

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; Yodzis, 1982) and in cases where the adult and larval
51 stages of a species have different diets it may make ecological sense (Clegg et al., 2018) meaning that it is
52 not uncommon that networks often have nodes that have different definitions of a ‘species’ *e.g.* consisting
53 of both taxonomic and trophic species. Practical implications of how we are aggregating the nodes is that
54 the resolution may not always be ‘pixel perfect’ *i.e.*, we may be unable to assess the co-extinction risk of a
55 species pair, however there is value in having nodes that represent an aggregation of species, as these convey
56 a much more general 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
60 the 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 one is interested in understanding the flow of energy through the network 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 (Banville et al., 2024; which quantifies how likely an interaction is to occur, Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of an interaction, Berlow et al., 2004).

1.0.3 Putting the parts together

The ingredients one uses to construct networks 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 which the resulting network can be used and applied within.

90 2 From Nodes and Edges to Scales, Context, and Processes

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

96 2.1 Understanding the processes that determine species interactions

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

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

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

111 [Figure 2 about here.]

112 Evolutionary compatibility

113 There is compelling evidence that the possibility of an interaction occurring between two species is the result
114 of their shared (co)evolutionary history (Dalla Riva & Stouffer, 2016; Gómez et al., 2010). In the more
115 proximal sense this is manifested as the ‘trait complementarity’ between two species, whereby one species
116 (the predator) has the ‘correct’ set of traits that allow it to chase, capture, kill, and consume the other species
117 (the prey). For species pairs where this condition is not met the link is deemed to be forbidden (Jordano,
118 2016b); *i.e.*, not physically possible and will always be absent within the network. In the context of trying

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

125 **(Co)occurrence**

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

136 **Abundance**

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

143 **Predator choice (energetic cost)**

144 Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume
145 prey, and is well described within optimal foraging theory [ref] and rests on the idea that the prey a predator
146 chooses to target is one that will have the greatest return on energy with the lowest energetic cost. There are
147 additional bodies of work that attempt to include the cost of movement that the environment imposes on an
148 individual (Cherif et al., 2024) as well as 2D/3D search space (Pawar et al., 2012). In terms of formalising
149 these processes in the context of predicting networks using diet models (Beckerman et al., 2006; Petchey et al.,

150 2008) that have predator choice determined by the handling time, energy content, prey density, and predator
151 attack rate. Wootton et al. (2023) developed a model that moves the energy of the system into different
152 modules related to the process of the predator acquiring energy from the prey *i.e.*, compartmentation in food
153 webs (Krause et al., 2003).

154 **Indirect interactions**

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

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

169 **downsampling paragraph??**

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
173 the resulting network is defined Section 1, which will ultimately delimit and define what inferences can
174 be made from the resulting network. Selecting a model for the task of network prediction should come
175 down to two things; what *aspect* of a food web one is interested in predicting, and what data are available,
176 necessary, and sufficient, and what is the purpose of wanting to predict a network? It is important that
177 a researcher is aware of this to ensure that the appropriate model is selected. Broadly researchers will be
178 interested in predicting/constructing two different types of networks; *metawebs*, which is essentially a list of
179 all interactions that are *possible* for a specific community (*i.e.*, at the scale of the species pairs), or being

able to predict 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/‘real-world’ 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 Models that predict structure

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

3.2 How do we predict food webs?

There as many ways to predict networks as what there is to define them and along with taking into consideration the points raised in the previous section it is also beneficial to think about the context in which the different models were developed - and how this will influence the networks that they produce... Also it is not

210 feasibly possible to list every single approach that has been developed to predict networks and so we will
211 present what we believe to be the broad families that represent the different approaches to predicting net-
212 works, particularly how these relate to the processes identified in Section 2.1, as well as models that predict
213 network structure (see Section 3.1).

214 In order for a model to formalise a ‘complete’ food web it is necessary to formalise two aspects of the network,
215 ‘who eats whom’ (to determine the links between nodes) as well as the structure of the network (to limit
216 the distribution of links), however most models are inclined to focus on one of the two aspects. As there
217 are many food web models to choose from it is perhaps useful to think about the models in terms of model
218 families, a summary of these families is presented in Table 1 highlights the differences and similarities of the
219 philosophies and assumptions that determine a network. A more extensive overview of the different models
220 that fall with in the different model families can be found in SuppMat 1 and for a more detailed breakdown
221 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.

Model family	Assumptions	Data/process	‘Limitation’	Network type	Key reference
null	Links are randomly distributed within a network		parameter assumptions, species agnostic	structural network	
neutral	Network structure is random, but species abundance determines links between nodes	abundance	parameter assumptions	structural network	Canard et al. (2012)
resource	Networks are interval, species can be ordered on a ‘niche axis’		parameter assumptions, species agnostic	structural network	Williams & Martinez (2008)

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
generative	Networks are determined by their structural features		need real world networks	structural network	
energetic	Interactions are determined by energetic costs	abundance + energy	does not account for forbidden links in terms of evolutionary compatibility	'energy' network	
graph embedding	Interactions can be predicted from the latent traits of networks	evolutionary compatibility	need real world networks	metaweb	Strydom et al. (2023)
trait matching	Interactions can be inferred by a mechanistic frame-work/relationships	evolutionary compatibility	well studied species/communities	metaweb	Morales-Castilla et al. (2015)
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	evolutionary compatibility	need real world networks	metaweb	Pichler et al. (2020)

