

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. 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...

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 many
38 forms (Poisot, Stouffer, et al., 2016). An awareness of variance in the way a food web can be defined is critical
39 as it represents the ‘object’ that is used to make inferences either about the interactions between species, or
40 how the structure influences ecosystem level processes. One thus needs to be aware of both the criteria that
41 is used to define nodes and edges, and what processes or mechanisms the aggregation of the two represents,
42 as this will ultimately determine and delimit the way in which a network should be used.

43 1.0.1 How do we define a node?

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

54 1.0.2 What is meant by an edge?

55 At its core, links within food webs can be thought of as a representation of either feeding links between
56 species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within
57 the community/system *e.g.*, energy transfer or material flow (Lindeman, 1942). How we specify links will
58 influence the resulting structure of the network - and the inferences we will make thereof. For example taking
59 a food web that consists of links representing all *potential* feeding links for a community (*i.e.*, a metaweb)
60 will be meaningless if one is interested in understanding the flow of energy through the network as the links
61 within a metaweb do not represent environmental/energetic constraints. 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 (Banville et al., 2024; which quantifies how likely an interaction is to occur, Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of an interaction, Berlow et al., 2004).

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 (Dunne, 2006), and realised networks; which is the subset of interactions in a metaweb that are *realised* ‘on the ground’. The fundamental difference between these two different types of networks 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 (Jordano, 2016b), or an idea of the *complete* diet of a species (Strydom et al., 2023). Although metawebs are typically ‘constrained’ to a collection of species that also co-occur, there is no reason that a metaweb can include species that do not co-occur (although this would require some degree of prediction/assumption to identify those possible interactions). In contrast realised networks are highly localised and 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. Thus, metawebs and realised networks are determined and constrained by a different set of assumptions as to what processes are determining the presence/absence of an interaction between two species as well as the resulting network structure.

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

Armed with these basics, it is now possible to review the scales and assumptions that are made by a wide range of tools to assist in constructing networks against poor data with the hope of capturing important processes that underpin accurate prediction. Our thesis centres on a five-tier conceptualization of networks: evolutionary compatibility, co-occurrence, feasibility, abundance, predator choice, and non-trophic interactions. In

92 the following sections we review each of these and then provide a synthesis among them.

93 2.1 Understanding the processes that determine species interactions

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

105 [Figure 1 about here.]

106 Evolutionary compatibility

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

119 (Co)occurrence

120 Although the outright assumption that because two species are co-occurring it must mean that they are
121 interacting is inherently flawed (Blanchet et al., 2020), 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 co-occurrence data alone is 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).

130 **Abundance**

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

137 **Predator choice (energetic cost)**

138 Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume
139 prey, and is well described within optimal foraging theory [ref] and rests on the idea that the prey a predator
140 chooses to target is one that will have the greatest return on energy with the lowest energetic cost. There are
141 additional bodies of work that attempt to include the cost of movement that the environment imposes on an
142 individual (Cherif et al., 2024) as well as 2D/3D search space (Pawar et al., 2012). In terms of formalising
143 these processes in the context of predicting networks using diet models (Beckerman et al., 2006; Petchey et al.,
144 2008) that have predator choice determined by the handling time, energy content, prey density, and predator
145 attack rate. Wootton et al. (2023) developed a model that moves the energy of the system into different
146 modules related to the process of the predator acquiring energy from the prey *i.e.*, compartmentation in food
147 webs (Krause et al., 2003).

