Food Webs

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Article Outline

Glossary

Connectance(C) The proportion of possible links in a food web that actually occur. There are many algorithms for calculating connectance. The simplest and most widely used algorithm, sometimes referred to as "directed connectance," is links per species^2 (L/S^2), where S^2 represents all possible directed feeding interactions among S species, and L is the total number of actual feeding links. Connectance ranges from ~ 0.03 to 0.3 in food webs, with a mean of ~ 0.10 to 0.15.

Consumer-resource interactions A generic way of referring to a wide variety of feeding interactions, such as predator-prey, herbivore-plant or parasite-host interactions. Similarly, "consumer" refers generically to anything that consumes or preys on something else, and "resource" refers to anything that is consumed or preyed upon. Many taxa are both consumers and resources within a particular food web.

Food web The network of feeding interactions among diverse co-occurring species in a particular habitat.

Trophic species (S) Defined within the context of a particular food web, a trophic species is comprised of a set of taxa that share the same set of consumers and resources. A particular trophic species is represented by a single node in the network, and that node is topologically distinct from all other nodes. "Trophic species" is a convention introduced to minimize bias due to uneven resolution in food web data and to focus analysis and modeling on functionally distinct network components. S is used to denote the number of trophic species in a food web. The terms "trophic species," "species," and "taxa" will be used somewhat interchangeably throughout this article to refer to nodes in a food web. "Original species" will be used specifically to denote the taxa found in the original dataset, prior to trophic species aggregation.

Definition of the Subject

Food webs refer to the networks of feeding ("trophic") interactions among species that co-occur within particular habitats. Research on food webs is one of the few subdisciplines within ecology that seeks to quantify and analyze direct and indirect interactions among diverse species, rather than focusing on particular types of taxa. Food webs ideally represent whole communities including plants, bacteria, fungi, invertebrates and vertebrates. Feeding links represent transfers of biomass and encompass a variety of trophic strategies including detritivory, herbivory, predation, cannibalism and parasitism. At the base of every food web are one or more types of autotrophs, organisms such as plants or chemoautotrophic bacteria, which produce complex organic compounds from an external energy source (e. g., light) and simple inorganic carbon molecules (e. g., CO_2). Food webs also have a detrital component—non-living particulate organic material that comes from the body tissues of organisms. Feeding-mediated transfers of organic material, which ultimately trace back to autotrophs or detritus via food chains of varying lengths, provide the energy, organic carbon and nutrients necessary to fuel metabolism in all other organisms, referred to as heterotrophs.

While food webs have been a topic of interest in ecology for many decades, some aspects of contemporary food web research fall within the scope of the broader cross-disciplinary research agenda focused on complex, "real-world" networks, both biotic and abiotic [2,83,101]. Using the language of graph theory and the framework of network analysis, species are represented by vertices (nodes) and feeding links are represented by edges (links) between vertices. As with any other network, the structure and dynamics of food webs can be quantified, analyzed and modeled. Links in food webs are generally considered directed, since biomass flows from a resource species to a consumer species ($A \rightarrow B$). However, trophic links are sometimes treated as undirected, since any given trophic interaction alters the population and biomass dynamics of both the consumer and resource species ($A \leftrightarrow B$). The types of questions explored in food web research range from "Do food webs from different habitats display universal topological characteristics, and how does their structure compare to that of other types of networks?" to "What factors promote different aspects of stability of complex food webs and their components given internal dynamics and external perturbations?" Two fundamental measures used to characterize food webs are S, the number of species or nodes in a web, and C, connectance—the proportion of possible feeding links that are actually realized in a web ($C = L/S^2$, where L is the number of observed directed feeding links, and S^2 is the number of possible directed feeding interactions among S taxa).

This article focuses on research that falls at the intersection of food webs and complex networks, with an emphasis on network structure augmented by a brief discussion of dynamics. This is a subset of a wide variety of ecological research that has been conducted on feeding interactions and food webs. Refer to the "Books and Reviews" in the bibliography for more information about a broader range of research related to food webs.

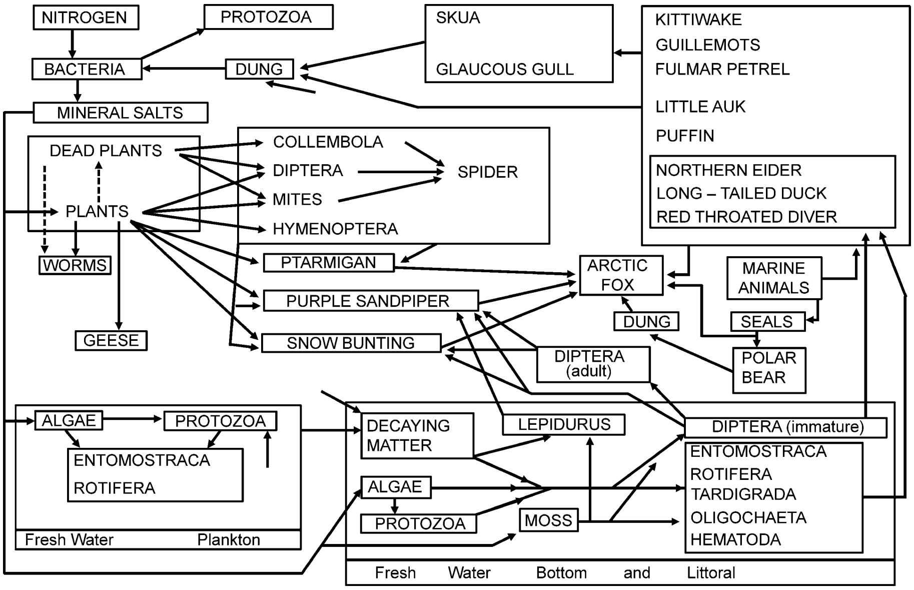
Introduction: Food Web Concepts and Data

The concept of food chains (e. g., grass is eaten by grasshoppers which are eaten by mice which are eaten by owls; $A \rightarrow B \rightarrow C \rightarrow D$) goes back at least several hundred years, as evidenced by two terrestrial and aquatic food chains briefly described by Carl Linnaeus in 1749 [42]. The earliest description of a food web may be the mostly detrital-based feeding interactions observed by Charles Darwin in 1832 on the island of St. Paul, which had only two bird species (Darwin 1939, as reported by Egerton [42]):

> By the side of many of these *[tern]* nests a small flying-fish was placed; which, I suppose, had been brought by the male bird for its partner … quickly a large and active crab (Craspus), which inhabits the crevices of the rock, stole the fish from the side of the nest, as soon as we had disturbed the birds. Not a single plant, not even a lichen, grows on this island; yet it is inhabited by several insects and spiders. The following list completes, I believe, the terrestrial fauna: a species of Feronia and an acarus, which must have come here as parasites on the birds; a small brown moth, belonging to a genus that feeds on feathers; a staphylinus (Quedius) and a woodlouse from beneath the dung; and lastly, numerous spiders, which I suppose prey on these small attendants on, and scavengers of the waterfowl.

The earliest known diagrams of generalized food chains and food webs appeared in the late 1800s, and diagrams of specific food webs, began appearing in the early 1900s, for example the network of insect predators and parasites on cotton-feeding weevils ("the boll weevil complex," [87]). By the late 1920s, diagrams and descriptions of terrestrial and marine food webs were becoming more common (e. g., Fig. 1 from [103], see also [48,104]). Charles Elton introduced the terms "food chain" and "food cycle" in his classic early textbook, *Animal Ecology* [43]. By the time Eugene Odum published a later classic textbook, *Fundamentals of Ecology* [84], the term "food web" was starting to replace "food cycle."

From the 1920s to the 1980s, dozens of system-specific food web diagrams and descriptions were published, as well as some webs that were more stylized (e. g., [60]) and that quantified link flows or species biomasses. In 1977, Joel Cohen published the first comparative studies of empirical food web network structure using up to 30 food webs collected from the literature [23,24]. To standardize the data, he transformed the diagrams and descriptions of webs in the literature into binary matrices with m rows and n columns [24]. Each column is headed by the number of



Food Webs, Figure 1
A diagram of a terrestrial Arctic food web, with a focus on nitrogen cycling, for Bear Island, published in 1923 [103]

one of the consumer taxa in a particular web, and each row is headed by the number of one of the resource taxa for that web. If w_{ij} represents the entry in the ith row and the jth column, it equals 1 if consumer j eats resource i or 0 if j does not eat i. This matrix-based representation of data is still often used, particularly in a full S by S format (where S is the number of taxa in the web), but for larger datasets a compressed two- or three-column notation for observed links is more efficient (Fig. 2).

By the mid-1980s, those 30 initial webs had expanded into a 113-web catalog [30] which included webs mostly culled from the literature, dating back to the 1923 Bear Island food web ([103], Fig. 1). However, it was apparent that there were many problems with the data. Most of the 113 food webs had very low diversity compared to the biodiversity known to be present in ecosystems, with a range of only 5 to 48 species in the original datasets and 3 to 48 trophic species. This low diversity was largely due to very uneven resolution and inclusion of taxa in most of these webs. The webs were put together in many different ways and for various purposes that did not include comparative, quantitative research. Many types of organisms were aggregated, underrepresented, or missing altogether, and in a few cases animal taxa had no food chains connecting them to basal species. In addition, cannibalistic links were purged when the webs were compiled into the 113-web catalog. To many ecologists, these food webs looked like little more than idiosyncratic cartoons of much richer and more complex species interactions found in natural systems, and they appeared to be an extremely unsound foundation on which to build understanding and theory [86,92].