Model family	Assumptions	Data/process	'Limitation'	Network type	Key reference
expert knowledge	'Boots on the ground' ecological knowledge and observations	evolutionary compatibility	well studied species/communities	metaweb	
data scavenging	Webscraping to create networks from online databases		need real world networks	metaweb	Poisot, Gravel, et al. (2016) (if you squint?)
co-occurrence	co-occurrence patterns arise from interactions so we can use these patterns to reverse engineer the interactions	co-occurrence	does not account for forbidden links in terms of evolutionary compatibility or account for energy constraints	co-occurrence network	

²²² 4 Making Progress with Networks

²²³ There is a bit of a ‘point of conflict’ between those calling for ‘pixel perfect’, regional scale data (Pringle, 2020; Pringle & Hutchinson, 2020) and for the means to generate networks that are ecologically plausible ²²⁵ representations (*sensu* structural networks). This represents two challenges; one is that models that represent ²²⁶ generalisations often lack the ability to retrieve any species/community specificity which limits their utility ²²⁷ for real world, species-driven scenarios *e.g.*, species driven conservation efforts, however networks that are ²²⁸ constructed through either empirical observations or through predictive means are fundamentally going to ²²⁹ represent metawebs, *i.e.*, lack constrained links.

²³⁰ In this section I want to highlight that we don’t actually have any clear guidelines as to how we can ‘use’ ²³¹ networks - which probably stems from both the fact that when I am talking about a network and when ²³² someone else is talking about a network we may actually be talking about two very different conceptualisations

²³³ of ‘a network’ (this should actually be a selling point in the intro - may have just found my *raison d’être*)
²³⁴ as well as that a lot of the ideas that we have about networks are not really tied to any sort of tangible
²³⁵ function (i.e. Tim’s GeoBon ms thing-y). However we can maybe at least try to present some guidelines -
²³⁶ but I think specifically within the sort of Petchey dilemma space and clearly tied to the ideas we discuss in
²³⁷ the ms. This includes: understanding the limits of how a network is defined and how the underlying theory
²³⁸ impacts the use as well as data?? IDK we need to shoehorn data in here somehow... We can also use this as a
²³⁹ gap identifying space and I think the framing can still rest under the limits concept particularly time, space,
²⁴⁰ and boundaries - which will all probably fall under some aspect of biological scale... We can also raise the
²⁴¹ idea of trust - as in which methods have more support/trust than others. Also what even a ‘real’ network
²⁴² entails (and this links again back to Tim’s stuff) as well as a subtle jab at Pringles notion that the most
²⁴³ critical issue in the world of food webs is being able to identify every. single. link. even though there is no
²⁴⁴ real discussion as to what is an ‘opportunistic’ link vs a link that represents a sustainable energy source for
²⁴⁵ a population (or would it be an individual)...

²⁴⁶ We need to be aware of the parameter space that is possible given a specific definition of a network and
²⁴⁷ operate within those parameters.

²⁴⁸ 5 Concluding remarks

²⁴⁹ I think the idea of time and how we are aggregating networks across that should be a prominent feature
²⁵⁰ here...

- ²⁵¹ In certain situations structure is ‘enough’ but there may be use cases where we are really interested in
²⁵² the node-level interactions *i.e.*, species identity is a thing we care about and need to be able to retrieve
²⁵³ specific interactions at specific nodes correctly.

- ²⁵⁴ Why do interaction models do so badly at predicting structure? Nuance of metaweb vs realisation but
²⁵⁵ also time? At the core of it interaction models are trained on existing interaction data; this is data
²⁵⁶ that are most likely closer to a metaweb than a local realisation even if they are being inventoried at a
²⁵⁷ small scale...

- ²⁵⁸ – We can briefly shoehorn downsampling here maybe??

- ²⁵⁹ It will be interesting to bring up the idea that if a model is missing a specific pairwise link but doing
²⁶⁰ well overall then when does it matter?

- ²⁶¹ – 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. (2008) but maybe not exactly in this context but vaguely adjacent.
 - I think this is sort of the crux of the argument presented in Brimacombe et al. (2024) as well.

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

- Do we need network models to predict interactions and interaction models to predict structure?
 - "Another argument for the joint prediction of networks and interactions is to reduce circularity and biases in the predictions. As an example, models like linear filtering generate probabilities of non-observed interactions existing, but do so based on measured network properties." - Strydom et al. (2021)
 - Aligning (dove-tailing) with this the idea of ensemble modelling as presented by Becker et al. (2022)
- Close out with a call to action that we have models that predict networks very well and models that predict interactions very well but nothing that is doing well at predicting both - this is where we should be focusing our attention when it comes to furthering model development...

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

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

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

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

303 **5.1 Time**

304 Look at Hutchinson et al. (2019) and in a way Rooney et al. (2008)

305 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a
306 ‘network’. Realistically most empirical networks are more aligned with ‘feasibility networks’ as opposed to
307 ‘realised networks’ as they are often the result of some sort of aggregation of observations across time. This
308 ‘problem’ is two-fold. Firstly we need to think about how this affects any sort of development of theory
309 that sits closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer
310 questions about realised networks using feasible networks? The second is that this lack of ‘direction’ as to
311 how we should define a network is (actually) probably one of the biggest barriers that is affecting the use of
312 networks in applied settings...

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

319 **Outstanding questions**

- 320 • non-consumptive effects
321 • how do we define the spatial and temporal ‘boundaries’ of a network?
322 • 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.

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

Figure 2: TODO.