Unveiling the Complexity of Food Webs: A Comprehensive Overview of Definitions, Scales, and Mechanisms

Tanya Strydom

Jennifer A. Dunne

Timothée Poisot

Andrew P. Beckerman

2024-11-25

Abstract

Food webs are a useful abstraction and representation of the feeding links between species in a community and are used to infer many ecosystem level processes. However, the different theories, mechanisms, and criteria that underpin how a food web is defined, and ultimately, constructed means that not all food webs are representing the same ecological process at the same scale. Here we present a synthesis of the different assumptions, scales, and mechanisms that are used to define the different ecological networks , leading to a revision of definitions for different types of networks. Additionally we explicitly link the different network representations to the broader methodological approaches (models) that are used to construct them. In explicitly outlining the assumptions, scales, and mechanisms of network inference allows for a formal categorisation of how to use networks to answer key ecological and conservation questions as wel as defining clear guidelines to prevent unintentional misuse or misinterpretation.

At the heart of modern biodiversity science are a set of concepts and theories about biodiversity, stability, and function [1]. These relate to the abundance, distribution, and services that biodiversity provides, and how biodiversity – as an interconnected set of species – responds to multiple stressors. Documenting interactions between and among species is thus one of the fundamental building blocks of community ecology, providing a powerful abstraction and platform for mathematical and statistical modelling of biodiversity in order to make predictions, mitigate threats, and manage services [2]. Such network representations of biodiversity are increasingly argued to be an asset to understanding and predicting the abundance, distribution, dynamics, and services provided by multiple species facing multiple stressors. However, there is a growing discourse around limitations to the interpretation and applied use of networks [3,4], primarily as the result of shortcomings regarding their conceptualisation [5].

Because an ‘interaction network’ can be defined and conceptualised in many ways, each method will be embed different assumptions about the determinants of interactions, and characterise patterns and process at different scales, which will ultimately influence the nature and scope of inference [6]. The different ways in which a network can be represented is the result of *how* the network is constructed, which represents an intersection of the data used to construct the network and the underlying theory as to what drives the occurrence of interactions between species. Although there have been extensive discussions as to the the challenges relating to the scale and nature of data collection/observation [*e.g.,* 5,7–12] we still lack a clear framework as to how different data sources result in networks that are fundamentally different [Section 1.3](#sec-representation).

In this perspective we aim to provide an overview of the different **food web** representations, particularly how these relate to the terminology used to define a food web, and how this is influenced by both the processes that determine interactions [Section 2](#sec-process), as well as how this relates to the way in which we construct the resulting networks [Section 3](#sec-construct). This allows us to deliver an overview of fundamental questions in ecology that we think can benefit from network thinking and a proposal that such thinking can accelerate our capacity to predict the impact of multiple stressors on biodiverse communities. Specifically, we finish this perspective with an overview of fundamental questions in ecology that we think can benefit from network thinking and a proposal that such thinking can accelerate our capacity to predict the impact of change on biodiverse communities.

# 1. Setting the Scene: The Not So Basics of Nodes and Edges

Defining a food web seems simple; it is the representation of feeding interactions (edges) between species (nodes) in the form of a network. However, the definition of ‘edges’ and ‘nodes’, as well as the levels of organization at which they are aggregated can take many forms [9], ultimately encoding a series of assumptions and criteria within a network. An awareness of variance in the way a food web can be defined is critical as a network (or its adjacency matrix) is both the ‘object’ from which inferences are made (*e.g.,* the interactions between species, or how the structure influences ecosystem level processes) as well as the ‘product’ of either the data collection [7] a prediction process [14], or both, and is an object form which downstream (*e.g.,* responses to stressors, dynamics or mapping structure to ecosystem level processes). One thus needs to be aware of both the criteria that define nodes and edges and the scale of the processes or mechanisms that define the collecting of species together.

## 1.1 How do we define a node?

Although this may seem an elementary question in the context of food webs — a node *should* represent a (taxonomic) species, the reality is that nodes can often represent non-taxonomic units such as trophic species [*e.g.,* 15,16], feeding guild [*e.g.,* 17], or segregation of species by life stages [*e.g.,* 18]. Practical implications of how we are aggregating the nodes is that the resolution may not always be ‘pixel perfect’, and may even vary within a single network. Such granularity and variation can limit the ability to make (taxonomic) species specific inferences (*e.g.,* does species eat species ?), and affect downstream inference made from networks, including estimates of complexity and structure [18,19]. There may also be value in having nodes that represent an aggregation of species, as the distribution of the links between them may be more meaningful in terms of understanding energy flow and distribution within the system.

## 1.2 What is captured by an edge?

At its core, links within food webs can be thought of as a representation of either feeding links between species (be that realised or potential [20,21]), or fluxes within a system *e.g.,* energy transfer or material flow as the result of the feeding links between species [22]. These correspond with different ‘currencies’ (the feasibility of links or the energy that is moving between nodes). How these links are specified will influence the resulting structure of the network. For example, taking a food web that consists of links representing all *potential* feeding links for a community will be meaningless if one is interested in understanding the flow of energy through the network as the links are not environmentally/energetically constrained. In addition to the various ways of defining the links between species pairs there are also a myriad of ways in which the links themselves can be quantified. Links between species are often treated as being present or absent (*i.e.,* binary) but it is also possible to use probabilities [14,which quantifies how likely an interaction is to occur, 23] or continuous measurements [which quantifies the strength of of an interaction, 24].

## 1.3 Network representations

Networks can be thought of to fall into two different ‘types’; namely metawebs; traditionally defined as all of the *potential* interactions for a specific species pool [20], and realised networks; which is the subset of interactions in a metaweb that are *realised* for a specific community at a given time and place. The fundamental differences between these two network representations are the spatial scale at which they are constructed, and the associated processes that are assumed to drive pattern at these scales.

