

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?** Maiorano et al. (2020)), actual
21 coverage of ‘real world’ interaction data remains sparse (Poisot et al., 2021). Against this practical challenge,
22 there is additionally high variance in the terminology we use to define networks. Finally, the mathematical
23 and statistical tools we use to construct, conceptualise, analyse and predict with these networks are also
24 highly variable.

25 1. what are the underlying assumptions about nodes, edges, scale and process that are made when we
26 attempt to delimit and describe a food webs;

27 2. are there families of commonly used tools that map onto assumptions about scales and processes;

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

32 thinking can accelerate our capacity to predict the impact of multiple stressors on biodiverse communities.

33 1 Setting the Scene: The Not So Basics of Nodes and Edges

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

45 [Figure 1 about here.]

46 1.0.1 How do we define a node?

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

57 1.0.2 What is meant by an edge?

58 At its core links within food webs can be thought of as a representation of either feeding links between
59 species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within the
60 community/system *e.g.*, 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 meaningless if you are interested in understanding the flow of energy through the system as the links within a metaweb do not represent environmental/energetic constraints. In addition to the various ways of defining the links between species pairs there are also a myriad of ways in which the links themselves can be quantified. Links between species are often treated as being present or absent (*i.e.*, binary) but it is also possible to use probabilities (which quantifies how likely an interaction is to occur, Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of of an interaction, Berlow et al., 2004). Moving away from a purely binary way of representing allows us to quantify a level of (un)certainty of our knowledge of interactions (*i.e.*, moving from being able to ask if they are occurring to quantifying how likely they are to occur) does add an additional level of ‘complexity’ to the construction and interpretation of networks, but ultimately it will allow us to capture more information at different scales (Banville et al., 2024).

1.0.3 Putting the parts together; what does it mean?

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

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

92 which the resulting network can be used and applied within.

93 **2 From Nodes and Edges to Scales, Context, and Processes**

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

99 **2.1 Understanding the processes that determine species interactions**

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

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

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

114 [Figure 2 about here.]

115 **Evolutionary compatibility**

116 There is compelling evidence that the possibility of an interaction occurring between two species is the result
117 of their shared (co)evolutionary history (Dalla Riva & Stouffer, 2016; Gómez et al., 2010). In the more
118 proximal sense this is manifested as the ‘trait complementarity’ between two species, whereby one species
119 (the predator) has the ‘correct’ set of traits that allow it to chase, capture, kill, and consume the other species

120 (the prey). For species pairs where this condition is not met the link is deemed to be forbidden (Jordano,
121 2016b); *i.e.*, not physically possible and will always be absent within the network. In the context of trying
122 to determine the feasibility (*i.e.*, the *possibility*) of an interaction, phylogeny is an excellent predictor (Fricke
123 et al., 2022; Strydom et al., 2022) and allows one to construct what can be considered to be a metaweb.
124 In terms of thinking about the anatomy of an ‘feasibility network’ one should be aware that it is possible
125 to represent interactions as either binary (feasible/forbidden; *i.e.*, the traditional definition of a metaweb
126 Dunne (2006)) or as a probability (Banville et al., 2024), where the probability represents how likely that
127 the interaction between two species is feasible (what is the possibility of this interaction occurring?).

128 **(Co)occurrence**

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

139 **Abundance**

140 The abundance of the different species within the community can influence the likelihood of an interaction
141 occurring in a myriad of ways. There is the argument that networks (and the interactions that make them up)
142 are driven by only the abundance of the different species and not the characteristics (traits), *sensu* neutral
143 processes (Canard et al., 2012). Alternatively the abundance of species in a community can influence which
144 interactions are ultimately realised (Banville et al., 2024; Poisot et al., 2015).

145 **Predator choice (energetic cost)**

146 Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume
147 prey, and is well described within optimal foraging theory [ref] and rests on the idea that the prey a predator
148 chooses to target is one that will have the greatest return on energy with the lowest energetic cost. There are
149 additional bodies of work that attempt to include the cost of movement that the environment imposes on an
150 individual (Cherif et al., 2024) as well as 2D/3D search space (Pawar et al., 2012). In terms of formalising

151 these processes in the context of predicting networks using diet models (Beckerman et al., 2006; Petchey
152 et al., 2008) that have predator choice determined by the handling time, energy content, prey density, and
153 predator attack rate. Wootton et al. (2023) developed a model that moves the energy of the system into
154 different modules related to the process of the predator acquiring energy from the prey.

