

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

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

Abstract: Food webs are a useful abstraction and representation of the feeding links between species in a community and are used to infer many ecosystem level processes. However, the different theories, mechanisms, and criteria that underpin how a food web is defined and, ultimately, constructed means that not all food webs are representing the same ecological process. Here we present a synthesis of the different assumptions, scales and mechanisms that are used to define different ecological networks ranging from metawebs (an inventory of all potential interactions) to fully realised networks (interactions that occur within a given community over a certain timescale). Illuminating the assumptions, scales, and mechanisms of network inference allows a formal categorisation of how to use networks to answer key ecological and conservation questions and defines guidelines to prevent unintentional misuse or misinterpretation.

Keywords: food web, network construction, scientific ignorance

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

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

19 With respect to data, it is extremely challenging to actually record species interactions in the field (Jordano,
20 2016a, 2016b). Despite notable herculean efforts (**Woodward? Benguela?**), 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.

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

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

[Figure 1 about here.]

1.0.1 How do we define a node?

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

1.0.2 What is meant by an edge?

At its core links within food webs can be thought of as a representation of either feeding links between species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within the community/system *e..*, energy transfer or material flow (Lindeman, 1942). How we specify links will influence the resulting structure of the network - and the inferences we will make thereof. For example taking a food 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 are they 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 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 drivers of species interactions**

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

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

109 [Figure 2 about here.]

110 **1. (Co)occurrence**

111 Although the outright assumption that because two species are co-occurring it must mean that they are
112 interacting is inherently flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at
113 least in terms of feeding links) if they are not co-occurring in time and space. Hence it is of course important
114 to take into consideration the co-occurrence of both the resource and the consumer. An example of this
115 would be the work from Dansereau et al. (2023), where a metaweb (feasibility network) is downsampled into
116 smaller realisations based on better data/knowledge as to which species are occurring at a specific location
117 - however arguably these are still firmly in the space of feasible interactions for the specific location but are
118 approaching a better approximation of ‘reality’...

119 **2. Feasibility**

120 This is based on the idea of forbidden links introduced by Jordano (2016b), specifically that there must

121 be some degree of *trait complementarity* that allows a predator to chase, capture, kill, and consume, its
122 prey. This is probably the level that the idea of a metaweb (Dunne, 2006) is most applicable to. Within
123 the network prediction ‘field’ this is perhaps the most developed space. Predictive models run the gamut
124 including mechanistic models (Morales-Castilla et al., 2015), binary classifiers (Pichler et al., 2020), and
125 graph embedding (Strydom et al., 2023) and use either traits (or phylogeny as a proxy for the conservation
126 thereof) as a means to ‘evaluate’ if an interaction is *possible* between two species (again not the likelihood
127 of it happening but the likelihood of its feasibility). It is probably worth having a brief interlude here to be
128 really clear that just because an interaction is probabilistic it does not make it weighted (at least not in the
129 traditional sense of weighted interactions, *e.g.*, J. T. Wootton & Emmerson (2005)) - it is still ‘binary’, it
130 just happens to be defined by a binomial distribution (*sensu* Banville et al. (2024)).

131 **3. Mass effect**

132 Not sure if there are models that ‘only’ consider abundance (barring the neutral model) and that it is rather
133 more of a building block in some of the models that are more relevant to the next steps. Maybe there is an
134 argument that this ‘rule’ is ‘irrelevant’ in the context of how I am presenting network prediction and more
135 so a data parameter one needs... maybe...

136 This is probably the point where we start to shift from a *potential* (presence/absence) way of defining
137 interactions and start moving into the ‘qualitative’/weighted interaction space - we are not ‘determining’ if
138 the interaction is feasible but rather making an assumption on prey selection based on the species’ likelihood
139 of ‘meeting’, although Banville et al. (2024) presents a compelling case that this could still be considered
140 something that falls under the ‘feasibility’ and not ‘reality’ side of the spectrum... (well at least past Tanya
141 seemed to think so)

142 **4. Energetics**

143 This is where we begin to move into the foraging ecology space - specifically consumption rate and how that
144 pertains to energy acquisition *i.e.*, optimal foraging theory. In the loosest sense I think this is the ‘prey choice’
145 space - but specifically in the context of how prey choice as informed by energetic cost (not just purely based
146 on *e.g.*, the most abundant species). If we think about ways that people have approached this there are the
147 diet models of (Beckerman et al., 2006) and (Petchey et al., 2008) as well as the ‘trait’ framework developed
148 by K. L. Wootton et al. (2023) that moves the ‘energy’ into different ‘modules’ related to the process of
149 the consumer acquiring energy from the resource (however there is a disregard for the ‘Rule 1’ requirement
150 of forbidden links, again not bad just pointing it out). The idea of the consumer search space developed
151 by Pawar et al. (2012) is also an interesting consideration. Finally the environment itself is also imposing

152 energy costs on the predator. Basically the ideas presented in Cherif et al. (2024), which is essentially a
153 take on movement ecology? What it boils down to is being able to quantify the cost of movement *i.e.*, the
154 physical constraints that the environment imposes on a species... Maybe we can also think of it more in terms
155 of metabolic rate?

