

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

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

119 2. Evolutionary compatibility

120 There is compelling evidence that the possibility of an interaction occurring between two species is the result

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

3. Mass effect

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

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

4. Energetics

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

152 by Pawar et al. (2012) is also an interesting consideration. Finally the environment itself is also imposing
153 energy costs on the predator. Basically the ideas presented in Cherif et al. (2024), which is essentially a
154 take on movement ecology? What it boils down to is being able to quantify the cost of movement *i.e.*, the
155 physical constraints that the environment imposes on a species... Maybe we can also think of it more in terms
156 of metabolic rate?

157 **5. Non-trophic interactions**

158 **3 Network prediction is scale dependent**

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

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

178 As discussed in Box 1 there are many ways to define a food web, meaning that there are equally as many
179 reasons one might be interested in predicting a food web. However we may think of two primary drivers
180 for wanting to predict networks (Panel B Figure 1), namely an interest in generating a set of ecologically

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

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

194 3.1 How do we predict food webs?

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

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

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

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

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

235 3.2 Categorizing Model Families

236 NEED A TRANSITION PARAGRAPH

237 As there are many food web models to choose from it is perhaps useful to think about the models in terms of
238 model families, a summary of these families is presented in Table 1 highlights the differences and similarities
239 of the philosophies and assumptions that determine a network. A more extensive overview of the different
240 models that fall with in the different model families can be found in SuppMat 1 and for a more detailed
241 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	

²⁴² 4 Making Progress with Networks

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

²⁵⁹ We need to be aware of the parameter space that is possible given a specific definition of a network and operate within those parameters.

²⁶¹ 5 Concluding remarks

²⁶² I think the idea of time and how we are aggregating networks across that should be a prominent feature
²⁶³ here...

- ²⁶⁴ • In certain situations structure is ‘enough’ but there may be use cases where we are really interested in
²⁶⁵ the node-level interactions *i.e.*, species identity is a thing we care about and need to be able to retrieve
²⁶⁶ specific interactions at specific nodes correctly.

- ²⁶⁷ • Why do interaction models do so badly at predicting structure? Nuance of metaweb vs realisation but
²⁶⁸ also time? At the core of it interaction models are trained on existing interaction data; this is data
²⁶⁹ that are most likely closer to a metaweb than a local realisation even if they are being inventoried at a
²⁷⁰ small scale...

²⁷¹ – We can briefly shoehorn downsampling here maybe??

- ²⁷² • It will be interesting to bring up the idea that if a model is missing a specific pairwise link but doing
²⁷³ well overall then when does it matter?

²⁷⁴ – The fact that *some* people are concerned about the taxonomic resolution and cascading effects
²⁷⁵ those might have on our understanding of network structure (Pringle, 2020; Pringle & Hutchinson,
²⁷⁶ 2020), but that puts us in a place where we are at risk of losing our ability to distinguish the wood
²⁷⁷ from the tree - are we not (at least at times) concerned more with understanding ecosystem level
²⁷⁸ processes than with needing to understand things *perfectly* at the species level.

²⁷⁹ – I don’t think these ‘rare’/nuanced links (e.g. carnivorous hippos) are going to rock the boat when
²⁸⁰ we think about networks at the structural level.

²⁸¹ “The resolution of food-web data is demonic because it can radically change network topology
²⁸² and associated biological inferences in ways that are unknowable in the absence of better data.” -
²⁸³ Pringle & Hutchinson (2020) The counter to this is that structural models are often not working
²⁸⁴ at the species level and thus the structure remains ‘unchanged’ when you increase the resolution
²⁸⁵ - I don’t think that people are that concerned with the structure of real world networks barring
²⁸⁶ connectance and since that scales with species richness anyway your final proportion will probably
²⁸⁷ still remain the same...

- ²⁸⁸ • I think a big take home will (hopefully) be how different approaches do better in different situations
²⁸⁹ and so you as an end user need to take this into consideration and pick accordingly. I think Petchey
²⁹⁰ et al. (2011) might have (and share) some thoughts on this. I feel like I need to look at Berlow et al.

291 (2008) but maybe not exactly in this context but vaguely adjacent.

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

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

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

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

300 – Aligning (dove-tailing) with this the idea of ensemble modelling as presented by Becker et al.
301 (2022)

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

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

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

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

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

316 5.1 Time

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

³¹⁹ ‘realised networks’ as they are often the result of some sort of aggregation of observations across time. This
³²⁰ ‘problem’ is two-fold. Firstly we need to think about how this affects any sort of development of theory
³²¹ that sits closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer
³²² questions about realised networks using feasible networks? The second is that this lack of ‘direction’ as to
³²³ how we should define a network is (actually) probably one of the biggest barriers that is affecting the use of
³²⁴ networks in applied settings...

³²⁵ Another time perspective question is when do we determine a link to be ‘real’... In the context of feasible
³²⁶ networks this is perhaps clearer - all things equal would the predator be able to consume the prey. However
³²⁷ in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction - just
³²⁸ because an interaction is possible in the now is it able to sustain a population in the long term. And what
³²⁹ is the scale for that long term - are we thinking at the generational scale? Because ultimately when we are
³³⁰ constructing a network we are aggregating not only across space but also across time.

³³¹ 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)

³³² Outstanding questions

- non-consumptive effects

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

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

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

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level of obj.		(mechanisms) what determines direct interaction		the "driver" of the interaction ≠ the underlying theory (l:1) & the way we get to the answer is diff e.g. co-occurrence is about sharing space/time but we use niche theory env. filtering as the means to determine co-occurrence.
6	Species	fund. niches (inv. filter)	co- occurrence	
15		buckbones (mora) truit-match	"capacity"	
21	Pop.	neutral. funct. resp.	pop size/ dynamics	
0	indiv.	"physics" 2D 3D prey choice	energy	
3		?? allometric scaling??		
		: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES		

Figure 2: TODO.