

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

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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.

Keywords: food web, network construction, scientific ignorance

1 At the heart of modern biodiversity science are a set of concepts and theories about biodiversity, stability
2 and function. These relate to the abundance, distribution and services that biodiversity provides, and how
3 biodiversity – as an interconnected set of species – responds to multiple stressors. The interaction between
4 species (or individuals) is one of the fundamental building blocks of ecological communities provide a powerful
5 abstraction that can help quantify, conceptualise, and understand biodiversity dynamics, and ultimately,
6 one hopes, make prediction, mitigate change and manage services [ref]. Such network representations of
7 biodiversity (including within species diversity) are increasingly argued to be an asset to predictive ecology,
8 climate change mitigation and resource management. Here, it is argued that characterising biodiversity in
9 a network will allow deeper capacity to understand and predict the abundance, distribution, dynamics and
10 services provided by multiple species facing multiple stressors.

11 However, the way that a network is constructed (encoded) defines an epistemology of the network concept
12 which, we argue, can influence the resulting observations and conclusions about pattern and mechanisms
13 that are made (Brimacombe et al., 2023; Proulx et al., 2005). This process of constructing networks has two
14 major pillars: the data and theory, the latter representing an expression of mechanism and process giving
15 rise to patterns that emerge from collating interactions among species. Each of these pillars carries with it
16 a set of practical, semantic and conceptual constraints that not only influence progress in making network
17 ecology more valuable and potentially predictive, but help define the spatial, temporal and evolutionary scale
18 of assumptions we make and predictions we might generate from the networks.

19 With respect to data, it is extremely challenging to actually record species interactions in the field (Jordano,
20 2016a, 2016b). Despite notable herculean efforts (**Woodward? Benguela?** Maiorano et al. (2020)), actual
21 coverage of ‘real world’ interaction data remains sparse (Poisot et al., 2021). Against this practical challenge,
22 there is additionally high variance in the terminology we use to define networks. Finally, the mathematical
23 and statistical tools we use to construct, conceptualise, analyse and predict with these networks are also
24 highly variable.

25 1. what are the underlying assumptions about nodes, edges, scale and process that are made when we
26 attempt to delimit and describe a food webs;

27 2. are there families of commonly used tools that map onto assumptions about scales and processes;

28 The provision of this detail ultimately leads to a set of insights and conclusions about whether, when and
29 under what conditions network representations of biodiversity can contribute to the advancement of ecological
30 theory and generate value in predictive ecology. Specifically, we finish this perspective with an overview of
31 fundamental questions in ecology that we think can benefit from network thinking and a proposal that such

32 thinking can accelerate our capacity to predict the impact of multiple stressors on biodiverse communities.

33 1 Setting the Scene: The Not So Basics of Nodes and Edges

34 Defining a food web seems simple; it is the representation of the interactions (edges) between species (nodes),
35 however the definition of ‘edges’ and ‘nodes’, as well as the scale at which they are aggregated can take many
36 forms (Poisot, Stouffer, et al., 2016). An awareness of variance in the way a food web can be defined is critical
37 as it represents the ‘object’ that is used to make inferences either about the interactions between species, or
38 how the structure influences ecosystem level processes. One thus needs to be aware of both the criteria that
39 is used to define nodes and edges, and what processes or mechanisms the aggregation of the two represents,
40 as this will ultimately determine and delimit the way in which a network should be used.

41 1.0.1 How do we define a node?

42 Although this may seem an elementary question in the context of food webs — a node *should* represent a
43 (taxonomic) species, the reality is that nodes can often represent an aggregation of different species - so called
44 ‘trophic species’ or segregation of species by life stages. Representing nodes as non-taxonomic species can be
45 useful in certain contexts (Williams & Martinez, 2000; Yodzis, 1982) and in cases where the adult and larval
46 stages of a species have different diets it may make ecological sense (Clegg et al., 2018) meaning that it is
47 not uncommon that networks often have nodes that have different definitions of a ‘species’ *e.g.* consisting
48 of both taxonomic and trophic species. Practical implications of how we are aggregating the nodes is that
49 the resolution may not always be ‘pixel perfect’ *i.e.*, we may be unable to assess the co-extinction risk of a
50 species pair, however there is value in having nodes that represent an aggregation of species, as these convey
51 a much more general overview of how the links are distributed within the community.

