

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

Tanya Strydom ¹; Jennifer A. Dunne ²; Timothée Poisot ^{3,4}; Andrew P. Beckerman ¹

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.

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 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 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.

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...

34

35 1 Setting the Scene: The Not So Basics of Nodes and Edges

36 Defining a food web seems simple; it is the representation of the interactions (edges) between species (nodes),
37 however the definition of ‘edges’ and ‘nodes’, as well as the scale at which they are aggregated can take
38 many forms (Poisot, Stouffer, et al., 2016). Networks can be constructed at the population (the links among
39 individuals), community (the links between species), or metacommunity (changes between locations) level.
40 Even if one were to limit their scope to thinking of interaction networks only in terms of food webs at the
41 community-level there are still many ways to define the various components of the network Panel A of 1,
42 one needs to understand the different intentions/assumptions that are made when a food web is constructed.
43 Although the main goal of constructing a food web is to capture and represent the feeding links between
44 species there are many ways to define the nodes (*e.g.*, species or taxonomic group), edges (*e.g.*, potential or
45 *realised* feeding links), the magnitude of the edges (*e.g.*, binary vs probabilistic), and even how the network
46 itself is delimited (does it represent an aggregation of interactions over time?).

47

[Figure 1 about here.]

48 1.0.1 How do we define a node?

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

59 **1.0.2 What is meant by an edge?**

60 At its core, links within food webs can be thought of as a representation of either feeding links between
61 species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within
62 the community/system *e.g.*, energy transfer or material flow (Lindeman, 1942). How we specify links will
63 influence the resulting structure of the network - and the inferences we will make thereof. For example taking
64 a food web that consists of links representing all *potential* feeding links for a community (*i.e.*, a metaweb)
65 will be meaningless if one is interested in understanding the flow of energy through the network as the links
66 within a metaweb do not represent environmental/energetic constraints. In addition to the various ways of
67 defining the links between species pairs there are also a myriad of ways in which the links themselves can
68 be quantified. Links between species are often treated as being present or absent (*i.e.*, binary) but it is
69 also possible to use probabilities (Banville et al., 2024; which quantifies how likely an interaction is to occur,
70 Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of of an interaction,
71 Berlow et al., 2004).

72 **1.0.3 Putting the parts together**

73 The ingredients one uses to construct networks generates a unique representation of the mechanisms (see
74 Section 2) that allow inference and reasoning about the structure, aspects of dynamics (*e.g.*, stability), and
75 potentially the function of communities (*e.g.*, flux). It is thus important to keep in mind that different
76 networks are going to be representing different processes and that can only be used for inference of some but
77 not all aspects of the community at large. Here it may be meaningful to contextualise the different ‘types’
78 of food webs within the larger research programmes (or even practical needs) that have been driving the
79 construction of them.

80 Before thinking about the ways in which we can predict networks it is perhaps meaningful to take a step
81 back and think about the different criteria that must be met in order for an interaction to be able to occur
82 between two species, specifically thinking of this in terms of distinguishing between the feasibility versus
83 realisation of an interaction and how these are determined (and defined by) different ‘rules’/mechanisms. If
84 we look at this feasibility-reality continuum (Figure 2) it is clear how the different predictive approaches
85 (methods) tend to fall within one of the broader categories identified (distinguished) in the triangle. This is
86 not to say that this shortcoming should be viewed as a ‘bug’ but rather a ‘feature’ of the field as it allows one
87 to engage with, as well as construct networks at different scales, which is particularly valuable if one takes
88 into consideration the considerable ‘data cost’ of predicting well resolved, realised networks in comparison to
89 constructing high-level metawebs. However, it is important that there is an awareness and acknowledgement

90 of where within this feasibility-reality one is working at and how this will impact and limit the contexts in
91 which the resulting network can be used and applied within.

92 **2 From Nodes and Edges to Scales, Context, and Processes**

93 Armed with these basics, it is now possible to review the scales and assumptions that are made by a wide
94 range of tools to assist in constructing networks against poor data with the hope of capturing important
95 processes that underpin accurate prediction. Our thesis centres on a four-tier conceptualization of networks:
96 evolutionary compatibility, co-occurrence, feasibility, abundance, predator choice, and non-trophic interac-
97 tions. In the following sections we review each of these and then provide a synthesis among them.

