

## A primer on the history of food web ecology: Fundamental contributions of fourteen researchers<sup>☆</sup>



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### ABSTRACT

Food webs are one of the primary frameworks on which the ecological sciences have been built. Research in this field has burgeoned over recent decades, expanding into diverse sub-disciplines and employing many different methodological approaches. Here we structure a historical review around 14 researchers and the specific contributions they have made to the field. Beginning with Charles Elton's insights into food web structure, and continuing to contemporary ecologists and emerging areas of study, we highlight some of the most important empirical and theoretical advances made over the last century. The review highlights that there are fundamentally different ways in which food webs are depicted and studied. Specifically, when one views systems through mathematical, energy flow or functional lenses, very different perspectives on food web structure and dynamics emerge. The contributions of these scientists illustrate the considerable advances that the field has undergone, and they provide the foundation for expansive on-going research programs that fall under the broad umbrella of food web ecology.

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## 1. Introduction

Food webs are one of the core thematic frameworks in the ecological sciences. Broadly defined, food webs are networks of consumer–resource interactions among a group of organisms, populations, or aggregate trophic units (see Table 1 for definitions of key terms in this review). These depictions of feeding relationships can provide insight into almost every area of ecological research, ranging from population dynamics to the cycling of nutrients through ecosystems. One of the most thorough syntheses of food web ecology came nearly two decades ago (Winemiller and Polis, 1996; see also Dunne, 2006, 2009; Morin, 2011). Since that review, the field has expanded substantially; a search in Web of Science (Thompson Reuters) with the keywords “food web” yields more than 55,000 entries since 1995. Because of the breadth of topics that are subsumed within, or relate

to, food web ecology, compiling a complete synthesis of the field would be a tremendous endeavor.

Here we craft a more targeted review focused on specific contributions that individual researchers have made to the field. Namely, for 14 scientists, we identified a critical advance he or she spearheaded that shaped the development of food web ecology. In choosing a subset of researchers, we necessarily omit the contributions of many others. However, our framework allowed for a tractable outline of the discipline’s history and major advances. The review is organized around four broad thematic areas (Fig. 1): Original foundations of the field (Sections 2–3); Mathematical food web constructs (Sections 4–7); Energy flow through food webs (Sections 8–11); and Functional food web relationships (Sections 12–15). These thematic areas allow us to isolate the very different approaches by which food webs are generally envisioned and studied. In doing so, we provide a starting point for reflecting on the history of the field, as well as outlining approaches that currently frame on-going research regarding the structure and function of food webs.

**Table 1**

Glossary summarizing definitions of key terms from the text.

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<i>Cascade model</i>	— A theoretical depiction of food web structure based on species richness and the total number of observed links, employing two constraints: species are randomly assigned to a one-dimensional feeding hierarchy and species can only feed on others lower in that established hierarchy.
<i>Connectance</i>	— The proportion of possible links in a food web that actually occur, often represented as some permutation of the ratio between actual links and the total number of species in a food web.
<i>Eco-evolutionary feedbacks</i>	— The cyclic interaction between ecology and evolution such that changes in ecological interactions drive evolutionary change in organismal traits that, in turn, alter the form of ecological interactions.
<i>Eltonian niche</i>	— Classification of an organism’s functional role, especially with respect to what it eats, as well as other the resources it utilizes or otherwise alters in an ecosystem.
<i>Food web</i>	— a network of consumer–resource interactions among a group of organisms, populations, or aggregate trophic units.
<i>Functional (or interaction) food webs</i>	— Webs based on the per capita effect (positive or negative) of one species on another.
<i>Indirect effect</i>	— Effect of one species on another, as mediated through one or more intervening species.
<i>Interaction strength</i>	— Per capita impact of one species on another’s population size or growth rate.
<i>Network theory</i>	— A subset of graph theory, which was developed to answer questions about connectivity and optimization of any system that can be represented by nodes and paths.
<i>Niche model</i>	— A theoretical depiction of food web structure similar to the cascade model, but instead of randomly assigning species to a position along the axis, it provides for more ecological realism by directly assigning individual species a particular niche value.
<i>Node</i>	— The core unit of organization in a food web model that is linked to another through direct feeding relationships; can be represented at the individual, population, species, or tropho-species (e.g., herbivore, parasite) level.
<i>Keystone species</i>	— A species which has disproportionate effects, relative to its biomass, on community structure or ecosystem function.
<i>Pyramid of numbers</i>	— A graphical representation of the number of organisms, standing biomass or overall productivity at each hierarchical trophic level.
<i>Realized food chain length</i>	— The total number of times energy or material is transferred from basal resources pools through consumers to a top predator.
<i>Scale-free networks</i>	— Networks characterized by a power-law degree distribution, where the majority of nodes have connections with a just a few very well-connected nodes.
<i>Small-world networks</i>	— Networks characterized by especially high clustering and short path lengths.
<i>Spatial subsidy</i>	— A donor-controlled resource flux moving from one habitat to another that increases productivity (primary or secondary) of the recipient habitat, which in turn alters consumer–resource dynamics.
<i>Stability–complexity relationship</i>	— The question of whether increased food web complexity (often represented as higher species richness) results in long-term constancy in the abundance of species within a food web.
<i>Topology</i>	— Detailed quantitative analysis of the structural properties of food webs, often assessed using metrics such as connectance, food chain length, and degree of omnivory.
<i>Trait-mediated indirect effect</i>	— An indirect effect in which one species influences another’s phenotype (via an intermediary species) rather than its population density.
<i>Trophic cascades</i>	— An indirect effect whereby predators control abundance (or a trait such as behavior) of prey which in turn affects the abundance (or trait) of organisms at the next lower trophic level.