156 3 Network prediction is scale dependent

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

- 168 • The way in which we predict networks is ‘constrained’/informed by the different theories shown in
169 Figure 2
- 170 • Need to be aware of this and be aware how/what we can use the networks - Petchey dilemma
- 171 • The ‘scale’ that a network is constructed should be a determinant of what we can learn about a system
172 *e.g.*, can’t use a feasibility network to learn something about energy flows. This is because they are
173 capturing different processes
- 174 • Link the ‘model families’ to the different scales/theories
- 175 • Data...

176 As discussed in Box 1 there are many ways to define a food web, meaning that there are equally as many
177 reasons one might be interested in predicting a food web. However we may think of two primary drivers
178 for wanting to predict networks (Panel B Figure 1), namely an interest in generating a set of ecologically
179 plausible networks (*i.e.*, being able to describe networks using a model) or being able to recover (predict)
180 location specific, ‘realised’, interactions for a specific species community (*i.e.*, being able to predict/infer the

181 interactions between species). Of course these two categories are not distinct, mutually exclusive, groups but
182 can rather be viewed as operating on a continuum ranging from a need for generality (*i.e.*, creating a network
183 that, when taken in aggregate, the distribution of links (interactions) between nodes (species) are ecologically
184 plausible) to a need for specificity (*i.e.*, local-level predictions between specific species pairs). Although the
185 ability to predict ‘real-world’ interactions (and the resulting food webs) can have more intuitive ‘real world’
186 applications *e.g.*, being able to ‘recover’ food webs that have since gone extinct (Dunne et al., 2008; Yeakel
187 et al., 2014), using pairwise interactions to understand species distributions (Pollock et al., 2014) or even
188 co-extinction risk (Dunn et al., 2009), a more structural approach to network construction affords one an
189 opportunity to interrogate some of the more high-level mechanisms that are structuring networks (Box 1).
190 It is perhaps more important that when one is talking about ‘why’ they want to predict networks to articulate
191 exactly what anatomical part of the food web we are interested in scrutinising.

192 3.1 How do we predict food webs?

193 Selecting a model for the task of network prediction should come down to two things; what *aspect* of a
194 food web one is interested in predicting, and what data are available, necessary, and sufficient. As shown
195 in panel B of Figure 1 the interest in a network is (usually) at either the ‘structural’ or ‘interaction’ level
196 and the development of models for the task of network prediction often focus on high fidelity (performance)
197 at one of these scales. With this in mind it is beneficial to think of the different model families relative
198 to these two different goals; here we refer to models that are used to predict the structure of a network as
199 **topology generators** and models developed to infer the interactions for a given species pool as **interaction**
200 **predictors**. It is meaningful to make this distinction because although it is possible to construct a food
201 web given using an *interaction predictor* the models themselves lack any sort of parametrisation of the
202 network structure and so the resulting network is a poor reflection of the actual network structure (Caron
203 et al., 2024). This is primarily because *interaction predictors* are models that evaluate the feasibility of
204 an interaction between species pairs and not in the context of feasibility at the community level. Models
205 themselves are a reflection of the different goals and intentions of the research program from which they are
206 developed and are often ‘described’ by a specific mechanism that will determine the resulting structure or
207 interactions (Box 1). Models such as the niche (Williams & Martinez, 2000) or cascade (Cohen et al., 1990)
208 were developed with the intent of being used to understand the *structural* aspects of food webs, specifically
209 how links are distributed amongst species in the community, whereas bayesian (Cirtwill et al., 2019) or trait
210 hierarchy (Shaw et al., 2024) models have been developed on the basis that the traits of a species are the
211 underlying mechanism in determining the feasibility of interactions (*i.e.*, species *a* has the capacity to eat

species *b*). Along with predicting different anatomical parts of a food web the different models have varying degrees of data that are needed to ‘parametrise’ the network. Once these two limitations are assessed and addressed it is then possible to select the model (or model family) that will best be able to capture food web feature that the researcher is most interested in (see Box 2 - Assessing model outputs). It is thus clear that (realistically) there will probably never be a ‘best fit’ tool that is able to construct a food web that will span the entire range of needs, and rather the responsibility lies with the researcher to be aware of not only the underlying philosophy of the specific toolset (as this could have knock-on effects when using those networks for downstream analyses/simulations; pers. comms. Beckerman, 2024), but also how well the tool can retrieve the specific network or interaction properties that is of interest.

