

# **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?**), actual coverage of ‘real world’  
21 interaction data remains sparse (Poisot et al., 2021). Against this practical challenge, there is additionally  
22 high variance in the terminology we use to define networks. Finally, the mathematical and statistical tools  
23 we use to construct, conceptualise, analyse and predict with these networks are also highly variable.

- 24 1. what are the underlying assumptions about nodes, edges, scale and process that are made when we  
25 attempt to delimit and describe a food webs;
- 26 2. are there families of commonly used tools that map onto assumptions about scales and processes;

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

## **32 1 Setting the Scene: The Not So Basics of Nodes and Edges**

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

44 [Figure 1 about here.]

### **45 1.0.1 How do we define a node?**

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

### **56 1.0.2 What is meant by an edge?**

57 At its core links within food webs can be thought of as a representation of either feeding links between  
58 species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within the  
59 community/system *e.g.*, energy transfer or material flow (Lindeman, 1942). How we specify links will influence  
60 the resulting structure of the network - and the inferences we will make thereof. For example taking a food  
61 web that consists of links representing all *potential* feeding links for a community (*i.e.*, a metaweb) will be

62 meaningless if you are interested in understanding the flow of energy through the system as the links within  
63 a metaweb do not represent environmental/energetic constraints. In addition to the various ways of defining  
64 the links between species pairs there are also a myriad of ways in which the links themselves can be quantified.  
65 Links between species are often treated as being present or absent (*i.e.*, binary) but it is also possible to  
66 use probabilities (which quantifies how likely an interaction is to occur, Poisot, Cirtwill, et al., 2016) or  
67 continuous measurements (which quantifies the strength of of an interaction, Berlow et al., 2004). Moving  
68 away from a purely binary way of representing allows us to quantify a level of (un)certainty of our knowledge  
69 of interactions (*i.e.*, moving from being able to ask if they are occurring to quantifying how likely they are  
70 to occur) does add an additional level of ‘complexity’ to the construction and interpretation of networks, but  
71 ultimately it will allow us to capture more information at different scales (Banville et al., 2024).

### 72 **1.0.3 Putting the parts together; what does it mean?**

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

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

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

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

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

99 Processes that are all-or-nothing (possibility) vs processes that are context dependent (likelihood). Processes  
100 form the underlying logic of models (and arguably even empirical data capture). Processes influence how we  
101 define the network (its anatomy). Ultimately when we put this all together it will influence how we can and  
102 should use the resulting network.

103 Important goal here is to introduce the idea that there are multiple facets as to what determines the interaction  
104 between species and that there is some sort of ‘scale of organisation’ Figure 2. We can then introduce these  
105 different scales/theories and I think some key points to highlights are the features, limits, and descriptions  
106 of these different scales (by that I mean what rules them, what finds them, and what binds them - sorry not  
107 sorry). I think it is also worth either in this section or in the one where we talk about model families to  
108 discuss the idea of ‘moving between’ different levels - e.g. downsampling but also feasibility - can we actually  
109 do that? Another interesting discussion here (or maybe actually something that can make its way into the  
110 concluding remarks) is thinking about what determines interactions vs what determines structure...

- 111 • These different theories are shown in Figure 2 and we can see there is some element of scaling (species  
112 - population - individual)

113 [Figure 2 about here.]

#### **114 Evolutionary compatibility**

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

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

### 127 **(Co)occurrence**

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

### 138 **Abundance**

139 The abundance of the different species within the community can influence the likelihood of an interaction  
140 occurring in a myriad of ways. There is the argument that networks (and the interactions that make them up)  
141 are driven by neutral processes and it is only the abundance of the different species within the community, *sensu*  
142 neutral processes (Canard et al., 2012). Alternatively, when one refers to feeding ecology [ref], the abundance  
143 of different prey will influence predator choice as this influences both the likelihood of meeting [ref] as well  
144 as predator specialisation based on learned behaviour [ref] (learned behaviour specialising capturing the  
145 more abundant prey species which will mean that in the weighted sense that is the strongest link). Finally,  
146 abundance *could* also be used as a way to further help in refining probabilistic metawebs (Banville et al.,  
147 2024).

