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

Tanya Strydom

Jennifer A. Dunne

Timothée Poisot

Andrew P. Beckerman

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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. Here we present a synthesis of the different assumptions, scales and mechanisms that are used to define different ecological networks ranging from metawebs (an inventory of all potential interactions) to fully realised networks (interactions that occur within a given community over a certain timescale). Illuminating the assumptions, scales, and mechanisms of network inference allows a formal categorisation of how to use networks to answer key ecological and conservation questions and defines 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. These relate to the abundance, distribution and services that biodiversity provides, and how biodiversity – as an interconnected set of species – responds to multiple stressors. The interaction between species is one of the fundamental building blocks of ecological communities, providing a powerful abstraction that can help quantify, conceptualise, and understand biodiversity dynamics, and ultimately, make predictions, mitigate change, and manage services. Such network representations of biodiversity (including within species diversity) are increasingly argued to be an asset to predictive ecology, climate change mitigation and resource management. Here, it is argued that characterising biodiversity in a network will allow deeper capacity to understand and predict the abundance, distribution, dynamics and services provided by multiple species facing multiple stressors.

A ‘network’ can be defined and conceptualised in a myriad of ways, which means that different networks will be embedding different processes (or determinants) of interactions, ultimately influencing the patterns and mechanisms that are inferred [1,2]. The different ways in which a network can be represented is the result of *how* the network is constructed, which itself rests on two pillars: the data used to construct the network and the underlying theory as to what drives the interactions between species. The latter represents an expression of mechanism and process that gives rise to the patterns that emerge from collating interactions among species, and will ultimately inform which data are deemed important in the determination of interactions occurring. Each of these pillars carries with it a set of practical, semantic and conceptual constraints that not only influence progress in making network ecology more valuable and potentially predictive, but help define the spatial, temporal, and evolutionary scale of assumptions we make and the predictions we might generate from different network representations.

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 network, and how this influenced by both the processes that determine networks as well as how this relates to the way in which we construct networks. The provision of this detail ultimately leads to a set of insights and conclusions about whether, when and under what conditions network representations of biodiversity can contribute to the advancement of ecological theory and generate value in predictive ecology. 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 multiple stressors 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 the interactions (edges) between species (nodes), however the definition of ‘edges’ and ‘nodes’, as well as the scale at which they are aggregated can take many forms [3], which ultimately encodes 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 [2] or prediction process [4]. One thus needs to be aware of both the criteria that is used to define nodes and edges, and what processes or mechanisms the aggregation of the two represents, as this will determine what the network can be used for.

### 1.0.1 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 an aggregation of different species - so called ‘trophic species’ [5,6] or segregation of species by life stages [7]. Practical implications of how we are aggregating the nodes is that the resolution may not always be ‘pixel perfect’, which limits the ability to make (taxonomic) species specific inferences *e.g.,* does species eat species , however there is value in having nodes that represent an aggregation of species, as the distribution of the links between them are more meaningful in terms of understanding energy flow and distribution within the system.

### 1.0.2 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 [8] or potential [9], alternative links can represent fluxes within the system *e.g.,* energy transfer or material flow as the result of the feeding links between species [10]. Fundamentally this means that the links within a network represent different ‘currencies’ (either the feasibility of a link existing between two species or the energy that is moving through the system) and how the links within a network 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 (*i.e.,* a metaweb) will be meaningless if one is interested in understanding the flow of energy through the network as the links within a metaweb do not represent environmental/energetic constraints, making them poor representations of which interactions are *realised* in a specific location [11]. 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 [4,which quantifies how likely an interaction is to occur, 12] or continuous measurements [which quantifies the strength of of an interaction, 13].

### 1.0.3 Network representations

Broadly, 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 [9], and realised networks; which is the subset of interactions in a metaweb that are *realised* at a given time and place. The fundamental difference between these two different network representations is that a metaweb provides insight as to the viability of an interaction between two species occurring and is a means to identify links that are not ecologically plausible, *i.e.,* forbidden links [14], or provide an idea of the *complete* diet of a species [15]. In contrast realised networks are highly localised and links between species are contingent on both the co-occurrence of species as well as the influence of the environment, and population and community dynamics on predator choice. In the context of definitions and semantics the links that are represented by a metaweb and a realised network are different; links that are absent in a metaweb can be treated as being truly absent, however links that are absent in a realised network cannot be considered to be truly absent but are 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 represents a shift towards capturing the 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 as well as the resulting network structure.

