ecological communities do not occur in highly stable environments, and some (perhaps most) only rarely or intermittently experience strong density-dependence or exhibit equilibrium population dynamics (Wiens 1984, Schoener 1982, Strong 1986, Menge and Sutherland 1987, Dunson and Travis 1991). Furthermore, few predators appear to forage on prey in constant ratios over time during their entire life cycle. Aquatic organisms, in particular, reveal much ontogenetic, size-dependent predation (Brooks and Dodson 1965, Werner and Gilliam 1984). In addition, diet composition frequently shifts in response to seasonal changes in the availability of preferred food resources. For example in the Venezuelan llanos, loriciid catfishes consume aquatic primary production mostly in the form of living algae during the wet season and in the form of dead macrophyte tissues (detritus) during the dry season (Table 6.1). This sort of seasonal variation in fish diets is more the norm than the exception (Werner and Gilliam 1984), even at less seasonal locations in the tropics (McKaye and Marsh 1983). Seasonal changes in fish species richness and abundance in the pelage zone of the Sea of Cortez was assumed to yield a more complex food web with longer chains during the summer (Klimley et al. 2005).

The behavior of individual organisms and temporal dynamics of populations within food webs can be interpreted in terms of the seasonal influence of specific environmental components, both abiotic and biotic. Large seasonal differences are observed in several properties of tropical aquatic food webs (Winemiller 1990, 1996). In the Venezuelan llanos, dry season contraction of aquatic habitats increases fish densities and results in more frequent predator-prey encounters. Thus the mean number of prey per predator node increases during the period of gradual drying (transition season) when prey densities are high. The number of prey consumed per predator node declines during the peak dry season when small species vulnerable to piscivores are reduced by predation mortality, then decreases further as fishes and other organisms are dispersed in expanded aquatic habitat during the wet season. The mean number of predators per node is about the same during the wet and transition seasons, because even though fish densities are very low in the expanded wet season environment, more different kinds of fishes are present in the local ecosystem due to immigration into the productive wetland. This example illustrates why certain food web parameters cannot be interpreted without knowledge of the physicochemical and production dynamics the system.

Food web properties vary in space and time under the influence of multiple factors associated with internal dynamics as well as external environmental

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Table 6.1. Seasonal composition of diets of two fishes in the Venezuelan llanos

	Food category	Wet	Dry
<i>Pterygoplichthys multiradiatus</i> (Loricariidae)	Fine detritus (2)	0.354	<u>0.817</u>
	Vegetative detritus (1)	<u>0.250</u>	0.104
	Diatoms, desmids (2)	<u>0.270</u>	0.027
	Filamentous algae (1)	0.034	0.022
	Spores (2)	0.013	0.006
	Protozoa, difflugiids (2)	<u>0.027</u>	0.006
	Copepods (1)	<u>0.007</u>	–
	Chitin fragments (1)	0.023	0.015
	Sample N	20	20
	Detritus (2)	0.004	0.009
	Seeds (1)	0.001	0.005
	Snails (1)	<u>0.119</u>	0.007
	Mussels (1)	0.012	–
<i>Pimelodella</i> sp. (Pimelodidae)	Copepods	–	0.021
	Cladocerans (1)	<u>0.049</u>	0.005
	Eubranchipods (1)	<u>0.070</u>	–
	Ostracods (1)	0.005	–
	Prawns (1)	<u>0.124</u>	0.004
	Ephemeroptera (1)	<u>0.096</u>	0.007
	Aquatic Coleoptera (2)	0.018	<u>0.247</u>
	Aquatic Diptera (3)	<u>0.318</u>	0.132
	Other aquatic insects (2)	0.082	0.144
	Scales (2)	0.077	0.054
	Fish eggs (1)	0.001	<u>0.243</u>
	Fish (1)	–	<u>0.088</u>
	Sample N	62	62