A metaweb provides insight as to the viability (feasibility) of an interaction between two species occurring, and captures some measure of the viability/feasibility of an interaction occurring between two species based on 1) the complementarity of their traits (a *global metaweb*) and 2) can be further refined by their co-occurrence (a *regional metaweb*). Metawebs thus provide a means to identify links that are not ecologically plausible, *i.e.,* forbidden links [25], or provide an idea of the *complete* diet of a species [26].

In contrast realised networks are relatively localised in space and time, and the links between species are contingent on both the co-occurrence of species, the role of the environment, and mechanisms of diet choice. Fundamentally this means that the presence/absence of a link is the result of the ‘behaviour’ of the species.

Ultimately this means that a metaweb and a realised network are different; links that are absent in a metaweb can (conceptually although not always practically) be treated as being truly absent, however links that are absent in a realised network cannot be considered to be truly absent but rather as absent due to the broader environmental/community context. Importantly, a realised network is *not* simply the downscaling of a metaweb to a smaller scale (*e.g.,* moving from the country to the 1x1 km2 scale based on fine-scale species co-occurrence) but rather represents a shift towards capturing the dynamic, higher level, processes that determine the *realisation* of an interaction, *i.e.,* the definition of an edges shifts from being determined by interaction feasibility to that of energetic choices/consequences. Thus, different network representations are determined and constrained by different sets of assumptions as to what the processes are that determine the presence/absence of an interaction between two species and will result in networks that are structurally different even if they contain the same species [27].

# 2. From Nodes and Edges to Process and Constraints

In the previous section we discussed how the nuances in defining a network (in terms of nodes, edges, and representation as a network) are broadly capturing different processes. Here we expand this discussion, introducing five core constraints that determine the links among species [Figure 1](#fig-process). The scale at which they operate leads to clear articulation of global metawebs as networks of all possible interactions for a collection of species, regional metawebs as networks representing all possible interactions of co-occurring species and realised networks representing interactions that occur and are framed by some kind of energetic constraint. We further develop these concepts in [Section 3](#sec-construct), where we will contextualise these process within the different bodies of theory as well as the set of tools and data required to construct the appropriate network, which will ultimately determine the context in which the resulting network is used [Section 4](#sec-progress).

The five core constraints we propose are evolutionary compatibility, co-occurrence, abundance, diet choice, and non-trophic interactions. In the following sections, we present details about how the constraints are defined, the scale at which they operate and how they deliver a network.

|  |
| --- |
| Figure 1: Aligning the various processes that determine interactions (right column) with the different network representations (left column). First we start with a **global metaweb** this network captures all possible interactions for a collection of species in the global context. However within the global environment different species occur in different regions (region one = yellow and region 2 = orange), and it is possible to construct two different metawebs (**regional metawebs**) for each region by taking accounting for the co-occurrence patterns of the difference species - as shown here we have two regions with some species (blue) that are found in both regions and others endemic to either region one (yellow) or region two (orange). However even within a region we do not expect that all interactions to be realised but rather that there are multiple configurations of the regional metaweb over both space and time. The ‘state’ of the different **realised networks** are ultimately influenced not just by the co-occurrence of a species pair but rather the larger community context such as the abundance of different species, maximisation of energy gain, or indirect/higher order interactions. |

## 2.1 Processes that determine the feasibility of an interaction

Here we will look at processes that ‘act’ at the species pair of interest, that is the *possibility* of an interaction being present/absent is assessed at the pairwise level and one is left with a ‘list’ of interactions that are present/absent. Although it is possible to build a network (*i.e.,* metaweb) from this information it is important to be aware that the structure of this network is not constrained by real-world dynamics or conditions (*i.e.,* the community context), and so just because species are able to interact does not mean that they will [28].

**Evolutionary compatibility**

This constraint is defined by shared (co)evolutionary history between consumers and resources [29–31] which, in the more proximal sense, is manifested as ‘trait complementarity’ between two species [32]. In this body of theory, one species (the consumer) has the ‘correct’ (multivariate) set of traits that allow it to chase, capture, kill, and consume the other species (the resource) and interactions that are not compatible are defined as forbidden links [25]; *i.e.,* not physically possible and will *always* be absent within a network.

Networks arising from this constraint can be binary (possible vs forbidden) or probabilistic [14], *e.g.,* the metaweb constructed by [33] uses probabilities to quantify their confidence with regards to the possibility of a specific interaction existing between two species. A network constructed on the basis of evolutionary compatibility is conceptually aligned with a ‘global metaweb’, and gives us information as to the feasibility of links between species despite the fact that they do not co-occur [as shown in 1](#fig-process).

**(Co)occurrence**

The co-occurrence of species in both time and space is a fundamental requirement for an interaction between two species to occur (at least in terms of feeding links). Although co-occurrence data alone is insufficient for building an accurate and ecologically meaningful representation of *feeding links* [34], it is still a critical process that determines the realisation of a feeding link and allows us to spatially constrain a global metaweb based on local communities [35], in the context of [Figure 1](#fig-process) this would be the metawebs for regions one and two.

## 2.2 Processes that modify the behaviour (preference) of species

Here we will showcase three processes that will ultimately influence the realisation of an interaction between species and form the conceptual basis for realised networks. As we show in [Figure 1](#fig-process) a ‘truly realised’ network is the product of different facets of both the properties of the community (**abundance** and **non-trophic interactions**) as well as the individual (**profitability**). This represents a contextual shift where the presence (realisation) of an interaction is no longer constrained to evaluating the viability between a *pair* of species but rather takes into consideration information about the community and the individual [36], and as discussed in [Section 1.3](#sec-representation), links are now *constrained* by consumer choice.