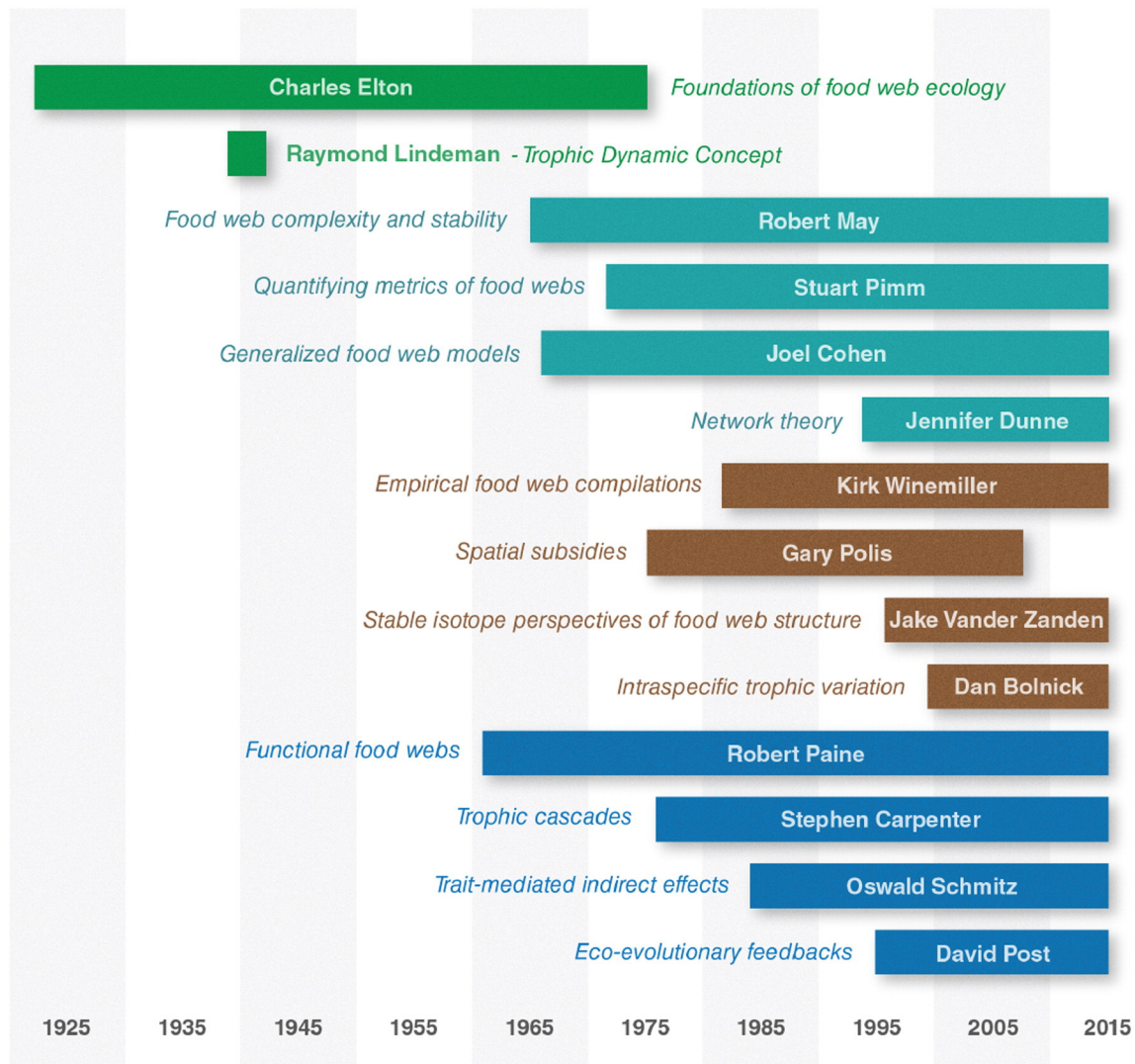
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## 2. Foundations of food web ecology — Charles Elton

Observations regarding food chains are deeply rooted in human history (Morris, 2014) with the first depictions of community-wide feeding relationships published in the early 20th century (Egerton, 2007). Yet, many people associate the dawn of food web ecology with Charles Elton who, at the age of 26, published the classic book *Animal Ecology* (Elton, 1927). Specifically, his discussion of food chains and food cycles (i.e., the sum total of all food chains in a system) foreshadowed the field of food web ecology. Elton believed that these models of trophic interactions offered the most direct framework to understand how entire ecosystems functioned. It is striking how many of his simple observations still resonate as the basis for some of the most important areas of research in the ecological sciences. For example, in Chapter 5 of *Animal Ecology* (The Animal Community), Elton emphasized several tenets relevant for food webs, e.g., (1) role of body size, (2) pyramid of numbers, (3) the niche, and (4) indirect food web effects.

First, Elton posited that size-structured interactions, namely that predators tend to be larger than their prey, are an intrinsic property of ecological systems and are fundamentally important for the structure of animal communities (although there are obviously exceptions, such as in systems with large herbivores, pack-hunting animals, and parasites). This idea has underpinned many subsequent efforts to characterize the architecture of food webs based on body size relationships (Brose et al., 2006; Cohen et al., 1993b, 2003; Woodward et al., 2005). Stemming from his observations that smaller organisms tended to reside lower in food webs, Elton also introduced the idea of the pyramid of numbers. In this graphical representation, the base of the pyramid is comprised of primary producers and herbivores, which are typically most abundant due to high reproductive rates and small size, whereas animals higher in webs tend to be rarer and large. This perspective influenced much subsequent work on the flow of energy through ecosystems, most notably Raymond Lindeman (see *Trophic dynamic concept* section), Howard Odum, and Eugene Odum’s seminal ideas on ecosystem ecology (Lindeman, 1942; Odum, 1953). Third, in contrast to Grinnell’s earlier definition of niche (which was based on habitat requirements Grinnell, 1917), Elton emphasized the niche as an animal’s functional role in a system, especially with respect to what it eats. This definition of the niche influenced ecological thought for decades (Bruno et al., 2003; Leibold, 1995; Odum, 1953; Pulliam, 2000). Finally, Elton’s observations of complex interspecific interactions forecasted what are now known as indirect effects, i.e., the effect of one species on another mediated through one or more intervening species (see *Trait-mediated indirect effects* section).

In the foreword to the most recent edition of *Animal Ecology*, Leibold and Wootton (2001) discuss a remarkable prescience in Elton’s ecological understanding, as revealed in his discourse on a core struggle in



**Fig. 1.** Time periods over which the featured scientists published scientific articles or books. The color codes represent four categories of contributions we used to organize the structure of the paper: Green – Original foundations of the field; Aqua – Mathematical food web constructs; Brown – Energy flow through food webs; Blue – Functional food web relationships. Figure credit Neil McCoy, North Carolina State University. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

environmental research, “...an ecologist is often balancing the search for simplifying theories with the recognition of the complexity in nature”. This exact theme is apparent in many sections of this review, underscoring how Elton’s contributions put in motion the development of food web ecology.

