

# **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 many  
36 forms (Poisot, Stouffer, et al., 2016), which ultimately encodes a series of assumptions and criteria within  
37 a network. An awareness of variance in the way a food web can be defined is critical as a network (or its  
38 adjacency matrix) is both the ‘object’ from which inferences are made (*e.g.*, the interactions between species,  
39 or how the structure influences ecosystem level processes) as well as the ‘product’ of either the data collection  
40 (Brimacombe et al., 2023) or prediction process (Banville et al., 2024). One thus needs to be aware of both  
41 the criteria that is used to define nodes and edges, and what processes or mechanisms the aggregation of the  
42 two represents, as this will determine what the network can be used for.

### 43 1.0.1 How do we define a node?

44 Although this may seem an elementary question in the context of food webs — a node *should* represent a  
45 (taxonomic) species, the reality is that nodes can often represent an aggregation of different species - so called  
46 ‘trophic species’ (Williams & Martinez, 2000; Yodzis, 1982) or segregation of species by life stages (Clegg  
47 et al., 2018). Practical implications of how we are aggregating the nodes is that the resolution may not  
48 always be ‘pixel perfect’, which limits the ability to make (taxonomic) species specific inferences *e.g.*, does  
49 species *a* eat species *b*, however there is value in having nodes that represent an aggregation of species, as  
50 the distribution of the links between them are more meaningful in terms of understanding energy flow and  
51 distribution within the system.

### 52 1.0.2 What is meant by an edge?

53 At its core, links within food webs can be thought of as a representation of either feeding links between  
54 species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within  
55 the community/system *e.g.*, energy transfer or material flow (Lindeman, 1942). How we specify links will  
56 influence the resulting structure of the network - and the inferences we will make thereof. For example taking  
57 a food web that consists of links representing all *potential* feeding links for a community (*i.e.*, a metaweb)  
58 will be meaningless if one is interested in understanding the flow of energy through the network as the links  
59 within a metaweb do not represent environmental/energetic constraints, making them poor representations  
60 of which interactions are *realised* in a specific location (Caron et al., 2024). In addition to the various ways

61 of defining the links between species pairs there are also a myriad of ways in which the links themselves  
62 can be quantified. Links between species are often treated as being present or absent (*i.e.*, binary) but it is  
63 also possible to use probabilities (Banville et al., 2024; which quantifies how likely an interaction is to occur,  
64 Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of of an interaction,  
65 Berlow et al., 2004).

66 **1.0.3 Network representations**

67 Broadly, networks can be thought of to fall into two different ‘types’; namely metawebs; traditionally defined  
68 as all of the *potential* interactions for a specific species pool (Dunne, 2006), and realised networks; which  
69 is the subset of interactions in a metaweb that are *realised* ‘on the ground’. The fundamental difference  
70 between these two different types of networks is that a metaweb provides insight as to the viability of an  
71 interaction between two species occurring and is a means to identify links that are not ecologically plausible,  
72 *i.e.*, forbidden links (Jordano, 2016b), or an idea of the *complete* diet of a species (Strydom et al., 2023).  
73 Although metawebs are typically ‘constrained’ to a collection of species that also co-occur, there is no reason  
74 that a metaweb cannot include species that do not co-occur (although this would require some degree of  
75 prediction/assumptions to identify those possible interactions). In contrast realised networks are highly  
76 localised and contingent on both the co-occurrence of species as well as the influence of the environment,  
77 and population and community dynamics on predator choice. In the context of definitions and semantics  
78 the links that are represented by a metaweb and a realised network are different; links that are absent in a  
79 metaweb can be treated as being truly absent, however links that are absent in a realised network cannot be  
80 considered to be truly absent but are rather as absent due to the broader environmental/community context.  
81 Importantly, a realised network is *not* simply the downscaling of a metaweb to a smaller scale (*e.g.*, moving  
82 from the country to the 1x1 km<sup>2</sup> scale based on fine-scale species co-occurrence) but represents a shift towards  
83 capturing the higher level processes that determine the *realisation* of an interaction. Thus, different network  
84 representations are determined and constrained by different sets of assumptions as to what the processes are  
85 that determine the presence/absence of an interaction between two species as well as the resulting network  
86 structure.