98 **2.1 Understanding the processes that determine species interactions**

99 Processes that are all-or-nothing (possibility) vs processes that are context dependent (likelihood). Processes
100 form the underlying logic of models (and arguably, no, for sure even empirical data) capture. This means
101 also the interplay of the two, *i.e.*, the use of models to ‘gap fill’ within existing empirical dataset (Biton et
102 al., 2024; Stock, 2021). Ultimately when we put this all together it will influence how we can (and should)
103 use the resulting network. Here we present Figure 2 some of the processes that have been shown to influence
104 either/or the feasibility (possibility) of an interaction occurring between two species or if a feasible interaction
105 is realised (likelihood of realisation) within the specific environmental/community context. Of course these
106 processes do not function in a vacuum and do interact with/influence one another but it is still beneficial
107 to present them as such as these are often the underlying processes that influence model development, the
108 criteria for data collection in the field, and the scale of organisation for which they are relevant (species,
109 population, community).

110 [Figure 2 about here.]

111 **Evolutionary compatibility**

112 There is compelling evidence that the possibility of an interaction occurring between two species is the result
113 of their shared (co)evolutionary history (Dalla Riva & Stouffer, 2016; Gómez et al., 2010; Segar et al., 2020).
114 In the more proximal sense this is manifested as the ‘trait complementarity’ between two species, whereby
115 one species (the predator) has the ‘correct’ set of traits that allow it to chase, capture, kill, and consume
116 the other species (the prey). For species pairs where this condition is not met the link is deemed to be
117 forbidden (Jordano, 2016b); *i.e.*, not physically possible and will always be absent within the network. In the
118 context of trying to determine the feasibility (*i.e.*, the *possibility*) of an interaction, phylogeny is an excellent

119 predictor (Fricke et al., 2022; Strydom et al., 2022) and allows one to construct what can be considered to
120 be a metaweb. In terms of thinking about the anatomy of an ‘feasibility network’ one should be aware that
121 it is possible to represent interactions as either binary (feasible/forbidden; *i.e.*, the traditional definition of a
122 metaweb Dunne (2006)) or as a probability (Banville et al., 2024), where the probability represents how likely
123 that the interaction between two species is feasible (what is the possibility of this interaction occurring?).

124 **(Co)occurrence**

125 Although the outright assumption that because two species are co-occurring it must mean that they are
126 interacting is inherently flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at
127 least in terms of feeding links) if they are not co-occurring in time and space. Thus co-occurrence data alone is
128 insufficient to build an accurate and ecologically meaningful representation of a food web having information
129 on the co-occurrence of species can further aid us in refining metawebs by allowing us to downsample the
130 network based on the species found in a specific location, or even add additional uncertainty based in how
131 likely species are to co-occur (Dansereau et al., 2023). Additionally the interplay between the interaction
132 between a species pair and their co-occurrence is meaningful when one is operating in the space of trying to
133 determine the distribution of a species (Higino et al., 2023), and forms a key component of some of the next
134 generation species distribution models *e.g.*, joint SDMs (Pollock et al., 2014).

135 **Abundance**

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

142 **Predator choice (energetic cost)**

143 Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume
144 prey, and is well described within optimal foraging theory [ref] and rests on the idea that the prey a predator
145 chooses to target is one that will have the greatest return on energy with the lowest energetic cost. There are
146 additional bodies of work that attempt to include the cost of movement that the environment imposes on an
147 individual (Cherif et al., 2024) as well as 2D/3D search space (Pawar et al., 2012). In terms of formalising
148 these processes in the context of predicting networks using diet models (Beckerman et al., 2006; Petchey et al.,
149 2008) that have predator choice determined by the handling time, energy content, prey density, and predator

150 attack rate. Wootton et al. (2023) developed a model that moves the energy of the system into different
151 modules related to the process of the predator acquiring energy from the prey *i.e.*, compartmentation in food
152 webs (Krause et al., 2003).

153 **Indirect interactions**

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

158 It should be self evident that the different processes discussed above are all ultimately going to influence the
159 realisation of interactions as well as the structure of a network, however they are acting at different scales of
160 organisation. Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of the
161 species pair of interest, that is the *possibility* of an interaction being present/absent is assessed at the pairwise
162 level and one is left with a ‘list’ of interactions that are present/absent. Although it is possible to build a
163 network (*i.e.*, metaweb) from this information it is important to be aware that the structure of this network
164 is not constrained by real-world dynamics or conditions (*i.e.*, community context), just because species are
165 able to interact does not mean that they will (Poisot et al., 2015). In order to construct a network who’s
166 structure is a closer approximation of reality (localised interactions) one needs to take into consideration
167 properties of the community as a whole and not just the two species of interest.