### 148 **4. Energetics**

149 This is where we begin to move into the foraging ecology space - specifically consumption rate and how  
150 that pertains to energy acquisition *i.e.*, optimal foraging theory. In the loosest sense I think this is the ‘prey  
151 choice’ space - but specifically in the context of how prey choice is informed by energetic cost (not just purely

152 based on *e.g.*, the most abundant species). If we think about ways that people have approached this there  
153 are the diet models of (Beckerman et al., 2006) and (Petchey et al., 2008) as well as the ‘trait’ framework  
154 developed by Wootton et al. (2023) that moves the ‘energy’ into different ‘modules’ related to the process of  
155 the consumer acquiring energy from the resource (however there is a disregard for the ‘Rule 1’ requirement  
156 of forbidden links, again not bad just pointing it out). The idea of the consumer search space developed  
157 by Pawar et al. (2012) is also an interesting consideration. Finally the environment itself is also imposing  
158 energy costs on the predator. Basically the ideas presented in Cherif et al. (2024), which is essentially a  
159 take on movement ecology? What it boils down to is being able to quantify the cost of movement *i.e.*, the  
160 physical constraints that the environment imposes on a species... Maybe we can also think of it more in terms  
161 of metabolic rate?

162 **5. Non-trophic interactions**

163 **3 Network prediction is scale dependent**

164 The way in which we predict a network is driven by the underlying theory Figure 2 which con-  
165 strains or informs the assumptions we make (this of course also has implications with regards  
166 to how the resulting network is defined (Box 1)). We can then spend a moment introducing  
167 the different model families Table 1. I think a clear messaging here might be that models can  
168 share a similar underlying theory but use different methods to get there (*e.g.*, using ecological  
169 rules (explicit), ecological expectations (pattern finders), or mathematical models (assumptions  
170 on the structure of the matrix - maybe even network)). Importantly different models will also  
171 have different ‘limits’ to them - this is probably a product of both where they are found within  
172 the ‘theory space’ Figure 2 as well as the definition of the network (Box 1) space. Should we  
173 also maybe revisit the idea of interaction vs structure predictors... I think it is still a point that  
174 is worth raising but no longer the framework on which we hang the different model families...

- 175 • The way in which we predict networks is ‘constrained’/informed by the different theories shown in  
176 Figure 2
- 177 • Need to be aware of this and be aware how/what we can use the networks - Petchey dilemma
- 178 • The ‘scale’ that a network is constructed should be a determinant of what we can learn about a system  
179 *e.g.*, can’t use a feasibility network to learn something about energy flows. This is because they are  
180 capturing different processes

181 • Link the ‘model families’ to the different scales/theories

182 • Data...

183 As discussed in Box 1 there are many ways to define a food web, meaning that there are equally as many  
184 reasons one might be interested in predicting a food web. However we may think of two primary drivers  
185 for wanting to predict networks (Panel B Figure 1), namely an interest in generating a set of ecologically  
186 plausible networks (*i.e.*, being able to describe networks using a model) or being able to recover (predict)  
187 location specific, ‘realised’, interactions for a specific species community (*i.e.*, being able to predict/infer the  
188 interactions between species). Of course these two categories are not distinct, mutually exclusive, groups but  
189 can rather be viewed as operating on a continuum ranging from a need for generality (*i.e.*, creating a network  
190 that, when taken in aggregate, the distribution of links (interactions) between nodes (species) are ecologically  
191 plausible) to a need for specificity (*i.e.*, local-level predictions between specific species pairs). Although the  
192 ability to predict ‘real-world’ interactions (and the resulting food webs) can have more intuitive ‘real world’  
193 applications *e.g.*, being able to ‘recover’ food webs that have since gone extinct (Dunne et al., 2008; Yeakel  
194 et al., 2014), using pairwise interactions to understand species distributions (Pollock et al., 2014) or even  
195 co-extinction risk (Dunn et al., 2009), a more structural approach to network construction affords one an  
196 opportunity to interrogate some of the more high-level mechanisms that are structuring networks (Box 1).

197 It is perhaps more important that when one is talking about ‘why’ they want to predict networks to articulate  
198 exactly what anatomical part of the food web we are interested in scrutinising.