Another catalog of "small" webs emerged in the late 1980s, a set of 60 insect-dominated webs with 2 to 87 original species (mean = 22) and 2 to 54 trophic species (mean = 12) [102]. Unlike the 113-web catalog, these webs are highly taxonomically resolved, mostly to the species level. However, they are still small due to their focus, in most cases, on insect interactions in ephemeral microhabitats such as phytotelmata (i. e., plant-held aquatic systems such as water in tree holes or pitcher plants) and singular detrital sources (e. g., dung paddies, rotting logs, animal carcasses). Thus, while the 113-web catalog presented food webs for communities at fairly broad temporal and spatial scales, but with low and uneven resolution, the 60-web catalog presented highly resolved but very small spatial and temporal slices of broader communities. These two very different catalogs were compiled into ECOWeB, the "Ecologists Co-Operative Web Bank," a machine readable database of food webs that was made available by Joel Cohen in 1989 [26]. The two catalogs, both separately and together as ECOWeB, were used in many studies of regularities in food web network structure, as discussed in the next Sect. "Early Food Web Structure Research".

A new level of detail, resolution and comprehensiveness in whole-community food web characterization was presented in two seminal papers in 1991. Gary Polis [92] published an enormous array of data for taxa found in the

	3	4	5	6
1	1	1	0	0
2	1	1	0	1
3	1	0	1	0
4	0	0	0	1
5	0	0	1	1
6	0	0	1	1

a

	1	2	3	4	5	6
1	0	0	1	1	0	0
2	0	0	1	1	0	1
3	0	0	1	0	1	0
4	0	0	0	0	0	1
5	0	0	0	0	1	1
6	0	0	0	0	1	1

b

3	1
3	2
3	3
4	1
4	2
5	3
5	5
5	6
6	2
6	4
6	5
6	6

c

3	1	3
4	1	2
5	3	
5	5	6
6	2	
6	4	6

d

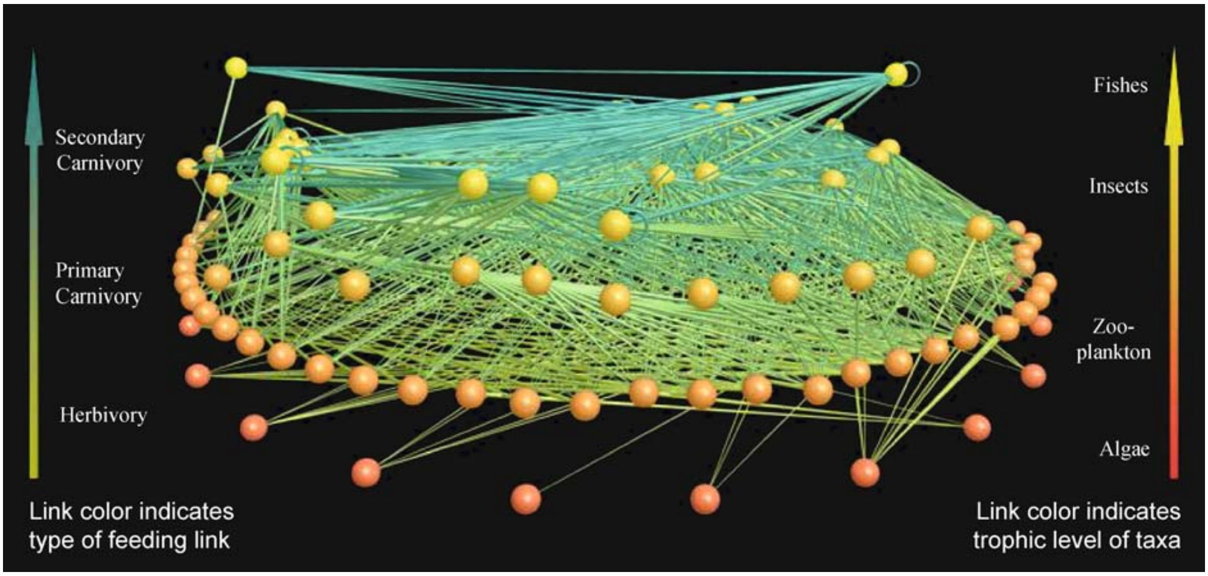
Food Webs, Figure 2

Examples of formats for standardized notation of binary food web data. A hypothetical web with 6 taxa and 12 links is used. *Numbers* 1–6 correspond to the different taxa. a Partial matrix format: the 1s or 0s inside the matrix denote the presence or absence of a feeding link between a consumer (whose numbers 3–6 head columns) and a resource (whose numbers 1–6 head rows); b Full matrix format: similar to a, but all 6 taxa are listed at the heads of columns and rows; c Two-column format: a consumer's number appears in the *first column*, and one of its resource's numbers appears in the *second column*; d Three-column format: similar to c, but where there is a third number, the second and third numbers refer to a range of resource taxa. In this hypothetical web, taxa numbers 1 and 2 are basal taxa (i. e., taxa that do not feed on other taxa—autotrophs or detritus), and taxa numbers 3, 5, and 6 have cannibalistic links to themselves

Coachella Valley desert (California). Over two decades, he collected taxonomic and trophic information on at least 174 vascular plant species, 138 vertebrate species, 55 spider species, thousands of insect species including parasitoids, and unknown numbers of microorganisms, acari, and nematodes. He did not compile a complete food web including all of that information, but instead reported a number of detailed subwebs (e. g., a soil web, a scorpion-focused web, a carnivore web, etc.), each of which was more diverse than most of the ECOWeB webs. On the basis of the subwebs and a simplified, aggregated 30-taxa web of the whole community, he concluded that "… *most catalogued webs are oversimplified caricatures of actual communities* … [they are]*grossly incomplete representations of communities in terms of both diversity and trophic connections.*"

At about the same time, Neo Martinez [63] published a detailed food web for Little Rock Lake (Wisconsin) that he compiled explicitly to test food web theory and patterns (see Sect. "Early Food Web Structure Research"). By piecing together diversity and trophic information from multiple investigators actively studying various types of taxa in the lake, he was able to put together a relatively complete and highly resolved food web of 182 taxa, most identified to the genus, species, or ontogentic life-stage level, including fishes, copepods, cladocera, rotifers, diptera and other insects, mollusks, worms, porifera, algae, and cyanobacteria. In later publications, Martinez modified the original dataset slightly into one with 181 taxa. The 181 taxa web aggregates into a 92 trophic-species web, with nearly 1000 links among the taxa (Fig. 3). This dataset, and the accompanying analysis, set a new standard for food web empiricism and analysis. It still stands as the best whole-community food web compiled, in terms of even, detailed, comprehensive resolution.

Since 2000, the use of the ECOWeB database for comparative analysis and modeling has mostly given way to a focus on a smaller set of more recently published food webs [10,37,39,99,110]. These webs, available through www.foodwebs.org or from individual researchers, are compiled for particular, broad-scale habitats such as St. Mark's Estuary [22], Little Rock Lake [63], the island of St. Martin [46], and the Northeast U.S. Marine Shelf [61]. Most of the food webs used in contemporary comparative research are still problematic—while they generally are more diverse and/or evenly resolved than the earlier webs, most could still be resolved more highly and evenly. Among several issues, organisms such as parasites are usually left out (but see [51,59,67,74]), microorganisms are either missing or highly aggregated, and there is still a tendency to resolve vertebrates more highly than lower level organisms. An important part of future food web research is the compilation of more inclusive, evenly resolved, and well-defined datasets. Meanwhile, the careful selection and justification of datasets to analyze is an important part of current research that all too often is ignored.



Food Webs, Figure 3
Food web of Little Rock Lake, Wisconsin [63]. 997 feeding links among 92 trophic species are shown. Image produced with FoodWeb3D, written by R.J. Williams, available at the Pacific Ecoinformatics and Computational Ecology Lab (www.foodwebs.org)

How exactly are food web data collected? In general, the approach is to compile as complete a species list as possible for a site, and then to determine the diets of each species present at that site. However, researchers have taken a number of different approaches to compiling food webs. In some cases, researchers base their food webs on observations they make themselves in the field. For example, ecologists in New Zealand have characterized the structure of stream food webs by taking samples from particular patches in the streams, identifying the species present in those samples, taking several individuals of each species present, and identifying their diets through gut-content analysis [106]. In other cases, researchers compile food web data by consulting with experts and conducting literature searches. For example, Martinez [63] compiled the Little Rock Lake (WI) food web by drawing on the expertise of more than a dozen biologists who were specialists on various types of taxa and who had been working at Little Rock Lake for many years. Combinations of these two approaches can also come into play—for example, a researcher might compile a relatively complete species list through field-based observations and sampling, and then assign trophic habits to those taxa through a combination of observation, consulting with experts, and searching the literature and online databases.

It is important to note that most of the webs used for comparative research can be considered "cumulative" webs. Contemporary food web data range from time- and space-averaged or "cumulative" (e. g., [63]) to more finely resolved in time (e. g., seasonal webs—[6]) and/or space (e. g., patch-scale webs—[106]; microhabitat webs—[94]). The generally implicit assumption underlying cumulative food web data is that the set of species in question co-exist within a habitat and individuals of those species have the opportunity over some span of time and space to interact directly. To the degree possible, such webs document who eats whom among all species within a macrohabitat, such as a lake or meadow, over multiple seasons or years, including interactions that are low frequency or represent a small proportion of consumption. Such cumulative webs are used widely for comparative research to look at whether there are regularities in food web structure across habitat (see Sect. "Food Webs Compared to Other Networks" and Sect. "Models of Food Web Structure"). More narrowly defined webs at finer scales of time or space, or that utilize strict evidence standards (e. g., recording links only through gut content sampling), have been useful for characterizing how such constraints influence perceived structure within habitats [105,106], but are not used as much to look for cross-system regularities in trophic network structure.