52 1.0.2 What is meant by an edge?

53 At its core, links within food webs can be thought of as a representation of either feeding links between
54 species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within
55 the community/system *e.g.*, energy transfer or material flow (Lindeman, 1942). How we specify links will
56 influence the resulting structure of the network - and the inferences we will make thereof. For example taking
57 a food web that consists of links representing all *potential* feeding links for a community (*i.e.*, a metaweb)
58 will be meaningless if one is interested in understanding the flow of energy through the network as the links
59 within a metaweb do not represent environmental/energetic constraints. In addition to the various ways of
60 defining the links between species pairs there are also a myriad of ways in which the links themselves can

61 be quantified. Links between species are often treated as being present or absent (*i.e.*, binary) but it is
62 also possible to use probabilities (Banville et al., 2024; which quantifies how likely an interaction is to occur,
63 Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of of an interaction,
64 Berlow et al., 2004).

65 **1.0.3 Network representations**

66 Broadly, networks can be thought of to fall into two different ‘types’; namely metawebs; traditionally defined
67 as all of the *potential* interactions for a specific species pool (Dunne, 2006), and realised networks; which is the
68 subset of interactions in a metaweb that are *realised* ‘on the ground’. The fundamental difference between these
69 two different types of networks is that a metaweb provides insight as to the viability of an interaction between
70 two species occurring and is a means to identify links that are not ecologically plausible, *i.e.*, forbidden links
71 (Jordano, 2016b), or an idea of the *complete* diet of a species (Strydom et al., 2023). Although metawebs
72 are typically ‘constrained’ to a collection of species that also co-occur, there is no reason that a metaweb
73 can include species that do not co-occur (although this would require some degree of prediction/assumption
74 to identify those possible interactions). In contrast realised networks are highly localised and contingent on
75 both the co-occurrence of species as well as the influence of the environment, and population and community
76 dynamics on predator choice. In the context of definitions and semantics the links that are represented by a
77 metaweb and a realised network are different; links that are absent in a metaweb can be treated as being truly
78 absent, however links that are absent in a realised network cannot be considered to be truly absent but are
79 rather as absent due to the broader environmental/community context. Importantly, a realised network is *not*
80 simply the downscaling of a metaweb to a smaller scale (*e.g.*, moving from the country to the 1x1 km² scale
81 based on fine-scale species co-occurrence) but represents a shift towards capturing the higher level processes
82 that determine the *realisation* of an interaction. Thus, metawebs and realised networks are determined and
83 constrained by a different set of assumptions as to what processes are determining the presence/absence of
84 an interaction between two species as well as the resulting network structure.

85 **2 From Nodes and Edges to Scales, Context, and Processes**

86 Armed with these basics, it is now possible to review the scales and assumptions that are made by a wide range
87 of tools to assist in constructing networks against poor data with the hope of capturing important processes
88 that underpin accurate prediction. Our thesis centres on a five-tier conceptualization of networks: evolution-
89 ary compatibility, co-occurrence, feasibility, abundance, predator choice, and non-trophic interactions. In
90 the following sections we review each of these and then provide a synthesis among them.

2.1 Understanding the processes that determine species interactions

92 Processes that are all-or-nothing (possibility) vs processes that are context dependent (likelihood). Processes
93 form the underlying logic of models (and arguably, no, for sure even empirical data). This means also the
94 interplay of the two, *i.e.*, the use of models to ‘gap fill’ within existing empirical dataset (Biton et al., 2024;
95 Stock, 2021). Ultimately when we put this all together it will influence how we can (and should) use the
96 resulting network. Here we present Figure 1 some of the processes that have been shown to influence either/or
97 the feasibility (possibility) of an interaction occurring between two species or if a feasible interaction is realised
98 (likelihood of realisation) within the specific environmental/community context. Of course these processes
99 do not function in a vacuum and do interact with/influence one another but it is still beneficial to present
100 them as such as these are often the underlying processes that influence model development, the criteria for
101 data collection in the field, and the scale of organisation for which they are relevant (species, population,
102 community).

[Figure 1 about here.]