### 199 3.1 How do we predict food webs?

200 Selecting a model for the task of network prediction should come down to two things; what *aspect* of a  
201 food web one is interested in predicting, and what data are available, necessary, and sufficient. As shown  
202 in panel B of Figure 1 the interest in a network is (usually) at either the ‘structural’ or ‘interaction’ level  
203 and the development of models for the task of network prediction often focus on high fidelity (performance)  
204 at one of these scales. With this in mind it is beneficial to think of the different model families relative  
205 to these two different goals; here we refer to models that are used to predict the structure of a network as  
206 **topology generators** and models developed to infer the interactions for a given species pool as **interaction**  
207 **predictors**. It is meaningful to make this distinction because although it is possible to construct a food  
208 web given using an *interaction predictor* the models themselves lack any sort of parametrisation of the  
209 network structure and so the resulting network is a poor reflection of the actual network structure (Caron  
210 et al., 2024). This is primarily because *interaction predictors* are models that evaluate the feasibility of  
211 an interaction between species pairs and not in the context of feasibility at the community level. Models

212 themselves are a reflection of the different goals and intentions of the research program from which they are  
213 developed and are often ‘described’ by a specific mechanism that will determine the resulting structure or  
214 interactions (Box 1). Models such as the niche (Williams & Martinez, 2000) or cascade (Cohen et al., 1990)  
215 were developed with the intent of being used to understand the *structural* aspects of food webs, specifically  
216 how links are distributed amongst species in the community, whereas bayesian (Cirtwill et al., 2019) or trait  
217 hierarchy (Shaw et al., 2024) models have been developed on the basis that the traits of a species are the  
218 underlying mechanism in determining the feasibility of interactions (*i.e.*, species *a* has the capacity to eat  
219 species *b*). Along with predicting different anatomical parts of a food web the different models have varying  
220 degrees of data that are needed to ‘parametrise’ the network. Once these two limitations are assessed and  
221 addressed it is then possible to select the model (or model family) that will best be able to capture food  
222 web feature that the researcher is most interested in (see Box 2 - Assessing model outputs). It is thus clear  
223 that (realistically) there will probably never be a ‘best fit’ tool that is able to construct a food web that  
224 will span the entire range of needs, and rather the responsibility lies with the researcher to be aware of not  
225 only the underlying philosophy of the specific toolset (as this could have knock-on effects when using those  
226 networks for downstream analyses/simulations; pers. comms. Beckerman, 2024), but also how well the tool  
227 can retrieve the specific network or interaction properties that is of interest.

228 In order for a model to formalise a ‘complete’ food web it is necessary to formalise two aspects  
229 of the network, ‘who eats whom’ (to determine the links between nodes) as well as the structure  
230 of the network (to limit the distribution of links), however most models are inclined to focus on  
231 one of the two aspects panel B of 1.

232 Crucially most topology generators lack some key data on the interaction between species (this  
233 can be because of how the model itself defines species or the way in which links are assigned in  
234 the network) and interaction predictors lack some sort of parametrisation of network structure  
235 (just because two species can interact it does not mean that they will, Poisot et al., 2015).

236 What is the purpose of generating a network? Is it an element of a bigger question we are asking,  
237 *e.g.*, I want to generate a series of networks to do some extinction simulations/bioenergetic stuff  
238 OR are we looking for a ‘final product’ network that is relevant to a specific location? (this can  
239 still be broad in geographic scope).

## 240 3.2 Categorizing Model Families

### 241 NEED A TRANSITION PARAGRAPH

242 As there are many food web models to choose from it is perhaps useful to think about the models in terms of  
243 model families, a summary of these families is presented in Table 1 highlights the differences and similarities  
244 of the philosophies and assumptions that determine a network. A more extensive overview of the different  
245 models that fall with in the different model families can be found in [SuppMat 1](#) and for a more detailed  
246 breakdown of the different ‘traits’ of the model families refer to [SuppMat 2](#).

Table 1: A summary of the different families of tools that can be used to generate food webs. Here ‘type’ leans on the ideas from Momal et al. (2020) in terms of reconstructing networks from other known (observed) interactions and inferring interactions without relying on observed interactions.

Model family	Assumption	Theory	Type	Key reference
null	Links are randomly distributed within a network		network	
			inference	
neutral	Network structure is random, but species abundance	abundance	network	Canard et al. (2012)
	determines links between nodes		inference	
resource	Networks are interval, species can be ordered on a ‘niche axis’		network	Williams & Martinez (2008)
			inference	
generative	Networks are determined by their structural features		network	
			reconstruction	
energetic	Interactions are determined by energetic costs	abundance + energy	network	
			reconstruction	
graph embedding	Interactions can be predicted from the latent traits of networks	feasibility	network	Strydom et al. (2023)
			reconstruction	
trait matching	Interactions can be inferred by a mechanistic framework/relationships	feasibility	network	Morales-Castilla et al. (2015)
			reconstruction	
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	feasibility	network	Pichler et al. (2020)
			reconstruction	