Note: Dominant diet items for each season are underlined. The number of operational taxonomic units used in related food web analyses appears in parentheses after each diet category

factors. Precise, accurate, and reliable estimates of empirical food webs would open up exciting new avenues of comparative research. For example, Briand (1983), Cohen and Briand (1984), and Briand and Cohen (1987) classified 62 food webs as being associated with either fluctuating or constant habitats. Aside from the questionable classification scheme used in producing Briand's environmental classifications, large variation in the units of comparison, methodologies, time intervals of study, and sample sizes among studies rendered this comparison essentially meaningless. This important topic could be approached with greater rigor by comparing a smaller number of systems based on more standard methods. If food webs are to provide greater insights into the relative roles of abiotic versus biotic factors and density-dependent versus density-independent influences on community properties, then variation in the strength of species interactions must be estimated quantitatively.

Spatial scales and boundaries profoundly influence ecosystem processes and the stability of food web elements (Holt 2002). Spatially structured population models have very different dynamics than unstructured models. In some cases, metapopulations of consumers may have variable and complex responses to variation in resource levels at the patch scale. At the landscape scale, movement of material and organisms between major habitat boundaries can profoundly influence food web dynamics (Polis et al. 1997). Holt (2002) developed theoretical models in which immigration could either stabilize or destabilize local population dynamics. In a three-level food web, top predators with larger ranges than their prey moderated unstable interactions between the second-level consumers and basal resources. Thus, food web dynamics are highly sensitive to spatial dynamics via multiple mechanisms, and these dynamics influence patterns observed in comparative studies. For example, food chain length in lakes has been shown to correlate with lake size more primary productivity (Post et al. 2000). It is now difficult to imagine how food web ecology could be separated from spatial ecology in any but the most trivial manner.

6.9 VARIANCE IN SPECIES ABUNDANCES AFFECT FOOD WEB PROPERTIES

Just as the magnitude of trophic interactions can vary with time and space, population densities and structures frequently vary over space and time. Schoenly and Cohen (1991) noted that, in addition to temporal variation in diets, seasonal changes in the residence time of species in the community cause temporal variation in food web structure. Likewise, Winemiller (1990) discussed the influence of seasonal hydrology, variation in production sources, reproduction, and local fish migrations on the properties of aquatic food webs in the tropics.

What are some potential implications of variance in population densities for food web structure and function? Consider a species with a broad diet. If the species is extremely rare, its overall effect on the system may be trivial. Conversely, a functionally significant prey species might be 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 appears to be no means for determining a priori which rare species should be excluded from the analysis. The current practice in comparative studies is to either omit rare species or to give them equal status with common species, neither of which seems very satisfactory.

Power (1990) discussed the implications of variable population densities on food web properties. The ecological significance of an observed trophic link is determined by the functional and numerical predation responses. Therefore, the structure of static topological food webs depends upon densities of predators and prey, which in turn are derived from rates of biomass accumulation,

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population growth rates, and predation rates during preceding time intervals. Models of ratio-dependent predation (where the functional response depends on the ratio of predator to prey rather than prey density) can yield dynamics quite different from simulations based on the familiar Holling (1966) predation model (Artidi and Ginzburg 1989). Berryman (1992) observed 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. By omitting species densities, static topological food webs have little or no relationship with their own dynamics. To achieve even modest coupling between web structure and dynamics requires data for community composition, species interactions, web architecture, and population densities (de Ruiter et al. 1995, Morin and Lawler 1995, Berlow et al. 2004).

6.10 INFLUENCE OF ABIOTIC AND BIOTIC ENVIRONMENTAL FACTORS

In much of the food web literature, the formulation of intriguing problems and clever analytical approaches seem to have taken precedence over environmental biology as well as concerns for how data are acquired and analyzed (see also discussions by Paine 1988, Lawton 1989, Winemiller 1990, Polis 1991). Once the empirical data and analytical methods manage to narrow the gap with theory, we may gain important new insights into some old, but fundamental problems. Much of food web theory implies an equilibrium or density-dependent world, however ecologists understand very well that ecological systems are influenced simultaneously by a host of density-independent and density-dependent factors that vary over time and space.