Early Food Web Structure Research

The earliest comparative studies of food web structure were published by Joel Cohen in 1977. Using data from the first 30-web catalog, one study focused on the ratio of predators to prey in food webs [23], and the other investigated whether food webs could be represented by single dimension interval graphs [24], a topic which continues to be of interest today (see Sect. "Food Webs Compared to Other Networks"). In both cases, he found regularities—(1) a ratio of prey to predators of $\sim 3/4$ regardless of the size of the web, and (2) most of the webs are interval, such that all species in a food web can be placed in a fixed order on a line such that each predator's set of prey forms a single contiguous segment of that line. The prey-predator ratio paper proved to be the first salvo in a quickly growing set of papers that suggested that a variety of food web properties were "scale-invariant." In its strong sense, scale invariance means that certain properties have constant values as the size (S) of food webs change. In its weak sense, scale-invariance refers to properties not changing systematically with changing S. Other scale-invariant patterns identified include constant proportions of top species (Top, species with no predators), intermediate species (Int, species with both predators and prey), and basal species (Bas, species with no prey), collectively called "species scaling laws" [12], and constant proportions of T-I, I-B, T-B, and I-I links between T, I, and B species, collectively called "link scaling laws" [27]. Other general properties of food webs were thought to include: food chains are short [31,43,50,89]; cycling/looping is rare (e. g., $A \rightarrow B \rightarrow C \rightarrow A$; [28]); compartments, or subwebs with many internal links that have few links to other subwebs, are rare [91]; omnivory, or feeding at more than one trophic level, is uncommon [90]; and webs tend to be interval, with instances of intervality decreasing as S increases [24,29,116]. Most of these patterns were reported for the 113-web catalog [31], and some of the regularities were also documented in a subset the 60 insect-dominated webs [102].

Another, related prominent line of early comparative food web research was inspired by Bob May's work from the early 1970s showing that simple, abstract communities of interacting species will tend to transition sharply from local stability to instability as the complexity of the system increases—in particular as the number of species (S), the connectance (C) *or* the average interaction strength (i) increase beyond critical values [69,70]. He formalized this as a criterion that ecological communities near equilibrium will tend to be stable if $i(SC)^{1/2} < 1$. This mathematical analysis flew in the face of the intuition of many ecologists (e. g., [44,50,62,84]) who felt that increased complexity (in terms of greater numbers of species and links between them) in ecosystems gives rise to stability.

May's criterion and the general question of how diversity is maintained in communities provided a framework within which to analyze some readily accessible empirical data, namely the numbers of links and species in food webs. Assuming that average interaction strength (i) is constant, May's criterion suggests that communities can be stable given increasing diversity (S) as long as connectance (C) decreases. This can be empirically demonstrated using food web data in three similar ways, by showing that 1) C hyperbolically declines as S increases, so that the product SC remains constant, 2) the ratio of links to species (L/S), also referred to as link or linkage density, remains constant as S increases, or 3) L plotted as a function of S on a log-log graph, producing a power-law relation of the form $L = \alpha S^{\beta}$, displays an exponent of $\beta = 1$ (the slope of the regression) indicating a linear relationship between L and S. These relationships were demonstrated across food webs in a variety of studies (see detailed review in [36]), culminating with support from the 113-web catalog and the 60 insect-dominated web catalog. Cohen and colleagues identified the "link-species scaling law" of $L/S \approx 2$ using the 113 web catalog (i. e., there are two links per species on average in any given food web, regardless of its size) [28,30], and SC was reported as "roughly independent of species number" in a subset of the 60 insect-dominated webs [102].

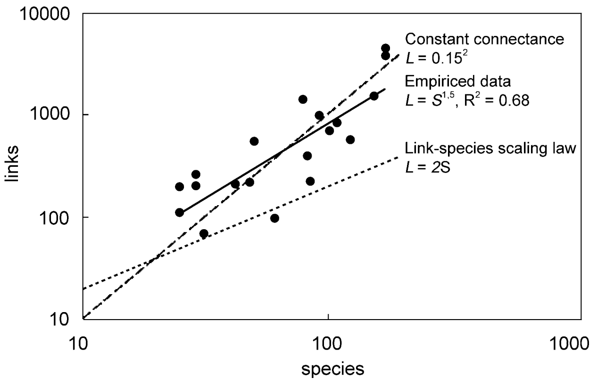
However, these early conclusions about patterns of food web structure began to crumble with the advent of improved data and new analysis methods that focused on the issues of species aggregation, sampling effort, and sampling consistency [36]. Even before there was access to improved data, Tom Schoener [93] set the stage for critiques of the conventional paradigm in his Ecological Society of America MacArthur Award lecture, in which he explored the ramifications of a simple conceptual model based on notions of "generality" (what Schoener referred to as "generalization") and "vulnerability." He adopted the basic notion underlying the "link-species scaling law": that how many different taxa something can eat is constrained, which results in the number of resource taxa per consumer taxon (generality) holding relatively steady with increasing S. However, he further hypothesized that the ability of resource taxa to defend again consumers is also constrained, such that the number of consumer taxa per resource taxon (vulnerability) should increase with increasing S. A major consequence of this conceptual model is that total links per species (L/S, which includes links to resources and consumers) and most other food web properties should display scale-dependence, not scale-invariance. A statistical reanalysis of a subset of the 113-web catalog supported this contention as well as the basic assumptions of his conceptual model about generality and vulnerability.

Shortly thereafter, more comprehensive, detailed datasets, like the ones for Coachella Valley [92] and Little

Rock Lake [63], began to appear in the literature. These and other new datasets provided direct empirical counterpoints to many of the prevailing notions about food webs: their connectance and links per species were much higher than expected from the "link-species scaling law," food chains could be quite long, omnivory and cannibalism and looping could be quite frequent, etc. In addition, analyzes such as the one by Martinez [63], in which he systematically aggregated the Little Rock Lake food web taxa and links to generate small webs that looked like the earlier data, demonstrated that "*most published food web patterns appear to be artifacts of poorly resolved data.*" Comparative studies incorporating newly available data further undermined the whole notion of "scale invariance" of most properties, particularly L/S(e. g., [65,66]).

For many researchers, the array of issues brought to light by the improved data and more sophisticated analyzes was enough for them to turn their back on structural food web research. A few hardy researchers sought to build new theory on top of the improved data. "Constant connectance" was suggested as an alternative hypothesis to constant L/S (the "link-species scaling law"), based on a comparative analysis of the relationship of L to S across a subset of available food webs including Little Rock Lake [64]. The mathematical difference between constant C and constant L/S can be simply stated using a log-log graph of links as a function of species (Fig. 4). If a power law exists of the form $L = \alpha S^{\beta}$, in the case of the link-species scaling law $\beta = 1$, which means that $L = \alpha S, L/S = \alpha$, indicating constant L/S. In the case of constant connectance, $\beta = 2$ and thus $L = \alpha S^2$, $L/S^2 = \alpha$, indicating constant C (L/S^2). Constant connectance means that L/S increases as a fixed proportion of S. One ecological interpretation of constant connectance is that consumers are likely to exploit an approximately constant fraction of available prey species, so as diversity increases, links per species increases [108].

Given the $L = \alpha S^{\beta}$ framework, $\beta = 2$ was reported for a set of 15 webs derived from an English pond [108], and $\beta = 1.9$ for a set of 50 Adirondack lakes [65], suggesting connectance may be constant across webs within a habitat or type of habitat. Across habitats, the picture is less clear. While $\beta = 2$ was reported for a small subset of the 5 most "credible" food webs then available from different habitats [64], several analyzes of both the old ECOWeB data and the more reliable newer data suggest that the exponent lies somewhere between 1 and 2, suggesting that C declines non-linearly with S (Fig. 4, [27,30,36,64,79,93]). For example, Schoener's reanalysis of the 113-web catalog suggested that $\beta = 1.5$, indicating that $L^{2/3}$ is proportional to S. A recent analysis of 19 recent trophic-species food webs with S of 25 to 172 also reported $\beta = 1.5$, with much scatter in the data (Fig. 4).



Food Webs, Figure 4
The relationship of links to species for 19 trophic-species food webs from a variety of habitats (*black circles*). The *solid line* shows the log-log regression for the empirical data, the *dashed line* shows the prediction for constant connectance, and the *dotted line* shows the prediction for the link-species scaling law (reproduced from [36], Fig. 1)

A recent analysis has provided a possible mechanistic basis for the observed constrained variation in C (~ 0.03 to 0.3 in cumulative community webs) as well as the scaling of C with S implied by β intermediate between 1 and 2 [10]. A simple diet breadth model based on optimal foraging theory predicts both of these patterns across food webs as an emergent consequence of individual foraging behavior of consumers. In particular, a contingency model of optimal foraging is used to predict mean diet breadth for S animal species in a food web, based on three parameters for an individual of species j: (1) net energy gain from consumption of an individual of species i, (2) the encounter rate of individuals of species i, and (3) the handling time spent attacking an individual of species i. This allows estimation of C for the animal portion of food webs, once data aggregation and cumulative sampling, well-known features of empirical datasets, are taken into account. The model does a good job of predicting values of C observed in empirical food webs and associated patterns of C across food webs.

Food Web Properties

Food webs have been characterized by a variety of properties or metrics, several of which have been mentioned previously (Sect. "Early Food Web Structure Research"). Many of these properties are quantifiable just using the basic network structure ("topology") of feeding interactions. These types of topological properties have been used to evaluate simple models of food web structure (Sect. "Food Web Properties"). Any number of properties can be calculated on a given network—ecologists tend to focus on properties that are meaningful within the context of ecological research, although other properties such as path length (**Path**) and clustering coefficient (**Cl**) have been borrowed from network research [109]. Examples of several types of food web network structure properties, with common abbreviations and definitions, follow.

