

## Causes and Effects in Food Webs: Do Generalities Exist?

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The problems concerning causality are classic in the philosophy of science, and sometimes they have also found their way into ecology and evolutionary biology (e.g., Levins and Lewontin, 1980; Simberloff, 1980; and Sober, 1984). In addition to unsolved philosophical issues, problems concerning general causes and effects in food webs, such as if population dynamic processes or energetics really are the causes for patterns in food web structure, arise because food web patterns and processes may affect each other reciprocally, as shown throughout this book (see also Levin, 1992). Hence it is useful to pragmatically rephrase the question: What factors affect what properties of food webs? This question brings into focus the interesting issues concerning the linkages between food web patterns and processes, as exemplified by many of the contributions to the following section.

### **Food Web Structure, Function, Pattern, Process, and Dynamics**

It is appropriate to define more precisely what is meant by the above terms in the present context. *Structure* is a property of a system referring to the "arrangements of parts or elements," according to the *Webster Universal Dictionary*, 1963 edition. Hence, *food web structure* refers to web topology, i.e., which components are linked or interacting. By necessity, this involves decisions about how links should be counted and how strong the interactions between the components (e.g.

herbivores) should be included in the web. *Function* is a statement about how components (e.g. herbivores) in a structure participate in a process (e.g., consumption; see also Martinez, in press). Function is a property of a component in a particular context. By *pattern* we mean structural regularities in food webs, whereas *process* refers to a series of actions producing patterns in food webs (cf. Fisher, 1994). Note that web structure, function, pattern, and process can change over time. We refer to such changes as *food web dynamics*. Population dynamics is regarded as one of the most important processes responsible for structure in communities and food webs (e.g., Watt, 1947; Pimm, 1982; Paine, 1988; and DeAngelis 1992). However, population dynamics are not the same as food web dynamics (see Winemiller and Polis, this volume), and dynamics in trophic structure, energy and nutrients, evolutionary changes, and other biotic and abiotic processes may also affect food web structure and function.

As evident in several of the following papers (Morin and Lawler, Chapter 21; Oksanen et al., Chapter 22; De Ruiter et al., Chapter 19), and noted by several previous authors (Levin, 1992; papers in Giller et al., 1994), patterns are not only consequences of processes, but they may also in turn influence processes. For food webs, pattern and process, or alternatively, structure and function, are different ways of looking at phenomena, and they are difficult to separate. For example, a species can be functionally characterized as a predator that strongly affects the population dynamics of several prey species.

The same species can be structurally characterized as a species that possesses direct trophic connections to 20% of the species in the web.

The importance of food web structure for population dynamics is demonstrated in the contribution by Morin and Lawler (Chapter 21). In their aquatic microcosms, changes in food web structure (e.g., addition of a trophic level) decrease density and increase population variability among prey species. Hairston and Hairston (1993) suggest another example. In their view, trophic structure, morphology, and the distributions of body sizes in different ecosystems affect the dynamics of energy and the component populations. This view is echoed in the paper by Oksanen et al. (Chapter 22), although productivity (or, alternatively, energy) is their starting point. Potential productivity affects trophic structure, which subsequently feeds back to both the actual productivity of an ecosystem and the dynamics of the trophic levels in that system (see also Persson et al., this volume). Morin and Lawler also suggest that population dynamics can determine food web structure, if high population variability increases extinction rates (cf. Pimm, 1982). Clearly, there is a multitude of reciprocal interactions between food web structure and a number of processes at both the population community and ecosystem level, and ecologists have just begun to examine them.

One way to investigate causal relationships between patterns and processes in food webs would be to look at the temporal sequences of changes in observed patterns and processes, for example by experimental manipulations in the laboratory or in the field. The microcosm approach suggested by Morin and Lawler is promising in this respect. DeRuiter et al. (Chapter 19) suggest another way in which the relationships among energetics, food web structure, and population dynamics can be investigated. They estimate interaction strengths between components in belowground food webs from empirical data on population sizes, feeding, and energetics. These estimates are then used to analyze the stability of the webs, and the impact on stability of different interactions in the web. An important finding is that impact on stability is not necessarily related to interaction strength.

