

Food webs versus interaction networks: principles, pitfalls and perspectives

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“Ecological network” and “food web” are summary terms covering a continuum from species-association based networks to quantified-links networks to interaction-specified ecosystem models. In particular “classical” one-mode (“unipartite”) food webs and bipartite (two-mode) interaction networks are two very active research fields. While often aiming to tackle similar topics (such as community stability and species coexistence) their data, methods and approaches often differ substantially. In this chapter we shall review the continuum of food web approaches along a set of questions:

- Which kind of data form the basis of the network? Are interactions observed or inferred?
- What do network nodes and links represent?
- What is the focus of scientific questions, which key features and topics are being investigated?
- Which methods are employed, and what are their potential pitfalls?

We find that the literature on food webs and bipartite networks reveals very different challenges, although the questions addressed are often very similar. For example, sampling artifacts and ecological interpretation of link strength are issues of vigorous discussion in many studies of bipartite networks, while being accepted largely unquestioned in classical food webs. In contrast, dynamic analyses and their mathematical challenges are behind many food webs papers, while being marginal to bipartite network research. In fact, several substantial criticisms leveled at one type of network are absent from the other for purely historic reasons. We identify challenges common to all network types and suggest avenues for a potentially fruitful transfer of approaches as well as applications between them.

1.1 Introduction

Food webs have aroused the interest and scientific analysis for many decades (Cohen, 1978). Especially Odum’s school of ecosystem thinking sought to quantify fluxes in ecosystems, based on feeding guilds (Odum, 1953). Later, the theoretical analysis of interactions among species took a prominent role, arguing that information fluxes are as important as energy fluxes (e.g. Pimm, 1982). These interaction network ideas still dominate models and experiments today (Rossberg, 2013). In contrast, interactions between two (trophic) levels (“bipartite” or “two-mode”

networks) are a more recent ecological mainstream activity. Pollination networks featured verbally in early scientific works (dating back to comments in the third chapter of Darwin, 1859), but it was only in the 1980s that data describing such interaction networks specifically received analytical attention (starting with the work of Jordano 1987). Today, food-web ecologists and network ecologists are still two largely separate scientific communities, with different data, methods, aims and interpretations. Attempts to bridge this gap are relatively few (e.g. Ings et al., 2009).

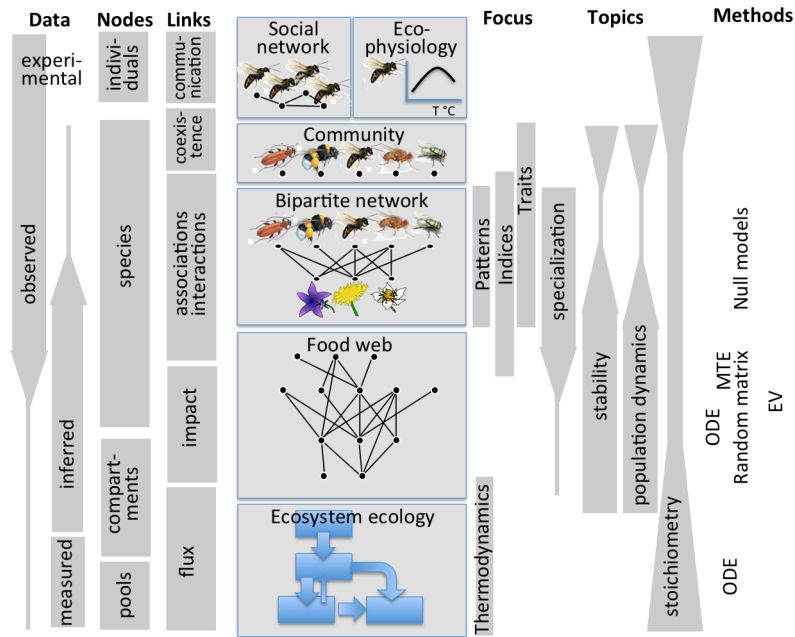


Fig. 1. Main changes in the scientific context when moving from individual-based ecophysiological studies to energy and nutrient flux-based ecosystem-level studies of food webs and networks. ODE and MTE refer to ordinary differential equations and metabolic theory of ecology, respectively.

Any food-web workshop (such as the one in Rauschholzhausen 2013) will typically bring together people from both sides and those already straddling the fields. Still, studies show a considerable separation, despite substantial intellectual overlap. In this chapter, we present an (necessarily incomplete) overview of current difference between food web and network ecology with the aim of highlighting the underlying similarities. We believe that both fields can profit from the expertise and experience present in the other, and we suggest specific steps towards incorporating so far neglected issues tackled in the other field. Specifically, we organize this chapter into four main dimensions (scientific focus; data; nodes and links; and methods), after a brief section defining the terms we use.