# 2. From Nodes and Edges to Scale, Context, and Process

The interplay between network representation and network (node and edge) definition is primarily governed by the process(es) that determine the interaction between species, however these processes are also scale and context dependent. Here we start by introducing the five core processes that determine either the feasibility or the realisation of interactions, namely: evolutionary compatibility, co-occurrence, abundance, predator choice, and non-trophic interactions; while simultaneously contextualising them within, and linking them to the different network representations [Figure 1](#fig-process). We can think of the different network representations to be conceptually analogous to the fundamental and realised niche, whereby the metaweb represents the ‘fundamental diet niche’ of a species and a realised network represents the ‘realised diet’ of a species. Of course these processes do not function in a vacuum and do interact with/influence one another, but it is still beneficial to present them in a categorical manner as these different processes are often the underpinning logic in the development of prediction/network models, the criteria for data collection in the field, and the scale of organisation for which they are relevant (species, population, or community).

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| Figure 1: Aligning the various processes that determine interactions with the different network representations. First we start with a ‘global metaweb’ this network which captures all possible interactions for an arbitrary collection of species, we can further refine this network by taking in to consideration the co-occurrence of these 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 (pink) or region two (orange). These regional metawebs to capture all possible interactions, however it only considers species that co-occur. However even within a region we do not expect 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 network realisations 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, maximising energy gain, or indirect/higher order interactions. |

## 2.1 The processes that determine species interactions

**Evolutionary compatibility**

There is compelling evidence that an interaction occurring between two species is the result of their shared (co)evolutionary history [16–18] which, in the more proximal sense, is manifested as the ‘trait complementarity’ between two species, whereby one species (the predator) has the ‘correct’ set of traits that allow it to chase, capture, kill, and consume the other species (the prey). For species pairs where this condition is not met the link is deemed to be forbidden [14]; *i.e.,* not physically possible and will always be absent within a network. A network constructed on the basis of evolutionary compatible links is most closely aligned with a metaweb, although it would not be required that the species co-occur (as shown in [Figure 1](#fig-process)), and arguably makes for a good approximation of the ‘Eltonian niche’ of species [19]. Finally, one should be aware that it is possible to represent evolutionary compatible interactions as either binary (possible vs forbidden) or as a probability [4], where the probability represents how likely the interaction between two species is to be possible.

**(Co)occurrence**

Although the outright assumption that because two species are co-occurring it must mean that they are interacting is flawed [20], it is of course impossible for two species to interact (at least in terms of feeding links) if they are not co-occurring in time and space. Thus, although co-occurrence data alone is insufficient to build an accurate and ecologically meaningful representation of *feeding links* it is still a critical process that determines the realisation of feeding links and allows us to constrain a global metaweb to only consider ‘realised’ communities [21] and an understanding of the intersection of species interactions and their co-occurrence is meaningful when one is operating in the space of trying to determine the distribution of a species [22,23].

**Abundance**

The abundance of different the species within the community is thought to influence the realisation of feeding links primarily in two ways. Firstly there is the argument that that structure of networks (and the interactions that they are composed of) are driven *only* by the abundance of the different species and that interactions are not contingent on there being any compatibility (trait matching) between them, *sensu* neutral processes [24,25]. However, a more ecologically sound assumption would be that the abundance of different prey species will influence which prey are targeted or preferred by the predator as abundance influences factors such as the likelihood of species meeting [4,26], or in the dynamic sense will influence the persistence of viable populations.

**Predator choice (energetic cost)**

Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume prey (where a predator will optimise energy while minimising handling and search time), and is well described within both optimal foraging [27] and metabolic theory [28]. The energetic cost of feeding is itself influenced by the interplay of both the energy content [*i.e.,* body size; [29]] as well as the density (abundance) of prey (as this influences search time) and as a process will influence which links are realised [Figure 1](#fig-process). Additional work on on understanding the energetic cost that the environment imposes on an individual [30] as well as the way a predator uses the landscape to search for prey [31] is bringing us closer to accounting for the energetic cost of realising feeding links.

**Non-trophic interactions**

Perhaps not as intuitive when thinking about the processes that determine feeding links (trophic interactions) is thinking about the role of the ability of non-trophic interactions to modify either the realisation or strength of trophic interactions [32,33]. 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 [34–36]. The ‘unobservable’ nature of non-trophic interactions makes them a challenge to quantify, however their importance in network dynamics should not be overlooked [37]

## 2.2 Contextualising the processes that determine species interactions

It should be self evident that the different processes discussed above are all ultimately going to influence the realisation of interactions as well as the structure of a network, however they are acting at different scales of organisation. Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of 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, and so just because species are able to interact does not mean that they will [26]. In order to construct a network who’s structure is a closer approximation of reality (localised interactions) one needs to take into consideration the properties of the community as a whole and not just the two species of interest, which requires more data at the community scale, such as the abundance of species.