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

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

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

3.2 Categorizing Model Families

NEED A TRANSITION PARAGRAPH

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

Table 1: A summary of the different families of tools that can be used to generate food webs. 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 determines links between nodes	abundance	network inference	Canard et al. (2012)
resource	Networks are interval, species can be ordered on a ‘niche axis’		network inference	Williams & Martinez (2008)
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 reconstruction	Strydom et al. (2023)
trait matching	Interactions can be inferred by a mechanistic framework/relationships	feasibility	network reconstruction	Morales-Castilla et al. (2015)
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	feasibility	network reconstruction	Pichler et al. (2020)
expert knowledge	‘Boots on the ground’ ecological knowledge and observations	feasibility	network reconstruction	

Model family	Assumption	Theory	Type	Key reference
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	

240 4 Making Progress with Networks

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

257 We need to be aware of the parameter space that is possible given a specific definition of a network and
258 operate within those parameters.

5 Concluding remarks

I think the idea of time and how we are aggregating networks across that should be a prominent feature here...

- In certain situations structure is ‘enough’ but there may be use cases where we are really interested in the node-level interactions *i.e.*, species identity is a thing we care about and need to be able to retrieve specific interactions at specific nodes correctly.
- Why do interaction models do so badly at predicting structure? Nuance of metaweb vs realisation but also time? At the core of it interaction models are trained on existing interaction data; this is data that are most likely closer to a metaweb than a local realisation even if they are being inventoried at a small scale...
 - We can briefly shoehorn downsampling here maybe??
- It will be interesting to bring up the idea that if a model is missing a specific pairwise link but doing well overall then when does it matter?
 - The fact that *some* people are concerned about the taxonomic resolution and cascading effects those might have on our understanding of network structure (Pringle, 2020; Pringle & Hutchinson, 2020), but that puts us in a place where we are at risk of losing our ability to distinguish the wood from the tree - are we not (at least at times) concerned more with understanding ecosystem level processes than with needing to understand things *perfectly* at the species level.
 - I don’t think these ‘rare’/nuanced links (e.g. carnivorous hippos) are going to rock the boat when we think about networks at the structural level.

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

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

289 (2008) but maybe not exactly in this context but vaguely adjacent.

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

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

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

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

298 – Aligning (dove-tailing) with this the idea of ensemble modelling as presented by Becker et al.
299 (2022)

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

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

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

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

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

314 5.1 Time

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

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

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

329 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)

330 **Outstanding questions**

- 331 • non-consumptive effects
- 332 • how do we define the spatial and temporal ‘boundaries’ of a network?

- how do we define a ‘real’ network?

References

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

- 364 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,
365 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The
366 environment to the rescue: Can physics help predict predator–prey interactions? *Biological Reviews*,
367 *n/a*(n/a). <https://doi.org/10.1111/brv.13105>
- 368 Cirtwill, A. R., Eklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for
369 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, *10*(6),
370 902–911. <https://doi.org/10.1111/2041-210X.13180>
- 371 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.
372 *Ecology*, *99*(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 373 Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag.
- 374 Dansereau, G., Barros, C., & Poisot, T. (2023). *Spatially explicit predictions of food web structure from*
375 *regional level data*.
- 376 Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction:
377 Are most endangered species parasites and mutualists? *Proceedings. Biological Sciences*, *276*(1670),
378 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- 379 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological*
380 *networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 381 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and
382 Network Analyses of Cambrian Food Webs. *PLOS Biology*, *6*(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 383
- 384 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks
385 over space. *Frontiers in Ecology and Evolution*, *11*.
- 386 Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings*
387 *of the Royal Society B: Biological Sciences*, *288*(1949), rspb.2020.1889, 20201889. <https://doi.org/10.1098/rspb.2020.1889>
- 388
- 389 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, *14*(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 390
- 391 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 392
- 393 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, *23*(4), 399–417. <https://doi.org/10.2307/1930126>
- 394
- 395 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from
396 abundance data. *Methods in Ecology and Evolution*, *11*(5), 621–632. <https://doi.org/10.1111/2041-210X.13180>