### 3. Trophic dynamic concept – Raymond Lindeman

Raymond Lindeman viewed feeding relationships from a largely different perspective than Elton, a view reflected in the title of his seminal paper as the “trophic dynamic aspect” of ecology (Lindeman, 1942). Whereas Elton wrote primarily about the direct interactions between species (such as in predator–prey relationships), Lindeman viewed interacting species through a prism of energy (or nutrient) flow, thereby creating a common currency for studying and comparing disparate aquatic ecosystems. His primary study system was a senescent lake in Minnesota, Cedar Creek Bog, where he was interested in how short term (daily) processes affected long-term (years) succession within the bog. Building from the trophic position hierarchy (e.g., primary producers, herbivores) outlined by Elton, he quantified energy flow through these trophic levels in the system. Using assumptions regarding efficiency of energy transfer, estimates of primary production and presumed feeding relationships (food web structure), he was able to

calculate the amount of biomass/production that could be supported at higher trophic levels.

A key insight in his characterization of the system was identifying both abiotic and biotic compartments through which organic matter was transformed. These components together, and the flow of matter among them, he referred to as an ecosystem (Golley, 1993), one of the first uses of this term in the ecological sciences (along with Tansley, 1935). Critically, Lindeman posited that food web structure affects both community-level patterns and ecosystem function, and thus quantifying aspects of food web structure is essential for understanding ecosystem-level ecology. As such, Lindeman was well before his time in relating food web dynamics to the functioning of ecosystems, research that continues to expand today (e.g., see Trophic cascades section).

### 4. Food web complexity and stability – Robert May

Robert May’s shaping of the field can be attributed to a single paper: “Will a large complex system be stable?” (May, 1972). His unique exploration of this simple question launched food web ecology into a new era. Decades before May’s contributions, ecologists often speculated whether the number of species in communities (diversity) affected the stability of those communities. In large part, the relationship between these two variables was assumed to be positive, i.e., ‘diversity

begets stability'. It's difficult to pinpoint where the hypothesized positive correlation between diversity and stability arose, but origins prior to the 20th century are certain (reviewed in Dunne, 2006; Ives, 2005; McCann, 2000, 2005). The idea received further support from prominent ecologists in the 1950s (Elton, 1958; MacArthur, 1955). As the 1970s dawned, there was a widespread prevailing assumption that higher diversity and/or complexity of food webs should support more stable communities.

Following work by Gardner and Ashby (1970), May approached the stability–complexity question from a different angle than ecologists had previously, namely, dynamical mathematical modeling. He varied attributes of an abstract network that roughly resembled a food web: the number of nodes (system size), the average number of links among nodes (system complexity), and interaction strength (how strong an effect one node has on another). Relative degree of stability was assessed by generating small perturbations to equilibrium values of nodes, and seeing whether values return to the previous equilibria; if so, systems were deemed stable. If population densities departed from equilibrium values, the systems were assumed to be unstable. The central finding was that structural properties of networks affected their stabilities, specifically increases in the number of nodes, complexity, or interaction strength tended to destabilize networks. In essence, large, complex networks should rarely occur simply because of their underlying structural properties.

May's paper also provided an initial effort to explore how covariation in structural properties relates to system stability. For instance, his analysis suggested that if interaction strength is held constant and species richness is increased in a presently stable system, the system can remain stable only if overall connectance decreases. An obvious corollary is that there should be an inverse relationship between connectance and species richness, a pattern that was widely investigated and drew subsequent support based on data from simple real-world food webs (Briand, 1983; Cohen et al., 1985; Pimm, 1982; Yodzis, 1980). More generally, predictions from May's model led to an explosion in efforts to quantify food web properties through mathematical examinations of food web topologies (e.g., see [Quantifying metrics of food webs](#) section).

May's abstraction of a food web as a randomly-connected set of nodes, linked by variable interaction strengths, received much criticism, as this was clearly an unrealistic representation of real world food webs. But this analysis served to revolutionize the field in terms of theory and practice. Robert May published relatively few papers on the ecology of food webs, yet their impact was lasting.

### 5. Quantifying metrics of food webs – Stuart Pimm

May's analysis (1972) led the field of food web ecology into detailed quantitative analysis of the structural properties of food webs, i.e., the topology of food webs. Much of this research was devoted to using a series of quantitative metrics to characterize food web properties. Commonly employed food web metrics include connectance, food chain length, degree of omnivory, and proportion of species in a web at a given trophic level, among many others. Stuart Pimm was in the vanguard of this pursuit, and we use one example to illustrate the type of topological studies that dominated the field in the 1970s and 1980s.

Pimm delved into how food web topology affects their stability (Pimm, 1979, 1982; Pimm and Lawton, 1977). In contrast with May, these approaches did not employ random networks of links, but simple community matrices with just a few species ( $n = 4$  in many cases) arranged to mimic the structure of real trophic interactions. Two metrics included food chain length (in this model, defined simply the total number of species linked in a chain) and omnivory (a species feeding at two different trophic levels below it). Stability was assessed based on the fraction of simulations in which population densities returned to equilibrium values, as well as the number of time steps it took to return to these values (more on definitions of stability can be found in Pimm,

1984). They found stability decreased with the number of trophic levels, whereas effects of omnivory were variable, and depended, in part, on the way stability was defined. From these models, testable predictions about real-world systems could be made, namely, that the number of trophic levels should be constrained by population dynamics and that omnivory should be rare. Simply by introducing a modicum of ecological realism (i.e., non-random trophic structure to simulated webs), predictions about food web complexity and stability diverged substantially from those based on randomly-assembled network models such as those proffered by May.

### 6. Generalized food web models – Joel Cohen

Joel Cohen published one of the first collections of real-world food webs and was a primary contributor to much of the early research on web structure using quantitative metrics (Cohen, 1978). Cohen and colleagues also sought to identify more general models, with defined sets of conditions, that could predict the structure of real-world food webs (Cohen, 1990; Cohen et al., 1990; Cohen and Newman, 1985). Notable was development of the cascade model, a construct based on just two variables: species richness and linkage density (i.e., the total number of observed links divided by the species richness), and two constraints: species are randomly assigned to a one-dimensional feeding hierarchy and species can only feed on others lower in that established hierarchy. Using binary webs (i.e., webs that just depict presence/absence of a feeding links between species, without a measure of the strength of the link), Cohen and Newman (1985) found evidence that the cascade model produced very similar general patterns to that of the available food webs. The fact that a simple model could emulate properties of real-world food webs suggested a consistent underlying structure across webs in diverse systems.