Fundamental Properties: These properties characterize very simple, overall attributes of food web network structure.

S: number of nodes in a food web
***L*:** number of links in a food web
***L*/*S*:** links per species
***C*, or *L*/*S*^{2}:** connectance, or the proportion of possible links that are realized

Types of Taxa: These properties characterize what proportion or percentage of taxa within a food web fall into particular topologically defined roles.

Bas: percentage of basal taxa (taxa without resources)
Int: percentage of intermediate taxa (taxa with both consumers and resources)
Top: percentage of top taxa (taxa with no consumers)
Herb: percentage of herbivores plus detritivores (taxa that feed on autotrophs or detritus)
Can: percentage of cannibals (taxa that feed on their own taxa)
Omn: percentage of omnivores (taxa that feed that feed on taxa at different trophic levels
Loop: percentage of taxa that are in loops, food chains in which a taxon occur twice (e. g., A → B → C → A)

Network Structure: These properties characterize other attributes of network structure, based on how links are distributed among taxa.

TL: trophic level averaged across taxa. Trophic level represents how many steps energy must take to get from an energy source to a taxon. Basal taxa have TL = 1, and obligate herbivores are TL = 2. TL can be calculated using many different algorithms that take into account multiple food chains that can connect higher level organisms to basal taxa (Williams and Martinez 2004).
ChLen: mean food chain length, averaged over all species
ChSD: standard deviation of ChLen
ChNum: log number of food chains
LinkSD: normalized standard deviation of links (# links per taxon)
GenSD: normalized standard deviation of generality (# resources per taxon)
VulSD: normalized standard deviation of vulnerability (# consumers per taxon)
MaxSim: mean across taxa of the maximum trophic similarity of each taxon to other taxa
Ddiet: the level of diet discontinuity—the proportion of triplets of taxa with an irreducible gap in feeding links over the number of possible triplets [19]—a local estimate of intervality
Cl: clustering coefficient (probability that two taxa linked to the same taxon are linked)
Path: characteristic path length, the mean shortest set of links (where links are treated as undirected) between species pairs

The previous properties (most of which are described in [110] and [39]) each provide a single metric that characterizes some aspect of food web structure. There are other properties, such as **Degree Distribution**, which are not single-number properties. "Degree" refers to the number of links that connect to a particular node, and the degree distribution of a network describes (in the format of a function or a graph) the total number of nodes in a network that have a given degree for each level of degree (Subsect. "Degree Distribution"). In food web analysis, **LinkSD**, **GenSD**, and **VulSD** characterize the variability of different aspects of degree distribution. Many food web structure properties are correlated with each other, and vary in predictable ways with *S* and/or *C*. This provides opportunities for topological modeling that are discussed below (Sect. "Models of Food Web Structure").

In addition to these types of metrics based on networks with unweighted links and nodes, it is possible to calculate a variety of metrics for food webs with nodes and/or links that are weighted by measures such as biomass, numerical abundance, frequency, interaction strength, or body size [11,33,67,81]. However, few food web datasets are "enriched" with such quantitative data and it remains to be seen whether such approaches are primarily a tool for richer description of particular ecosystems or whether they can give rise to novel generalities, models and predictions. One potential generality was suggested by a study of interaction strengths in seven soil food webs, where interaction strength reflects the size of the effects of species on each other's dynamics near equilibrium. Interaction strengths appear to be organized such that long loops contain many weak links, a pattern which enhances stability of complex food webs [81].

Food Webs Compared to Other Networks

Small-World Properties

How does the structure of food webs compare to that of other kinds of networks? One common way that various networks have been compared is in terms of whether they are "small-world" networks. Small-world networks are characterized by two of the properties described previously, characteristic path length (**Path**) and clustering coefficient (**Cl**) [109]. Most real-world networks appear to have high clustering, like what is seen on some types of regular spatial lattices (such as a planar triangular lattice, where many of a node's neighbors are neighbors of one another), but have short path lengths, like what is seen on "random graphs" (i. e., networks in which links are distributed randomly). Food webs do display short path lengths that are similar to what is seen in random webs (Table 1, [16,37,78,113]). On average, taxa are about two links from other taxa in a food web ("two degrees of separation"), and path length decreases with increasing connectance [113].

However, clustering tends to be quite low in many food webs, closer to the clustering expected on a random network (Table 1). This relatively low clustering in food webs appears consistent with their small size compared to most other kinds of networks studied, since the ratio of clustering in empirical versus comparable random networks increases linearly with the size of the network (Fig. 5).

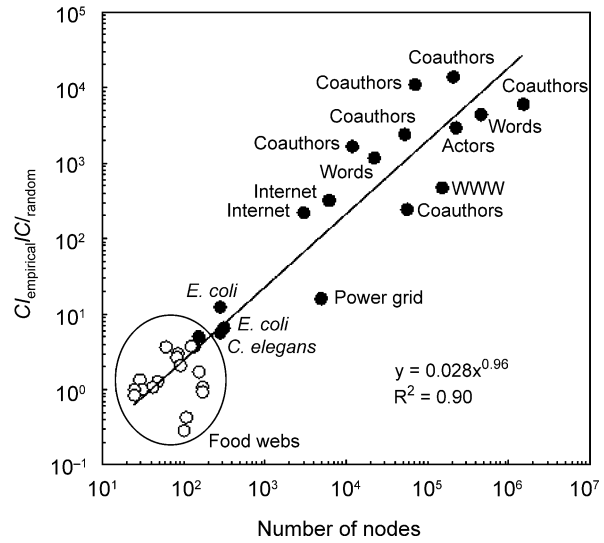
Degree Distribution

In addition to small-world properties, many real-world networks appear to display power-law degree distributions [2]. Whereas regular graphs have the same number of links per node, and random graphs display a Poisson degree distribution, many empirical networks, both biotic and abiotic, display a highly skewed power-law ("scale-free") degree distribution, where most nodes have few links and a few nodes have many links. However, some empirical networks display less-skewed distributions such as exponential distributions [4]. Most empirical food webs display exponential or uniform degree distributions, not power-law distributions [16,37], and it has been suggested that normalized degree distributions in food webs follow universal functional forms [16] although there is a quite a bit of scatter when a wide range of data are considered (Fig. 6, [37]). Variable degree distributions, like what is seen in individual food webs, could result from simple mechanisms. For example, exponential and uniform food web degree distributions are generated by a model that combines (1) random immigration to local webs from a randomly linked regional set of taxa, and (2) random extinctions in the local webs [5]. The general lack of power-

Food Webs, Table 1

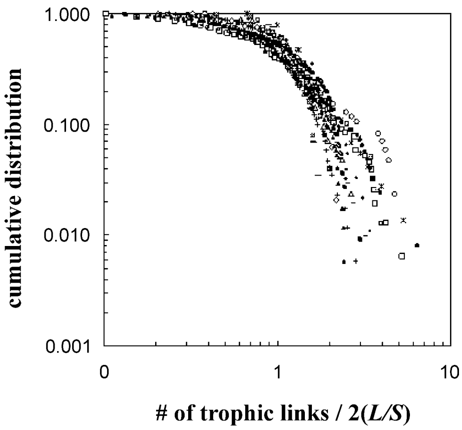
Topological properties of empirical and random food webs, listed in order of increasing connectance. *Path* refers to characteristic path length, and *Cl* refers to the clustering coefficient. $Path_r$ and Cl_r refer to the mean *D* and *Cl* for 100 random webs with the same *S* and *C*. Modified from [37] Table 1

Food Web	S	$C(L/S^2)$	L/S	$Path$	$Path_r$	Cl	Cl_r	Cl/Cl_r
Grassland	61	0.026	1.59	3.74	3.63	0.11	0.03	3.7
Scotch Broom	85	0.031	2.62	3.11	2.82	0.12	0.04	3.0
Ythan Estuary 1	124	0.038	4.67	2.34	2.39	0.15	0.04	3.8
Ythan Estuary 2	83	0.057	4.76	2.20	2.19	0.16	0.06	2.7
El Verde Rainforest	155	0.063	9.74	2.20	1.95	0.12	0.07	1.4
Canton Creek	102	0.067	6.83	2.27	2.01	0.02	0.07	0.3
Stony Stream	109	0.070	7.61	2.31	1.96	0.03	0.07	0.4
Chesapeake Bay	31	0.071	2.19	2.65	2.40	0.09	0.09	1.0
St. Marks Seagrass	48	0.096	4.60	2.04	1.94	0.14	0.11	1.3
St. Martin Island	42	0.116	4.88	1.88	1.85	0.14	0.13	1.1
Little Rock Lake	92	0.118	10.84	1.89	1.77	0.25	0.12	2.1
Lake Tahoe	172	0.131	22.59	1.81	1.74	0.14	0.13	1.1
Mirror Lake	172	0.146	25.13	1.76	1.72	0.14	0.15	0.9
Bridge Brook Lake	25	0.171	4.28	1.85	1.68	0.16	0.19	0.8
Coachella Valley	29	0.312	9.03	1.42	1.43	0.43	0.32	1.3
Skipwith Pond	25	0.315	7.88	1.33	1.41	0.33	0.33	1.0



Food Webs, Figure 5

Trends in clustering coefficient across networks. The ratio of clustering in empirical networks ($\mathrm{Cl}_{\text{empirical}}$) to clustering in random networks with the same number of nodes and links ($\mathrm{Cl}_{\text{random}}$) is shown as a function of the size of the network (number of nodes). Reproduced from [37], Fig. 1



Food Webs, Figure 6

Log-log overlay plot of the cumulative distributions of links per species in 16 food webs. The link data are normalized by the average number of links/species in each web. If the distributions followed a power law, the data would tend to follow a straight line. Instead, they follow a roughly exponential shape. Reproduced from [37], Fig. 3

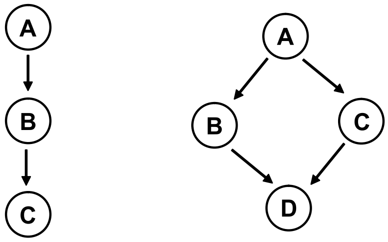
law degree distributions in food webs may result partly from the small size and large connectance of such networks, which limits the potential for highly skewed distributions. Many of the networks displaying power-law degree distributions are much larger and much more sparsely connected than food webs.