168 **downsampling paragraph??**

169 **3 Network prediction is nuanced**

170 The different models that are used to either predict or construct networks have an underlying philosophy
171 that often only captures one or a few of the processes discussed in Section 2.1, has implications for how the
172 resulting network is defined Section 1, which will ultimately delimit and define what inferences can be made
173 from the resulting network. Selecting a model for the task of network prediction should come down to two
174 things; what *aspect* of a food web one is interested in predicting, and what data are available, necessary,
175 and sufficient, and what is the purpose of wanting to predict a network? It is important that a researcher
176 is aware of this to ensure that the appropriate model is selected. Broadly researchers will be interested in
177 predicting/constructing two different types of networks; *metawebs*, which is essentially a list of all interactions
178 that are *possible* for a specific community (*i.e.*, at the scale of the species pairs), or being able to predict
179 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.

3.1 Models that predict structure

Although we identify mechanisms that determine species interactions in Section 2.1 not all models that are used to predict networks operate at this ‘mechanistic’ level (at least in absolute terms), but rather represent the *structure* of a network based on a series of *a priori* assumptions of network connectance (*e.g.*, the niche model Williams & Martinez (2000); although see Allesina & Pascual (2009) for a parameter-free model) or other structural features of a *realised* network (*e.g.*, stochastic block model, Xie et al. (2017)). 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 *a* eats species *b*). Although this means this suite of models are unsuitable as tools for predicting interactions, they have been shown to be sufficient tools to predict the structure of networks (Williams & Martinez, 2008).

3.2 How do we predict food webs?

There as many ways to predict networks as what there is to define them and along with taking into consideration the points raised in the previous section it is also beneficial to think about the context in which the different models were developed - and how this will influence the networks that they produce... Also it is not feasibly possible to list every single approach that has been developed to predict networks and so we will present what we believe to be the broad families that represent the different approaches to predicting networks Table 1, particularly how these relate to the processes identified in Section 2.1, as well as models that predict network structure (see Section 3.1). A more extensive overview of the different models that fall with in the different model families can be found in SuppMat 1 and for a more detailed breakdown of the different ‘traits’ of the model families refer to SuppMat 2.

Table 1: A summary of the different families of tools that can be used to generate food webs.

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
null	Links are randomly distributed within a network		parameter assumptions, species agnostic	structural network	
neutral	Network structure is random, but species abundance determines links between nodes	abundance	parameter assumptions	structural network	Canard et al. (2012)
resource	Networks are interval, species can be ordered on a 'niche axis'		parameter assumptions, species agnostic	structural network	Williams & Martinez (2008)
generative	Networks are determined by their structural features		need real world networks	structural network	
energetic	Interactions are determined by energetic costs	abundance + energy	does not account for forbidden links in terms of evolutionary compatibility	'energy' network	
graph embedding	Interactions can be predicted from the latent traits of networks	evolutionary compatibility	need real world networks	metaweb	Strydom et al. (2023)

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
trait matching	Interactions can be inferred by a mechanistic frame-work/relationships	evolutionary compatibility	well studied species/communities	metaweb	Morales-Castilla et al. (2015)
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	evolutionary compatibility	need real world networks	metaweb	Pichler et al. (2020)
expert knowledge	'Boots on the ground'	evolutionary compatibility	well studied species/communities	metaweb	
data scavenging	Webscraping to create networks from online databases		need real world networks	metaweb	Poisot, Gravel, et al. (2016) (if you squint?)

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
co-occurrence	co-occurrence patterns arise from interactions so we can use these patterns to reverse engineer the interactions	co-occurrence	does not account for forbidden links in terms of evolutionary compatibility or account for energy constraints	co-occurrence network	

²¹⁰ There is a bit of a ‘point of conflict’ between those calling for ‘pixel perfect’, regional scale data (Pringle,
²¹¹ 2020; Pringle & Hutchinson, 2020) and for the means to generate networks that are ecologically plausible
²¹² *representations* (*sensu* structural networks). This represents two challenges; one is that models that repre-
²¹³ sent generalisations of networks often lack the ability to retrieve any species/community specificity which
²¹⁴ limits their utility for real world, species-driven scenarios *e.g.*, species driven conservation efforts (Dunn et
²¹⁵ al., 2009), however networks that are constructed through either (most) empirical observations or through
²¹⁶ predictive means are fundamentally going to represent metawebs, *i.e.*, lack constrained links, a representation
²¹⁷ of structure, or energy flow...