Cohen's efforts spawned other attempts to develop such models. Of particular note was the niche model of Williams and Martinez (2000). Like the cascade model, it is based on a single dimension along which species are arranged. But instead of randomly assigning species to a position along the axis, each species is given a niche value. This value is the midpoint of an interval (where this interval width is randomly assigned from a given distribution), and then the particular species feeds on all other species that fall within this range. This design provided a more realistic representation of real-world food webs because it allowed for additional diversity in feeding interactions, e.g., cannibalism, and higher degrees of niche overlap among species. Williams and Martinez (2000) tested the niche model, cascade model, and a random model by evaluating how well each predicted the structural properties of seven food webs. They found the niche model performed substantially better than the others (see also Dunne et al., 2004). These successes led to other attempts to increase the realistic nature of these predictive models while retaining their base simplicity; much more detail on these type of approaches to modeling food webs can be found in Dunne (2006).

### 7. Network theory – Jennifer Dunne

Network theory provides a novel framework to view food webs from a mathematical perspective, and Jennifer Dunne has been at the forefront of this endeavor (Dunne et al., 2002a, 2013; Thompson et al., 2012; Williams et al., 2002). Network theory is a subset of graph theory, which was developed to answer questions about connectivity and optimization of systems that can be represented by nodes and paths. This theoretical framework has been used to answer questions regarding the stability and functionality of power grids, human social networks, and food web dynamics. As interest in network structure grew, several generalities began to surface, in particular, many networks can be described as having (1) 'small world' and (2) 'scale-free' structure. Small world networks, first described by Watts and Strogatz (1998), are characterized by high clustering and short path lengths. This means that the

number of other nodes needed to travel from A to B is smaller than in a regularly distributed lattice. This network topology results in rapid propagation of signals or disturbances, a desirable characteristic for networks such as the World Wide Web or power grids. Scale-free network structure refers to the degree distribution, or the distribution of the number of connections per node within the network. Specifically, scale-free networks are characterized by a power-law degree distribution, where the majority of nodes have connections with a few well-connected nodes (Barabási, 2009; Barabási and Albert, 1999). This results in networks that are highly sensitive to the removal of a few well-connected nodes, but robust to the removal of others.

Similar to small world networks, research suggests food webs tend to have short path lengths (Williams et al., 2002). Yet, food webs are not scale-free, as their degree distributions tend towards uniform rather than power-law distributions. This deviation from scale-free structure in networks means that food webs should be more robust to species extinction than other forms of networks, largely as a result of the high level of connectance in many webs. Alternatively, food webs with lower connectance may be more sensitive to species extinctions (Dunne et al., 2002b). For example, in networks with high numbers of trophic specialists, extinctions may be more likely to propagate throughout the network (Dunne et al., 2002b; Srinivasan et al., 2007). By focusing on food web network structure, and identifying their similarities and differences with other well-studied networks, Dunne and colleagues' research continues to advance our understanding of under what conditions we may expect predictable patterns in food web topology. These efforts extend those of May, Pimm and Cohen decades before, and demonstrate the primacy of mathematical approaches to depicting food web structure over the last five decades.

## 8. Empirical food web compilations – Kirk Winemiller

A principal criticism of food web metrics and models discussed in the previous sections is that the empirical data used to parameterize and test them insufficiently depicts real-world feeding relationships (Cohen et al., 1993a; Winemiller and Layman, 2005). For example, much of the effort expended on quantifying food web characteristics relied on simple binary webs that lacked estimates of the strength of species interactions (Briand and Cohen, 1984). Consequently, such binary depictions did not allow for quantification of the energy (or nutrient) flow among nodes in the web. Kirk Winemiller devoted effort to compiling extensive empirical data sets on feeding relationships, and in doing so provided very different perspectives than that of binary (or other types of simplified) webs (Jepsen and Winemiller, 2002; Jepsen et al., 1997; Layman et al., 2005; Winemiller, 1989b, 1990; Winemiller et al., 2007).

Of particular note was his compilation of trophic relationships in species-rich tropical streams (Winemiller, 1990), systems far more diverse than other published food webs (Winemiller and Layman, 2005). For example, the 113 binary webs assembled by Briand and Cohen (1987) averaged 17 nodes, whereas the tropical stream webs averaged 75. Winemiller did not sacrifice resolution in his compilation of trophic relationships: fish and invertebrate prey were identified to lowest taxonomic levels feasible and operational taxonomic units were defined at the base of the food webs (e.g., diatoms, algae, aquatic macrophytes, detritus, and terrestrial plant seeds, flowers, spores, and fruits). This specificity allowed volume-based measures of each prey category which were employed to estimate the relative strength of predator–prey interactions. The number of stomachs examined in each stream (mean  $n = 4822$ ) is among the largest data sets for any empirical food web study.

One of the most compelling findings was the extremely high degree of connectance in these stream webs. For example, the Briand and Cohen (1987) webs averaged just 34 links, whereas the stream webs averaged 514. This complexity is even more striking considering that only the fish component of the food webs were examined. Including aquatic

invertebrates or terrestrial animals that feed on aquatic organisms would have added significant complexity. Other findings from his compilation also ran counter with prevailing thoughts on food web properties. As discussed above, it was often suggested that food webs might have consistent properties, such as the inverse relationship between connectance and species richness (Briand, 1983; Pimm, 1982). The stream webs offered stark contrast. Winemiller found a positive relationship between connectance and species richness, such that more diverse webs had much higher connectance – a nearly 5-fold difference in the average number of trophic links between the least and most diverse streams. These findings casted doubt on the validity of using binary (or other simplified) food web depictions as subjects for rigorous quantitative analysis (Winemiller, 1989a, 1990).