## Do Generalities Exist in Food Webs?

Sometimes ecologists experience difficulties finding general patterns in population dynamics, food webs, and ecosystems. The legacy of natural history, as well as the results from a number of theoretical analyses exemplified by the contributions of Yodzis (Chapter 18) and Hastings (Chapter 20), have suggested that idiosyncracies of individual species and their dynamics may preclude many generalities. In food web studies, the poor quality of much of the previous data has also contributed to a healthy skepticism toward many proposed generalities (e.g., Paine, 1988; Polis, 1991; 1994; and Hall and Raffaelli, 1993).

Nonetheless, studies of food webs have produced some generalities, or at least regularities that should lead to further inquiry. This is so for structural webs (i.e., webs with binary links) as well as interaction webs. In principle, the use of structural webs should facilitate intersystem comparisons of food web attributes, albeit on a coarser level of resolution with regard to population dynamics and population interactions. However, most examinations of structural webs suffer from the data being vastly incomplete, and many regularities suggested in the 1980s have not stood up to closer scrutiny, e.g., the link species scaling law (Martinez, 1992; Hall and Raffaelli, 1993).

In recent years, the use of better data as well as novel methods of analysis have led some authors to argue that there are more robust generalities in structural webs (e.g., Martinez, 1991, 1992, 1993; and Bengtsson, 1994). Although these may still be artifacts of poor data (e.g., Paine, 1988; Hall & Raffaelli, 1993), the search for structural regularities in food webs is important, because they are among the patterns at the community level that should be linked to processes at lower levels, for example population dynamics. As Bengtsson (1994) argued, potentially confounding variables such as web size (species richness) may have to be accounted for before such patterns can be interpreted in ecologically sensible ways.

One example of such a regularity is variation in food chain length across food webs.

Chain length appears to increase with diversity (species richness) (Martinez, 1991; Hall and Raffaelli, 1993; Bengtsson, 1994; Martinez and Lawton, 1995) and to vary among ecosystems (Schoener, 1989; Bengtsson, 1994). On the other hand, no consistent relationship between productivity and food chain length has been found (Persson et al., but see Oksanen et al., Chapter 22).

The number of links per species also appears to vary a regular way with diversity (Schoener, 1989; Warren, 1990; Martinez, 1992) and among ecosystems (Bengtsson, 1994). It increases with species richness in a way that suggests that each species feeds on approximately 10% of the species in the web regardless of web size (Martinez, 1992, 1993), although Bengtsson (1994) advocated great caution when discussing the exact form of this relationship. Future comparative studies of patterns such as these among habitats and ecosystems may provide insights regarding certain aspects of how food webs and communities are organized, provided the data are adequate, links are defined in consistent ways and methodological biases are identified and accounted for (cf. Polis and Winemiller, this volume). For example, analyses of connectance or the number of links per species could reveal if species differ in the degree of food specialization between ecosystems (cf. Warren, 1990), and how habitat structure may affect food web properties.

Some general patterns have also begun to emerge in studies of interaction webs. Most interactions in food webs seem to be weak (Juliano and Lawton, 1990; Paine, 1992). Raffaelli and Hall (Chapter 17) examined the distribution of per capita interaction strengths in an estuary by field experiments, and found that most values were near zero. A similar result was obtained for the soil food webs examined by DeRuiter et al. (Chapter 19), using a combination of observation and modeling. Another potentially general finding, at least in intertidal webs, is that indirect effects are common (Menge, 1995). This is likely to be the case also in other systems such as soils (Bengtsson et al., this volume). Menge (1995) suggests that indirect effects scale with species richness as does links in structural webs.

Hence, both approaches to the study of

food webs appear capable of producing general patterns. What is needed now is the formalization of these patterns into specific predictions about the relationships between food web patterns and processes. These should be tested by manipulative or nonmanipulative (natural) experiments capable of distinguishing between processes hypothesized to be responsible for the patterns.

### **Interaction Webs—The Solution?**

To some ecologists, interaction webs are the most useful tools for analyzing food webs, especially when combined with detailed observational data (e.g., Paine, 1988; Polis, 1994; Polis, this volume; Menge, this volume; and Raffaelli and Hall, Chapter 17), while structural approaches such as Cohen et al. (1990) and Martinez (1991, 1992) are regarded as less useful. To a large degree, this view is based on the fact that interaction strength, the central issue in interaction webs, appears to provide a direct link to the population dynamics of the component species in the food web. However, as can be illustrated by some of the chapters in this section, there are a number of potential problems concerning interaction webs that need to be recognized in future studies.