**Abundance**

The most basic abundance constraint linked to foraging biology is the principle that organisms feeding randomly will consume resources in proportion to their abundance [37], and interactions are not necessarily contingent on there being any **compatibility** between them [38–40]. However, a more ecologically sound assumption would be that the abundance of different prey species will influence the distribution of links in a network [41], by influencing which prey are targeted or preferred by the predator, as abundance influences factors such as the likelihood of two species (individuals) meeting [14,28]. Thus, if abundance data are combined with a derived metaweb, there is a rule-set that defines the distribution and potentially strength (preference via abundance) of links and thus delivers structure.

**Profitability**

Ultimately, consumer choice is underpinned by the energetic cost-benefit (profitability) of trying to find, catch, kill, and consume a resource (where a consumer will optimise energy intake while minimising handling and search time (energy cost)). Although energetic constrains can be invoked in a myriad of ways [*e.g.,* 42,43,44] profitability represents a well described within both optimal foraging [45] and metabolic theory [46], making it a good ‘umbrella concept’ for capturing the energetic cost of interactions.

**Non-trophic interactions**

Perhaps not as intuitive when thinking about the processes that determine feeding links is non-trophic interactions [47], specifically accounting for their ability to modify either the realisation or strength of trophic interactions [48–51]. Non-trophic interactions can modify interactions either ‘directly’ *e.g.,* predator *a* outcompetes predator *b* or ‘indirectly’ *e.g.,* mutualistic/facilitative interactions will alter the fine-scale distribution and abundance of species as well as their persistence [52–54].

# 3. Linking theory to network construction: a case for models

The suite of different network representations [Section 1.3](#sec-representation) that we have at our disposal allow us to isolate and operate within one (or a few) of the constraints discussed in [Section 2](#sec-process), and have an influence on the way we construct networks, specifically in terms of the development of different models. The act of constructing a ‘real world’ network through the empirical collection of interaction data is both costly and challenging to execute [25,55], thus we often turn to models to either predict networks (be that the interaction between two species, or network structure [56]), identify missing interactions (gap fill) within an existing empirical dataset [*e.g.,* 57,58,59]. In the context of this discussion food web models are also a valuable to that will allow us to better understand the different constraints determining interactions [60,61], allowing us to interrogate, generate, and reflect upon different ecological theories.

Here we will present the broader bodies of theory that have underpinned the development of different food web models, specifically in terms of understanding what drives the presence of interactions between species. Broadly we can think of interactions being ‘stochastic’, determined by the feasibility of traits (*sensu* [Section 2.1](#sec-process-feasibility)), and more broadly the behaviour and dynamics of biological systems (*sensu* [Section 2.2](#sec-process-realisation)). Each of these categories have their own set of accompanying theories and modelling approaches that have been developed within them and mapping these out is beneficial for two reasons 1) it is critical that the ‘correct’ network (and thus underlying models and assumptions) are used if we truly want to understand how different processes determine interactions [9,12,62,63] and constructively move the field forward, and 2) provide guidance as to the identifying the appropriate networks for different research questions [64, see also [Section 4](#sec-progress) and Box 1].

|  |
| --- |
| Box 1 - Why we need to aggregate networks at different scales: A hypothetical case study |
| Although it might seem most prudent to be predicting, constructing, and defining networks that are the closest representation of reality there are pros and cons of constructing both realised networks as well as metawebs. Let us take for example a community that experiences a degree of species turnover between seasons. In this community we expect species to be either present or absent depending on the season (*i.e.,* changes in co-occurrence) as well as some species exhibiting seasonal shifts in their diets (be that due to changes in species occurrence or predator choice). If one were to construct a metaweb that disregards these season shifts (*i.e.,* a global metaweb) it is clear that these finer nuances would be lost. It is of course possible to construct either smaller metawebs for the different seasonal communities (thereby capturing the changes in community diversity), or realised networks for each season (to capture diet or ecosystem process shifts *e.g.,* [65]). However, these small-scale networks lack the context of the bigger picture that is available at the metaweb - that is it gives us a more holistic idea of the entire diet range of a specific species, which is important when one needs to make conservation-based/applied decisions (*e.g.,* conserving the entire diet of a species and not just seasonal prey items) as well as providing information on interactions that may be possible regardless of the environmental/community context (species may have the capacity to consume certain prey items but do not do so due to local conditions). With this is mind let us see how the different network aggregations can be used:  **1. A ‘global’ metaweb:** Knowledge of the entire diet breadth of a species is valuable especially in terms of understanding how a species will respond to changes in the community - *e.g.* invasions/rewilding scenarios (where does the new species ‘fit’ within the network?) as well as potential capacity to shift its diet. There is also the argument that a metaweb will allow us to identify species that act as links across the landscape.  **2. A seasonal metaweb:** Knowledge at the finer scale is also valuable to understand and provide insight on the differences in diets between seasons (and identify key species within the network in different environments).  **3. A realised network:** Provide insight as to the different network configurations for a given time and place, which is a better approximation of the energy flows/ecosystem processes as they are occurring (that is the *structure* of the network is also meaningful). A realised network will also allow one to detect more nuanced shifts diet - *i.e.,* not only changes in links due to species turnover between seasons. |

## 3.1 Stochastic networks

Within stochastic networks the assumption is that the interactions between species occurs irrespective of the identity of the species (*i.e.,* species have no agency) and links are *randomly* distributed throughout the network. Alternatively it can be assumed that interactions are still independent of a species’ trait but are rater driven by its abundance, *sensu* neutral theory [66].

Practically there is little support that networks are truly stochastic, however null models [*e.g.,* 67,68] are often used as a ‘null hypothesis’ that can be used to ask questions about deviations in observed network structure [*e.g.,* 69,70]. Conversely, neutral models [71,72], and by extension processes, are most likely relevant at local scales [40], *i.e.,* should be considered to play a role when constructing realised networks but are superseded by trait-based processes at a metaweb scale.