- 398 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from
399 proxies. *Trends in Ecology & Evolution*, *30*(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 400 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic
401 interaction strengths. *Nature*, *486*(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 402 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web
403 structure. *Proceedings of the National Academy of Sciences*, *105*(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 404 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some
405 thoughts on judging food web models. *Journal of Theoretical Biology*, *279*(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 406 Pichler, M., Boreux, V., Klein, A.-M., Schleunig, M., & Hartig, F. (2020). Machine learning algorithms
407 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and
408 Evolution*, *11*(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- 409 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods
410 in Ecology and Evolution*, *14*(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 411 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
412 Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,
413 *48*(7), 1552–1563. <https://doi.org/10.1111/jbi.14127>
- 414 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of
415 probabilistic networks. *Methods in Ecology and Evolution*, *7*(3), 303–312. <https://doi.org/10.1111/2041-210X.12180>
- 416 Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B.,
417 & Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological
418 hypotheses. *Ecography*, *39*(4), 402–408. <https://doi.org/10.1111/ecog.01941>
- 419 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
420 through space and time. *Oikos*, *124*(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 421 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks
422 in ecology? *Functional Ecology*, *30*(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 423 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., &
424 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint
425 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*(5), 397–406. <https://doi.org/10.1111/2041-210X.12180>
- 426 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton

University Press. <https://doi.org/10.1515/9780691195322-020>

Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology, Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>

Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>

Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3), 630–642. <https://doi.org/10.1111/1365-2656.13652>

Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>

Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer learning can help predict potential species interaction networks despite data limitations. *Methods in Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>

Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz, N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap towards predicting species interaction networks (across space and time). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>

Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047. <https://doi.org/10.1002/ecy.3047>

Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183. <https://doi.org/10.1038/35004572>

Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>

Wootton, J. T., & Emmerson, M. (2005). Measurement of Interaction Strength in Nature. *Annual Review of Ecology, Evolution, and Systematics*, 36(1), 419–444. <https://doi.org/10.1146/annurev.ecolsys.36.091704.175535>

Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>

Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014). Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1407211111>

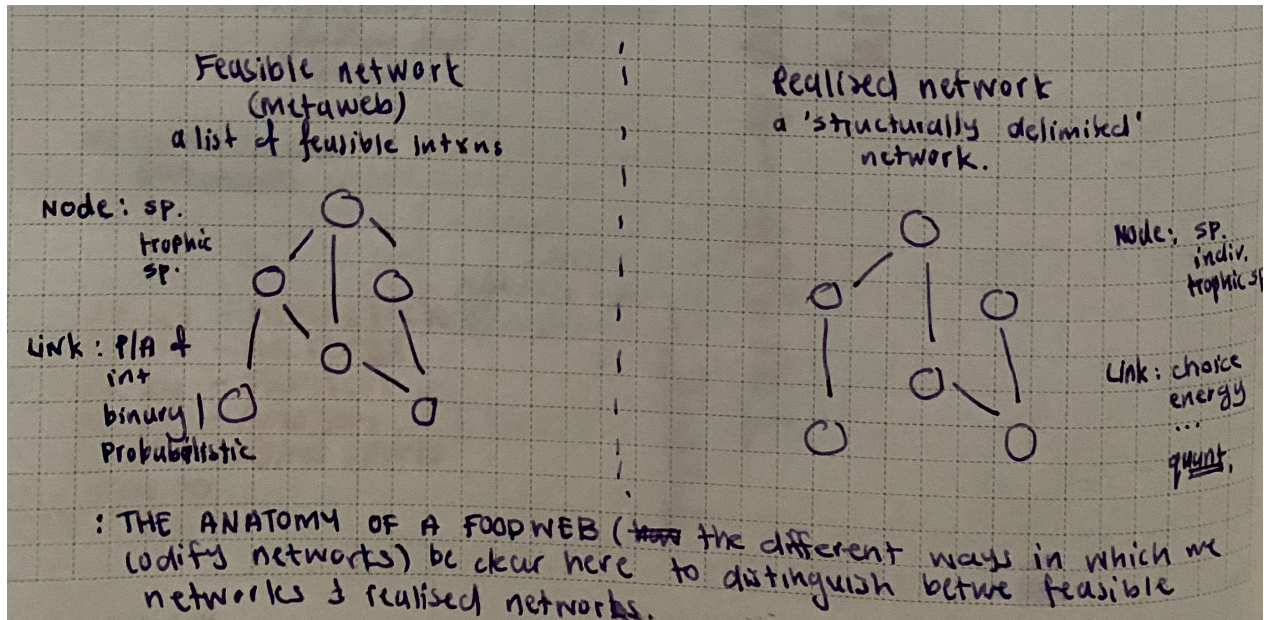


Figure 1: The many ways in which a food web can be defined and described at the node, edge, and even network level.

the "driver" of the interaction \neq the underlying theory (1:1) $\hat{=}$ 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.

level of org.	Bodies of theory	(mechanisms) what determines / drives interaction
"realizability" interactions (mechanisms)	species	fund. niche / env. filter
		co-occurrence
"realized" networks		backbones (mora) / trait-match
	pop.	neutral. / funct. resp.
		"capacity"
indiv.	"physics" / 2D / 3D / prey choice	POP size / dynamics
		energy

?? allometric scaling??

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

Figure 2: TODO.