Other Properties

Assortative mixing, or the tendency of nodes with similar degree to be linked to each other, appears to be a pervasive phenomenon in a variety of social networks [82]. However, other kinds of networks, including technological and biological networks, tend to show disassortative mixing, where nodes with high degree tend to link to nodes with low degree. Biological networks, and particularly two food webs examined, show strong disassortativity [82]. Some of this may relate to a finite-size effect in systems like food webs that have limits on how many links are recorded between pairs of nodes. However, in food webs it may also result from the stabilizing effects of having feeding specialists linked to feeding generalists, as has been suggested for plant-animal pollination and frugivory (fruit-eating) networks ([7], Sect. "Ecological Networks").

Another aspect of structure that has been directly compared across several types of networks including food webs are "motifs," defined as "recurring, significant patterns of interconnections" [77]. A variety of networks (transcriptional gene regulation, neuron connectivity, food webs, two types of electronic circuits, the World Wide Web) were scanned for all possible subgraphs that could be constructed out of 3 or 4 nodes (13 and 199 possible subgraphs, respectively). Subgraphs that appeared significantly more often in empirical webs than in their randomized counterparts (i. e., networks with the same number of nodes and links, and the same degree for each node, but with links otherwise randomly distributed) were identified. For the seven food webs examined, there were two "consensus motifs" shared by most of the webs—a three-node food chain, and a four-species diamond where a predator has two prey, which in turn prey on the same species (Fig. 7). The four-node motif was shared by two other types of networks (neuron connectivity, one type of electronic circuit), and nothing shared the three-node chain. The WWW and food web networks appear most dissimilar to other types of networks (and to each other) in terms of significant motifs.

Complex networks can be decomposed into minimum spanning trees (MST). A MST is a simplified version of a network created by removing links to minimize the distance between nodes and some destination. For example, a food web can be turned into MST by adding an "environment" node that all basal taxa link to, tracing the shortest food chain from each species to the environment node, and removing links that do not appear in the shortest chains. Given this algorithm, a MST removes links that



Food Webs, Figure 7
The two 3 or 4-node network motifs found to occur significantly more often than expected in most of seven food webs examined. There is one significant 3-node motif (out of 13 possible motifs), a food chain of the form A eats B eats C. There is one significant 4-node motif (out of 199 possible motifs), a trophic diamond ("bi-parallel") of the form A eats B and C, which both eat D

occur in loops and retains a basic backbone that has a tree-like structure. In a MST, the quantity A_i is defined as the number of nodes in a subtree rooted at node i, and can be regarded as the transportation rate through that node. C_i is defined as the integral of A_i (i. e., the sum of A_i for all nodes rooted at node i) and can be regarded as the transportation cost at node i. These properties can be used to plot C_i versus A_i for each node in a networks, or to plot whole-system C_o versus A_o across multiple networks, to identify whether scaling relationships of the form $C(A) \propto A^n$ are present, indicating self-similarity in the structure of the MST (see [18] for review). In a food web MST, the most efficient configuration is a star, where every species links directly to the environment node, resulting in an exponent of 1, and the least efficient configuration is a single chain, where resources have to pass through each species in a line, resulting in an exponent of 2. It has been suggested that food webs display a universal exponent of 1.13 [18,45], reflecting an invariant functional food web property relating to very efficient resource transportation within an ecosystem. However, analyzes based on a larger set of webs (17 webs versus 7) suggest that exponents for C_i as a function of A_i range from 1.09 to 1.26 and are thus not universal, that the exponents are quite sensitive to small changes in food web structure, and that the observed range of exponent values would be similarly constrained in any network with only 3 levels, as is seen in food web MSTs [15].

Models of Food Web Structure

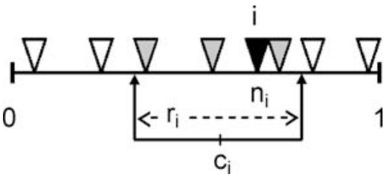
An important area of research on food webs has been whether their observed structure, which often appears quite complex, can emerge from simple rules or models. As with other kinds of "real-world" networks, models that assign links among nodes randomly, according to fixed probabilities, fail to reproduce the network structure of empirically observed food webs [24,28,110]. Instead, several models that combine stochastic elements with simple link assignment rules have been proposed to generate and predict the network structure of empirical food webs.

The models share a basic formulation [110]. There are two empirically quantifiable parameters: (1) S, the number of trophic species in a food web, and (2) C, the connectance of a food web, defined as links per species squared, L/S^2. Thus, S specifies the number of nodes in a network, and C specifies the number of links in a network with S nodes. Each species is assigned a "niche value" n_i drawn randomly and uniformly from the interval [0,1]. The models differ in the rules used to distribute links among species. The link distribution rules follow in the order the models were introduced in the literature:

Cascade Model (Cohen and Newman [28]): Each species has the fixed probability $P = 2CS/(S-1)$ of consuming species with niche values less than its own. This creates a food web with hierarchical feeding, since it does not allow feeding on taxa with the same niche value (cannibalism) or taxa with higher niche values (looping/cycling). This formulation [110] is a modified version of the original cascade model that allows L/S, equivalent to the CS term in the probability statement above, to vary as a tunable parameter, rather than be fixed as a constant [28].

Niche Model (Williams and Martinez [110], Fig. 8): Each species consumes all species within a segment of the [0,1] interval whose size r_i is calculated using the feeding range width algorithm described below. The r_i's center c_i is set at a random value drawn uniformly from the interval $[r_i/2, n_i]$ or $[r_i/2, 1 - r_i/2]$ if $n_i > 1 - r_i/2$, which places c_i equal to or lower than the niche value n_i and keeps the r_i segment within [0,1]. The c_i rule relaxes the strict feeding hierarchy of the cascade model and allows for the possibility of cannibalism and looping. Also, the r_i rule ensures that species feed on a contiguous range of species, necessarily creating interval graphs (i. e., species can be lined up along a single interval such that all of their resource species are located in contiguous segments along the interval).

Feeding range width algorithm: The value of $r_i = xn_i$, where $0 < x < 1$ is randomly drawn from the probability density function $p(x) = \beta(1-x)^{b-1}$ (the beta distribution), where $\beta = (1/2C) - 1$ to obtain a C close to the desired C.



Food Webs, Figure 8
Graphical representation of the niche model: Species *i* feeds on 4 taxa including itself and one with a higher niche value

Nested-Hierarchy Model (Cattin et al. [19]): Like the niche model, the number of prey items for each species is drawn randomly from a beta distribution that constrains C close to a target value. Once the number of prey items for each species is set, those links are assigned in a multistep process. First, a link is randomly assigned from species i to a species j with a lower n_i. If j is fed on by other species, the next feeding links for i are selected randomly from the pool of prey species fed on by a set of consumer species defined as follows: they share at least one prey species and at least one of them feeds on j. If more links need to be distributed, they are then randomly assigned to species without predators and with niche values $< n_i$, and finally to those with niche value $\geq n_i$. These rules were chosen to relax the contiguity rule of the niche model and to allow for trophic habit overlap among taxa in a manner which the authors suggest evokes phylogenetic constraints.

Generalized Cascade Model (Stouffer et al. [99]): Species i feeds on species j if $n_j \leq n_i$ with a probability drawn from the interval [0,1] using the beta or an exponential distribution. This model combines the beta distribution introduced in the niche model with the hierarchical, non-contiguous feeding of the cascade model.

These models have been evaluated with respect to their relative fit to empirical data in a variety of ways. In a series of six papers published from 1985 to 1990 with the common title "A stochastic theory of community food webs," the cascade model was proposed as a means of explaining "*the phenomenology of observed food web structure, using a minimum of hypotheses*" [31]. This was not the first simple model proposed for generating food web structure [25,88,89,116], but it was the most well-developed model. Cohen and colleagues also examined several model variations, most of which performed poorly. While the cascade model appeared to generate structures that qualitatively fit general patterns in the data from the 113-web catalog, subsequent statistical analyzes suggested that the fit between the model and that early data was poor [93,96,97]. Once improved data began to emerge, it became clear that some of the basic assumptions built in to the cascade model, such as no looping and minimal overlap and no clustering of feeding habits across taxa, are violated by common features of multi-species interactions.

The niche model was introduced in 2000, along with a new approach to analysis: numerical simulations to compare statistically the ability of the niche model, the cascade model, and one type of random network model to fit empirical food web data [110]. Because of stochastic variation in how species and links are distributed in any particular model web, analysis begins with the generation of hundreds to thousands of model webs with the same S and similar C as an empirical food web of interest. Model webs that fall within 3% of the target C are retained. Model-generated webs occasionally contain species with no links to other species, or species that are trophically identical. Either those webs are thrown out, or those species are eliminated and replaced, until every model web has no disconnected or identical species. Also, each model web must contain at least one basal species. These requirements ensure that model webs can be sensibly comparable to empirical trophic-species webs.