155 **Indirect interactions**

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

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

170 **3 Network prediction is nuanced**

171 The different models that are used to either predict or construct networks have an underlying philosophy
172 that often only captures one or a few of the processes discussed in Section 2.1, has implications for how the
173 resulting network is defined Section 1, which will ultimately delimit and define what inferences can be made
174 from the resulting network. Selecting a model for the task of network prediction should come down to two
175 things; what *aspect* of a food web one is interested in predicting, and what data are available, necessary,
176 and sufficient, and what is the purpose of wanting to predict a network? It is important that a researcher
177 is aware of this to ensure that the appropriate model is selected. Broadly researchers will be interested in
178 predicting/constructing two different types of networks; *metawebs*, which is essentially a list of all interactions
179 that are *possible* for a specific community (*i.e.*, at the scale of the species pairs), or being able to predict
180 location specific, *realised*, networks for the community (*i.e.*, at the scale of the community). The nature of

metawebs means that they are unable to capture the structural metrics of realised networks (Caron et al., 2024). The researcher is also constrained by the data needs of both the model as well as the network type; for example in order to predict a realised network one needs additional data (*e.g.*, abundance), making metawebs a more feasible choice in data-poor contexts (*e.g.*, Strydom et al. (2023) construct a metaweb using a species list and a phylogenetic tree). The final question is assessing the purpose of predicting a network - is it to create a series of simulated, species agnostic but still ecologically plausible, networks [*e.g.*] or to predict a network for a specific community at a specific location. It is these three points that will ultimately dictate which model is going to best allow one to predict the appropriate network.

Although the ability to predict ‘real-world’ interactions (and the resulting food webs) can have more intuitive ‘real world’ applications *e.g.*, being able to ‘recover’ food webs that have since gone extinct (Dunne et al., 2008; Yeakel et al., 2014), using pairwise interactions to understand species distributions (Pollock et al., 2014) or even co-extinction risk (Dunn et al., 2009), a more structural approach to network construction affords one an opportunity to interrogate some of the more high-level mechanisms that are structuring networks.

3.1 How do we predict food webs?

NEED A TRANSITION PARAGRAPH

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.

assumptions

Models such as the niche (Williams & Martinez, 2000) or cascade (Cohen et al., 1990) were developed with the intent of being used to understand the *structural* aspects of food webs, specifically how links are distributed amongst species in the community, whereas bayesian (Cirtwill et al., 2019) or trait hierarchy (Shaw et al., 2024) models have been developed on the basis that the traits of a species are the underlying mechanism in determining the feasibility of interactions (*i.e.*, species *a* has the capacity to eat species *b*).

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 with in 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	

211 4 Making Progress with Networks

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

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

230 5 Concluding remarks

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

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

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

240 – We can briefly shoehorn downsampling here maybe??

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

243 – The fact that *some* people are concerned about the taxonomic resolution and cascading effects
244 those might have on our understanding of network structure (Pringle, 2020; Pringle & Hutchinson,
245 2020), but that puts us in a place where we are at risk of losing our ability to distinguish the wood
246 from the tree - are we not (at least at times) concerned more with understanding ecosystem level
247 processes than with needing to understand things *perfectly* at the species level.

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

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

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

260 (2008) but maybe not exactly in this context but vaguely adjacent.

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

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

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

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

269 – Aligning (dove-tailing) with this the idea of ensemble modelling as presented by Becker et al.
270 (2022)

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

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

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

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

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

285 5.1 Time

286 Look at Hutchinson et al. (2019)

287 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a

²⁸⁸ ‘network’. Realistically most empirical networks are more aligned with ‘feasibility networks’ as opposed to
²⁸⁹ ‘realised networks’ as they are often the result of some sort of aggregation of observations across time. This
²⁹⁰ ‘problem’ is two-fold. Firstly we need to think about how this affects any sort of development of theory
²⁹¹ that sits closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer
²⁹² questions about realised networks using feasible networks? The second is that this lack of ‘direction’ as to
²⁹³ how we should define a network is (actually) probably one of the biggest barriers that is affecting the use of
²⁹⁴ networks in applied settings...