## 3.2 Feasibility networks (metawebs)

Metawebs (depending on the aggregation) can help us develop our understanding of the intersection of species interactions and their co-occurrence [*sensu* a fusion of the the Eltonian (interactions) and Grinnellian (environmental) niches, 73,74]. Whereby a *global metaweb* presents an approximation of the fundamental Eltonian niche of a species (*i.e.,* its relation to its food source), whereas as *regional metawebs* represent an intersection of Elton and Grinnell. As discussed in [Section 2.1](#sec-process-feasibility) the feasibility of an interaction is typically assessed on a pairwise basis, and is often assessed based on the idea that interactions are governed by a set of ‘feeding rules’ [75], and are broadly elucidated in two different ways; *mechanistic models*, [*e.g.,* 76,77,78] and *pattern finding models* [*e.g.,* 26,33,79–84]. The fundamental difference between these two model groups is that *mechanistic models* rely on expert knowledge and make explicit assumptions on trait-feeding relationships, whereas the *pattern finding models* are dependent on existing interaction datasets from feeding rules can be elucidated. It perhaps also bears repeating that these models are often only presenting a list of feasible interactions and that the rresulting netowrk is ‘unstructured’, as it is uconstrained by any processes or conditions that generate structure. While these networks can be imprinted with external definitions of trophic position and guild identity to deliver hypothetical structure, this structure is not an emergent property of the links and species pairs [27].

Feasibility networks are useful for determining all feasible interactions for a specific community, and the models that have been developed in this context have the potential to allow us to construct first draft networks for communities for which we have no interaction data [33], and are valuable not only in data poor regions but also for predicting interactions for ‘unobservable’ communities *e.g.,* prehistoric networks [85–87] or future, novel community assemblages. Conceptually this is particularly valuable if we want to understand interactions between novel communitites, as well as the rewiring capacity of species. Additionally, an understanding of the role of interactions between species has allowed us to better determine the distribution of a species by accounting not only for the role of the environment but also the role of species interactions [88,89].

## 3.3 ‘Behavioural’ networks

Ultimately realised networks and capture some aspect of how the behavior of a species determines if a link is realised or not and can be modelled in two ways; models that predict realised interactions (whereby he behaiour of a secies is modelled *i.e.,* its diet choice), and models that predict the structure of realised networks (whereby the behvaiour of the system is modelled and assumptions are made with regards to the structure of a network). In terms predicting interactions current models are rooted in feeding theory and allocate the links between species based on energy *e.g.,* diet models [19,90] have been used construct networks based on both profitability (as determined by the handling time, energy content, and predator attack rate) as well as abundance (prey density), and modular models [91,92] are based on the compartmentation and aquisition of energy for species at different trophic levels. Models that determine structure are based on the idea that networks follow a trophic hierarchy and that network structure can be determined by distributing interactions along single dimension [the “niche axis”; [93]], while parametrising an aspect of the network structure [although see 94 for a parameter-free model].

As behavioural networks are are build on the concept of dynamic processes (*e.g.,* the abundance of species will always be in flux) these networks are valuable for understanding the behaviour of networks over time, or their response to change [95–97]. However, they are ‘costly’ to construct (requiring data about the entire community, as it is the behaviour of the system that determines the behaviour of the part) and also lack the larger diet niche context afforded by metawebs. Structural models provide a data-light (the models often only require species richness) but assumption heavy (the resulting network structure is determined by an assumption of network structure) alternative, however they do not make species specific predictions and so cannot be used to determine if an interaction is either possible *or* realised between two species (*i.e.,* one cannot use these models to determine if species eats species ). Although this means this suite of models are unsuitable as tools for predicting species-specific interactions, they have been shown to be sufficient tools to predict the structure of networks [98], and are useful in synthetic simulations.

# 4. Making Progress with Networks

It should be clear that there is a high degree of interrelatedness and overlap between the way in which a network is constructed and the process(es) that it captures [Figure 1](#fig-process), these are encoded (embedded) within the network representation and ultimately influences how the network can and should be used [64,99], with different network representations (and models) yielding different interpretations of processes [100].

It is probably both this nuance as well as a lack of clear boundaries and guidelines as to the links between network form and function [although see 101] that has stifled the ‘productive use’ of networks beyond the inventorying the interactions between species. Although progress with using networks as a means to address questions within larger bodies of ecological theory *e.g.,* invasion biology [102] and co-existence theory [17] has been made we still lack explicit guidelines as to what the appropriate network representation for the task at hand would be, and as highlighted in Box 1, underscores the need to evaluate exactly what process a specific network representation captures as well as its suitability for the question of interest. Below we present a mapping of what we believe are some of the key questions for which interaction networks can be used to the different networks representations that are most suitable, as well as highlight some of the methodological challenges that still need to be improved upon.

## 4.1 Making use of the different network representations

**Methodological challenges**

1. Tools that allow us to estimate both the feasibility as well as realisation of links: Currently most approaches to modelling relaised networks fail to explicitly account for any form of evolutionary constraint [although see 103] and we need to develop either an ensemble modelling approach [104,105] or tools that will allow for the downsampling of metawebs into realised networks [*e.g.,* 106].
2. Modelling interaction strength: Although realised networks are more closely aligned with *explicitly* capturing interaction strength we lack models that allow us to quantify this [56,107].
3. How do we validate our predictions?: Progress has been made to assess how well a model recovers pairwise interactions [56,108], but we still lack clear set of guidelines for benchmarking the ability of models to recover structure [93]

**Theory challenges**

1. Core Theory Advancement: Do the decades of insights arrived at for stability-diversity-productivity relationships with tri-trophic or diamond shaped models hold for complex communities (10’s-100s) [109]; How will spatial and temporal variation in climate and productivity drive change in complex ecosystems. Necessary to move to predicting changes in biodiversity per se, ecosystem functions and identifying sensitive and robust species and portions of communities.
2. How will novel communities interact? How will range shifts and invasions result in new/novel community assemblages. And then also the intentional changes of species compositions through rewilding.
3. Does rewiring happen and does it deliver robustness? Specific sub points to consider here is persistence, especially persistence to perturbation. Again, dynamic networks and network/community assembly and finally extinctions [87].
4. When do invasive species enhance or decimate communities? When do reintroductions work? [110]
5. Are there temperature threshold to community collapse
6. Can socioeconomic networks combined with biological networks drive understanding of externalities?
7. Can paleoecological data from deep time hyperthermal events provide sufficient insight into the targets, pace and recovery times from rapid climate events?