87 **2 From Nodes and Edges to Scales, Context, and Processes**

88 The interplay between network representation and network definition is primarily governed by the process(es)  
89 that determine the interaction between species, however these processes are also scale and context dependent.  
90 Here we start by introducing the five core processes that determine either the feasibility or realisation of

91 interactions, namely: evolutionary compatibility, co-occurrence, feasibility, abundance, predator choice, and  
92 non-trophic interactions; while simultaneously contextualising them within, and linking them to the different  
93 network representations Figure 1; specifically if the processes captures an all-or-nothing (possibility) vs  
94 context dependent (likelihood) determination of interactions between species. Of course these processes do  
95 not function in a vacuum and do interact with/influence one another, but it is still beneficial to present them  
96 in a categorical manner as these different processes are often the underpinning logic in the development of  
97 prediction/network models, the criteria for data collection in the field, and the scale of organisation for which  
98 they are relevant (species, population, or community).

99 [Figure 1 about here.]

## 100 2.1 The processes that determine species interactions

### 101 Evolutionary compatibility

102 There is compelling evidence that the possibility of an interaction occurring between two species is the result  
103 of their shared (co)evolutionary history (Dalla Riva & Stouffer, 2016; Gómez et al., 2010; Segar et al., 2020).  
104 In the more proximal sense this is manifested as the ‘trait complementarity’ between two species, whereby  
105 one species (the predator) has the ‘correct’ set of traits that allow it to chase, capture, kill, and consume  
106 the other species (the prey). For species pairs where this condition is not met the link is deemed to be  
107 forbidden (Jordano, 2016b); *i.e.*, not physically possible and will always be absent within the network. In the  
108 context of trying to determine the feasibility (*i.e.*, the *possibility*) of an interaction, phylogeny is an excellent  
109 predictor (Fricke et al., 2022; Strydom et al., 2022) and allows one to construct what can be considered to  
110 be a metaweb. In terms of thinking about the anatomy of an ‘feasibility network’ one should be aware that  
111 it is possible to represent interactions as either binary (feasible/forbidden; *i.e.*, the traditional definition of a  
112 metaweb Dunne (2006)) or as a probability (Banville et al., 2024), where the probability represents how likely  
113 that the interaction between two species is feasible (what is the possibility of this interaction occurring?).

### 114 (Co)occurrence

115 Although the outright assumption that because two species are co-occurring it must mean that they are  
116 interacting is inherently flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at  
117 least in terms of feeding links) if they are not co-occurring in time and space. Thus co-occurrence data alone is  
118 insufficient to build an accurate and ecologically meaningful representation of a food web having information  
119 on the co-occurrence of species can further aid us in refining metawebs by allowing us to downsample the  
120 network based on the species found in a specific location, or even add additional uncertainty based in how

121 likely species are to co-occur (Dansereau et al., 2024). Additionally the interplay between the interaction  
122 between a species pair and their co-occurrence is meaningful when one is operating in the space of trying to  
123 determine the distribution of a species (Higino et al., 2023), and forms a key component of some of the next  
124 generation species distribution models *e.g.*, joint SDMs (Pollock et al., 2014).

125 **Abundance**

126 The abundance of the different species within the community can influence the likelihood of an interaction  
127 occurring in a myriad of ways *e.g.*, the likelihood of two species meeting, or the long term availability of  
128 prey. There is the argument that structure of networks (and the interactions that they are composed of)  
129 are driven by only the abundance of the different species and not their characteristics (traits), *sensu* neutral  
130 processes (Canard et al., 2012; Momal et al., 2020). Alternatively the abundance of species in a community  
131 can influence which interactions are ultimately realised (Banville et al., 2024; Poisot et al., 2015).

132 **Predator choice (energetic cost)**

133 Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume  
134 prey, and is well described within both optimal foraging theory [ref] and metabolic theory [ref], which rests  
135 on the idea that the prey a predator chooses to target is one that will have the greatest return on energy  
136 with the lowest energetic cost. With a body of evidence that suggests that body size might be the underlying  
137 driver, and thus suitable proxy for understanding these processes (Yodzis & Innes, 1992) There are additional  
138 bodies of work that attempt to include the cost of movement that the environment imposes on an individual  
139 (Cherif et al., 2024) as well as 2D/3D search space (Pawar et al., 2012).