²¹⁸ 4 Making Progress with Networks

²¹⁹ 4.1 Further development of models and tools

²²⁰ As we show in Table 1 there has been a suite of models that have been developed to predict trophic links,
²²¹ however we are lacking in tools that are explicitly taking into consideration estimating both the feasibility
²²² as well as realisation of links, *i.e.*, both interactions and structure simultaneously (Strydom et al., 2021).
²²³ This could be addressed either through the development of tools that do both (predict both interactions and
²²⁴ structure), or it might be possible to do a ensemble modelling approach (Becker et al., 2022). Alternatively
²²⁵ the development of tools that will allow for the downsampling of metawebs into realised networks (*e.g.*,
²²⁶ Roopnarine, 2006), although deciding exactly what is driving differences between local networks and the
²²⁷ regional metaweb might not be that simple (Saravia et al., 2022). Probably also something that aligns with
²²⁸ trying to predict interaction strength - because that would be the gold standard. Probably also worth just

229 plainly stating that feasibility of developing a model that is both broadly generalisable, but also has local
230 specificity is probably not attainable (Stouffer, 2019)

231 **4.2 At what scale should we be predicting/using networks?**

232 Look at Hutchinson et al. (2019)

233 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a
234 ‘network’. Realistically most empirical networks are more aligned with metawebs as opposed to realised
235 networks as they are often the result of some sort of aggregation of observations across time, this creates a
236 two-fold problem. Firstly, we need to think about how this affects any sort of development of theory that sits
237 closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer questions
238 about realised networks using feasible networks? The second is that this lack of ‘direction’ as to how we
239 should define a network is (actually) probably one of the biggest barriers that is affecting the use of networks
240 in applied settings... By define I mean both delimiting the time and geographic scale at which a network is
241 aggregated at (Estay et al., 2023). This is important because it can influence the inferences made, *e.g.*, the
242 large body of work (landscape theory for food web architecture) that showcases how different species use the
243 landscape will influence network dynamics (Rooney et al., 2008). There is also a bit of an interplay with
244 time and data and the different scales that they may be integrated at - co-occurrence may span decades and
245 just because two species have been recorded in the same space does not mean it was at the same timescale
246 (Brimacombe et al., 2024)

247 **4.3 How should we use different networks?**

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

255 **4.4 Feasible, realised, or sustainable?**

256 When do we determine a link to be ‘real’... In the context of feasible networks this is perhaps clearer - if all
257 things were equal (*i.e.*, community context is irrelevant) would the predator be able to consume the prey.

258 However in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction
259 - just because an interaction is possible in the now is it able to sustain a population in the long term. And
260 what is the scale for that long term - are we thinking at the generational scale? Because ultimately when we
261 are constructing a network we are aggregating not only across space but also across time... This is probably
262 again a Lokta-Volterra space question and something that the dynamic foodweb model (BEFW, Curtsdotter
263 et al. (2019)) is addressing, but again it is integrating this with the feasible/realised axis.

264 5 Concluding remarks

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

270 Do we expect there to be differences when thinking about unipartite vs bipartite networks? Is there underlying
271 ecology/theory that would assume that different mechanisms (and thus models) are relevant in these two
272 ‘systems’.

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

274 References

- 275 Allesina, S., & Pascual, M. (2009). Food web models: A plea for groups. *Ecology Letters*, 12(7), 652–662.
276 <https://doi.org/10.1111/j.1461-0248.2009.01321.x>
- 277 Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas,
278 T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction*
279 *networks*. EcoEvoRxiv. <https://doi.org/10.32942/X28G8Z>
- 280 Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.
281 A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,
282 E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic
283 reservoirs. *The Lancet Microbe*, 3(8), e625–e637. [https://doi.org/10.1016/S2666-5247\(21\)00245-7](https://doi.org/10.1016/S2666-5247(21)00245-7)
- 284 Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.
285 *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>