Winemiller's research was used as a primary example in critiques of the way food webs are compiled and studied (Cohen et al., 1993a; Winemiller and Layman, 2005; Winemiller and Polis, 1996), and we note five of those criticisms here. First, as mentioned above, many model webs don't include quantification of energy flow between nodes. Second, even those food webs regarded as 'comprehensive' in the literature are actually composites based on suspected, but unverified, feeding relationships (e.g., those gleaned from the literature). They are not real depictions of the actual feeding links that are manifest at a given time and place. Third, the level at which nodes are identified (e.g., the way species are lumped together to create nodes representing "trophospecies") greatly affects the structure of the modeled web. Since these lumping approaches vary greatly across studies, it is difficult to make direct comparisons using web metrics. And even within a single data set of trophic relationships, food web patterns may look very different depending on the level at which the nodes are defined. Fourth, the spatial and temporal boundaries of food webs are always arbitrary (see Spatial subsidies section), and are necessarily a subset of all feeding interactions in a region. Finally, environmental heterogeneity results in highly variable feeding relationships both spatially and temporally. Together, these observations suggest the great difficulty in generating accurate representations of all feeding relationships within a particular ecosystem.

## 9. Spatial subsidies – Gary Polis

Gary Polis also grounded his research in the empirical study of trophic relationships and called for more direct, detailed, assessments of real-world webs (Polis, 1991). In this context, Polis was at the forefront of integrating food web and landscape ecology, particularly how ecosystems are linked by the flux of resources across arbitrary boundaries. He defined a "spatial subsidy" as a donor-controlled resource (e.g., animal prey, detritus, or nutrients) from one habitat to another, with increased productivity (primary or secondary) of the recipient, thereby altering consumer–resource dynamics (Polis et al., 1997). Polis was not the first to describe the importance of energy flow among ecosystems. For example, Likens and Bormann (1974) emphasized how various terrestrial inputs affected ecosystem function in freshwater ecosystems, and part of the River Continuum Concept (Vannote et al., 1980) was based on the role of allochthonous material in headwater streams. Polis took such observations further and began to quantify the magnitude of subsidy effects on recipient ecosystems in a food web context.

Much of Polis' food web research focused on impacts that marine subsidies had on terrestrial food webs, with coastal deserts of Baja California as a model (Anderson and Polis, 1999, 2004; Due and Polis, 1985; Polis et al., 1997; Polis and Hurd, 1995, 1996; Rose and Polis, 1998). These systems were supported by various marine-derived subsidies, including algal wrack, dead aquatic animals, and seabird guano, the effects of which varied by subsidy type. For example, this work showed that marine algae and carrion washing ashore were substantial and important subsidies, directly supporting orders of magnitude higher densities of scavenging insects along shorelines (Polis and Hurd, 1995). In other locations, inland areas also received a marine subsidy in the form of seabird guano, which increased localized primary production and plant

nutrient content (e.g., herbaceous species on islands with birds could have as much as 2.5 times greater nitrogen content). In turn, this high-quality forage contributed to greater herbivore growth rate and reproductive capacity in these inland areas. In each case, these subsidy effects would propagate up from the base of the food web to induce pronounced shifts in the abundance and behavior of higher-level consumers such as scorpions (*Vaejovis littoralis*, Vaejovidae, Scorpiones) and coyotes (*Canis latrans*, Canidae, Carnivora).

Polis' work spurred similar studies in other systems, e.g., streams (Nakano and Murakami, 2001), lakes (Vadeboncoeur et al., 2002), and terrestrial systems (Giery et al., 2013), suggesting that some degree of cross-boundary resource flux is expected in most ecosystems (Polis et al., 2004a). This work also led efforts to identify the specific environmental conditions under which spatial subsidies are most prevalent and relevant for ecosystem dynamics (Dreyer and Gratton, 2014; Marcarelli et al., 2011; Marczak et al., 2007; Polis et al., 2004b; Whitman et al., 2004), several of which are now well-understood. For example, subsidies are generally important when adjacent systems differ substantially in productivity. This observation explains why marine-to-terrestrial subsidies are important, as shallow coastal waters are typically extremely productive relative to adjacent terrestrial ecosystems. The permeability of habitat boundaries is also key determinant because the nature of the transferred material, the distance it must move, and the biological and physical structure of habitat edges affect the type and magnitude of subsidies delivered across boundaries. Perimeter:area ratio is especially important for islands that receive food web subsidies, with smaller islands having a greater per unit area effect of the subsidy. Each of these variables illustrates the importance of landscape ecology for understanding food web dynamics, a viewpoint that Polis pioneered decades ago and that continues to frame many research programs today (Marleau et al., 2014; Massol et al., 2011; McCann et al., 2005).

## 10. Stable isotope perspectives of food web structure — Jake Vander Zanden

As discussed in the two previous sections, a common way to compile energy flow through food webs is to use direct empirical information on consumer diets, e.g., through stomach content or scat analysis. Stable isotopes are now emerging as another, and perhaps even the primary, tool to infer trophic relationships and the flow of energy through food webs (Layman et al., 2012). This approach is especially useful because stable isotopes provide time- and space-integrated insights into trophic relationships among organisms, whereas stomach content analysis only provides a snapshot of recent prey items. Two elements, nitrogen (N) and carbon (C), are most commonly employed in a food web context (Layman et al., 2012). The ratio of  $^{15}\text{N}$  to  $^{14}\text{N}$  (expressed relative to a standard,  $\delta^{15}\text{N}$ ) exhibits stepwise enrichment with trophic transfers and thus is used to estimate trophic position of consumers. Ratios of carbon isotopes ( $\delta^{13}\text{C}$ ) vary substantially among primary producers with different photosynthetic pathways (e.g., C3 versus C4 photosynthetic pathways), but change little with trophic transfers. Therefore,  $\delta^{13}\text{C}$  can be used to determine original sources of dietary carbon. Peterson and Fry (1987) were among the first to illustrate the broad utility of isotope methods in the ecological sciences. This new analytical tool opened up many new research directions, such as the early advances made by Keith Hobson who implemented stable isotopes to study the trophic ecology of seabirds (Hobson, 1999; Hobson et al., 1993; Hobson and Clark, 1992a,b; Hobson and Welch, 1992). Here we highlight some of the ways stable isotopes are employed in a more general food web context, using the research of Jake Vander Zanden and colleagues as examples.