1.2 Definitions

Food webs describe who-eats-whom-relationships in an $n \times n$ adjacency matrix. Since every food-web entity may interact with any other, this matrix has the dimensions of the number of entities (species, guilds) and is called *one-mode* or *unipartite*. If interactions

are restricted to those between, and not amongst, two trophic levels, the resulting $k \times l$ matrix describes *bipartite* networks. Food webs are typically interpreted along trophic relationships (and often contain only data on trophic interactions, as revealed e.g. in the 113 webs in <http://ipmnet.org/loop/foodweb.aspx>). Interaction networks, in contrast, include a large diversity of relationships between species, e.g. mutualism, facilitation or commensalism. Usually, a network focuses on a specific function for a better interpretation and does not attempt to mix pollinators and predators in a single matrix, although some attempts have now been doing so (e.g. Pocock, Evans and Memmott, 2012). In line with most current publications we shall henceforth use “food web” for one-mode trophic relationships, and “interaction network” for other relationships which are most often bipartite (even those of plant facilitation networks: Verdú and Valiente-Banuet, 2011). Note that other definitions have been proposed (e.g. food webs being binary adjacency matrices, while networks have weighted links: Allesina, 2009).

We refer to any kind of food web or network as *binary* if the data in the adjacency matrix are 0/1 (for absent and existing links, respectively) and as *weighted* if data are quantitative (e.g. predation rates or number of observed interactions). Each cell with a value different from 0 is called a *link*, while the actual events underlying a link are called *interactions*.

For reasons of presentational clarity we make statements about the prevalent patterns, and the reader may want to mentally add qualifying phrases such as “mainly”, “largely” or “generally” to most of them. At the same time, we cite and discuss studies successfully reaching beyond the dominant research modes. Figure 1 summarizes the main trends we discuss in this chapter.

1.3 Scientific focus and applications

Species interactions have been studied for very different reasons. Food webs originally were models of ecosystems, representing the main **pathways of mass flow** (typically carbon or total biomass: Odum, 1953). Scientific questions were related to population sizes of particular species, for example those commercially or culturally important to humans (fish harvests, top predator abundances). Soon the **stability** of such ecosystems was being analysed (i.e. resistance to disturbance, resilience to overexploitation; Fig. 2), and the role **complexity** plays for species coexistence and hence food web stability (e.g. May, 1973). The first such analyses were largely theoretical, using oversimplified “Tinkertoy models” (Pimm, 1982; Montoya, Pimm and Solé, 2006), but models of real food webs and applications to human effects soon followed. The interest in such strategic theoretical models has not diminished and still dominates the literature on food webs today (see Fussmann and Heber, 2002; Murdoch et al., 2002; Solé, Alonso and McKane, 2002; Melian and Bascompte, 2002; Ives and Cardinale, 2004; Kéfi et al., 2012; Allesina and Tang, 2012; Thompson et al., 2012 for some of many examples).

The literature on *bipartite* networks, in particular mutualist and host-parasitoid networks, has a very different focus. Here **spe-**

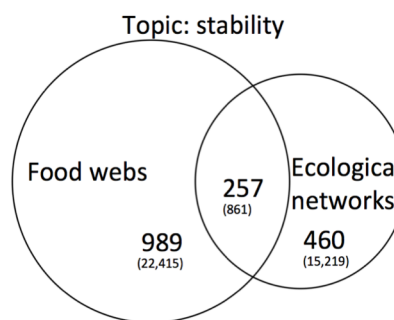


Fig. 2. Venn diagram showing the number of publications on food webs and/or ecological networks that include the topic “stability.” Web of Science search in September 2014 using the search terms “ecolog* network*”, “food-web” and “stability.” Slight modifications of the terms yield similar results. Total numbers of papers without “stability” are given in parentheses. 5.4% of the food-web articles, and 4.5% of the network articles include “stability.”

cialisation of its members is of central interest, particularly **coevolution** in mutualistic networks (such as plant-pollinator or seed-disperser networks: Schleuning et al., 2012; Morris et al., 2014). Related to specialization, many studies investigated how **trait matching** between interacting species contributes to the distribution of links or their relative weight (Vázquez, Chacoff and Cagnolo, 2009). Another topic largely confined to bipartite networks is the asymmetry of interaction strengths. One may argue that indeed all network metrics – from connectance over betweenness to nestedness – are quantifying the effect of specialization, from different angles or at different levels. The description of these patterns is still the main preoccupation of network ecologists, although only few studies experimentally or empirically demonstrate causes and consequences of such patterns, e.g. in predicting land-use effects on species' population declines (Winfrey et al., 2007; Weiner et al., 2014).