Once a set of model webs are generated with the same S and C as an empirical web, model means and standard deviations are calculated for each food web property of interest, which can then be compared to empirical values. Raw error, the difference between the value of an empirical property and a model mean for that property, is normalized by dividing it by the standard deviation of the property's simulated distribution. This approach allows assessment not only of whether a model over- or under-estimates empirical properties as indicated by the raw error, but also to what degree a model's mean deviates from the empirical value. Normalized errors within ±2 are considered to indicate a good fit between the model prediction and the empirical value. This approach has also been used to analyze network motifs [77] (Subsect. "Other Properties").

The initial niche model analyzes examined seven more recent, diverse food webs ($S = 24$ to 92) and up to 12 network structure properties for each web [110]. The random model (links are distributed randomly among nodes) performs poorly, with an average normalized error (ANE) of 27.1 (SD = 202). The cascade model performs better, with ANE of -3.0 (SD = 14.1). The niche model performs an order of magnitude better than the cascade model, with ANE of 0.22 (SD = 1.8). Only the niche model falls within ±2 ANE considered to show a good fit to the data. Not surprisingly, there is variability in how all three models fit different food webs and properties. For example, the niche model generally overestimates food-chain length. Specific mismatches are generally attributable either to limitations of the models or biases in the data [110]. A separate test of the niche and cascade models with three marine food webs, a type of habitat not included in the original analysis, obtained similar results [39]. These analyzes demonstrate that the structure of food webs is far from random and that simple link distribution rules can yield apparently complex network structure, similar to that observed in empirical data. In addition, the analyzes suggest that food webs from a variety of habitats share a fundamentally similar network structure, and that the structure is scale-dependent in predictable ways with S and C.

The nested-hierarchy model [19] and generalized cascade model [99], variants of the niche model, do not appear to improve on the niche model, and in fact may be worse at representing several aspects of empirical network structure. Although the nested-hierarchy model breaks the intervality of the niche model and uses a complicated-sounding set of link distribution rules to try to mimic phylogenetic constraints on trophic structure, it "*generates webs characterized by the same universal distributions of numbers of prey, predators, and links*" as the niche model [99]. Both the niche and nested-hierarchy models have a beta distribution at their core. The beta distribution is reasonably approximated by an exponential distribution for $C < 0.12$ [99], and thus reproduces the exponential degree distributions observed in many empirical webs, particularly those with average or less-than-average C [37]. The generalized cascade model was proposed as a simplified model that would return the same distributions of taxa and links as the niche and nested-hierarchy models. It is defined using only two criteria: (1) taxa form a totally ordered set—this is fulfilled by the arrangement of taxa along a single "niche" interval or dimension, and (2) each species has an exponentially decaying probability of preying on a given fraction of species with lower niche values [99].

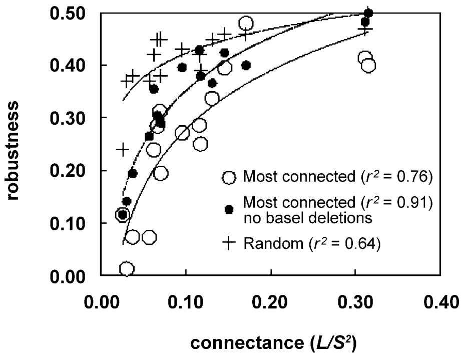
Although the generalized cascade model does capture a central tendency of successful food web models, only some food web properties are derivable from link distributions (e. g., Top, Bas, Can, VulSD, GenSD, Clus). There are a variety of food web structure properties of interest that are not derivable from degree distributions (e. g., Loop, Omn, Herb, TL, food-chain statistics, intervality statistics). The accurate representation of these types of properties may depend on additional factors, for example the contiguous feeding ranges specified by the niche model but absent from the cascade, nested-hierarchy, and generalized cascade models. While it is known that empirical food webs are not interval, until recently it was not clear how non-interval they are. Intervality is a brittle property that is broken by a single gap in a single feeding range (i. e., a single missing link in a food web), and trying to arrange species in a food web into their most interval ordering is a computationally challenging problem. A more robust measure of intervality in food webs has been developed, in conjunction with the use of simulated annealing to estimate the most interval ordering of empirical food webs [100]. This analysis suggests that complex food webs "*do exhibit a strong bias toward contiguity of prey, that is, toward intervality*" when compared to several alternative "null" models, including the generalized cascade model. Thus, the intervality assumption of the niche model, initially critiqued as a flaw of the model [19], helps to produce a better fit to empirical data than the non-interval alternate models.

Structural Robustness of Food Webs

A series of papers have examined the response of a variety of networks including the Internet and WWW web pages [1] and metabolic and protein networks [52,53] to the simulated loss of nodes. In each case, the networks, all of which display highly skewed power-law degree distributions, appear very sensitive to the targeted loss of highly-connected nodes but relatively robust to random loss of nodes. When highly-connected nodes are removed from scale-free networks, the average path length tends to increase rapidly, and the networks quickly fragment into isolated clusters. In essence, paths of information flow in highly skewed networks are easily disrupted by loss of nodes that are directly connected to an unusually large number of other nodes. In contrast, random networks with much less skewed Poisson degree distributions display similar responses to targeted loss of highly-connected nodes versus random node loss [101].

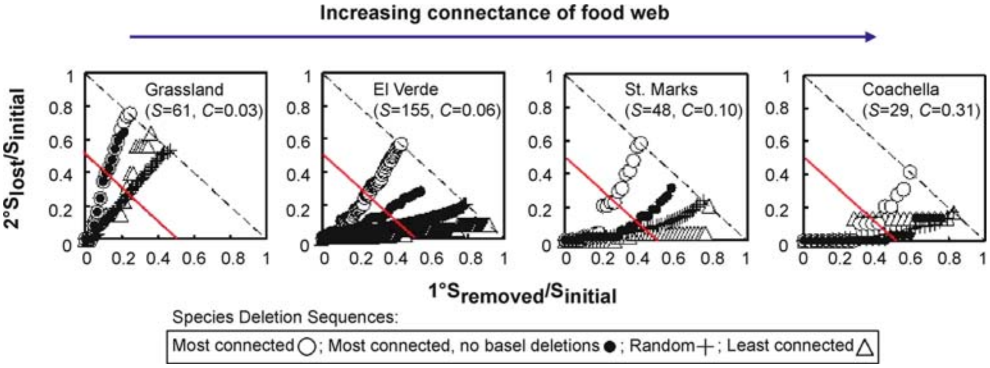
Within ecology, species deletions on small ($S < 14$) hypothetical food web networks as well as a subset of the 113-web catalog have been used to examine the reliability of network flow, or the probability that sources (producers) are connected to sinks (consumers) in food webs [54]. The structure of the empirical webs appears to conform to reliable flow patterns identified using the hypothetical webs, but that result is based on low diversity, poorly resolved data. The use of more highly resolved data with node knock-out algorithms to simulate the loss of species allows assessment of potential secondary extinctions in complex empirical food webs. Secondary extinctions result when the removal of taxa results in one or more consumers losing all of their resource taxa. Even though most food webs do not have power-law degree distributions, they show similar patterns of robustness to other networks: removal of highly-connected species results in much higher rates of secondary extinctions than random loss of species ([38,39,95], Fig. 9). In addition, loss of high-degree species results in more rapid fragmentation of the webs [95]. Protecting basal taxa from primary removal increases the robustness of the web (i. e., fewer secondary extinctions occur) ([38], Fig. 9). While removing species with few links generally results in few secondary extinctions, in a quarter of the food webs examined, removing low-degree species results in secondary extinctions comparable to or greater than what is seen with removal of high-degree species [38]. This tends to occur in webs with relatively high *C*.

Beyond differential impacts of various sequences of species loss in food webs, food web 'structural robustness' can be defined as the fraction of primary species loss that induces some level of species loss (primary + secondary extinctions) for a particular trophic-species web. Analysis of R_{50} (i. e., what proportion of species have to be removed to achieve $\geq$ 50% total species loss) across multiple food webs shows that robustness increases approximately logarithmically with increasing connectance ([38,39], Fig. 9, 10). In essence, from a topological perspective food webs with more densely interconnected taxa are better protected from species loss, since it takes greater species loss for consumers to lose all of their resources.



Food Webs, Figure 10
The proportion of primary species removals required to induce a total loss (primary removals plus secondary extinctions) of 50% of the species in each of 16 food webs ("robustness," see the shorter red line of Fig. 9 for visual representation) as a function of the connectance of each web. Logarithmic fits to the three data sets are shown, with a *solid line* for the most connected deletion order, a *long dashed line* for the most connected with basal species preserved deletion order, and a *short dashed* line for random deletion order. The maximum possible y value is 0.50. The equations for the fits are: $y = 0.162 \ln(x) + 0.651$ for most connected species removals, $y = 0.148 \ln(x) + 0.691$ for most connected species removals with basal species preserved, and $y = 0.067 \ln(x) + 0.571$ for random species removals. Reproduced from [38], Fig. 2

It is also potentially important from a conservation perspective to identify particular species likely to result in the greatest number of secondary extinctions through their loss. The loss of a particular highly-connected species may or may not result in secondary extinctions. One way to identify critical taxa is to reduce the topological structure of empirical food webs into linear pathways that define the essential chains of energy delivery in each web. A particular species can be said to "dominate" other



Food Webs, Figure 9
Secondary extinctions resulting from primary species loss in 4 food webs ordered by increasing connectance (*C*). The *y-axis* shows the cumulative secondary extinctions as a fraction of initial S, and the *x-axis* shows the primary removals of species as a fraction of initial *S*. 95% error bars for the random removals fall within the size of the symbols and are not shown. For the most connected (*circles*), least connected (*triangles*), and random removal (*plus symbols*) sequences, the data series end at the *black diagonal dashed line*, where primary removals plus secondary extinctions equal *S* and the web disappears. For the most connected species removals with basal species preserved (*black dots*), the data points end when only basal species remain. The shorter *red diagonal lines* show the points at which 50% of species are lost through combined primary removals and secondary extinctions ("robustness" or R_{50})

species if it passes energy to them along a chain in the dominator tree. The higher the number of species that a particular species dominates, the greater the secondary extinctions that may result from its removal [3]. This approach has the advantage of going beyond assessment of direct interactions to include indirect interactions.