- 287 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of*
288 *the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- 289 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,
290 V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.
291 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),
292 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 293 Biton, B., Puzis, R., & Pilosof, S. (2024). *Inductive link prediction boosts data availability and enables*
294 *cross-community link prediction in ecological networks*.
- 295 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.
296 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 297 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A*
298 *cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 299 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings
300 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),
301 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 302 Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of
303 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- 304 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models
305 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,
306 33(4), e13807. <https://doi.org/10.1111/geb.13807>
- 307 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,
308 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The
309 environment to the rescue: Can physics help predict predator-prey interactions? *Biological Reviews*,
310 n/a(n/a). <https://doi.org/10.1111/brv.13105>
- 311 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.
312 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 313 Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., Traugott, M., &
314 Bommarco, R. (2019). Ecosystem function in predator-prey food webs—confronting dynamic models with
315 empirical data. *Journal of Animal Ecology*, 88(2), 196–210. <https://doi.org/10.1111/1365-2656.12892>
- 316 Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs’ backbones
317 using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>
- 318 Dansereau, G., Barros, C., & Poisot, T. (2023). *Spatially explicit predictions of food web structure from*

- 320 regional level data.
- 321 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,
322 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).
323 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brv.12433>
- 324
- 325 Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction:
326 Are most endangered species parasites and mutualists? *Proceedings. Biological Sciences*, 276(1670),
327 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- 328 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological
329 networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 330 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks
331 over space. *Frontiers in Ecology and Evolution*, 11.
- 332 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,
333 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.
334 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 335 Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions
336 interact? *Journal of Animal Ecology*, 80(5), 1097–1108. <https://doi.org/10.1111/j.1365-2656.2011.01852.x>
- 337
- 338 Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across
339 the entire tree of life. *Nature*, 465(7300), 918–921. <https://doi.org/10.1038/nature09113>
- 340 Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch
341 between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*,
342 11, e14620. <https://doi.org/10.7717/peerj.14620>
- 343 Hutchinson, M. C., Bramon Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., Jordano, P., &
344 Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community
345 ecology. *Functional Ecology*, 33(2), 206–217. <https://doi.org/10.1111/1365-2435.13237>
- 346 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 347
- 348 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 349
- 350 Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015).
351 Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky
352 shores. *Ecology*, 96(1), 291–303. <https://doi.org/10.1890/13-1424.1>

- 353 Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N.,
354 Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., & Brose,
355 U. (2012). More than a meal... integrating non-feeding interactions into food webs: More than a meal
356 *Ecology Letters*, 15(4), 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- 357 Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments
358 revealed in food-web structure. *Nature*, 426(6964), 282–285. <https://doi.org/10.1038/nature02115>
- 359 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 360 Maiorano, L., Montemaggiore, A., Ficetola, G. F., O'Connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A
361 species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, 29(9), 1452–1457.
362 <https://doi.org/10.1111/geb.13138>
- 363 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from
364 abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.13380>
- 365 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from
366 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 367 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic
368 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 369 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web
370 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 371 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some
372 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 373 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms
374 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and
375 Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- 376 Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks.
377 *Nature Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 378 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods
379 in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 380 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
381 Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,

- 386 48(7), 1552–1563. <https://doi.org/10.1111/jbi.14127>
- 387 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of
388 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/mec.12703>
- 389 Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B.,
390 & Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological
391 hypotheses. *Ecography*, 39(4), 402–408. <https://doi.org/10.1111/ecog.01941>
- 392 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
393 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 394 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks
395 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 396 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O’Hara, R. B., Parris, K. M., Vesk, P. A., &
397 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint
398 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/10.1111/2041-210X.12180>
- 400 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton
401 University Press. <https://doi.org/10.1515/9780691195322-020>
- 402 Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology,
403 Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>
- 405 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.
406 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 407 Rooney, N., McCann, K. S., & Moore, J. C. (2008). A landscape theory for food web architecture. *Ecology
408 Letters*, 11(8), 867–881. <https://doi.org/10.1111/j.1461-0248.2008.01193.x>
- 409 Roopnarine, P. D. (2006). Extinction Cascades and Catastrophe in Ancient Food Webs. *Paleobiology*, 32(1),
410 1–19. <https://www.jstor.org/stable/4096814>
- 411 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network
412 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),
413 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 414 Segar, S. T., Fayle, T. M., Srivastava, D. S., Lewinson, T. M., Lewis, O. T., Novotny, V., Kitching, R. L.,
415 & Maunsell, S. C. (2020). The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology &
416 Evolution*, 35(5), 454–466. <https://doi.org/10.1016/j.tree.2020.01.004>
- 417 Stock, M. (2021). Pairwise learning for predicting pollination interactions based on traits and phylogeny.
418 *Ecological Modelling*, 14.