140 **Indirect/higher order interactions**

141 The realisation (presence/absence) or strength of trophic interactions themselves can also be modified by  
142 other, indirect (non-trophic), interactions (Golubski & Abrams, 2011; Pilosof et al., 2017), this can be either  
143 ‘directly’ through *e.g.*, competition or ‘indirectly’ *e.g.*, mutualistic/facilitative interactions will alter the fine-  
144 scale distribution and abundance of some species (Kéfi et al., 2012, 2015) as well as persistence (Buche et al.,  
145 2024).

146 **2.2 Contextualising the processes that determine species interactions**

147 It should be self evident that the different processes discussed above are all ultimately going to influence the  
148 realisation of interactions as well as the structure of a network, however they are acting at different scales  
149 of organisation. Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of  
150 the species pair of interest, that is the *possibility* of an interaction being present/absent is assessed at the

pairwise level and one is left with a ‘list’ of interactions that are present/absent. Although it is possible to build a network (*i.e.*, metaweb) from this information it is important to be aware that the structure of this network is not constrained by real-world dynamics or conditions (*i.e.*, community context), and so just because species are able to interact does not mean that they will (Poisot et al., 2015). In order to construct a network whose structure is a closer approximation of reality (localised interactions) one needs to take into consideration properties of the community as a whole and not just the two species of interest, which requires more data at the community scale, such as the abundance of species.

*something about ‘physical’/landscape scale as well as time scale??*

### 3 Network construction is nuanced

The act of constructing a ‘real world’ network will ultimately be delimited by its intended use, however the reality is that the empirical collection of interaction data is both costly [ref] and challenging to execute in a way that captures the different processes (owing to the different time and spatial scales they may be operating at). Thus we often turn to models to either predict networks, be that the interaction between two species, or its structure (Strydom, Catchen, et al., 2021), or as a means to identify missing interactions (gap fill) within existing empirical dataset (Biton et al., 2024; Stock, 2021), and so for the purpose of this discussion network construction will be synonymous with using a model as a means to represent or predict a network — it can be argued that even the collection of empirical data is in and of itself a ‘model’ as it is still only a *representation* of the system. Different models have different underlying philosophies that often only capture one or a few of the processes discussed in Section 2, has implications for how the resulting network is defined Section 1, which will ultimately delimit and define what inferences can be made from the resulting network. Here we will introduce the three different types of network representations, how they link back to the different processes determining interactions Figure 1, and broadly discuss some of the modelling approaches that are used to construct these different network types. This is paralleled by a hypothetical case study (Box 1) where we showcase the utility/applicability of the different network representation in the context of trying to understand the feeding dynamics of a seasonal community.

#### **i** Box 1 - Why we need to aggregate networks at different scales: A hypothetical case study

Although it might seem most prudent to be predicting, constructing, and defining networks that are the closest representation of reality there are pros and cons of constructing both realised networks as well as metawebs. Let us take for example a community across time/through seasons. In this community we

expect species to be either present or absent depending on the season (*i.e.*, changes in co-occurrence) as well as some species exhibiting seasonal diet shifts, these details would be lost at the scale of the metaweb and it would be valuable to construct either smaller metawebs for the different seasonal communities (thereby capturing the changes in community diversity), or realised networks for each season (to capture diet or ecosystem process shifts). However, these small-scale networks lack the context of the bigger picture that is available at the metaweb - that is it gives us a more holistic idea of the entire diet range of a specific species, which is important when one needs to make conservation-based/applied decisions (*e.g.*, conserving the entire diet of a species and not just seasonal prey items) as well as providing information on interactions that may be possible regardless of the environmental/community context (species may have the capacity to consume certain prey items but do not do so due to local conditions).

With this in mind let us see how the different network aggregations can be used

#### **1: A global metaweb**

Knowledge of the entire diet breadth of a species is valuable especially in terms of understanding how a species will respond to changes in the community - *e.g.*, invasions/rewilding exercises (where does the new species ‘fit’ within the network?) as well as potential capacity to shift its diet. Although this might make sense across space and not time but certain species act as links across the landscape [Rooney]

#### **2: A seasonal metaweb**

Knowledge at the finer scale is also valuable to understand/identify that there are in fact differences between the seasons

#### **3: A seasonal realised network**

Dynamics are useful because they are a representation of the different configurations/energy flows/ecosystem processes. Also to detect more nuanced shifts in diet - *e.g.*, seasonal diet shifts.

