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A primer on the history of food web ecology: Fundamental contributions of fourteen researchers☆

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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

Table 1
Glossary summarizing definitions of key terms from the text.

Cascade model — 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.
Connectance — 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.
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.
Eltonian niche — 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.
Food web — a network of consumer–resource interactions among a group of organisms, populations, or aggregate trophic units.
Functional (or interaction) food webs — Webs based on the per capita effect (positive or negative) of one species on another.
Indirect effect — Effect of one species on another, as mediated through one or more intervening species.
Interaction strength — Per capita impact of one species on another's population size or growth rate.
Network theory — 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.
Niche model — 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.
Node — 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.
Keystone species — A species which has disproportionate effects, relative to its biomass, on community structure or ecosystem function.
Pyramid of numbers — A graphical representation of the number of organisms, standing biomass or overall productivity at each hierarchical trophic level.
Realized food chain length — The total number of times energy or material is transferred from basal resources pools through consumers to a top predator.
Scale-free networks — Networks characterized by a power-law degree distribution, where the majority of nodes have connections with a just a few very well-connected nodes.
Small-world networks — Networks characterized by especially high clustering and short path lengths.
Spatial subsidy — A donor-controlled resource flux moving from one habitat to another that increases productivity (primary or secondary) of the recipient habitat, which in turns alters consumer–resource dynamics.
Stability–complexity relationship — 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.
Topology — Detailed quantitative analysis of the structural properties of food webs, often assessed using metrics such as connectance, food chain length, and degree of omnivory.
Trait-mediated indirect effect — An indirect effect in which one species influences another's phenotype (via an intermediary species) rather than its population density.
Trophic cascades — 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.

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.

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