One of the most common applications of stable isotopes in food web ecology is to provide time-integrated estimates of trophic position. That is, instead of assigning individuals to discrete trophic positions based on assumed trophic roles, or conducting extensive diet analysis to identify the exact prey on which consumers feed,  $\delta^{15}\text{N}$  values of a consumer can

be used to quantify trophic position expressed as a continuous variable. Vander Zanden and Rasmussen (1999) applied this approach in a food web context, calculating trophic position of lake trout (*Salvelinus namaycush*, Salmonidae, Salmoniformes) in a series of Canadian lakes. Estimates of trophic position based on stable isotopes allowed him to quantify one of the most fundamental food web metrics — food chain length. Specifically, stable isotopes provide for estimates of realized food chain length, a metric quantifying the total number of times energy or material is transferred through consumers to a top predator. Using the group of Canadian lakes, Vander Zanden et al. (1999) estimated food chain length leading to lake trout. Despite all having the same top predator, food chain length varied substantially among lakes, an illustration of how stable isotopes could provide insights that may not have emerged using other techniques. This research was among a bevy of contemporaneous studies that utilized stable isotopes for exploring basic tenets of food web theory, e.g., identifying the exact mechanisms explaining variation in food chain length across ecosystems (Jennings and Warr, 2003; Post, 2002a,b; Post et al., 2000). Vander Zanden provided empirical evidence that food chain length could be partially explained by the productive-space hypothesis, i.e., a variable derived as an ecosystem size multiplied by its productivity (Schoener, 1989). Such studies also were early indications of the sensitivity of stable isotopes to numerous underlying methodological assumptions (Vander Zanden and Rasmussen, 2001), considerations that remain at the forefront of discussions regarding application of stable isotopes to examine aspects of food web structure (Layman et al., 2012).

Vander Zanden was in the vanguard of other various applications of stable isotopes in a food web context. He demonstrated that because benthic and pelagic primary producers in lakes had distinct  $\delta^{13}\text{C}$  signatures, one can estimate the degree to which fishes were utilizing benthic resources (Vander Zanden and Vadeboncoeur, 2002). The simple mixing model employed in that paper was an influential precursor to the extremely advanced Bayesian approaches that typify current applications (Layman et al., 2012). From a temporal perspective, Vander Zanden et al. (2003) showed how isotopes can describe the structure of historic food webs and document changes in food web structure over time. Vander Zanden and Rasmussen (1996) also demonstrated the utility of stable isotopes in assessing bioaccumulation of contaminants in aquatic consumers. Vander Zanden and colleagues' research provide numerous examples of how important stable isotopes can be for quantifying multiple aspects of food web structure.

## 11. Intraspecific trophic variation — Dan Bolnick

Ecologists long have recognized that individuals within a population vary with respect to their trophic role (Roughgarden, 1972; Schoener, 1986; Van Valen, 1965). Conversely, in the development of food web ecology, conspecific individuals were often treated as ecological equivalents represented by a single node. Thus, energy flow typically is depicted as flowing through species, ignoring the role of individuals in food web structure and dynamics. Daniel Bolnick and colleagues revived interest in intraspecific trophic variation with several publications in the early 2000s, including Bolnick et al. (2003) in which the term "individual specialist" was explicitly defined: an individual whose trophic niche is substantially narrower than its population's niche for reasons not attributable to sex, age, or discrete polymorphisms. The important point here was that substantial cryptic variation in trophic role may exist within superficially similar conspecifics, and this variation can have important implications for the way food webs are structured and function (Tur et al., 2015). The empirical data to date illustrate numerous examples of apparently generalist taxa that are actually composed of individuals with rather specialized diets (Araújo et al., 2007, 2011; Bolnick et al., 2007, 2010; Snowberg et al., 2015).

Three recent papers outline how far research on individual specialization has progressed in the years following Bolnick et al. (2003). First, Araújo et al. (2011) found 107 new examples of individual

specialization (93 vertebrates, 13 invertebrates, and one plant), and outlined the primary ecological mechanisms affecting the incidence of individual specialization, including intra- and inter-specific competition, predation, and ecological opportunity. One of the most important drivers appears to be the strength of intraspecific competition. Individuals of the same species may exhibit high overlap in resources use at low population densities (and correspondingly low intensity of competition). But at higher conspecific densities, individuals will diverge in trophic ecology to minimize intraspecific competition. The result is that individuals become more specialized in their diet, consuming just a portion of the population-level diet (Svanback and Bolnick, 2007). Considering that almost all food webs are assembled at the species level, such context dependency at an individual level further complicates our ability to model real-world food webs.

Second, Bolnick et al. (2011) outlined six reasons why individual specialization matters for our understanding of ecological dynamics, including food web structure. For example, a high degree of individual specialization within a taxa results in a broader population-level dietary niche breadth. Therefore, there is a direct link between individual variation in trophic niche and basic structural attributes of food webs, connectance in particular. A high degree of specialization also may promote strong eco-evolutionary feedbacks, which can lead to rapid shifts in food web structure and function (more detail in the *Eco-evolutionary feedbacks* section).

Third, Dall et al. (2012) pointed out similarities in the study of trophic niche specialization across three sub-disciplines in the biological sciences: trophic niche variation in population and community ecology studies, the division of labor within insect societies, and animal “personality” variation from a behavioral ecology perspective. This provides an example of how studies of food web ecology can inform other areas of ecological research, in this case, extending the role of the individual in food webs to other areas of biological inquiry. Likewise, it suggests that further advances in the field may arise by drawing from very different areas of research (another example of this discussed in the *Network theory* section).

## 12. Functional food webs — Robert Paine

The previous 4 sections illustrate how empirical diet data or stable isotopes can be used to model the flow of energy or nutrients among nodes in a food web, but these data alone cannot be used to determine the demographic control of one species on another. Food web models based on the per capita effect of one species on another are often termed functional (or interaction) webs, and are fundamentally different than those based on energy flow. Experiments are central to developing functional webs, as they are the most direct way to identify which species have strong effects on population and community dynamics. Although energy flow and functional webs are often conflated by ecologists, they do not necessarily map onto each other. A strong link, as quantified based on energy flow, does not necessarily imply that the consumer species has strong control on population size or growth rates of that particular prey species (and vice versa).