- 419 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*,
420 88(2), 192–195. <https://doi.org/10.1111/1365-2656.12949>
- 421 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,
422 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction
423 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,
424 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- 425 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,
426 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer
427 learning can help predict potential species interaction networks despite data limitations. *Methods in
428 Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 429 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
430 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap
431 towards predicting species interaction networks (across space and time). *Philosophical Transactions of
432 the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 433 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.
434 <https://doi.org/10.1002/ecy.3047>
- 435 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
436 <https://doi.org/10.1038/35004572>
- 437 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food
438 webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 439 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory
440 of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 441 Xie, J.-R., Zhang, P., Zhang, H.-F., & Wang, B.-H. (2017). Completeness of Community Structure in
442 Networks. *Scientific Reports*, 7(1), 5269. <https://doi.org/10.1038/s41598-017-05585-6>
- 443 Yodzis, P. (1982). The Compartmentation of Real and Assembled Ecosystems. *The American Naturalist*,
444 120(5), 551–570. <https://doi.org/10.1086/284013>

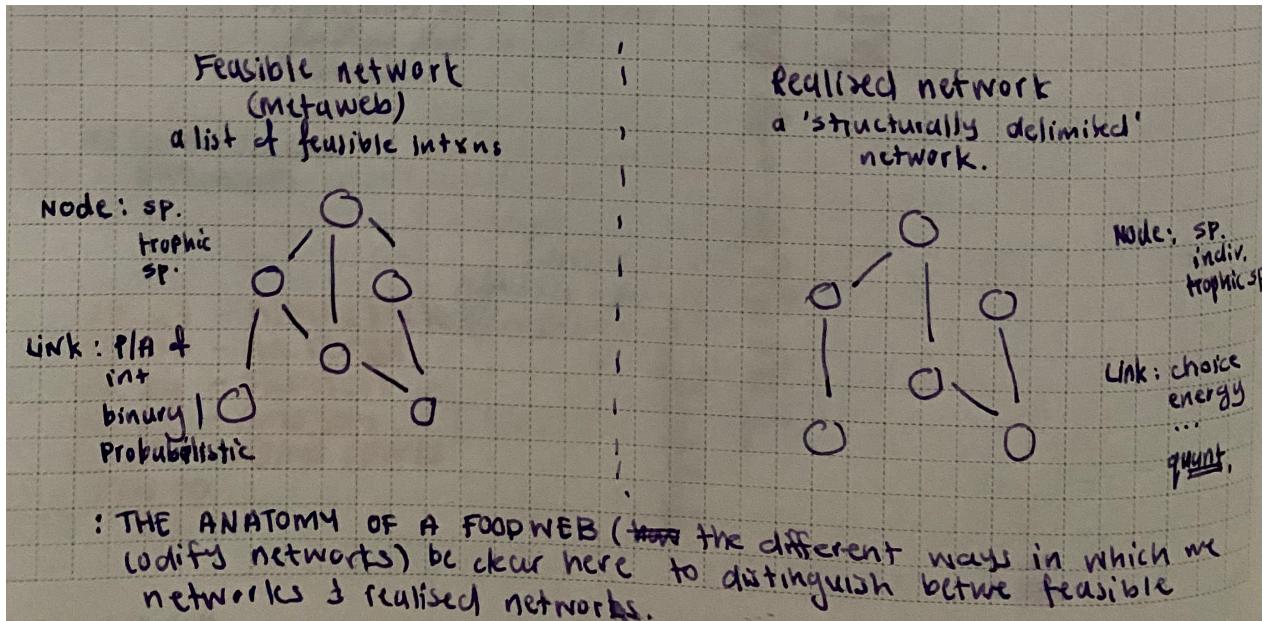


Figure 1: The many ways in which a food web can be defined and described at the node, edge, and even network level.

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
			(mechanism)	
			what determines	
			interaction	
6		Body of theory		
15	Species	fund. niches env. filter	co- occurrence	
21		buck bones (mora)	"capacity"	
0	pop.	truit-match		
3	indiv.	neutral. funct. resp.	pop size / dynamics	
15		"physicw" 2D 3D prey choice	energy	
0				?? allometric scaling ??
3				: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES

Figure 2: TODO.