# 3. Network construction is nuanced

The act of constructing a ‘real world’ network will ultimately be delimited by its intended use, however the reality is that the empirical collection of interaction data is both costly and challenging to execute [14,38], especially if one wants to capture *all* aspects of the processes discussed in [Section 2](#sec-process) (owing to the different time and spatial scales they may be operating at). Thus we often turn to models to either predict networks (be that the interaction between two species, or network structure [39]), or as a means to identify missing interactions (gap fill) within an existing empirical dataset [40–42], and so for the purpose of this discussion network construction will be synonymous with using a model as a means to represent or predict a network. That is not to say that there is no need for empirical data collection but rather that using a model for food web prediction (or reconstruction) is a more feasible approach as it allows us to make inferences about interactions that are not happening in the ‘observable now’ [39], with the added benefit that one is able to build some uncertainty into the resulting network [4]. Additionally different models have different underlying philosophies that allow us to capture one or a few of the processes discussed in [Section 2](#sec-process), and although the delimits and defines what inferences can be made from the resulting network it also allows us to isolate and understand how different processes determine interactions [43,44]. Here we will introduce the three different types of network representations (metawebs, realised networks, and structural networks), how they link back to (and encode) the different processes determining interactions [Figure 1](#fig-process), and broadly discuss some of the modelling approaches that are used to construct these different network types. This is paralleled by a hypothetical case study (Box 1) where we showcase the utility/applicability of the different network representations in the context of trying to understand the feeding dynamics of a seasonal community.

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| 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 across time/through 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 diet shifts, these details would be lost at the scale of the metaweb an it would be valuable 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). 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 exercises (where does the new species ‘fit’ within the network?) as well as potential capacity to shift its diet. ALthough this might make sense across space and not time but certain species act as links across the landscape.  **2: A seasonal metaweb**  Knowledge at the finer scale is also valuable to understand/identify that there are in fact differences between the seasons  **3: A seasonal realised network**  Dynamics are useful because they are a representation of the different configurations/energy flows/ecosystem processes. Also to detect more nuanced shifts in diet - *e.g.,* seasonal diet shifts.  **4: A structural network**  **Data trade off**  Above we highlight the practical uses of the different network configurations but we also need to take into consideration the barriers to construction/associated data needs/cost and acknowledge them. Basically in the ideal world we would have all this information at hand but in reality we might be sitting with seasonal metawebs… |

## 3.1 Models that predict metawebs (feasible interactions)

This is perhaps the most developed group of models; with a variety of approaches having been developed that typically determine the feasibility of an interaction using the trait compatibility between predator and prey (*i.e.* their evolutionary compatibility) to determine ‘feeding rules’ [45]. These feeding rules are broadly elucidated in two different ways; mechanistic feeding rules can be explicitly defined and applied to a community [*e.g.,* 46,47] or they are inferred from a community for which there are interaction data and the ‘rules’ are then applied to a different community [*e.g.,* 15,48–54]. 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 datasets from which to elucidate feeding rules. These models are useful for determining all feasible interactions for a specific community, and owing to the availability of empirical interaction datasets [*e.g.,* 55,56,57], as well as the development of model testing/benchmarking tools [58], means that these models can be validated and (with relative confidence) be used to construct first draft networks for communities for which we have no interaction data [49], and are valuable not only in data poor regions but also for predicting interactions for ‘unobservable’ communities *e.g.,* prehistoric networks [59,60] or future, novel community assemblages. Importantly metawebs are inherently ‘static’ in the sense that they are *not* able to capture dynamic processes (since the notion of feasibility is all or nothing), however they provide a bigger picture context (*e.g.,* understanding the *entire* diet breadth of a species) and often require little data to construct.

## 3.2 Models that predict realised networks (realised interactions)

In order to construct realised networks models need to incorporate *both* the feasibility of interactions (*i.e.,* determine the entire diet breadth of a species) as well as then determine which interactions are realised (*i.e.,* incorporate the ‘cost’ of interactions). As far as we are aware there is no model that explicitly accounts for both of these ‘rules’ and rather *only* account for processes that determine the realisation of an interaction (*i.e.,* abundance, predator choice, or non-trophic interactions). Although the use of allometry *i.e.,* body size [*e.g.,* 61,62] may represent a first step in capturing ‘evolutionary compatibility’ alongside more energy (predator choice) driven processes we still need to account for other traits that determine feeding compatibility [*e.g.,* 63 show how incorporating prey defensive properties alongside body size improves predictions]. In terms of constructing realised networks, diet models [62,64] have been used construct networks based on both predator choice (as determined by the handling time, energy content, and predator attack rate) as well as abundance (prey density) and progress has also been made in understanding the compartmentation of energy in networks and how this influences energy acquisition [65,66]. As realised networks are are build on the concept of dynamic processes (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 [67–69]. However, the 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 context afforded by metawebs.