²⁹⁵ Another time perspective question is when do we determine a link to be ‘real’... In the context of feasible
²⁹⁶ networks this is perhaps clearer - all things equal would the predator be bale to consume the prey. However
²⁹⁷ in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction - just
²⁹⁸ because an interaction is possible in the now is it able to sustain a population in the long term. And what
²⁹⁹ is the scale for that long term - are we thinking at the generational scale? Because ultimately when we are
³⁰⁰ constructing a network we are aggregating not only across space but also across time.

³⁰¹ **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)

³⁰² Outstanding questions

- non-consumptive effects

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

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

306 **References**

- 307 Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas,
308 T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction*
309 *networks*. EcoEvoRxiv. <https://doi.org/10.32942/X28G8Z>
- 310 Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.
311 A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,
312 E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic
313 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)
- 314 Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.
315 *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- 316 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of
317 the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- 318 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,
319 V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.
320 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),
321 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 322 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.
323 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 324 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A
325 cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 326 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings
327 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),
328 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 329 Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of
330 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- 331 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models
332 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,
333 33(4), e13807. <https://doi.org/10.1111/geb.13807>

- 336 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,
337 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The
338 environment to the rescue: Can physics help predict predator-prey interactions? *Biological Reviews*,
339 n/a(n/a). <https://doi.org/10.1111/brv.13105>
- 340 Cirtwill, A. R., Ekklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for
341 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10(6),
342 902–911. <https://doi.org/10.1111/2041-210X.13180>
- 343 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.
344 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 345 Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag.
- 346 Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones
347 using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>
- 348 Dansereau, G., Barros, C., & Poisot, T. (2023). *Spatially explicit predictions of food web structure from*
349 *regional level data*.
- 350 Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction:
351 Are most endangered species parasites and mutualists? *Proceedings. Biological Sciences*, 276(1670),
352 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- 353 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological*
354 *networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 355 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and
356 Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 357 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks
358 over space. *Frontiers in Ecology and Evolution*, 11.
- 359 Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings*
360 *of the Royal Society B: Biological Sciences*, 288(1949), rspb.2020.1889, 20201889. <https://doi.org/10.1098/rspb.2020.1889>
- 361 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,
362 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.
363 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 364 Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions
365 interact? *Journal of Animal Ecology*, 80(5), 1097–1108. <https://doi.org/10.1111/j.1365-2656.2011.01852.x>

- 369 Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across
370 the entire tree of life. *Nature*, 465(7300), 918–921. <https://doi.org/10.1038/nature09113>
- 371 Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch
372 between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*,
373 11, e14620. <https://doi.org/10.7717/peerj.14620>
- 374 Hutchinson, M. C., Bramon Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., Jordano, P., &
375 Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community
376 ecology. *Functional Ecology*, 33(2), 206–217. <https://doi.org/10.1111/1365-2435.13237>
- 377 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 378 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 381 Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015).
382 Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky
383 shores. *Ecology*, 96(1), 291–303. <https://doi.org/10.1890/13-1424.1>
- 384 Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N.,
385 Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., & Brose,
386 U. (2012). More than a meal... integrating non-feeding interactions into food webs: More than a meal
387 *Ecology Letters*, 15(4), 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- 388 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 390 Maiorano, L., Montemaggiore, A., Ficetola, G. F., O'Connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A
391 species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, 29(9), 1452–1457.
392 <https://doi.org/10.1111/geb.13138>
- 393 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from
394 abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.13380>
- 396 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from
397 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 398 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic
399 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 400 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web
401 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0711111105>