104 Evolutionary compatibility

105 There is compelling evidence that the possibility of an interaction occurring between two species is the result
106 of their shared (co)evolutionary history (Dalla Riva & Stouffer, 2016; Gómez et al., 2010; Segar et al., 2020).
107 In the more proximal sense this is manifested as the ‘trait complementarity’ between two species, whereby
108 one species (the predator) has the ‘correct’ set of traits that allow it to chase, capture, kill, and consume
109 the other species (the prey). For species pairs where this condition is not met the link is deemed to be
110 forbidden (Jordano, 2016b); *i.e.*, not physically possible and will always be absent within the network. In the
111 context of trying to determine the feasibility (*i.e.*, the *possibility*) of an interaction, phylogeny is an excellent
112 predictor (Fricke et al., 2022; Strydom et al., 2022) and allows one to construct what can be considered to
113 be a metaweb. In terms of thinking about the anatomy of an ‘feasibility network’ one should be aware that
114 it is possible to represent interactions as either binary (feasible/forbidden; *i.e.*, the traditional definition of a
115 metaweb Dunne (2006)) or as a probability (Banville et al., 2024), where the probability represents how likely
116 that the interaction between two species is feasible (what is the possibility of this interaction occurring?).

117 (Co)occurrence

118 Although the outright assumption that because two species are co-occurring it must mean that they are
119 interacting is inherently flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at
120 least in terms of feeding links) if they are not co-occurring in time and space. Thus co-occurrence data alone is
121 insufficient to build an accurate and ecologically meaningful representation of a food web having information

on the co-occurrence of species can further aid us in refining metawebs by allowing us to downsample the network based on the species found in a specific location, or even add additional uncertainty based in how likely species are to co-occur (**dansereauSpatiallyExplicitPredictions2023?**). Additionally the interplay between the interaction between a species pair and their co-occurrence is meaningful when one is operating in the space of trying to determine the distribution of a species (Higino et al., 2023), and forms a key component of some of the next generation species distribution models *e.g.*, joint SDMs (Pollock et al., 2014).

128 **Abundance**

The abundance of the different species within the community can influence the likelihood of an interaction occurring in a myriad of ways. There is the argument that networks (and the interactions that make them up) are driven by only the abundance of the different species and not the characteristics (traits), *sensu* neutral processes and have been formalised with the neutral model (Canard et al., 2012), as well as statistical tools (Momal et al., 2020). Alternatively the abundance of species in a community can influence which interactions are ultimately realised (Banville et al., 2024; Poisot et al., 2015).

135 **Predator choice (energetic cost)**

Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume prey, and is well described within optimal foraging theory [ref] and rests on the idea that the prey a predator chooses to target is one that will have the greatest return on energy with the lowest energetic cost. There are additional bodies of work that attempt to include the cost of movement that the environment imposes on an individual (Cherif et al., 2024) as well as 2D/3D search space (Pawar et al., 2012). In terms of formalising these processes in the context of predicting networks using diet models (Beckerman et al., 2006; Petchey et al., 2008) that have predator choice determined by the handling time, energy content, prey density, and predator attack rate. Wootton et al. (2023) developed a model that moves the energy of the system into different modules related to the process of the predator acquiring energy from the prey *i.e.*, compartmentation in food webs (Krause et al., 2003).

146 **Indirect interactions**

The realisation (presence/absence) or strength of trophic interactions themselves can also be modified by other, indirect (non-trophic), interactions (Golubski & Abrams, 2011; Pilosof et al., 2017), this can be either ‘directly’ through *e.g.*, competition or ‘indirectly’ *e.g.*, mutualistic/facilitative interactions will alter the fine-scale distribution and abundance of some species (Kéfi et al., 2012, 2015).

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 (*i.e.*, community context), just because species are able to interact does not mean that they will (Poisot et al., 2015). In order to construct a network who’s structure is a closer approximation of reality (localised interactions) one needs to take into consideration properties of the community as a whole and not just the two species of interest.

downsampling paragraph??