Two themes common to both food web and network research are the relation between diversity (and hence complexity) and coexistence or stability, and the community organization from subgroups (modularity). The mathematical aspects differ, however, as we will see below.

1.4 Data

Possibly because mathematical properties of food-web models are complex, model structure received more attention than data (and still does). The typical empirical data are simply lists of species or taxa, at least in traditional food webs. Links are then **inferred** from co-occurrences of species, reports of interactions in the literature or cafeteria experiments in the lab (“refectory experiments”), rather than based on field observations or *in situ* food choice experiments (“picnic experiments”). Reasons and challenges for inferring links and even interaction strengths are multi-fold (Morales-Castilla et al., 2015). Whenever actual fluxes have been measured in food webs, these studies tend to take a more ecosystem-level standpoint (e.g. Neutel and Thorne, 2014). This is in stark contrast to bipartite interaction networks, where interactions are **observed** in the field and are thus much more certain to be real. However, gut content analyses – morphological or molecular identification of the organisms consumed by an individual predator – recently contributed to more empirical, quantitative data on interactions. Stable isotope analyses or fatty acids play an important role in resolving trophic relationships, but particularly molecular gut content analyses allow for a better taxonomic resolution of prey items consumed by predators and are increasingly employed in food web studies (Traugott, Kamenova and Ruess, 2013). The methodological progress of food webs based on gut contents now increasingly approaches data properties of interaction networks – and inherit their advantages as well as disadvantages.

Empirical data on interactions do not come problemfree, however. The effect of variation in sampling intensity and the resulting number of observations per species (ranging from singletons to species with many hundreds of observations), have been investigated in several food web and network studies (Goldwasser and Roughgarden, 1997; Martinez et al., 1999; Banašek-Richter, Cattin and Bersier, 2004; Nielsen and Bascompte, 2007; Dormann et al., 2009). Interaction networks are notoriously incomplete and many links are missed in any given sample

(Sørensen et al., 2011). The influence of such variation in number of observations on network patterns is now routinely accounted for by using null models (see below). In food webs, **data uncertainty**, statistical artifacts incurred through externally driven species abundance, and sampling intensity are non-issues and (implicitly) assumed irrelevant relative to model structural uncertainty (but see Martinez et al., 1999). This assumption is likely to be wrong. Many links possible *in principle* or elsewhere may be absent at the study site. Binary data may suggest a generalist behavior of a predator despite huge but unquantified differences between prey preferences, effectively making the predator seem to behave highly specialized. Thus, **quantitative links** give a more realistic impression of the importance of a link. For example, easily a third of all links in a network are singleton observations, adding (more or less) random noise with large effects on qualitative network structure but small effects on weighted metrics (Blüthgen, 2010).

Binary adjacency matrices are generally insufficient to gauge the importance of a link for food-web and network structure. The *quality* of link information is hugely important for food webs and networks alike. Over the last decade or so food webs became more quantitative, but still lag network analyses when it comes to assessing the effects of sampling intensity on food web structure.

1.5 Nodes and links: what actually is your network?

Any ecosystem, even those in extreme environments, easily comprises hundreds, thousands or even millions of “species” (although it remains a point of contention how to delineate microbial species). Soils as well as benthic sediments can be immensely species rich, even above the bacterial realm (think of fungi, nematodes, algae, crustaceans). It is thus common practice (and technical necessity) in food-web science to **lump species into guilds** (e.g. “decomposers”) or taxonomic units (e.g. “diatoms”). Larger species are thus often represented as a single compartment (“sea otter”), while lower trophic levels are pooled (“kelp”). The nodes of a food web are thus heterogene-

ous: sometimes a species, sometimes a guild. Taxonomic resolution is indeed a long-standing debate in food-web ecology, since it heavily affects food-web structure and hence stability analyses and population dynamics (e.g. Williams and Martinez, 2008; Boit et al., 2012).

Bipartite networks are much better resolved, and even if some species remain unidentified: nodes are species. An interaction in a network actually refers to an observed event, rather than a potential connection (see previous section). This is, in itself, not sufficient for most of the questions that network ecologists try to address. One line of interest is in rates (pollen transfer, parasitism, etc.), rather than observed events. One visit by a pollinator need not be sufficient to transfer the required pollen for fertilization, and a single parasite may itself become hyper-parasitized. The higher resolution of bipartite networks thus needs to be backed up by additional measurements of specific interaction efficiency (as provided, e.g., by Vázquez, Morris and Jordano, 2005), rather than generic conversion coefficients (for herbivores or predators). Another line of interest is in specialization and partitioning of interactions (**niche theory**). Both niche-based and frequency- or rate-related questions require appropriate treatment of the observed interaction data and/or careful consideration of sampling limitations (Blüthgen, 2010).