148 **Indirect interactions**

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

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

163 **downsampling paragraph??**

164 **3 Network prediction is nuanced**

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

184 **3.1 Models that predict structure**

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

195 **3.2 How do we predict food webs?**

196 There as many ways to predict networks as what there is to define them and along with taking into con-
197 sideration the points raised in the previous section it is also beneficial to think about the context in which
198 the different models were developed - and how this will influence the networks that they produce... Also it
199 is not feasibly possible to list every single approach that has been developed to predict networks and so we
200 will present what we believe to be the broad families that represent the different approaches to predicting
201 networks Table 1, particularly how these relate to the processes identified in Section 2.1, as well as models
202 that predict network structure (see Section 3.1). A more extensive overview of the different models that fall
203 with in the different model families can be found in SuppMat 1 and for a more detailed breakdown of the
204 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	

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
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 energy and 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)
trait matching	Interactions can be inferred by a mechanistic frame-work/relationships	evolutionary compatibility	well studied species/communities	metaweb	Morales-Castilla et al. (2015)

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
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' ecological knowledge and observations	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?)
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	

²⁰⁵ There is a bit of a ‘point of conflict’ between those calling for ‘pixel perfect’, regional scale data (Pringle, 2020; Pringle & Hutchinson, 2020) and for the means to generate networks that are ecologically plausible representations (*sensu* structural networks). This represents two challenges; one is that models that repre-

208 sent generalisations of networks often lack the ability to retrieve any species/community specificity which
209 limits their utility for real world, species-driven scenarios *e.g.*, species driven conservation efforts (Dunn et
210 al., 2009), however networks that are constructed through either (most) empirical observations or through
211 predictive means are fundamentally going to represent metawebs, *i.e.*, lack constrained links, a representation
212 of structure, or energy flow...

213 4 Making Progress with Networks

214 4.1 Further development of models and tools

215 As we show in Table 1 there has been a suite of models that have been developed to predict trophic links,
216 however we are lacking in tools that are explicitly taking into consideration estimating both the feasibility
217 as well as realisation of links, *i.e.*, both interactions and structure simultaneously (Strydom et al., 2021).
218 This could be addressed either through the development of tools that do both (predict both interactions and
219 structure), or it might be possible to do a ensemble modelling approach (Becker et al., 2022). Alternatively
220 the development of tools that will allow for the downsampling of metawebs into realised networks (*e.g.*,
221 Roopnarine, 2006), although deciding exactly what is driving differences between local networks and the
222 regional metaweb might not be that simple (Saravia et al., 2022). Probably also something that aligns with
223 trying to predict interaction strength - because that would be the gold standard. Probably also worth just
224 plainly stating that feasibility of developing a model that is both broadly generalisable, but also has local
225 specificity is probably not attainable (Stouffer, 2019)

226 4.2 At what scale should we be predicting/using networks?

227 Look at Hutchinson et al. (2019)

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

237 large body of work (landscape theory for food web architecture) that showcases how different species use the
238 landscape will influence network dynamics (Rooney et al., 2008). There is also a bit of an interplay with
239 time and data and the different scales that they may be integrated at - co-occurrence may span decades and
240 just because two species have been recorded in teh same space does not mean it was at the same timescale
241 (Brimacombe et al., 2024)

242 **4.3 How should we use different networks?**

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

250 **4.4 Feasible, realised, or sustainable?**

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

260 **5 Concluding remarks**

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

²⁶⁶ Do we expect there to be differences when thinking about unipartite vs bipartite networks? Is there underlying
²⁶⁷ ecology/theory that would assume that different mechanisms (and thus models) are relevant in these two
²⁶⁸ ‘systems’.

- ²⁶⁹ • The Terry & Lewis (2020) paper looks at some methods but is specifically looking at a bipartite world...

²⁷⁰ References

- ²⁷¹ Allesina, S., & Pascual, M. (2009). Food web models: A plea for groups. *Ecology Letters*, 12(7), 652–662.
²⁷² <https://doi.org/10.1111/j.1461-0248.2009.01321.x>
- ²⁷³ Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas,
²⁷⁴ T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction*
²⁷⁵ *networks*. EcoEvoRxiv. <https://doi.org/10.32942/X28G8Z>
- ²⁷⁶ Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.
²⁷⁷ A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,
²⁷⁸ E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic
²⁷⁹ 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)
- ²⁸⁰ Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.
²⁸¹ *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- ²⁸² Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of
the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- ²⁸³ Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,
²⁸⁴ V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.
²⁸⁵ (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),
²⁸⁶ 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- ²⁸⁷ Biton, B., Puzis, R., & Pilosof, S. (2024). *Inductive link prediction boosts data availability and enables
cross-community link prediction in ecological networks*.
- ²⁸⁸ Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.
²⁸⁹ *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- ²⁹⁰ Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A
cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- ²⁹¹ Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings
²⁹² of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),