Table 6.2 lists some of the major factors known to influence population dynamics. Only two of the seven factors (predation/parasitism and food availability) are explicitly represented in food webs. In any large food web, some feeding relationships will have disproportionate and major impacts on the community. Consider, e.g., the major role that African elephants play as architects of savanna ecosystems. In contrast, consider the food chain of leaf-cutter ants (*Atta* sp.)—fungi—vegetation (3 nodes, 2 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 in a manner that meets their physiological requirements, and are therefore dependent upon their association with fungi. If leaf-cutters were to suddenly evolve their own biochemical capacity to digest and assimilate plants directly, what kind of ramifications would the elimination of the fungus (1 node, 1 link) have at the level of the overall food web? According to the energetic view of food webs, there would be a major effect. In terms of the network of population interactions, it might be very insignificant.

Whether or not they choose to deal with it directly, most ecologists are keenly aware of the role that historical biogeography plays in setting the stage for

Table 6.2. Factors that influence local population densities

1.	Abiotic (climatic) density-independent influences
*2.	Predation, parasitism
*3.	Nutrients, food availability
4.	Available space and physical habitat
5.	Mutualism (e.g., pollinators, seed dispersers)
6.	Commensalism (e.g., enhancement of physical habitats, enhanced foraging success, enhanced predator deterrence)
7.	Intrinsic genetic factors (e.g., inbreeding depression, sex ratio, mating systems, life history strategy)
8.	Emigration and immigration from other habitats or regions (e.g., spatial subsidies)

Note: Asterisks denote factors that are explicit in food web models

contemporary ecological interactions. Yet few methodologies have been developed for identifying or adjusting for the influence of historical constraints on community features (Endler 1982, Ricklefs 1987). The influence of historical factors (invasions, local extinctions, and succession) on food web features has been investigated from both theoretical and experimental standpoints (Yodzis 1984, Post and Pimm 1983, Drake 1990, 1991, Fukami and Morin 2003), but only superficially from a comparative standpoint (Beaver 1983, Kitching 1987, Winemiller 1990). Priority effects in contemporary biological interactions can greatly influence community dynamics and structure (Drake 1991, Fukami and Morin 2003). The food web structure and dynamics of some, perhaps even most, ecosystems would be impossible to interpret or predict without fundamental understanding of abiotic drivers, such as coastal upwelling or advective currents that deliver resources and new population recruits (Menge et al. 2003).

6.11 LIFE HISTORY STRATEGIES INFLUENCE POPULATION DYNAMICS

The influence of alternative life history strategies on food web structure and function has scarcely been addressed (Polis et al. 1996, Scharler et al. 2005). 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. Species life histories vary in their demographic responses to seasonal environmental variation as well as manifestation of the storage effect (Chesson and Huntley 1989). According to Chesson (2000), the storage effect promotes species coexistence via three mechanisms: buffered population dynamics (e.g., long-lived life stages that can endure periods of unfavorable environmental conditions), interspecific differences in response to environmental variation (see also Tilman 1982), or covariance between environmental conditions and competition (i.e., as environmental conditions improve for a species, its demand for resources increases which eventually results in greater competition).

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Stochastic environmental disturbances can actually favor populations with buffered population dynamics and high recruitment variation (Higgins et al. 2000).

Terrestrial and aquatic food webs seem to differ in at least one fundamental aspect associated with life history strategies. Terrestrial food webs contain many long-lived (environmentally buffered) plants (especially trees and shrubs) that are grazed by animals with considerably shorter life spans. Many of these herbivores, both vertebrates and invertebrates, are in turn consumed by carnivores that may or may not have longer life spans and greater environmental buffering (e.g., vertebrate carnivores versus parasitoids). In aquatic food webs, the most important primary producers consumed by herbivores are short-lived algae with high population turnover rates. The predominant consumers of algae are small invertebrates (microcystacea and immature stages of insects), which in turn are consumed by larger vertebrates. This trend of increasing body size with trophic level has long been noted (Elton 1927) and sometimes used as a basis for explaining food web structure (Cohen and Newman 1985, Warren and Lawton 1987). Analysis of a version of the Ythan estuary web (Hall and Raffaelli 1991) that included parasites demonstrated very weak body size—trophic position relationships, which suggested body size relationships may be poor predictors of interaction strength for dynamic models (Leaper and Huxham 2002).