3 Network prediction is nuanced

The different models that are used to either predict or construct networks have an underlying philosophy that often only captures one or a few of the processes discussed in Section 2.1, has implications for how the resulting network is defined Section 1, which will ultimately delimit and define what inferences can be made from the resulting network. Selecting a model for the task of network prediction should come down to two things; what *aspect* of a food web one is interested in predicting, and what data are available, necessary, and sufficient, and what is the purpose of wanting to predict a network? It is important that a researcher is aware of this to ensure that the appropriate model is selected. Broadly researchers will be interested in predicting/constructing two different types of networks; *metawebs*, which is essentially a list of all interactions that are *possible* for a specific community (*i.e.*, at the scale of the species pairs), or being able to predict location specific, *realised*, networks for the community (*i.e.*, at the scale of the community). The nature of metawebs means that they are unable to capture the structural metrics of realised/‘real-world’ networks (Caron et al., 2024). The researcher is also constrained by the data needs of both the model as well as the network type; for example in order to predict a realised network one needs additional community/population level data (*e.g.*, abundance), making metawebs a more feasible choice in data-poor contexts (*e.g.*, Strydom et al. (2023) construct a metaweb using a species list and a phylogenetic tree). The final question is assessing the purpose of predicting a network - is it to create a series of simulated, species agnostic but still ecologically plausible, networks [*e.g.*,] or to predict a network for a specific community at a specific location. It is these three points that will ultimately dictate which model is going to best allow one to predict the appropriate network.

182 **3.1 How do we predict food webs?**

183 There as many ways to predict networks as what there is to define them and along with taking into consid-
184 eration the points raised in the previous section it is also beneficial to think about the context in which the
185 different models were developed - and how this will influence the networks that they produce...

186 There is a bit of a ‘point of conflict’ between those calling for ‘pixel perfect’, regional scale data (Pringle,
187 2020; Pringle & Hutchinson, 2020) and for the means to generate networks that are ecologically plausible
188 *representations* (*sensu* structural networks). This represents two challenges; one is that models that repre-
189 sent generalisations of networks often lack the ability to retrieve any species/community specificity which
190 limits their utility for real world, species-driven scenarios *e.g.*, species driven conservation efforts (Dunn et
191 al., 2009), however networks that are constructed through either (most) empirical observations or through
192 predictive means are fundamentally going to represent metawebs, *i.e.*, lack constrained links, a representation
193 of structure, or energy flow...

i 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 and 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 in 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
[Rooney]

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.

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...

195

196 3.1.1 Models that predict structure

197 Although we identify mechanisms that determine species interactions in Section 2.1 not all models that are
198 used to predict networks operate at this ‘mechanistic’ level (at least in absolute terms), but rather represent
199 the *structure* of a network based on a series of *a priori* assumptions of network connectance (*e.g.*, the niche
200 model Williams & Martinez (2000); although see Allesina & Pascual (2009) for a parameter-free model) or
201 other structural features of a *realised* network (*e.g.*, stochastic block model, Xie et al. (2017)). Importantly
202 these structural models do not make species specific predictions (they are usually species agnostic and treat
203 nodes as trophic species) and so cannot be used to determine if an interaction is either possible *or* realised
204 between two species (*i.e.*, one cannot use these models to determine if species *a* eats species *b*). Although this
205 means this suite of models are unsuitable as tools for predicting interactions, they have been shown to be
206 sufficient tools to predict the structure of networks (Williams & Martinez, 2008).

207 **3.1.2 Models that predict metawebs (feasible interactions)**

208 **3.1.3 Models that predict realised networks (realised interactions)**

209 **4 Making Progress with Networks**

210 **4.1 Further development of models and tools**

211 As we show in `?@tbl-families` there has been a suite of models that have been developed to predict trophic
212 links, however we are lacking in tools that are explicitly taking into consideration estimating both the feasibil-
213 ity as well as realisation of links, *i.e.*, both interactions and structure simultaneously (Strydom et al., 2021).
214 This could be addressed either through the development of tools that do both (predict both interactions
215 and structure), or it might be possible to do a ensemble modelling approach (Becker et al., 2022). Alter-
216 natively the development of tools that will allow for the downsampling of metawebs into realised networks
217 (*e.g.*, Roopnarine, 2006), although deciding exactly what is driving differences between local networks and
218 the regional metaweb might not be that simple (Saravia et al., 2022). Probably also something that aligns
219 with trying to predict interaction strength - because that would be the gold standard. Probably also worth
220 just plainly stating that feasibility of developing a model that is both broadly generalisable, but also cas-
221 local specificity is probably not attainable (Stouffer, 2019), and more specifically the potential use un models
222 untangling/identifying the different processes (Song & Levine, 2024)