Model family	Assumption	Theory	Type	Key reference
expert knowledge	'Boots on the ground' ecological knowledge and observations	feasibility	network reconstruction	
data scavenging	Webscraping to create networks from online databases		network reconstruction	Poisot, Gravel, et al. (2016) (f you squint?)
co-occurrence	co-occurrence patterns arise from interactions so we can use these patterns to reverse engineer the interactions	co-occurrence	network inference	

## <sup>247</sup> 4 Making Progress with Networks

<sup>248</sup> In this section I want to highlight that we don't actually have any clear guidelines as to how we can 'use'  
<sup>249</sup> networks - which probably stems from both the fact that when I am talking about a network and when  
<sup>250</sup> someone else is talking about a network we may actually be talking about two very different conceptualisations  
<sup>251</sup> of 'a network' (this should actually be a selling point in the intro - may have just found my *raison d'être*) as  
<sup>252</sup> well as that a lot of the ideas that we have about networks are not really tied to any sort of tangible function  
<sup>253</sup> (i.e. Tim's GeoBon ms thing-y). However we can maybe at least try to present some guidelines - but I think  
<sup>254</sup> specifically within the sort of Petchy dilemma space and clearly tied to the ideas we discuss in the ms. This  
<sup>255</sup> includes: understanding the limits of how a network is defined and how the underlying theory impacts the use  
<sup>256</sup> as well as data?? IDK we need to shoehorn data in here somehow... We can also use this as a gap identifying  
<sup>257</sup> space and I think the framing can still rest under the limits concept particularly time, space, and boundaries  
<sup>258</sup> - which will all probably fall under some aspect of biological scale... We can also raise the idea of trust - as in  
<sup>259</sup> which methods have more support/trust than others. Also what even a 'real' network entails (and this links  
<sup>260</sup> again back to Tim's stuff) as well as a subtle jab at Pringles notion that the most critical issue in the world  
<sup>261</sup> of food webs is being able to identify every. single. link. even though there is no real discussion as to what  
<sup>262</sup> is an 'opportunistic' link vs a link that represents a sustainable energy source for a population (or would it  
<sup>263</sup> be an individual)...

<sup>264</sup> We need to be aware of the parameter space that is possible given a specific definition of a network and  
<sup>265</sup> operate within those parameters.

## <sup>266</sup> 5 Concluding remarks

<sup>267</sup> I think the idea of time and how we are aggregating networks across that should be a prominent feature  
<sup>268</sup> here...

<sup>269</sup> • In certain situations structure is ‘enough’ but there may be use cases where we are really interested in  
<sup>270</sup> the node-level interactions *i.e.*, species identity is a thing we care about and need to be able to retrieve  
<sup>271</sup> specific interactions at specific nodes correctly.

<sup>272</sup> • Why do interaction models do so badly at predicting structure? Nuance of metaweb vs realisation but  
<sup>273</sup> also time? At the core of it interaction models are trained on existing interaction data; this is data  
<sup>274</sup> that are most likely closer to a metaweb than a local realisation even if they are being inventoried at a  
<sup>275</sup> small scale...

<sup>276</sup> – We can briefly shoehorn downsampling here maybe??

<sup>277</sup> • It will be interesting to bring up the idea that if a model is missing a specific pairwise link but doing  
<sup>278</sup> well overall then when does it matter?

<sup>279</sup> – The fact that *some* people are concerned about the taxonomic resolution and cascading effects  
<sup>280</sup> those might have on our understanding of network structure (Pringle, 2020; Pringle & Hutchinson,  
<sup>281</sup> 2020), but that puts us in a place where we are at risk of losing our ability to distinguish the wood  
<sup>282</sup> from the tree - are we not (at least at times) concerned more with understanding ecosystem level  
<sup>283</sup> processes than with needing to understand things *perfectly* at the species level.

<sup>284</sup> – I don’t think these ‘rare’/nuanced links (e.g. carnivorous hippos) are going to rock the boat when  
<sup>285</sup> we think about networks at the structural level.

<sup>286</sup> “The resolution of food-web data is demonic because it can radically change network topology  
<sup>287</sup> and associated biological inferences in ways that are unknowable in the absence of better data.” -  
<sup>288</sup> Pringle & Hutchinson (2020) The counter to this is that structural models are often not working  
<sup>289</sup> at the species level and thus the structure remains ‘unchanged’ when you increase the resolution  
<sup>290</sup> - I don’t think that people are that concerned with the structure of real world networks barring  
<sup>291</sup> connectance and since that scales with species richness anyway your final proportion will probably  
<sup>292</sup> still remain the same...