Life history strategies have been incorporated into a variety of dynamic modeling approaches, but, aside from using body size, how can this critical source of variation affecting population and community dynamics be captured by an empirical description of food webs? The manner that species with different life history traits to different aspects and spatiotemporal scales of environmental variation will differ in ways that are difficult to build into dynamic food web models. Winemiller (1996) categorized species in river food webs according to a triangular life history gradient with three endpoint strategies. This triangular gradient seems to describe patterns of variation among basic life history traits of fishes reasonably well, and also can be derived from fundamental demographic relationships (Winemiller and Rose 1992, Winemiller 2005). The problem with this application to empirical food webs is that species lying on a continuous gradient are forced into discrete categories. Nonetheless, it represents one empirical means of integrating variation in life history strategies with food web structure. The effects of population structure (McCann et al. 1998) and life history strategies on food web structure and dynamics surely will be a fruitful area for inquiry.

6.12 DEALING WITH COMPLEXITY AND VARIABILITY: FOOD WEB RESEARCH ON A TROPICAL RIVER

The remainder of this chapter examines these issues from the perspective of empirical field research in a tropical river. The Cinaruco River, Venezuela is a dynamic and spatially heterogenous ecosystem that supports extremely high

species richness and ecological diversity. The river contains more than 280 fish species with trophic niches ranging from detritivores to herbivores, invertivores, and piscivores spanning a wide range of body sizes and life history strategies. Can this high diversity and complexity be examined in units that permit prediction of ecological dynamics? It probably is not reasonable to seek set of universal, standardized methods for empirical research on every element of the food web from bacteria to river dolphins (*Inia geoffrensis*). To some extent, protocols must be devised and adapted in response to the characteristics of the system. My colleagues and I are attempting to understand the structure and dynamics of the Cinaruco food web by dealing with components on scales of time, space, and taxonomy that are defined by rather obvious spatiotemporal boundaries as well as practical constraints. We organize the food web into modules defined on the basis of habitat features and associated biota (habitat modules) and sink or source webs (trophic modules) that may or may not be associated with a single habitat module (Figure 6.1). Trophic modules that are sink webs defined by large mobile predators will unite habitat modules in the manner described by Holt's (1996) spatial food web model. Holt's model, which builds on ideas from the island biogeography theory, describes well the spatial patterning of littoral zone species assemblages that are mixtures of relatively