223 **4.2 At what scale should we be predicting/using networks?**

224 Look at Hutchinson et al. (2019)

225 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a
226 ‘network’. Realistically most empirical networks are more aligned with metawebs as opposed to realised
227 networks as they are often the result of some sort of aggregation of observations across time, this creates a
228 two-fold problem. Firstly, we need to think about how this affects any sort of development of theory that sits
229 closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer questions
230 about realised networks using feasible networks? The second is that this lack of ‘direction’ as to how we
231 should define a network is (actually) probably one of the biggest barriers that is affecting the use of networks
232 in applied settings... By define I mean both delimiting the time and geographic scale at which a network is
233 aggregated at (Estay et al., 2023). This is important because it can influence the inferences made, *e.g.*, the
234 large body of work (landscape theory for food web architecture) that showcases how different species use the
235 landscape will influence network dynamics (Rooney et al., 2008). There is also a bit of an interplay with

236 time and data and the different scales that they may be integrated at - co-occurrence may span decades and
237 just because two species have been recorded in teh same space does not mean it was at the same timescale
238 (Brimacombe et al., 2024)

239 4.3 How should we use different networks?

240 What for and how we can use networks is perhaps one of the biggest ‘gaps’ we have in network ecology
241 (Tim’s EBV ms), and there is a serious need to start drawing clear, ecological links between network form
242 and function (although see Delmas et al., 2019). That being said one of the most important things we can
243 do is to be aware of the parameter space that is possible given a specific definition of a network and operate
244 within those parameters. And we should use this in how we also evaluate/benchmark the performance of the
245 different models as well; Poisot (2023) presents a set of guidelines for assessing how well a model recovers
246 pairwise interactions but we lack any clear strategies for benchmarking structure.

247 4.4 Feasible, realised, or sustainable?

248 When do we determine a link to be ‘real’... In the context of feasible networks this is perhaps clearer - if
249 all things were equal (*i.e.*, community context is irrelevant) would the predator be able to consume the
250 prey. However in the realised space there is also the question of the long term ‘energetic feasibility’ of an
251 interaction - just because an interaction is possible in the now is it able to sustain a population in the long
252 term. And what is the scale for that long term - are we thinking at the generational scale? Because ultimately
253 when we are constructing a network we are aggregating not only across space but also across time... This is
254 probably again a Lokta-Volterra space question and something that the dynamic foodweb model (Curtsdotter
255 et al., 2019; Delmas et al., 2017; Lajaaiti et al., 2024) is addressing, but again it is integrating this with the
256 feasible/realised axis.

257 5 Concluding remarks

258 I think a big take home will (hopefully) be how different approaches do better in different situations and so
259 you as an end user need to take this into consideration and pick accordingly. I think Petchey et al. (2011)
260 might have (and share) some thoughts on this. I feel like I need to look at Berlow et al. (2008) but maybe
261 not exactly in this context but vaguely adjacent. This is sort of the crux of the argument presented in
262 Brimacombe et al. (2024) as well.

263 Do we expect there to be differences when thinking about unipartite vs bipartite networks? Is there underlying

264 ecology/theory that would assume that different mechanisms (and thus models) are relevant in these two
265 ‘systems’.

- 266 • The Terry & Lewis (2020) paper looks at some methods but is specifically looking at a bipartite world...

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the "driver" of the interaction
≠ the underlying theory (1:1) & the
'way' we get to the answer is diff
e.g. co-occurrence is about sharing
space/time but we use niche theory/
env. filtering as the means to determine
co-occurrence.

JUN 27		THU 木	179
	level of obj.	(mechanism) what determines interaction	
6	Species	fund. niche/ env. filter	co- occurrence
15	pop.	buck bones (mora)	"capacity"
21	indiv.	fruit-match neutral. funct. resp.	pop size/ dynamics
0		"physiological" 2D 3D prey choice	energy
3		?? allometric scaling ??	
		: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES	

Figure 1: TODO.