## 3.3 Models that predict structure (interaction agnostic)

Although we identify mechanisms that determine species interactions in [Section 2](#sec-process) not all models that are used to predict networks explicitly operate at the ‘process’ level, but rather represent the *structure* of a network based on a series of *a priori* assumptions as to the distribution of links between species (typically trophic not taxonomic species). These models operate by parametrising an aspect of the network structure, (*e.g.,* the niche model [6] makes an assumption as to the expected connectance of the network,although see [70] for a parameter-free model) or alternatively uses structural features of an exiting *realised* network (*e.g.,* stochastic block model, [71]). Importantly these structural models do not make species specific predictions (they are usually species agnostic and treat nodes as trophic species) 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 [72], and 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) way to construct a network.

# 4. Making Progress with Networks

## 4.1 Further development of models and tools

There has been a suite of models that have been developed to predict feeding links, however we are lacking in tools that are explicitly taking into consideration estimating both the feasibility as well as realisation of links, *i.e.,* both interactions and structure simultaneously [39]. This could be addressed either through the development of tools that do both (predict both interactions and structure), or to develop an ensemble modelling approach [73,74] or tools that will allow for the downsampling of metawebs into realised networks [*e.g.,* 75]. Additionally although realised networks are more closely aligned with capturing interaction strength we lack models that allow us to quantify this [39,76]. In addition to the more intentional development of models we also need to consider the validation of these models, there have been developments and discussions for assessing how well a model recovers pairwise interactions [39,58], although the rate of false-negatives that may be present in the testing data still present a challenge [77], we still lack clear set of guidelines for benchmarking the ability of models to recover structure [78].

## 4.2 At what scale should we be predicting and using networks?

We lack an understanding of which processes drive the differences between different scales [79], as well as to what the appropriate level of aggregation is for a ‘network’ [80]. Which presents a challenge both in deciding what the appropriate spatial and time scales are for constructing not only a network but also which type of network representation. Space influences both network properties [81], as well as dynamics [82,83], and time has implications when it comes to accounting for seasonal turnover in communities [84,85] as well as thinking co-occurrence, particularly the records used to determine it [86]. Although multilayer networks may allow us to encode the nuances of space and time [87] we still need to understand the implications of *e.g.,* constructing networks that are not at ecologically but rather politically relevant scales [49] and what we can learn or infer from networks a these scales.

# 5. The future value of networks

developing a dictionary of use… that helps navigate between the levels and assumptions

It should be clear that there is a high degree of interrelatedness and overlap between the way a network is constructed (modelled or predicted) and the process(es) it captures, these are encoded (embedded) within the network representation and ultimately influences how the network can and should be used [88,89]. 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 90] that has stifled the ‘productive use’ of networks beyond 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 [91] and co-existence theory [92], has been made we still need to have a discussion on what the appropriate network representation for the task at hand would be. This is highlighted in Box 1, and underscores that we need to evaluate exactly what process a specific network representation captures as well as its suitability for the question of interest.

An informative table

| Question (broad) | Question (specific) | Network representation |
| --- | --- | --- |
| Species invasions | What species will the invading species interact with? | Regional metaweb but need to derive information from a global metaweb since these are interactions that are ‘novel’ |
| Species invasions | How does the invading species alter network dynamics and function? | Realised network (after having moved through the global metaweb to understand which interactions are feasible) |
| Range shifts and novel communities | Under global change how will novel community assemblages interact? | Global metaweb, need context of broader community |
| Extinctions | Cascading effect of the loss of a species from the network | Regional metaweb - need to account for entire diet, a realised network will exclude the entire diet but will allow to elucidate the final structure |
| Species/community persistence | Dynamics over time. Stability/resilience. How does a change in pop *A* affect pop *B*? | Realised networks - but dynamic! |
| Synthetic networks | Creating ecologically plausible communities for synthetic analyses | Structural networks - data light! |
| Practical use | What is both attainable (data constraints) but also of practical use to ‘real world’ decision making. So moving from theory to applied | ??Regional metawebs?? |

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