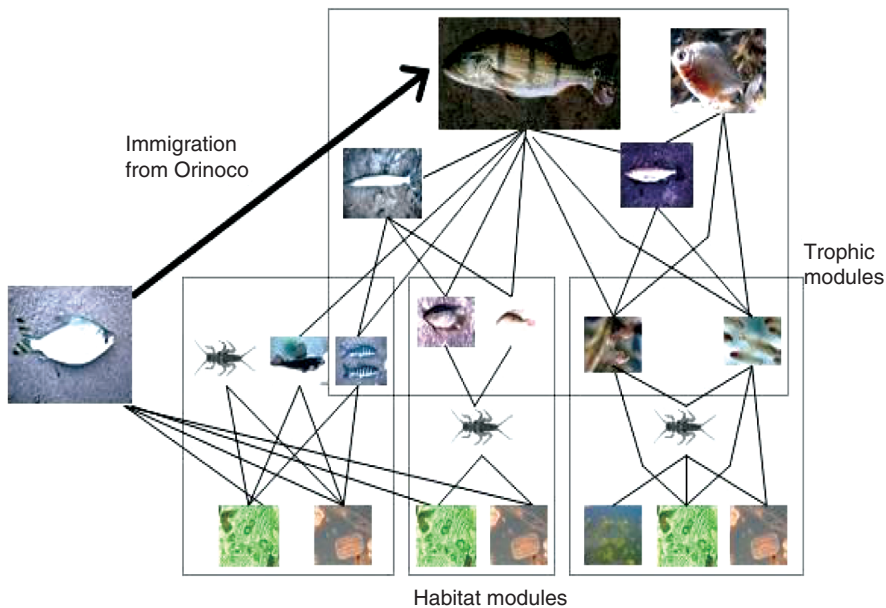


Figure 6.1. Schematic diagram of the Cinaruco River food web modules (e.g., rocky shoals, woody debris, sandbank), trophic modules (sink subwebs at top, and source subwebs at bottom), and a food web spatial subsidy in the form of a migratory benthivorous fish (*S. kneri*) consumed by predatory *Cichla temensis*.

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sedentary species with strong habitat affinities and relatively mobile species that move frequently among habitats (see Jepsen et al. 1997, Hoeinghaus et al. 2003, Arrington and Winemiller 2005a, b, Arrington et al. 2005, Layman et al. 2005a).

We have adopted three approaches to reveal the structure and dynamics of food web modules. First, we estimate species distribution and abundance patterns over time (hydrologic seasons in this lowland river) and space (habitats), and then quantify diets via stomach contents analysis (Layman et al. 2005a, b). Stomach contents analysis allows identification of prey taxa with relatively high resolution, but requires large samples, especially for consumers with broad diets. Because these efforts are time and labor intensive, we are also examining aspects of the food web using stable isotopes of carbon (useful for estimating certain terrestrial and aquatic primary production sources) and nitrogen (useful for estimating trophic positions of consumers). Stable isotope research provides an estimate of the overall structure of the river food web (see Jepsen and Winemiller 2002), the relative importance of autochthonous and allochthonous food resources supporting omnivores and carnivores (Layman et al. 2005a, b). For example, species of herbivorous characid fishes show significant interspecific variation in carbon and nitrogen stable isotope signatures that reflects partitioning of aquatic and terrestrial food resources, such as plankton, insects, fruits, seeds, and leaves (Figure 6.2). Stable isotope data also have assisted in revealing the importance of a spatial food web subsidy in the form of benthivorous fish that migrate seasonally between the highly productive Orinoco River and the unproductive Cinaruco River (Winemiller and Jepsen 2004). The basis for the latter estimates is small but consistent differences in the carbon isotopic signatures of biota living in acidic “black waters” of the Cinaruco River compared with biota from the neutral “white waters” of the Orinoco.

The third approach is field experimentation in which various species or functional groups are excluded or confined to areas of habitat in order to discover their effects on other food web elements. When large piscivores were excluded from large areas of sand bank, there were significant increases in the abundance and diversity of fishes in the range of prey sizes consumed by these predators (as determined from stomach contents analysis), but no responses were observed within the assemblage of smaller fishes (see Layman and Winemiller 2004). Similar results were obtained when assemblages of entire lagoons were manipulated by commercial net fishers (Layman et al. 2005a). Like the mesh on our fish exclosures, the mesh of commercial seine nets remove the largest fishes while allowing smaller fishes to pass unharmed. The consistent results from these manipulations conducted in two different habitats at two different spatial scales (500 m² on river channel shorelines versus several thousand m² in lagoons) give us confidence that field manipulations scale up to entire habitat patches on the landscape. Removal of large piscivores and detritivorous fishes that are their principal prey results in shorter, and presumably less energetically efficient food chains that start with algae and lead to aquatic invertebrates, small invertivorous fishes and small piscivores (Layman et al. 2005a).