<sup>293</sup> • I think a big take home will (hopefully) be how different approaches do better in different situations  
<sup>294</sup> and so you as an end user need to take this into consideration and pick accordingly. I think Petchey  
<sup>295</sup> et al. (2011) might have (and share) some thoughts on this. I feel like I need to look at Berlow et al.

296 (2008) but maybe not exactly in this context but vaguely adjacent.

297 – I think this is sort of the crux of the argument presented in Brimacombe et al. (2024) as well.

298 “we highlight an interesting paradox: the models with the best performance measures are not  
299 necessarily the models with the closest reconstructed network structure.” - Poisot (2023)

- 300 • Do we need network models to predict interactions and interaction models to predict structure?

301 – “Another argument for the joint prediction of networks and interactions is to reduce circularity  
302 and biases in the predictions. As an example, models like linear filtering generate probabilities of  
303 non-observed interactions existing, but do so based on measured network properties.” - Strydom  
304 et al. (2021)

305 – Aligning (dove-tailing) with this the idea of ensemble modelling as presented by Becker et al.  
306 (2022)

- 307 • Close out with a call to action that we have models that predict networks very well and models that  
308 predict interactions very well but nothing that is doing well at predicting both - this is where we should  
309 be focusing our attention when it comes to furthering model development...

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

313 – The Terry & Lewis (2020) paper looks at some methods but is specifically looking at a bipartite  
314 world...

315 do we bring this up? this could be a box... if we have the ‘finances’ for it... otherwise it should go to the  
316 outstanding questions fur sure

317 “That being said, there is a compelling argument for the need to ‘combine’ these smaller functional units  
318 with larger spatial networks (Fortin et al., 2021) and that we should also start thinking about the interplay  
319 of time and space (Estay et al., 2023). Although deciding exactly what measure might actually be driving  
320 differences between local networks and the regional metaweb might not be that simple (Saravia et al., 2022).”

321 **5.1 Time**

322 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a  
323 ‘network’. Realistically most empirical networks are more aligned with ‘feasibility networks’ as opposed to

<sup>324</sup> ‘realised networks’ as they are often the result of some sort of aggregation of observations across time. This  
<sup>325</sup> ‘problem’ is two-fold. Firstly we need to think about how this affects any sort of development of theory  
<sup>326</sup> that sits closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer  
<sup>327</sup> questions about realised networks using feasible networks? The second is that this lack of ‘direction’ as to  
<sup>328</sup> how we should define a network is (actually) probably one of the biggest barriers that is affecting the use of  
<sup>329</sup> networks in applied settings...

<sup>330</sup> Another time perspective question is when do we determine a link to be ‘real’... In the context of feasible  
<sup>331</sup> networks this is perhaps clearer - all things equal would the predator be able to consume the prey. However  
<sup>332</sup> in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction - just  
<sup>333</sup> because an interaction is possible in the now is it able to sustain a population in the long term. And what  
<sup>334</sup> is the scale for that long term - are we thinking at the generational scale? Because ultimately when we are  
<sup>335</sup> constructing a network we are aggregating not only across space but also across time.

## <sup>336</sup> Glossary

---

Term	Definition
food web	a representation of feeding links between species
topology generator	a model that predicts a network based on assumptions of structure, this network is species agnostic in the sense that it does not necessarily contain information at the node level
interaction predictor	a model that predicts species interactions, these interactions can be used to construct a network but there are no <i>a priori</i> assumptions as that will constrain the network structure
model	A tool that can be used to construct food webs, where the resulting network is a representation of a real world network. Models typically only capture specific elements of real world networks and are intended to be used in specific settings

Term	Definition
model family	A family of models that share an underlying philosophy when it comes to the mapping, pragmatism, and reduction of a network. Families have the same underlying philosophies and assumptions that determine the links between nodes as well as how these may be encoded
metaweb	A network that represents <i>all</i> the potential links between species. Importantly these links will not necessarily all be realised in a specific location for a specific time
realised network	A network that represents the links between species that are occurring. These networks represent a very localised network...
potential feeding link	links that indicate that an interaction is ecologically feasible but not realised <i>per se</i> (a metaweb would contain potential feeding links)
realised feeding link	links that indicate that the interaction is realised ‘in the field’. (a realised network contains realised feeding links)
confusion matrix	captures the number of true positives (interaction predicted as present when it is present), false negatives (interaction predicted as absent when it is present), false positives (interaction predicted as present when it is absent), and true negatives (interaction predicted as absent when it is absent)

## <sup>337</sup> Outstanding questions

- non-consumptive effects

- how do we define the spatial and temporal ‘boundaries’ of a network?