- 297 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 298 Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of
299 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- 300
- 301 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models
302 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,
303 33(4), e13807. <https://doi.org/10.1111/geb.13807>
- 304 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,
305 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The
306 environment to the rescue: Can physics help predict predator-prey interactions? *Biological Reviews*,
307 n/a(n/a). <https://doi.org/10.1111/brv.13105>
- 308 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.
309 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 310 Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., Traugott, M., &
311 Bommarco, R. (2019). Ecosystem function in predator-prey food webs—confronting dynamic models with
312 empirical data. *Journal of Animal Ecology*, 88(2), 196–210. <https://doi.org/10.1111/1365-2656.12892>
- 313 Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones
314 using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>
- 315 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,
316 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).
317 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brv.12433>
- 318
- 319 Delmas, E., Brose, U., Gravel, D., Stouffer, D. B., & Poisot, T. (2017). Simulations of biomass dynamics in
320 community food webs. *Methods in Ecology and Evolution*, 8(7), 881–886. <https://doi.org/10.1111/2041-210X.12713>
- 321
- 322 Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction:
323 Are most endangered species parasites and mutualists? *Proceedings. Biological Sciences*, 276(1670),
324 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- 325 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological
326 networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 327 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks
328 over space. *Frontiers in Ecology and Evolution*, 11.
- 329 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,

- 330 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.
331 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 332 Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions
333 interact? *Journal of Animal Ecology*, 80(5), 1097–1108. <https://doi.org/10.1111/j.1365-2656.2011.01852.x>
- 334 x
- 335 Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across
336 the entire tree of life. *Nature*, 465(7300), 918–921. <https://doi.org/10.1038/nature09113>
- 337 Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch
338 between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*,
339 11, e14620. <https://doi.org/10.7717/peerj.14620>
- 340 Hutchinson, M. C., Bramon Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., Jordano, P., &
341 Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community
342 ecology. *Functional Ecology*, 33(2), 206–217. <https://doi.org/10.1111/1365-2435.13237>
- 343 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 344 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 345 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 346 Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015).
347 Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky
348 shores. *Ecology*, 96(1), 291–303. <https://doi.org/10.1890/13-1424.1>
- 349 Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N.,
350 Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., & Brose,
351 U. (2012). More than a meal... integrating non-feeding interactions into food webs: More than a meal
352 *Ecology Letters*, 15(4), 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- 353 Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments
354 revealed in food-web structure. *Nature*, 426(6964), 282–285. <https://doi.org/10.1038/nature02115>
- 355 Lajaaiti, I., Bonnici, I., Kéfi, S., Mayall, H., Danet, A., Beckerman, A. P., Malpas, T., & Delmas, E. (2024).
356 *EcologicalNetworksDynamics.jl* A Julia package to simulate the temporal dynamics of complex ecological
357 networks (p. 2024.03.20.585899). bioRxiv. <https://doi.org/10.1101/2024.03.20.585899>
- 358 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 359 Maiorano, L., Montemaggioli, A., Ficetola, G. F., O'Connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A
360 species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, 29(9), 1452–1457.

- 363 <https://doi.org/10.1111/geb.13138>
- 364 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from
365 abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.13380>
- 367 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from
368 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 369 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic
370 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 371 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web
372 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 374 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some
375 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 377 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms
378 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and
379 Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- 380 Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks.
381 *Nature Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 382 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods
383 in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 384 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
385 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/10.1111/2041-210X.12441>
- 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., Lewinsohn, 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>

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	
?? allometric scaling ??				
				: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES

Figure 1: TODO.