|  |
| --- |
| Figure 2: Here we highlight some of the outstanding questions in both network as well as general ecology, as well as some of the outstanding methodological challenges with regards to constructing food webs (shown in orange) that we are faced with. |

# 5. Concluding remarks

Having a clear understanding of the interplay between network representations and the processes that they are capable of encoding is critical if we are to understand exactly which networks can be used to answer which questions. As we highlight in Box 1 the different network representations have different potential uses and it should be clear that there is no ‘best’ network representation but rather a network representation that is best suited to its intended purpose. In providing a formalisation regards to the assumptions and mechanisms that need to be explicitly taken into consideration when deciding to use (and construct) networks we hope to prevent the unintentional misuse or misinterpretation of networks as well as provide a starting point from which we can develop a better framework for the applied use of networks to answer questions that are not only pressing within the field but also within broader biodiversity science.

# References

1. Loreau, M. and de Mazancourt, C. (2013) [Biodiversity and ecosystem stability: A synthesis of underlying mechanisms](https://doi.org/10.1111/ele.12073). *Ecology Letters* 16, 106–115

2. Windsor, F.M. *et al.* (2023) [Using ecological networks to answer questions in global biogeography and ecology](https://doi.org/10.1111/jbi.14447). *Journal of Biogeography* 50, 57–69

3. Dormann, C.F. (2023) The rise, and possible fall, of network ecology. In *Defining Agroecology – A Festschrift for Teja Tscharntke*, pp. 143–159., Tredition

4. Blüthgen, N. (2010) [Why network analysis is often disconnected from community ecology: A critique and an ecologist’s guide](https://doi.org/10.1016/j.baae.2010.01.001). *Basic and Applied Ecology* 11, 185–195

5. Blüthgen, N. and Staab, M. (2024) [A Critical Evaluation of Network Approaches for Studying Species Interactions](https://doi.org/10.1146/annurev-ecolsys-102722-021904). *Annual Review of Ecology, Evolution, and Systematics* 55, 65–88

6. Proulx, S.R. *et al.* (2005) [Network thinking in ecology and evolution](https://doi.org/10.1016/j.tree.2005.04.004). *Trends in Ecology & Evolution* 20, 345–353

7. Brimacombe, C. *et al.* (2023) [Shortcomings of reusing species interaction networks created by different sets of researchers](https://doi.org/10.1371/journal.pbio.3002068). *PLOS Biology* 21, e3002068

8. Brimacombe, C. *et al.* (2024) [Publication-driven consistency in food web structures: Implications for comparative ecology](https://doi.org/10.1002/ecy.4467). *Ecology* n/a, e4467

9. Moulatlet, G. *et al.* (2024) [The scaling of trophic specialization in interaction networks across levels of organization](https://doi.org/10.22541/au.172977303.33335171/v1)Authorea

10. Pringle, R.M. and Hutchinson, M.C. (2020) [Resolving Food-Web Structure](https://doi.org/10.1146/annurev-ecolsys-110218-024908). *Annual Review of Ecology, Evolution and Systematics* 51, 55–80

11. Polis, G.A. (1991) [Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory](https://doi.org/10.1086/285208). *The American Naturalist* 138, 123–155

12. Saberski, E. *et al.* (2024) [The impact of data resolution on dynamic causal inference in multiscale ecological networks](https://doi.org/10.1038/s42003-024-07054-z). *Communications Biology* 7, 1–10

13. Poisot, T. *et al.* (2016) [Describe, understand and predict: Why do we need networks in ecology?](https://www.jstor.org/stable/48582345) *Functional Ecology* 30, 1878–1882

14. Banville, F. *et al.* (2024) [Deciphering probabilistic species interaction networks](https://doi.org/10.32942/X28G8Z)EcoEvoRxiv

15. Yodzis, P. (1982) [The Compartmentation of Real and Assembled Ecosystems](https://doi.org/10.1086/284013). *The American Naturalist* 120, 551–570

16. Williams, R.J. and Martinez, N.D. (2000) [Simple rules yield complex food webs](https://doi.org/10.1038/35004572). *Nature* 404, 180–183

17. García-Callejas, D. *et al.* (2023) [Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological communities](https://doi.org/10.1111/ele.14206). *Ecology Letters* 26, 831–842

18. Clegg, T. *et al.* (2018) [The impact of intraspecific variation on food web structure](https://doi.org/10.1002/ecy.2523). *Ecology* 99, 2712–2720

19. Beckerman, A.P. *et al.* (2006) [Foraging biology predicts food web complexity](https://doi.org/10.1073/pnas.0603039103). *Proceedings of the National Academy of Sciences* 103, 13745–13749

20. Dunne, J.A. (2006) The Network Structure of Food Webs. In *Ecological networks: Linking structure and dynamics* (Dunne, J. A. and Pascual, M., eds), pp. 27–86, Oxford University Press

21. Pringle, R.M. (2020) [Untangling Food Webs](https://doi.org/10.1515/9780691195322-020). In *Unsolved Problems in Ecology*, pp. 225–238, Princeton University Press

22. Lindeman, R.L. (1942) [The Trophic-Dynamic Aspect of Ecology](https://doi.org/10.2307/1930126). *Ecology* 23, 399–417

23. Poisot, T. *et al.* (2016) [The structure of probabilistic networks](https://doi.org/10). *Methods in Ecology and Evolution* 7, 303–312

24. Berlow, E.L. *et al.* (2004) [Interaction strengths in food webs: Issues and opportunities](https://doi.org/10.1111/j.0021-8790.2004.00833.x). *Journal of Animal Ecology* 73, 585–598