- 402 1073/pnas.0710672105
- 403 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some
404 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 405
- 406 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, 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 Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks.
410 *Nature Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 411 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods
412 in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 413 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
414 Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,
415 48(7), 1552–1563. <https://doi.org/10.1111/jbi.14127>
- 416 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of
417 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/mec.12450>
- 418 Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B.,
419 & Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological
420 hypotheses. *Ecography*, 39(4), 402–408. <https://doi.org/10.1111/ecog.01941>
- 421 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
422 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 423 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks
424 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 425 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O’Hara, R. B., Parris, K. M., Vesk, P. A., &
426 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint
427 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/10.1111/2041-210X.12180>
- 428
- 429 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton
430 University Press. <https://doi.org/10.1515/9780691195322-020>
- 431 Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology,
432 Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>
- 433
- 434 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.

- 435 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 436 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network
437 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),
438 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 439 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*
440 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 441 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,
442 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction
443 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,
444 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- 445 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,
446 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer
447 learning can help predict potential species interaction networks despite data limitations. *Methods in*
448 *Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 449 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
450 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap
451 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*
452 *the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 453 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.
454 <https://doi.org/10.1002/ecy.3047>
- 455 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
456 <https://doi.org/10.1038/35004572>
- 457 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food
458 webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 459 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory
460 of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 461 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).
462 Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>

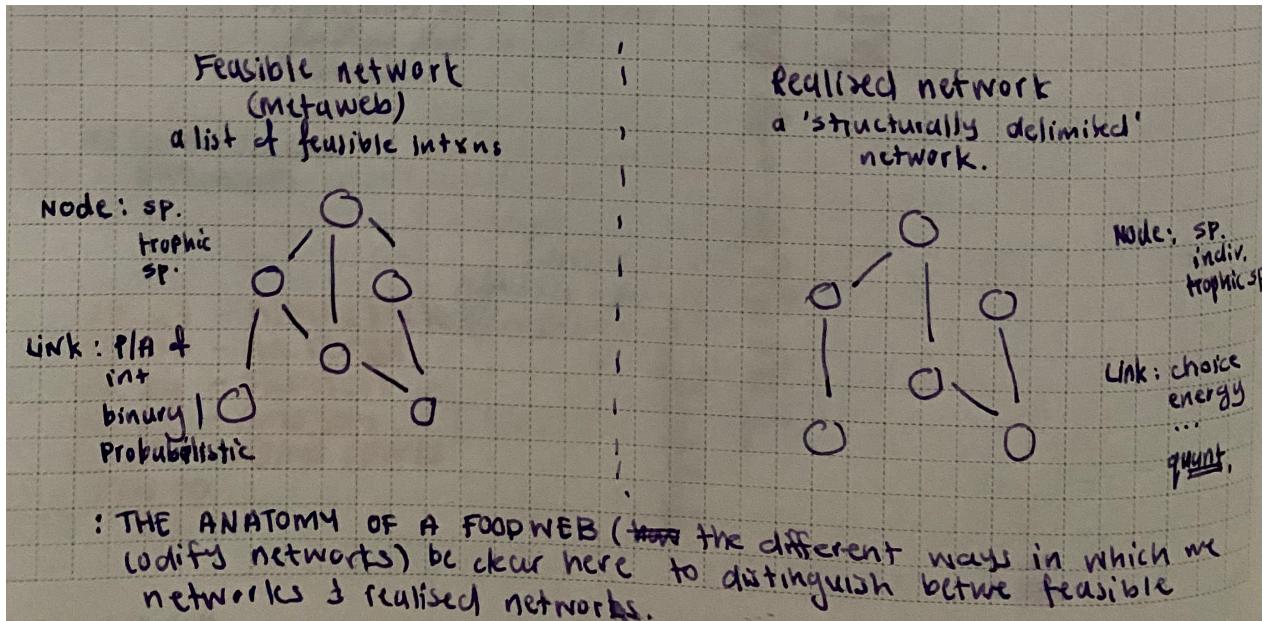


Figure 1: The many ways in which a food web can be defined and described at the node, edge, and even network level.

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.

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			(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	
15		"physicw" 2D 3D prey choice	energy	
0				?? allometric scaling ??
3				: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES

Figure 2: TODO.