Food webs commonly aggregate some of its members into manageable ecological units, while bipartite networks remain resolved to species level. In combination with quantitative information on the strength of link (see last section) this information determines interaction probabilities and hence the flow of energy and control in both food webs and networks. Lumping may be inevitable, but its consequences may be severe and are not well understood. Also common to both types is the **lumping in space** (i.e. from different locations) **and/or time** (i.e. over hours, seasons, years). Again, spatio-temporal pooling of interactions obscures the potentially fine-balanced nature of species interactions (Fründ, Dormann and Tschamntke, 2011). Food webs or networks from adjacent ponds

or valleys are likely to have overlapping species, but their internal structure may differ substantially due to some differences (e.g. predatory fish in ephemeral ponds, shifts in flower abundance due to grazing). In seasonal environments, species often have temporal niches and phenologies, and food-web structure and dynamics will change constantly (e.g. Olesen et al., 2008; Boit et al., 2012). Both food-web and network ecology still have to develop strategies to sample and represent spatio-temporal dynamics (Fortuna, Krishna and Bascompte, 2012; Wells, Feldhaar and O'Hara, 2014; Cazelles et al., 2015).

1.6 Methods

Food-web models describe the temporal (and occasionally spatial) population dynamics of its members (be it species or guilds). Ordinary differential equations (ODEs; in the case of spatial models: partial differential equations) and difference equations are most commonly employed and in the more simple cases their behavior at equilibrium can be analysed using algebraic stability analysis (e.g. Case, 2000). Achieving coexistence of the whole food web is already a major success, since these models are very sensitive to initial conditions and parameter settings (Rossberg, 2013). Comparisons with data is mostly informal or qualitatively. Quantitative matches between food-web models and observed data are rare (Reuman et al., 2008; Boit et al., 2012).

Analyses of bipartite networks are static, with a few notable exceptions (Bastolla et al., 2009; Benadi et al., 2012; James, Pitchford and Plank, 2012; Suweis et al., 2013). This seems surprising, as the system under investigation is much simpler. However, this simplicity also reduces the possibilities for coexistence (Benadi et al., 2012), and in some cases this is only achieved by allowing resource space to increase with species numbers (Bastolla et al., 2009). While it is possible to actually fit network models to data (Wells and O'Hara, 2014), the ecological realism of such models currently remains low. Instead, the vast number of publications on bipartite networks contents itself with describing patterns, rather than understanding the underlying dynamic processes. Network

indices are plentiful, directly or indirectly related to specialization and typically over-interpreted. If abundances of species are not modeled as part of the network structure, observed patterns cannot be distinguished from random interactions of differently abundant species, as seen when using null models that maintain species abundance (Vázquez and Aizen, 2003, 2006; Blüthgen et al., 2008; Dormann et al., 2009; Joppa et al., 2009). Such simple, parsimonious explanations are surprisingly often ignored. For example, James et al. (2012) emphasized that “the question of why real ecological networks often have a highly nested architecture remains unanswered” (page 229).

Network analyses should profit greatly from embracing the dynamic modeling approach common in food-web ecology. Capturing the way species are interacting more realistically will, in the long run, certainly prove superior to statistical descriptions of static snapshots. Using null models for food webs may be useful, but is seen by theoretical ecologists as an inferior, transient option.

1.7 Conclusions

Different areas of ecology come with a different research tradition. As food-web ecology

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and interaction-network ecology start to overlap, each sub-discipline can benefit from the teething experiences of the other. In particular, the more statistical view point of interaction networks seems to acknowledge the importance of sampling errors and biases introduced by binary data, at least more so than the arena of food-web ecology currently does. In exchange, food-web ecologists have a long-standing tradition, and the tools, to embrace static data as snapshots of a dynamic system, a position that would also serve network ecologists well. Once the main technical and semantic trenches have been bridged, both directions will have to address unresolved issues, of which we find two particularly challenging but important. Firstly, the common aggregation of data across time (e.g. over months and years) and space (different locations), distorting the actual interactions at any point in time and space into a non-existent average. Secondly, the structural model error emerging from sampling problems (spurious interactions and non-detected real ones). The real test for both fields is predictive accuracy beyond the data – and a tight integration with experimental studies.

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