25. Jordano, P. (2016) Sampling networks of ecological interactions. *Functional Ecology* DOI: [10.1111/1365-2435.12763](https://doi.org/10.1111/1365-2435.12763)

26. Strydom, T. *et al.* (2023) [Graph embedding and transfer learning can help predict potential species interaction networks despite data limitations](https://doi.org/10.1111/2041-210X.14228). *Methods in Ecology and Evolution* 14, 2917–2930

27. Caron, D. *et al.* (2024) [Trait-matching models predict pairwise interactions across regions, not food web properties](https://doi.org/10.1111/geb.13807). *Global Ecology and Biogeography* 33, e13807

28. Poisot, T. *et al.* (2015) [Beyond species: Why ecological interaction networks vary through space and time](https://doi.org/10.1111/oik.01719). *Oikos* 124, 243–251

29. Segar, S.T. *et al.* (2020) [The Role of Evolution in Shaping Ecological Networks](https://doi.org/10.1016/j.tree.2020.01.004). *Trends in Ecology & Evolution* 35, 454–466

30. Gómez, J.M. *et al.* (2010) [Ecological interactions are evolutionarily conserved across the entire tree of life](https://doi.org/10.1038/nature09113). *Nature* 465, 918–921

31. Dalla Riva, G.V. and Stouffer, D.B. (2016) [Exploring the evolutionary signature of food webs’ backbones using functional traits](https://doi.org/10.1111/oik.02305). *Oikos* 125, 446–456

32. Benadi, G. *et al.* (2022) [Quantitative Prediction of Interactions in Bipartite Networks Based on Traits, Abundances, and Phylogeny](https://doi.org/10.1086/714420). *The American Naturalist* 199, 841–854

33. Strydom, T. *et al.* (2022) [Food web reconstruction through phylogenetic transfer of low-rank network representation](https://doi.org/10.1111/2041-210X.13835). *Methods in Ecology and Evolution* 13, 2838–2849

34. Blanchet, F.G. *et al.* (2020) [Co-occurrence is not evidence of ecological interactions](https://doi.org/10.1111/ele.13525). *Ecology Letters* 23, 1050–1063

35. Dansereau, G. *et al.* (2024) [Spatially explicit predictions of food web structure from regional-level data](https://doi.org/10.1098/rstb.2023.0166). *Philosophical Transactions of the Royal Society B: Biological Sciences* 379

36. Quintero, E. *et al.* (2024) [Downscaling mutualistic networks from species to individuals reveals consistent interaction niches and roles within plant populations](https://doi.org/10.1101/2024.02.02.578595)bioRxiv, 2024.02.02.578595

37. Stephens, D.W. and Krebs, J.R. (1986) [*Foraging Theory*](https://doi.org/10.2307/j.ctvs32s6b), 1, Princeton University Press

38. Canard, E. *et al.* (2012) [Emergence of Structural Patterns in Neutral Trophic Networks](https://doi.org/10.1371/journal.pone.0038295). *PLOS ONE* 7, e38295

39. Momal, R. *et al.* (2020) [Tree-based inference of species interaction networks from abundance data](https://doi.org/10.1111/2041-210X.13380). *Methods in Ecology and Evolution* 11, 621–632

40. Pomeranz, J.P.F. *et al.* (2019) [Inferring predator–prey interactions in food webs](https://doi.org/10.1111/2041-210X.13125). *Methods in Ecology and Evolution* 10, 356–367

41. Vázquez, D.P. *et al.* (2009) [Uniting pattern and process in plant–animal mutualistic networks: A review](https://doi.org/10.1093/aob/mcp057). *Annals of Botany* 103, 1445–1457

42. Pawar, S. *et al.* (2012) [Dimensionality of consumer search space drives trophic interaction strengths](https://doi.org/10.1038/nature11131). *Nature* 486, 485–489

43. Portalier, S.M.J. *et al.* (2019) [The mechanics of predator–prey interactions: First principles of physics predict predator–prey size ratios](https://doi.org/10.1111/1365-2435.13254). *Functional Ecology* 33, 323–334

44. Cherif, M. *et al.* (2024) [The environment to the rescue: Can physics help predict predator–prey interactions?](https://doi.org/10.1111/brv.13105) *Biological Reviews* 138

45. Pyke, G. (1984) [Optimal Foraging Theory: A Critical Review](https://doi.org/10.1146/annurev.ecolsys.15.1.523). *Annual Review of Ecology, Evolution and Systematic* 15, 523–575

46. Brown, J.H. *et al.* (2004) [Toward a Metabolic Theory of Ecology](https://doi.org/10.1890/03-9000). *Ecology* 85, 1771–1789

47. Ings, T.C. *et al.* (2009) [Ecological networks–beyond food webs](https://doi.org/10.1111/j.1365-2656.2008.01460.x). *The Journal of Animal Ecology* 78, 253–269

48. Golubski, A.J. and Abrams, P.A. (2011) [Modifying modifiers: What happens when interspecific interactions interact?](https://doi.org/10.1111/j.1365-2656.2011.01852.x) *Journal of Animal Ecology* 80, 1097–1108

49. Pilosof, S. *et al.* (2017) [The multilayer nature of ecological networks](https://doi.org/10.1038/s41559-017-0101). *Nature Ecology & Evolution* 1, 101

50. Staniczenko, P.P.A. *et al.* (2010) [Structural dynamics and robustness of food webs](https://doi.org/10.1111/j.1461-0248.2010.01485.x). *Ecology Letters* 13, 891–899

51. Kamaru, D.N. *et al.* (2024) [Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey](https://doi.org/10.1126/science.adg1464). *Science* 383, 433–438

52. Kéfi, S. *et al.* (2012) [More than a meal… integrating non-feeding interactions into food webs: More than a meal …](https://doi.org/10.1111/j.1461-0248.2011.01732.x). *Ecology Letters* 15, 291–300