Such a distinction between energy flow webs and functional webs was articulated by Robert Paine (1980) based on a series of influential experiments involving *Pisaster ochraceus* (Asteroidea, Forcipulatida), a predatory starfish (Paine, 1966, 1969a, 1969b, 1974). Paine found that removing starfish resulted in a decrease in species richness because the population size of a dominant competitor, a bivalve mollusk, increased thereby excluding inferior competitors. Paine termed the starfish a keystone species, because it exerted substantial control over community composition and stability (Paine, 1969a). Decades after its initial inception, the role (and definition) of keystone species remains a highly influential and much-discussed idea in ecology and conservation biology (Jones et al., 1994; Mills et al., 1993; Power et al., 1996; Tews et al., 2004).

Implicit in the construction of functional food webs is the concept of interaction strength, the per capita impact of one species on another's population size or growth rate. As discussed above, experimentation is the primary tool to this end, i.e., adding or removing a species and assessing the demographic effects on other species in the study system. Species are considered strong interactors if they induce substantial changes in population and/or community dynamics. In many systems, few species strongly interact, whereas most have relatively weak interactions (McCann and Rooney, 2009). The amount of attention devoted to how to best quantify interaction strength (Berlow, 1999; Laska and Wootton, 1998; Novak and Wootton, 2010; Paine, 1992) reflects how important this concept is for understanding functional relationships within food webs.

## 13. Trophic cascades — Stephen Carpenter

Parallel to Paine's contributions from the rocky intertidal, Stephen Carpenter and colleagues used experimental approaches to explore functional food webs in northern temperate lakes (Carpenter et al., 1985, 1987, 2001; Carpenter and Kitchell, 1993). In particular, this research explored the dynamics of trophic cascades. The original trophic cascade hypothesis suggested that nutrient inputs establish the potential productivity of a system and that deviations from that potential are due to various interactions between predator and prey. In whole lake manipulations, the top predator (piscivorous bass, *Micropterus salmoides*, Centrarchidae, Perciformes) was removed from one lake and added to another. Increased abundance of piscivores led to decreased planktivorous fish biomass, increased zooplankton biomass (and a shift in zooplankton community composition), and reduced phytoplankton biomass. As such, the base of the food web was fundamentally affected by manipulating top predators that were three trophic levels removed from primary producers, an empirical example of a trophic cascade. Another important advance was placing these findings in the context of ecosystem ecology. That is, the presence or absence of a top predator not only influenced community composition, but also various ecosystem processes. Most apparent was how the shifts in food web structure affected primary productivity, but other ecosystem processes, such as carbon sequestration, were also affected. These classic experiments provided the background for extensive debate over the conditions favoring the occurrence of trophic cascades and the strength of cascading effects across trophic levels (Schmitz et al., 2000, 2004; Shurin et al., 2002; Strong, 1992).

The ubiquity of trophic cascades is now well recognized (Pace et al., 1999). In many cases, the cascading effects were made obvious as the result of human-driven loss of top predators, recently termed “The trophic downgrading of Planet Earth” (Estes et al., 2011). Of note is the vast array of ecosystem processes affected by cascading effects of top predator loss, e.g., incidence of disease, fire frequency, nutrient cycling, carbon storage, water quality, and the relative invasibility of ecosystems (Estes et al., 2011). As such, understanding the nature of trophic cascades has become a central part of conservation planning and decision-making. Take, for instance, the complicated case of reintroducing wolves (*Canis lupus*, Canidae, Carnivora) to Yellowstone, and whether this has induced cascading effects on constituent habitats and ecosystem processes (Dobson, 2014). The simple trophic cascade idea has broad implications for understanding food web dynamics and ecosystem function.

## 14. Trait-mediated indirect effects — Oswald Schmitz

Implicit in this review is that food web structure is a function of the total sum of direct feeding interactions between consumers and their resources in a particular system. But species are also affected by non-trophic interactions that feed back to affect consumer–resource links. Such interactions can be best contextualized within the broad classification of indirect effects, i.e., when the influence of one species is transmitted to another via an intermediary. These effects can be manifest in two

ways. First, density-mediated indirect interactions occur when one species alters the abundance of another via an intervening species. The trophic cascades in northern temperate lakes (see previous section) are paradigmatic examples, where densities of a top predator indirectly mediate the abundance of zooplankton and phytoplankton through changes in abundance of planktivorous fish. Second are trait-mediated indirect interactions, in which one species influences another's phenotype, rather than (or in addition to) its population density, subsequently affecting consumer–resource patterns among other species. For example, a predator can restrict a prey to a particular habitat, resulting in a shift in the prey's resource use, thereby altering the prey's functional role within that food web. The ubiquity and importance of these indirect interactions is now well recognized (Peacor and Werner, 2001; Peckarsky et al., 2008; Schmitz et al., 2000; Schmitz et al., 2004; Werner and Peacor, 2003).

Oswald Schmitz and colleagues' research illustrates the importance of understanding indirect effects for elucidating functional food web structure, using old field systems in Connecticut as a model study system (Beckerman et al., 1997; Schmitz, 1998; Schmitz et al., 1997; Schmitz and Suttle, 2001). Spiders are the dominant predators and grasshoppers the most common herbivore within a diverse grass and herb plant community. In a series of experiments, Schmitz and colleagues quantified spider effects on grasshoppers and resulting cascading effects on plants, specifically partitioning the relative importance of density- and trait-mediated mechanisms. Identifying the strength of the two was facilitated by the fact that spider species were characterized by different hunting strategies, including sit-and-wait and active hunting modes. Grasshopper prey shifted behavior only in the presence of sit-and-wait predators, residing in a different part of the old field canopy in order to minimize predation risk. In this microhabitat, they consumed less nutritious herbs instead of their preferred grasses. This behavioral shift lowered the impact of herbivores on grasses, and generated a trait-mediated trophic cascade on herbs. As was discussed in the lake examples from the previous section, shifts in food web structure also influenced ecosystem-level processes. Actively hunting spiders reduced net localized primary productivity and nitrogen remineralization, while sit-and-wait had the opposite effect. This research program provides an elaborate example of how direct feeding interactions are insufficient to encapsulate the real complexity of food webs, and why behavior (and other phenotypic traits) is also critical to consider when examining food web dynamics.