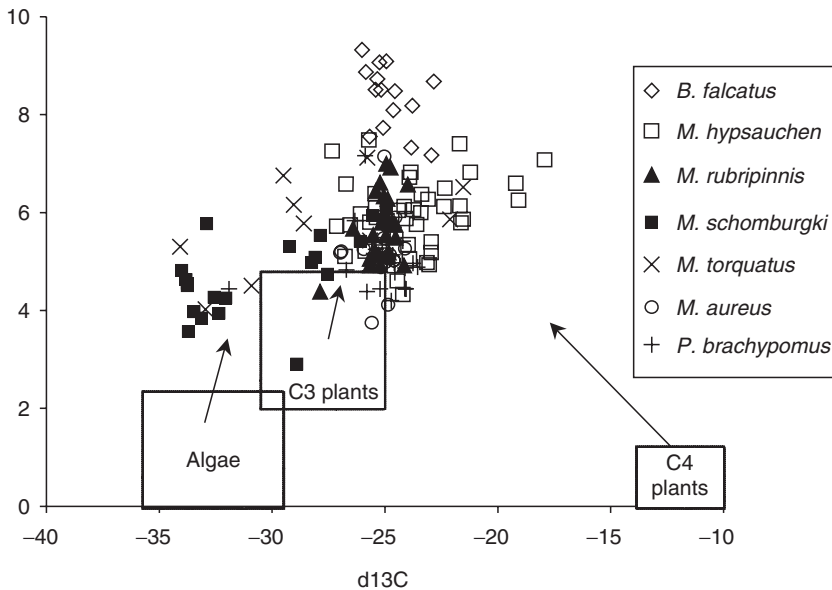


Figure 6.2. Plot of stable isotopic signatures of carbon and nitrogen for herbivorous characid fishes of the Cinaruco River in relation to the range of variation in carbon and nitrogen signatures for three basal sources. Carbon ratios of consumers are a proportional assimilation of sources, whereas nitrogen ratios are fractionated (2–3%) with each successive trophic level. The plot reveals high overlap in trophic niches among some species (e.g., *Metynnis hypsauchen*, *M. rubripinnis*, and *Myleus aureus*), and a high degree of resource partitioning between certain species pairs (e.g., *Brycon falcatus*—*M. schomburgki*, *B. falcatus*—*M. torquatus*, *M. hypsauchen*—*Piaractus brachypomus*).

We conducted fish exclusion and enclosure experiments to examine the role of benthivorous fish on sediments of the littoral zone module in channel and lagoon habitats. Selective exclusion of large or small fishes revealed strong fish effects on organic sediments and chlorophyll during the low water season, but not during the rising water period (Winemiller et al. 2005). The species that reduces most of the organic material from the surface of sediments is the migratory fish, *Semaprochilodus kneri*, which is abundant in the river during the low water period, but absent during the flood period when it spawns and feeds in the Orinoco River. Ongoing studies are examining effects of these fish manipulations on sediment particle size, rates of nutrient regeneration in sediments, and meiofauna community structure.

At the same time we are investigating food web modules, we also are investigating spatial and temporal variation in abiotic environmental factors and primary production (Cotner et al. 2005, Montoya et al. 2005, Roelke et al. 2005) and biota–habitat relationships (Arrington and Winemiller 2005a, b, Willis et al. 2005). These studies have revealed a strong and pervasive influence of the annual hydrological regime on water chemistry, dissolved nutrient

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concentrations, phytoplankton, and densities of aquatic organisms. Significant spatial variation in limnological and faunal attributes is observed both within and between major habitat types, particularly during the low water period when the landscape becomes more strongly differentiated, and nutrients, phytoplankton, and organisms are more concentrated in the reduced volume of aquatic habitat.

We have only scratched the surface in understanding the spatial and temporal variation in the structure of the Cinaruco River food web. New and sometimes surprising findings from descriptive research and experimental manipulations of food web modules are increasing our ability to predict changes in response to seasonal variation as well as human impacts. A reliable and detailed description of the taxonomically complete Cinaruco food web may not be a realistic expectation. Nonetheless, as our understanding of modules increases, we hope to expand geographic scales by joining the pieces together in a great interactive network that spans a variety of habitat types. We agree with Reagan and Waide (1996), that complex, species-rich food webs can only be understood through sustained efforts of long-term field research involving multiple, interacting components and processes.

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Author Queries

- AQ1: Please update
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