53. Kéfi, S. *et al.* (2015) [Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores](https://doi.org/10.1890/13-1424.1). *Ecology* 96, 291–303

54. Buche, L. *et al.* (2024) [Multitrophic Higher-Order Interactions Modulate Species Persistence](https://doi.org/10.1086/729222). *The American Naturalist* 203, 458–472

55. Jordano, P. (2016) [Chasing Ecological Interactions](https://doi.org/10.1371/journal.pbio.1002559). *PLOS Biology* 14, e1002559

56. Strydom, T. *et al.* (2021) [A roadmap towards predicting species interaction networks (across space and time)](https://doi.org/10.1098/rstb.2021.0063). *Philosophical Transactions of the Royal Society B: Biological Sciences* 376, 20210063

57. Biton, B. *et al.* (2024) Inductive link prediction boosts data availability and enables cross-community link prediction in ecological networks

58. Stock, M. (2021) Pairwise learning for predicting pollination interactions based on traits and phylogeny. *Ecological Modelling*

59. Dallas, T. *et al.* (2017) [Predicting cryptic links in host-parasite networks](https://doi.org/10.1371/journal.pcbi.1005557). *PLOS Computational Biology* 13, e1005557

60. Stouffer, D.B. (2019) [All ecological models are wrong, but some are useful](https://doi.org/10.1111/1365-2656.12949). *Journal of Animal Ecology* 88, 192–195

61. Song, C. and Levine, J.M. (2024) [Rigorous (in)validation of ecological models](https://doi.org/10.1101/2024.09.19.613075)bioRxiv, 2024.09.19.613075

62. Estay, S.A. *et al.* (2023) Editorial: Patterns and processes in ecological networks over space. *Frontiers in Ecology and Evolution* 11

63. Saravia, L.A. *et al.* (2022) [Ecological network assembly: How the regional metaweb influences local food webs](https://doi.org/10.1111/1365-2656.13652). *Journal of Animal Ecology* 91, 630–642

64. Petchey, O.L. *et al.* (2011) [Fit, efficiency, and biology: Some thoughts on judging food web models](https://doi.org/10.1016/j.jtbi.2011.03.019). *Journal of Theoretical Biology* 279, 169–171

65. Schwarz, B. *et al.* (2020) [Temporal scale-dependence of plant–pollinator networks](https://doi.org/10.1111/oik.07303). *Oikos* 129, 1289–1302

66. Hubbell, S.P. (2001) [*The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*](https://www.jstor.org/stable/j.ctt7rj8w), Princeton University Press

67. Fortuna, M.A. and Bascompte, J. (2006) [Habitat loss and the structure of plant-animal mutualistic networks: Mutualistic networks and habitat loss](https://doi.org/10.1111/j.1461-0248.2005.00868.x). *Ecology Letters* 9, 281–286

68. Bascompte, J. *et al.* (2003) [The nested assembly of plant-animal mutualistic networks](https://doi.org/10.1073/pnas.1633576100). *Proceedings of the National Academy of Sciences* 100, 9383–9387

69. Banville, F. *et al.* (2023) [What constrains food webs? A maximum entropy framework for predicting their structure with minimal biases](https://doi.org/10.1371/journal.pcbi.1011458). *PLOS Computational Biology* 19, e1011458

70. Strydom, T. *et al.* (2021) [SVD Entropy Reveals the High Complexity of Ecological Networks](https://doi.org/10.3389/fevo.2021.623141). *Frontiers in Ecology and Evolution* 9

71. Canard, E.F. *et al.* (2014) [Empirical Evaluation of Neutral Interactions in Host-Parasite Networks.](https://doi.org/10.1086/675363) *The American Naturalist* 183, 468–479

72. Krishna, A. *et al.* (2008) [A neutral-niche theory of nestedness in mutualistic networks](https://doi.org/10.1111/j.1600-0706.2008.16540.x). *Oikos* 117, 1609–1618

73. Soberón, J. (2007) [Grinnellian and Eltonian niches and geographic distributions of species](https://doi.org/10.1111/j.1461-0248.2007.01107.x). *Ecology Letters* 10, 1115–1123

74. Gravel, D. *et al.* (2019) [Bringing Elton and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks](https://doi.org/10.1111/ecog.04006). *Ecography* 42, 401–415

75. Morales-Castilla, I. *et al.* (2015) [Inferring biotic interactions from proxies](https://doi.org/10.1016/j.tree.2015.03.014). *Trends in Ecology & Evolution* 30, 347–356

76. Shaw, J.O. *et al.* (2024) [A framework for reconstructing ancient food webs using functional trait data](https://doi.org/10.1101/2024.01.30.578036)bioRxiv, 2024.01.30.578036

77. Dunne, J.A. *et al.* (2008) [Compilation and Network Analyses of Cambrian Food Webs](https://doi.org/10.1371/journal.pbio.0060102). *PLOS Biology* 6, e102

78. Roopnarine, P.D. (2017) Ecological Modelling of Paleocommunity Food Webs. In *Conservation Paleobiology: Using the Past to Manage for the Future*, pp. 201–226, University of Chicago Press

79. Pichler, M. *et al.* (2020) [Machine learning algorithms to infer trait-matching and predict species interactions in ecological networks](https://doi.org/10.1111/2041-210X.13329). *Methods in Ecology and Evolution* 11, 281–293

80. Caron, D. *et al.* (2022) [Addressing the Eltonian shortfall with trait-based interaction models](https://doi.org/10.1111/ele.13966). *Ecology Letters* 25, 889–899

81. Llewelyn, J. *et al.* (2023) [Predicting predator–prey interactions in terrestrial endotherms using random forest](https://doi.org/10.1111/ecog.06619). *Ecography* 2023, e06619

82. Desjardins-Proulx, P. *et al.* (2017) [Ecological interactions and the Netflix problem](https://doi.org/10.7717/peerj.3644). *PeerJ* 5, e3644