- 340 • how do we define a ‘real’ network?

341 **References**

- 342 Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas,  
343 T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction*  
344 *networks*. EcoEvoRxiv. <https://doi.org/10.32942/X28G8Z>
- 345 Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.  
346 A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,  
347 E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic  
348 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)
- 349 Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.  
350 *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- 352 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of  
353 the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- 354 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,  
355 V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.  
356 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),  
357 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 358 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.  
359 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 360 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A  
361 cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 362 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings  
363 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),  
364 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 365 Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of  
366 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- 368 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models  
369 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,  
370 33(4), e13807. <https://doi.org/10.1111/geb.13807>

- 371 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,  
372 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The  
373 environment to the rescue: Can physics help predict predator-prey interactions? *Biological Reviews*,  
374 n/a(n/a). <https://doi.org/10.1111/brv.13105>
- 375 Cirtwill, A. R., Ekklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for  
376 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10(6),  
377 902–911. <https://doi.org/10.1111/2041-210X.13180>
- 378 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.  
379 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 380 Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag.
- 381 Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones  
382 using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>
- 383 Dansereau, G., Barros, C., & Poisot, T. (2023). *Spatially explicit predictions of food web structure from*  
384 *regional level data*.
- 385 Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction:  
386 Are most endangered species parasites and mutualists? *Proceedings. Biological Sciences*, 276(1670),  
387 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- 388 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological*  
389 *networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 390 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and  
391 Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal. pbio.0060102>
- 392 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks  
393 over space. *Frontiers in Ecology and Evolution*, 11.
- 394 Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings*  
395 *of the Royal Society B: Biological Sciences*, 288(1949), rspb.2020.1889, 20201889. <https://doi.org/10.1098/ rspb.2020.1889>
- 396 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,  
397 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.  
398 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 399 Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch  
400 between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*,  
401 11, e14620. <https://doi.org/10.7717/peerj.14620>

- 404 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 405
- 406 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 407
- 408 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 409
- 410 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from  
411 abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.13380>
- 412
- 413 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from  
414 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 415 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic  
416 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 417 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web  
418 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 419
- 420 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some  
421 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 422
- 423 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms  
424 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and  
425 Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- 426
- 427 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods  
in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 428
- 429 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &  
Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,  
430 48(7), 1552–1563. <https://doi.org/10.1111/jbi.14127>
- 431
- 432 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of  
probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/2041-210X.12602>
- 433
- 434 Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B.,  
& Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological  
435 hypotheses. *Ecography*, 39(4), 402–408. <https://doi.org/10.1111/ecog.01941>
- 436 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary

- 437 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 438 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks  
439 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 440 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O’Hara, R. B., Parris, K. M., Vesk, P. A., &  
441 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint  
442 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/10.1111/2041-210X.12180>
- 443 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton  
444 University Press. <https://doi.org/10.1515/9780691195322-020>
- 445 Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology,  
446 Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>
- 447 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.  
448 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 449 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network  
450 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),  
451 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 452 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for  
453 reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 454 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,  
455 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction  
456 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,  
457 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- 458 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,  
459 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer  
460 learning can help predict potential species interaction networks despite data limitations. *Methods in  
461 Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 462 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
463 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
464 towards predicting species interaction networks (across space and time). *Philosophical Transactions of  
465 the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 466 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.

- 470      <https://doi.org/10.1002/ecy.3047>
- 471      Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
- 472      <https://doi.org/10.1038/35004572>
- 473      Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food  
474      webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 475      Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory  
476      of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 477      Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).  
478      Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>
- 479



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

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

JUN	27	THU	木	179
			(mechanism)	
			what determines	
			interaction	
6		Body of theory		
15	Species	fund. niches env. filter	co- occurrence	
21		buck bones (mora)	"capacity"	
0	pop.	truit-match		
3	indiv.	neutral. funct. resp.	pop size / dynamics	
?? allometric scaling ??				
				: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES

Figure 2: TODO.