

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

Tanya Strydom <sup>1</sup>; Jennifer A. Dunne <sup>2</sup>; Timothée Poisot <sup>3,4</sup>; Andrew P. Beckerman <sup>1</sup>

**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

<sup>32</sup> 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. Thus, metawebs and realised networks are representing different mechanisms that are determining and constraining both the interactions between species as well as the resulting network structure, specifically providing context as to either the *potential* of an interaction occurring between two species (metawebs) or the subset of potential interactions that are *realised* in the field (realised networks).

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

92 **2.1 Understanding the processes that determine species interactions**

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

104 [Figure 1 about here.]

105 **Evolutionary compatibility**

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

118 **(Co)occurrence**

119 Although the outright assumption that because two species are co-occurring it must mean that they are  
120 interacting is inherently flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at  
121 least in terms of feeding links) if they are not co-occurring in time and space. Thus co-occurrence data alone is  
122 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 (Dansereau et al., 2023). 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).

## 129 Abundance

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

## 136 Predator choice (energetic cost)

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

## 147 Indirect interactions

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

It should be self evident that the different processes discussed above are all ultimately going to influence the realisation of interactions as well as the structure of a network, however they are acting at different scales of

organisation. Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of the species pair of interest, that is the *possibility* of an interaction being present/absent is assessed at the pairwise level and one is left with a ‘list’ of interactions that are present/absent. Although it is possible to build a network (*i.e.*, metaweb) from this information it is important to be aware that the structure of this network is not constrained by real-world dynamics or conditions (*i.e.*, community context), just because species are able to interact does not mean that they will (Poisot et al., 2015). In order to construct a network who’s structure is a closer approximation of reality (localised interactions) one needs to take into consideration properties of the community as a whole and not just the two species of interest.

162 **downsampling paragraph??**

### 163 **3 Network prediction is nuanced**

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

183 **3.1 Models that predict structure**

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

194 **3.2 How do we predict food webs?**

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

<sup>204</sup> 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-

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

## 212 4 Making Progress with Networks

### 213 4.1 Further development of models and tools

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

### 225 4.2 At what scale should we be predicting/using networks?

226 Look at Hutchinson et al. (2019)

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

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

#### 241 **4.3 How should we use different networks?**

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

#### 249 **4.4 Feasible, realised, or sustainable?**

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

### 259 **5 Concluding remarks**

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

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

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

## 269 References

- 270 Allesina, S., & Pascual, M. (2009). Food web models: A plea for groups. *Ecology Letters*, 12(7), 652–662.  
271 <https://doi.org/10.1111/j.1461-0248.2009.01321.x>
- 272 Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas,  
273 T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction*  
274 *networks*. EcoEvoRxiv. <https://doi.org/10.32942/X28G8Z>
- 275 Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.  
276 A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,  
277 E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic  
278 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)
- 279 Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.  
280 *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- 281 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of  
282 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  
288 cross-community link prediction in ecological networks*.
- 289 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.  
290 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 291 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A  
292 cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 293 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings  
294 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),

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

- 329 over space. *Frontiers in Ecology and Evolution*, 11.
- 330 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,  
331 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.  
332 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 333 Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions  
334 interact? *Journal of Animal Ecology*, 80(5), 1097–1108. <https://doi.org/10.1111/j.1365-2656.2011.01852.x>
- 335 **X**
- 336 Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across  
337 the entire tree of life. *Nature*, 465(7300), 918–921. <https://doi.org/10.1038/nature09113>
- 338 Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch  
339 between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*,  
340 11, e14620. <https://doi.org/10.7717/peerj.14620>
- 341 Hutchinson, M. C., Bramon Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., Jordano, P., &  
342 Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community  
343 ecology. *Functional Ecology*, 33(2), 206–217. <https://doi.org/10.1111/1365-2435.13237>
- 344 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 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
- 360

- 362 Maiorano, L., Montemaggiori, A., Ficetola, G. F., O'Connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A  
363 species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, 29(9), 1452–1457.  
364 <https://doi.org/10.1111/geb.13138>
- 365 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from  
366 abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.X.13380>
- 368 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from  
369 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 370 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic  
371 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 372 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web  
373 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 375 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some  
376 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 378 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms  
379 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and  
380 Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- 381 Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks.  
382 *Nature Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 383 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods  
384 in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 385 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &  
386 Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,  
387 48(7), 1552–1563. <https://doi.org/10.1111/jbi.14127>
- 388 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of  
389 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/2041-210X.13329>
- 390 Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B.,  
391 & Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological  
392 hypotheses. *Ecography*, 39(4), 402–408. <https://doi.org/10.1111/ecog.01941>
- 393 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
394 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>

- 395 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks  
396 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 397 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O’Hara, R. B., Parris, K. M., Vesk, P. A., &  
398 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint  
399 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>
- 404 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.  
405 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 406 Rooney, N., McCann, K. S., & Moore, J. C. (2008). A landscape theory for food web architecture. *Ecology  
Letters*, 11(8), 867–881. <https://doi.org/10.1111/j.1461-0248.2008.01193.x>
- 407 Roopnarine, P. D. (2006). Extinction Cascades and Catastrophe in Ancient Food Webs. *Paleobiology*, 32(1),  
408 1–19. <https://www.jstor.org/stable/4096814>
- 409 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network  
410 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),  
411 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 412 Segar, S. T., Fayle, T. M., Srivastava, D. S., Lewinsohn, T. M., Lewis, O. T., Novotny, V., Kitching, R. L.,  
413 & Maunsell, S. C. (2020). The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology &  
414 Evolution*, 35(5), 454–466. <https://doi.org/10.1016/j.tree.2020.01.004>
- 415 Stock, M. (2021). Pairwise learning for predicting pollination interactions based on traits and phylogeny.  
416 *Ecological Modelling*, 14.
- 417 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*,  
418 88(2), 192–195. <https://doi.org/10.1111/1365-2656.12949>
- 419 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,  
420 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction  
421 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,  
422 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- 423 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,  
424 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer  
425

- 428 learning can help predict potential species interaction networks despite data limitations. *Methods in*  
429 *Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 430 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
431 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
432 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*  
433 *the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 434 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.  
435 <https://doi.org/10.1002/ecy.3047>
- 436 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.  
437 <https://doi.org/10.1038/35004572>
- 438 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food  
439 webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 440 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory  
441 of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 442 Xie, J.-R., Zhang, P., Zhang, H.-F., & Wang, B.-H. (2017). Completeness of Community Structure in  
443 Networks. *Scientific Reports*, 7(1), 5269. <https://doi.org/10.1038/s41598-017-05585-6>
- 444 Yodzis, P. (1982). The Compartmentation of Real and Assembled Ecosystems. *The American Naturalist*,  
445 120(5), 551–570. <https://doi.org/10.1086/284013>

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		木	179	
level of obj.		(mechanisms) what determines direct interaction		
6	Species	fund. niche (inv. filter)	co- occurrence	
15		buckbones (mora) truit-match	"capacity"	
21	Pop.	neutral. funct. resp.	pop size/ dynamics	
0	indiv.	"physics" 2D   3D prey choice	energy	
3		?? allometric scaling??		
		: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES		

the "driver" of the interaction  
 ≠ the underlying theory (l: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.

Figure 1: TODO.