### 15. Eco-evolutionary feedbacks — David Post

Other sections in this essay highlight many of the ways food web-based perspectives have influenced population, community, and ecosystem sub-disciplines of ecology. Recently, another intriguing area of research is emerging — using food web ecology as a context to examine questions in evolutionary biology, in particular as a way to explore contemporary evolution. More generally, such research addresses what are termed eco-evolutionary feedbacks, the cyclic interaction between ecology and evolution such that changes in ecological interactions drive evolutionary change in organismal traits that, in turn, alter the form of ecological interactions (Schoener, 2011). This dynamic is possible when (1) time-scales for ecological and evolutionary change are congruent, (2) the organism (due to its phenotype) exerts a strong effect on the environment, (3) the altered environment is sufficient to create a selection gradient, and (4) there is sufficient genetic variation within the focal population to allow for evolutionary change. Relevant for this review are cases where eco-evolutionary feedbacks directly affect aspects of food web structure, which can then alter the direction of evolutionary change for constituent organisms (Post and Palkovacs, 2009).

A model example is David Post and colleagues' study of contemporary evolution in alewives (*Alosa pseudoharengus*, Clupeidae, Clupeiformes) and the associated drivers of, and implications for, shifts in food web structure. This research is based on comparisons among New England

lakes inhabited by alewives with two divergent life histories: an anadromous form that migrates between freshwater lakes and the ocean, and a landlocked form that spends its entire life in a lake. Important differences between the two forms include variation in feeding morphology and diet, where anadromous alewives preferentially feed on large-bodied zooplankton while landlocked individuals are better adapted to feed on small-bodied zooplankton. In anadromous lakes, seasonal migrations and subsequent feeding of alewives results in reductions in mean body size and biomass of zooplankton. Yet when anadromous alewives migrate back to marine environments, populations of large-bodied zooplankton are able to recover such that they are again available for planktivores in the subsequent spring/summer. Conversely, in landlocked populations, alewives feed throughout the year and this consistent predation pressure permanently eliminates large prey. This creates a strong selection gradient for feeding on the remaining small-bodied zooplankton. As a result, landlocked populations are characterized by individuals with a smaller gape and narrower spacing between gill rakers, both traits that are associated with more efficient foraging on small prey. These phenotypic traits are what drive a very different food web structure, with small-bodied zooplankton dominating the community and providing the primary prey for alewives and other planktivores. The crux of eco-evolutionary feedback is that changes in food web structure generate selective pressure on alewives, driving distinct phenotypic shifts in individuals. Shifts in individual phenotypes ultimately result in further changes in food web structure over time (Howeth et al., 2013; Jones and Post, 2013; Palkovacs and Post, 2008, 2009).

These eco-evolutionary feedbacks give rise to fundamentally different food webs in lakes with anadromous and landlocked populations. As for the latter, changes are manifest not only in the ecology and trophic role of alewives, but also other aspects of food web structure. For example, bluegill (*Lepomis macrochirus*, Centrarchidae, Perciformes) from lakes with landlocked alewives also target the available smaller-bodied zooplankton, resulting in shifts in bluegill trophic role (Huss et al., 2014). Competitive interactions between the two species can be high, which may further strengthen selective pressure for phenotypes that allow for the most efficient feeding strategies. Effects are also apparent at higher trophic levels. Chain pickerel (*Esox niger*, Esocidae, Esociformes) is typically a littoral predator, but in lakes with landlocked alewives, a portion of the chain pickerel population has undergone a habitat shift and forages in pelagic habitats. The alewife system provides a clear example of how food web perspectives may be critical for our understanding of contemporary evolutionary change, as well describing how this evolutionary change feeds back to affect the structure and function of present day food webs.

### 16. Conclusion

Four summary observations emerged from this review of food web ecology, as viewed through the key contributions of these 14 scientists. First, a vast array of concepts, research perspectives, and methodological tools fall under the umbrella of food web research. It is challenging to find a specific sub-discipline of ecology that is not related to, or relevant for, an understanding of food webs. For example, just in this review, contributions illustrate that food webs have implications at population (e.g., Winemiller, Polis), community (e.g., Paine), ecosystem (e.g., Carpenter, Schmitz) and evolutionary (e.g., Bolnick, Post) levels. These examples illustrate the extremely diverse areas of research related to food web ecology.

Second, scientists with different backgrounds and interests approach the study of food webs with vastly divergent viewpoints. Although this seems like a self-evident statement, its importance should not be under-estimated. Thomas Kuhn wrote: "What a man sees depends both upon what he looks at and also upon what his previous visual–conceptual experience has taught him to see (Kuhn, 1962)". A classic (admittedly simple) example used to illustrate this concept is the ambiguous duck–rabbit figure, a drawing that could look like either a duck or a rabbit



depending on observational perspective (Jastrow, 1899). A person that has no prior experience of a rabbit will surely see a duck, but one who doesn't know that ducks exist will see a rabbit. As such, previous experience and knowledge will result in very different research trajectories.

Such different perspectives underlie a continuing tension among food web ecologists, specifically a debate regarding the relative strengths and weaknesses of empirical- and theoretical-based approaches. Researchers trained as quantitative scientists may see food webs as mathematical entities that allow for exploration of universal structural properties within ecosystems, whereas researchers with a background grounded in basic natural history may argue that the only way to truly understand food web structure and function is through rigorous empirical investigation. Almost 90 years since publication of *Animal Ecology* (Elton, 1927), these two approaches often remain rather divergent in practice. But each remains critical to further our understanding of food web structure, and especially to provide predictive ability regarding food web dynamics in the context of rapid, on-going, environmental change.

Finally, this review is limited in its scope because of the focus on specific contributions of just 14 scientists; dozens of others would certainly warrant inclusion in a more comprehensive effort. Further, it was beyond the scope of this effort to explore various emerging areas in the ecological sciences relevant for the study of food webs. For example, ecological stoichiometry (Sterner and Elser, 2002), positive interactions (Bascompte, 2009; Bruno et al., 2003), temperature-based models (Gilbert et al., 2014; Humphries and McCann, 2014; Sentis et al., 2014), and novel approaches to identify universal food web patterns (Riede et al., 2011) all contribute to a more dynamic and seemingly ever-expanding breadth and relevance of food web ecology. Those two caveats aside, by focusing on particular scientists and their specific contributions, we were able to track the most critical advances that have framed the study of food webs. We hope our approach provokes more discussion and debate regarding food web ecology, and provides a foundation that will be useful for other researchers as the field continues to expand and evolve.

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