As in food webs, the order of pollinator loss has an effect on potential plant extinction patterns in plant-pollinator networks [75] (see Sect. "Ecological Networks"). Loss of plant diversity associated with targeted removal of highly-connected pollinators is not as extreme as comparable secondary extinctions in food webs, which may be due to pollinator redundancy and the nested topology of those networks.

While the order in which species go locally extinct clearly affects the potential for secondary extinctions in ecosystems, the focus on high-degree, random, or even dominator species does not provide insight on ecologically plausible species loss scenarios, whether the focus is on human perturbations or natural dynamics. The issue of what realistic natural extinction sequences might look like has been explored using a set of pelagic-focused food webs for 50 Adirondack lakes [49] with up to 75 species [98]. The geographic nestedness of species composition across the lakes is used to derive an ecologically plausible extinction sequence scenario, with the most restricted taxa the most likely to go extinct. This sequence is corroborated by the pH tolerances of the species. Species removal simulations show that the food webs are highly robust in terms of secondary extinctions to the "realistic" extinction order and highly sensitive to the reverse order. This suggests that nested geographical distribution patterns coupled with local food web interaction patterns appear to buffer effects of likely species losses. This highlights important aspects of community organization that may help to minimize biodiversity loss in the face of a naturally changing environment. However, anthropogenic disturbances may disrupt the inherent buffering of how taxa are organized geographically and trophically, reducing the robustness of ecosystems.

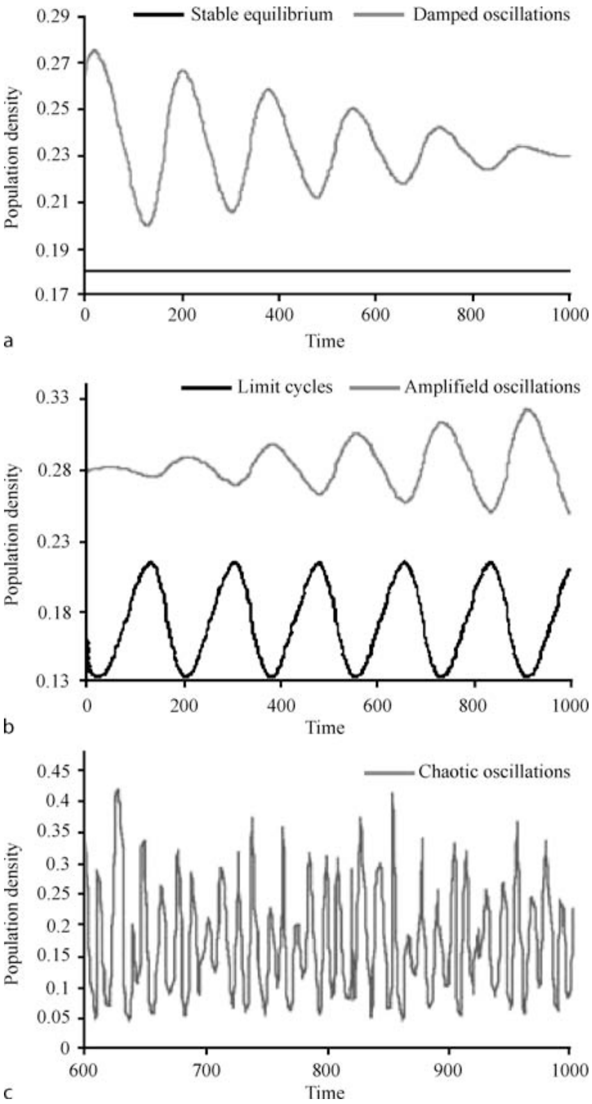
Food Web Dynamics

Analysis of the topology of food webs has proven very useful for exploring basic patterns and generalities of "who eats whom" in ecosystems. This approach seeks to identify "*the most universal, high-level, persistent elements of organization*" [35] in trophic networks, and to leverage understanding of such organization for thinking about ecosystem robustness. However, food webs are inherently dynamical systems, since feeding interactions involve biomass flows among species whose "stocks" can be characterized by numbers of individuals and/or aggregate population biomass. All of these stocks and flows change through time in response to direct and indirect trophic and other types of interactions. Determining the interplay among network structure, network dynamics, and various aspects of stability such as persistence, robustness, and resilience in complex "real-world" networks is one of the great current challenges in network research [101]. It is particularly important in the study of ecosystems, since they face a variety of anthropogenic perturbations such as climate change, habitat loss, and invasions, and since humans depend on them for a variety of "ecosystem services" such as supply of clean water and pollination of crops [34].

Because it is nearly impossible to compile detailed, long-term empirical data for dynamics of more than two interacting species, most research on species interaction dynamics relies on analytical or simulation modeling. Most modeling studies of trophic dynamics have focused narrowly on predator-prey or parasite-host interactions. However, as the previous sections should make clear, in natural ecosystems such interaction dyads are embedded in diverse, complex networks, where many additional taxa and their direct and indirect interactions can play important roles for the stability of focal species as well as the stability or persistence of the broader community. Moving beyond the two-species population dynamics modeling paradigm, there is a strong tradition of research that looks at interactions among 3–8 species, exploring dynamics and simple variations in structure in slightly more complex systems (see reviews in [40,55]). However, these interaction modules still present a drastic simplification of the diversity and structure of natural ecosystems. Other dynamical approaches have focused on higher diversity model systems [69], but ignore network structure in order to conduct analytically tractable analyzes.

Researchers are increasingly integrating dynamics with complex food web structure in modeling studies that move beyond small modules. The Lotka–Volterra cascade model [20,21,32] was an early incarnation of this type of integration. As its name suggests, the Lotka–Volterra cascade model runs classic L-V dynamics, including a non-saturating linear functional response, on sets of species interactions structured according to the cascade model [28]. The cascade model was also used to generate the structural framework for a dynamical food web model with a linear functional response [58] used to study the effects of prey-switching on ecosystem stability. Improving on aspects of biological realism of both dynamics and structure, a bioenergetic dynamical model with nonlinear functional responses [119] was used in conjunction with empirically-defined food web structure among 29 species to simulate the biomass dynamics of a marine fisheries food web [117,118]. This type of nonlinear bioenergetic dynamical modeling approach has been integrated with niche model network structure and used to study more complex networks [13,14,68,112]. A variety of types of dynamics are observed in these non-linear models, including equilibrium, limit cycle, and chaotic dynamics, which may or may not be persistent over short or long time scales (Fig. 11). Other approaches model ecological and evolutionary dynamics to assemble species into networks, rather than imposing a particular structure on them. These models, which typically employ an enormous amount of parameters, are evaluated as to whether they generate plausible persistence, diversity, and network structure (see review by [72]). All of these approaches are generally used to examine stability, characterized in a diversity of ways, in ecosystems with complex structure and dynamics [71,85].

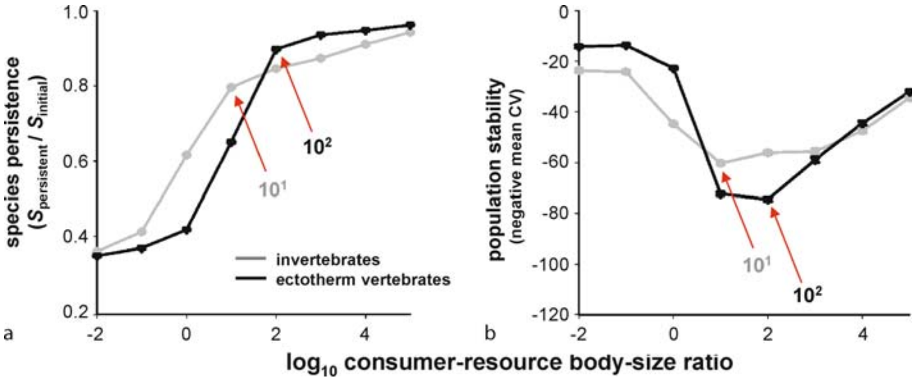
While it is basically impossible to empirically validate models of integrated structure and dynamics for complex ecological networks, in some situations it is possible to draw interesting connections between models and data at more aggregated levels. This provides opportunities to move beyond the merely heuristic role that such models generally play. For example, nonlinear bioenergetic models of population dynamics parametrized by biological rates allometrically scaled to populations' average body masses have been run on various types of model food web structures [14]. This approach has allowed the comparison of trends in two different measures of food web stability, and how they relate to consumer-resource body-size ratios and to initial network structure. One measure of stability is the fraction of original species that display persistent dynamics, i. e., what fraction of species do not go extinct in the model when it is run over many time steps ("species persistence"). Another measure of stability is how variable the densities of all of the persistent species are ("population stability")—greater variability across all the species indicates decreased stability in terms of population dynamics.