First, measuring interaction strength is problematic. Even good experimental protocols may, in cases where predators and prey differ in density, yield a huge variability in this measure, as pointed out by Raffaelli and Hall (Chapter 17). Perhaps interaction strengths could be more profitably measured per unit biomass (as in DeRuiter et al., Chapter 19), and thus the results may become more comparable between ecosystems and species.

Second, the concept of interaction webs is linked to theories of strong population interactions between predators and prey, such as Lotka-Volterra models. However, we see no reason that the interactions in natural ecosystems are of these types only. The recent debates on predator-prey theory (Matson and Berryman, 1992; Diehl et al., 1993) and the bottom-up vs. top-down controversy (Matson and Hunter 1992; Strong, 1992; Polis and Strong, in press) emphasize this point (see also Persson et al., this volume, and Osen-

berg and Mittelbach, this volume). The presently available analyses based on interaction strength carry many implicit and untested assumptions regarding the forms of the trophic relationships between food web components. If the types of trophic interactions differ greatly between ecosystems, a value of interaction strength  $i$  in one study may be something quite different than  $i$  in another study. These are issues that need more careful thought and formalization of the concepts before further progress can be made.

This problem can be illustrated by the contribution by DeRuiter et al. (Chapter 19). They devised an ingenious way to derive interaction strength from feeding rates and energetics in observed natural food webs. They subsequently impose Lotka-Volterra dynamics on their systems, when in fact the forms of the interactions in their detrital-based food webs are unknown. Although the method holds promise for the future, one wonders how the results may differ when other forms of the trophic interactions, such as donor control, are used in their model.

Finally, it is an open question how useful are results from short-term experiments on interaction strength at small spatial scales for long-term predictions of food web behavior. For example, in many food webs population dynamics of different species may be on vastly different spatial and temporal scales. The contributions by Hastings (Chapter 20) and Yodzis (Chapter 18) suggest that strong interactions in food webs may result in chaotic dynamics and many indirect effects that are slow to manifest themselves. This makes interpretation of interaction strengths in complex webs more difficult, and predictions of long-term behavior and responses to perturbations also seem problematic. Yodzis also points out that environmental variability may add to the unpredictability of responses. It is not clear how the conclusions of these authors depend on the forms of the interactions between the components of the webs, but in any case, the possibility of inherent unpredictability of population dynamics within food webs is evident in a number of theoretical studies.

Hence, for several reasons, the likelihood that interaction webs will yield more generalities than structural webs concerning the structure and function of community food webs

seems uncertain (but for the counter point of view, see e.g. Paine, 1988; Menge, this volume; and Polis, 1994, this volume). Although the interaction-strength approach will lead to important insights, the results of Hastings and Yodzis and Abrams (this volume) suggest that in the near future it will be a difficult task to find generalities in interaction webs unless there are special circumstances. A promising example is the analyses of indirect effects in intertidal webs (Menge, 1995). It would be useful to pursue this type of analysis in other well-studied habitats, such as lakes.

### Defining Food Webs and Links

Another problem in food web research is the definition of the food web and its components. Cousins (Chapter 23) discusses the problem that in earlier food web research, the spatial and temporal extents of the food web have not been consistently defined (see also Polis et al., this volume). He suggests that energy concentration is the core process in food webs, and that the boundaries of the food web should be tied to the activity of the top predators, i.e., he advocates a particular type of sink web. On the other hand, food webs could also be defined as ecosystem food webs using explicit spatial and temporal boundaries (Martinez, 1991). In many cases, this will correspond to obvious habitat boundaries, e.g. the water-land boundary in lakes. Polis et al. (this volume) discuss the implications of defining food webs based on habitat boundaries.

Finally, different criteria for including and weighting trophic links have been used—energy flow, frequency of feeding, selectivity, interaction strength, etc. The papers in the section offer a variety of approaches to this issue, but it is yet to be determined how the different criteria relate to each other in a way that would make the results from different approaches comparable. For example, DeRuiter et al. (Chapter 19) estimated interaction strengths based on feeding and energetics, but Polis (1994) argued that there is usually little concordance between energetics and interaction strength. These and other issues were recently discussed in more detail

by Winemiller (1990), Cohen et al. (1993) and Hall and Raffaelli (1993).

To summarize, the chapters in this section highlight the diversity of perspectives and approaches to the basic question of whether general patterns are to be found among food webs. A consensus on these generalities has yet to emerge. In our view, this diversity is a sign of a healthy research field, where different perspectives and methods of analysis provide complementary views on food web structure and function, and their interrelationships.

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# FOOD WEBS

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