83. Eklöf, A. *et al.* (2013) [Secondary extinctions in food webs: A Bayesian network approach](https://doi.org/10.1111/2041-210X.12062). *Methods in Ecology and Evolution* 4, 760–770

84. Cirtwill, A.R. *et al.* (2019) [A quantitative framework for investigating the reliability of empirical network construction](https://doi.org/10.1111/2041-210X.13180). *Methods in Ecology and Evolution* 10, 902–911

85. Yeakel, J.D. *et al.* (2014) [Collapse of an ecological network in Ancient Egypt](https://doi.org/10.1073/pnas.1408471111). *PNAS* 111, 14472–14477

86. Fricke, E.C. *et al.* (2022) [Collapse of terrestrial mammal food webs since the Late Pleistocene](https://doi.org/10.1126/science.abn4012). *Science* 377, 1008–1011

87. Dunhill, A.M. *et al.* (2024) [Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event](https://doi.org/10.1038/s41467-024-53000-2). *Nature Communications* 15, 8599

88. Higino, G.T. *et al.* (2023) [Mismatch between IUCN range maps and species interactions data illustrated using the Serengeti food web](https://doi.org/10.7717/peerj.14620). *PeerJ* 11, e14620

89. Pollock, L.J. *et al.* (2014) [Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM)](https://doi.org/10.1111/2041-210X.12180). *Methods in Ecology and Evolution* 5, 397–406

90. Petchey, O.L. *et al.* (2008) [Size, foraging, and food web structure](https://doi.org/10.1073/pnas.0710672105). *Proceedings of the National Academy of Sciences* 105, 4191–4196

91. Wootton, K.L. *et al.* (2023) [Towards a modular theory of trophic interactions](https://doi.org/10.1111/1365-2435.13954). *Functional Ecology* 37, 26–43

92. Krause, A.E. *et al.* (2003) [Compartments revealed in food-web structure](https://doi.org/10.1038/nature02115). *Nature* 426, 282–285

93. Allesina, S. *et al.* (2008) [A General Model for Food Web Structure](https://doi.org/10.1126/science.1156269). *Science* 320, 658–661

94. Allesina, S. and Pascual, M. (2009) [Food web models: A plea for groups](https://doi.org/10.1111/j.1461-0248.2009.01321.x). *Ecology Letters* 12, 652–662

95. Lajaaiti, I. *et al.* (2024) [EcologicalNetworksDynamics.jl A Julia package to simulate the temporal dynamics of complex ecological networks](https://doi.org/10.1101/2024.03.20.585899)bioRxiv, 2024.03.20.585899

96. Delmas, E. *et al.* (2017) [Simulations of biomass dynamics in community food webs](https://doi.org/10.1111/2041-210X.12713). *Methods in Ecology and Evolution* 8, 881–886

97. Curtsdotter, A. *et al.* (2019) [Ecosystem function in predator–prey food webs—confronting dynamic models with empirical data](https://doi.org/10.1111/1365-2656.12892). *Journal of Animal Ecology* 88, 196–210

98. Williams, R.J. and Martinez, N.D. (2008) [Success and its limits among structural models of complex food webs](https://doi.org/10.1111/j.1365-2656.2008.01362.x). *Journal of Animal Ecology* 77, 512–519

99. Berlow, E.L. *et al.* (2008) [The “Goldilocks factor” in food webs](https://doi.org/10.1073/pnas.0800967105). *Proceedings of the National Academy of Sciences* 105, 4079–4080

100. Keyes, A.A. *et al.* (2024) [Synthesising the Relationships Between Food Web Structure and Robustness](https://doi.org/10.1111/ele.14533). *Ecology Letters* 27, e14533

101. Delmas, E. *et al.* (2019) [Analysing ecological networks of species interactions](https://doi.org/10.1111/brv.12433). *Biological Reviews* 94, 16–36

102. Hui, C. and Richardson, D.M. (2019) [How to Invade an Ecological Network](https://doi.org/10.1016/j.tree.2018.11.003). *Trends in Ecology & Evolution* 34, 121–131

103. Van De Walle, R. *et al.* (2023) [Arthropod food webs predicted from body size ratios are improved by incorporating prey defensive properties](https://doi.org/10.1111/1365-2656.13905). *Journal of Animal Ecology* 92, 913–924

104. Becker, D.J. *et al.* (2022) [Optimising predictive models to prioritise viral discovery in zoonotic reservoirs](https://doi.org/10.1016/S2666-5247(21)00245-7). *The Lancet Microbe* 3, e625–e637

105. Terry, J.C.D. and Lewis, O.T. (2020) [Finding missing links in interaction networks](https://doi.org/10.1002/ecy.3047). *Ecology* 101, e03047

106. Roopnarine, P.D. (2006) [Extinction Cascades and Catastrophe in Ancient Food Webs](https://www.jstor.org/stable/4096814). *Paleobiology* 32, 1–19

107. Wells, K. and O’Hara, R.B. (2013) [Species interactions: Estimating per-individual interaction strength and covariates before simplifying data into per-species ecological networks](https://doi.org/10.1111/j.2041-210x.2012.00249.x). *Methods in Ecology and Evolution* 4, 1–8

108. Poisot, T. (2023) [Guidelines for the prediction of species interactions through binary classification](https://doi.org/10.1111/2041-210X.14071). *Methods in Ecology and Evolution* 14, 1333–1345

109. Danet, A. *et al.* (2024) [Response diversity is a major driver of temporal stability in complex food webs](https://doi.org/10.1101/2024.08.29.610288)bioRxiv, 2024.08.29.610288

110. Wooster, E.I.F. *et al.* (2024) [Australia’s recently established predators restore complexity to food webs simplified by extinction](https://doi.org/10.1016/j.cub.2024.09.049). *Current Biology* 34, 5164–5172.e2