Food Webs, Figure 11

5 different types of population dynamics shown as time series of population density (from [40], Fig. 10.1). The types of dynamics shown include a stable equilibrium, damped oscillations, limit cycles, amplified oscillations, and chaotic oscillations

Brose and colleagues [14] ran the model using different hypothetical consumer-resource body-size ratios that range from 10^{-2} (consumers are 100 times smaller than their resources) to 10^5 (consumers are 100,000 times larger than their resources) (Fig. 12). Species persistence increases dramatically with increasing body-size ratios, until inflection points are reached at which persistence shifts to high levels (~ 0.80) of persistence (Fig. 12a). However, population stability decreases with increasing body-size ratios until inflection points are reached that show the lowest stability, and then increases again beyond those points (Fig. 12b). In both cases, the inflection points correspond to empirically observed consumer-resource body-size ratios, both for webs parametrized to represent invertebrate dominated webs, and for webs parametrized to represent ectotherm vertebrate dominated webs. Thus, across thousands of observations, invertebrate consumer-resource body size ratios are $\sim 10^1$, and ectotherm vertebrate consumer-resource body size ratios are $\sim 10^2$, which correspond to the model's inflection points for species persistence and population stability (Fig. 12). It is interesting



Food Webs, Figure 12

a shows the fraction of species that display persistent dynamics as a function of consumer-resource body-size ratios for model food webs parametrized for invertebrates (*gray line*) and ectotherm vertebrates (*black line*). The inflection points for shifts to high-persistence dynamics are indicated by *red arrows* for both curves, and those inflection points correspond to empirically observed consumer-resource body size ratios for invertebrate dominated webs (10^1—consumers are on average 10 times larger than their resources) and ectotherm vertebrate dominated webs (10^2—consumers are on average 100 times larger than their resources). b shows results for population stability, the mean of how variable species population biomasses are in persistent webs. In this case, the inflection points for shifts to low population stability are indicated by red arrows, and those inflection points also correspond to the empirically observed body-size ratios for consumers and resources. Figure adapted from [14]

to note that high species persistence is coupled to low population stability—i. e., an aspect of increased stability of the whole system (species persistence) is linked to an aspect of decreased stability of components of that system (population stability). It is also interesting to note that in this formulation, using initial cascade versus niche model structure had little impact on species persistence or population stability [14], although other formulations show increased persistence when dynamics are initiated with niche model versus other structures [68]. How structure influences dynamics, and vice-versa, is an open question.

Ecological Networks

This article has focused on food webs, which generally concern classic predator-herbivore-primary producer feeding interactions. However, the basic concept of food webs can be extended to a broader framework of "ecological networks" that is more inclusive of different components of ecosystem biomass flow, and that takes into consideration different kinds of species interactions that are not classic "predator-prey" interactions. Three examples are mentioned here. First, parasites have typically been given short shrift in traditional food webs, although exceptions exist (e. g., [51,67,74]). This is changing as it becomes clear that parasites are ubiquitous, often have significant impacts on predator-prey dynamics, and may be the dominant trophic habitat in most food webs, potentially altering our understanding of structure and dynamics [59]. The dynamical models described previously have been parametrized with more conventional, non-parasite consumers in mind. An interesting open question is how altering dynamical model parameters such as metabolic rate, functional response, and consumer-resource body size ratios to reflect parasite characteristics will affect our understanding of food web stability.

Second, the role of detritus, or dead organic matter, in food webs has yet to be adequately resolved in either structural or dynamical approaches. Detritus has typically been included as one or several separate nodes in many binary-link and flow-weighted food webs. In some cases, it is treated as an additional "primary producer," while in other cases both primary producers and detritivores connect to it. Researchers must think much more carefully about how to include detritus in all kinds of ecological studies [80], given that it plays a fundamental role in most ecosystems and has particular characteristics that differ from other food web nodes: it is non-living organic matter, all species contribute to detrital pools, it is a major resource for many species, and the forms it takes are extremely heterogeneous (e. g., suspended organic matter in water columns; fecal material; rotting trees; dead animal bodies; small bits of plants and molted cuticle, skin, and hair mixed in soil; etc.).

Third, there are many interactions that species participate in that go beyond strictly trophic interactions. Plant-animal mutualistic networks, particularly pollination and seed dispersal or "frugivory" networks, have received the most attention thus far. They are characterized as "bipartite" (two-level) graphs, with links from animals to plants, but no links among plants or among animals [7,9,56,57,73,107]. While both pollination and seed dispersal do involve a trophic interaction, with animals gaining nutrition from plants during the interactions, unlike in classic predator-prey relationships a positive benefit is conferred upon both partners in the interaction. The evolutionary and ecological dynamics of such mutualistic relationships place unique constraints on the network structure of these interactions and the dynamical stability of such networks. For example, plant-animal mutualistic networks are highly nested and thus asymmetric, such that generalist plants and generalist animals tend to interact among themselves, but specialist species (whether plants or animals) also tend to interact with the most generalist species [7,107]. When simple dynamics are run on these types of "coevolutionary" bipartite networks, it appears that the asymmetric structure enhances long-term species coexistence and thus biodiversity maintenance [9].

Future Directions

Food web research of all kinds has expanded greatly over the last several years, and there are many opportunities for exciting new work at the intersection of ecology and network structure and dynamics. In terms of empiricism, there is still a paucity of detailed, evenly resolved community food webs in every habitat type. Current theory, models, and applications need to be tested against more diverse, more complete, and more highly quantified data. In addition, there are many types of datasets that could be compiled which would support novel research. For example, certain kinds of fossil assemblages may allow the compilation of detailed paleo food webs, which in turn could allow examination of questions about how and why food web structure does or does not change over deep time or in response to major extinction events. Another example is data illustrating the assembly of food [41] webs in particular habitats over ecological time. In particular, areas undergoing rapid successional dynamics would be excellent candidates, such as an area covered by volcanic lava flows, a field exposed by a retreating glacier, a hillside denuded by an earth slide, or a forest burned in a large fire. This type of data would allow empirically-based research on the topological dynamics of food webs. Another empirical frontier is the integration of multiple kinds of ecological interaction data into networks with multiple kinds of links—for example, networks that combine mutualistic interactions such as pollination and antagonistic interactions such as predator-prey relationships. In addition, more spatially explicit food web data can be compiled across microhabitats or linked macrohabitats [8]. Most current food web data is effectively aspatial even though trophic interactions occur within a spatial context. More could also be done to collect food web data based on specific instances of trophic interactions. This was done for the insects that live inside the stems of grasses in British fields. The web includes multiple grass species, grass herbivores, their parasitoids, hyper-parasitoids, and hyper-hyper parasitoids [67]. Dissection of over 160,000 grass stems allowed detailed quantification of the frequency with which the species ($S = 77$ insect plus 10 grass species) and different trophic interactions ($L = 126$) were observed.

Better empiricism will support improved and novel analysis, modeling, and theory development and testing. For example, while food webs appear fundamentally different in some ways from other kinds of "real-world" networks (e. g., they don't display power-law degree distributions), they also appear to share a common core network structure that is scale-dependent with species richness and connectance in predicable ways, as suggested by the success of the niche and related models. Some of the disparity with other kinds of networks, and the shared structure across food webs, may be explicable through finite-size effects or other methodological or empirical constraints or artifacts. However, aspects of these patterns may reflect attributes of ecosystems that relate to particular ecological, evolutionary, or thermodynamic mechanisms underlying how species are organized in complex bioenergetic networks of feeding interactions. Untangling artifacts from attributes [63] and determining potential mechanisms underlying robust phenomenological patterns (e. g., [10]) is an important area of ongoing and future research. As a part of this, there is much work to be done to continue to integrate structure and dynamics of complex ecological networks. This is critical for gaining a more comprehensive understanding of the conditions that underlie and promote different aspects of stability, at different levels of organization, in response to external perturbations and to endogenous short- and long-term dynamics.

As the empiricism, analysis and modeling of food web structure and dynamics improves, food web network research can play a more central and critical role in conservation and management [76]. It is increasingly apparent that an ecological network perspective, which encompasses direct and indirect effects among interacting taxa, is critical for understanding, predicting, and managing the impacts of species loss and invasion, habitat conversion, and climate change. Far too often, critical issues of ecosystem management have been decided on extremely limited knowledge of one or a very few taxa. For example, this has been an ongoing problem in fisheries science. The narrow focus of most research driving fisheries management decisions has resulted in overly optimistic assessments of sustainable fishing levels. Coupled with climate stressors, over-fishing appears to be driving steep, rapid declines in diversity of common predator target species, and probably many other kinds of associated taxa [114]. Until we acknowledge that species of interest to humans are embedded within complex networks of interactions that can produce unexpected effects through the interplay of direct and indirect effects, we will continue to experience negative outcomes from our management decisions [118]. An important part of minimizing and mitigating human impacts on ecosystems also involves research that explicitly integrates human and natural dynamics. Network research provides a natural framework for analyzing and modeling the complex ways in which humans interact with and impact the world's ecosystems, whether through local foraging or large-scale commercial harvesting driven by global economic markets.

These and other related research directions will depend on efficient management of increasingly dispersed and diversely formatted ecological and environmental data. Ecoinformatic tools—the technologies and practices for gathering, synthesizing, analyzing, visualizing, storing, retrieving and otherwise managing ecological knowledge and information—are playing an increasingly important role in the study of complex ecosystems, including food web research [47]. Indeed, ecology provides an excellent testbed for developing, implementing, and testing new information technologies in a biocomplexity research context (e. g., Semantic Prototypes in Research Ecoinformatics/SPiRE: spire.umbc.edu/us/; Science Environment for Ecological Knowledge/SEEK: seek.ecoinformatics.org; Webs on the Web/WoW: www.foodwebs.org). Synergistic ties between ecology, physics, computer science and other disciplines will dramatically increase the efficacy of research that takes advantage of such interdisciplinary approaches, as is currently happening in food web and related research.

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