#### **4: A structural network**

##### **Data trade off**

Above we highlight the practical uses of the different network configurations but we also need to take into consideration the barriers to construction/associated data needs/cost and acknowledge them. Basically in the ideal world we would have all this information at hand but in reality we might be sitting with seasonal metawebs...

178 **3.1 How do we predict food webs?**

179 There as many ways to predict networks as what there is to define them and along with taking into consid-  
180 eration the points raised in the previous section it is also beneficial to think about the context in which the  
181 different models were developed - and how this will influence the networks that they produce...

182 There is a bit of a ‘point of conflict’ between those calling for ‘pixel perfect’, regional scale data (Pringle,  
183 2020; Pringle & Hutchinson, 2020) and for the means to generate networks that are ecologically plausible  
184 *representations* (*sensu* structural networks). This represents two challenges; one is that models that repre-  
185 sent generalisations of networks often lack the ability to retrieve any species/community specificity which  
186 limits their utility for real world, species-driven scenarios *e.g.*, species driven conservation efforts (Dunn et  
187 al., 2009), however networks that are constructed through either (most) empirical observations or through  
188 predictive means are fundamentally going to represent metawebs, *i.e.*, lack constrained links, a representation  
189 of structure, or energy flow...

190 **3.1.1 Models that predict metawebs (feasible interactions)**

191 This is perhaps the most developed group of models; with a variety of approaches having been developed that  
192 typically determine the feasibility of an interaction based on the trait compatibility between predator and  
193 prey (*i.e.* their evolutionary compatibility) to determine ‘feeding rules’ (Morales-Castilla et al., 2015). These  
194 feeding rules are broadly elucidated in two different ways; mechanistic feeding rules can be explicitly defined  
195 and applied to a community (Dunne et al., 2008; *e.g.*, Shaw et al., 2024) or they are inferred from a community  
196 for which there is interaction data and the ‘rules’ are then applied to a different community (Caron et al.,  
197 2022; Cirtwill et al., 2019; Desjardins-Proulx et al., 2017; Eklöf et al., 2013; Llewelyn et al., 2023; Pichler et  
198 al., 2020; Strydom et al., 2022; *e.g.*, Strydom et al., 2023). The fundamental difference between these two  
199 model groups is that ‘mechanistic models’ rely on expert knowledge and make assumptions on trait-feeding  
200 relationships, whereas the ‘pattern finding’ models are dependent on existing datasets from which to elucidate  
201 feeding rules. These models are useful for determining all feasible interactions for a specific community, and  
202 owing to the availability of datasets (Gray et al., 2015; *e.g.*, Poelen et al., 2014; Poisot, Baiser, et al., 2016),  
203 as well as the development of model testing/benchmarking tools (Poisot, 2023), means that these models  
204 can be validated and (with relative confidence) be used to construct first draft networks for communities for  
205 which we have no data (Strydom et al., 2022), and are valuable for constructing networks where we lack any  
206 interaction data *e.g.*, prehistoric networks (Fricke et al., 2022; Yeakel et al., 2014).

207 **3.1.2 Models that predict realised networks (realised interactions)**

208 In order to construct realised networks models need to incorporate *both* the feasibility of interactions (*i.e.*,  
209 determine the entire diet breadth of a species) as well as then determine which interactions are realised (*i.e.*,  
210 incorporate the ‘cost’ of interactions). As far as we are aware there is no model that explicitly accounts for  
211 both of these ‘rules’ and rather *only* account for processes that determine the realisation of an interaction  
212 (*i.e.*, abundance, predator choice, or non-trophic interactions). Although the use of allometry *i.e.*, body size  
213 (Beckerman et al., 2006; *e.g.*, Valdovinos et al., 2023) may represent a first step in capturing ‘evolutionary  
214 compatibility’ alongside more energy (predator choice) driven processes accounting for additional traits is still  
215 needed (*e.g.*, Van De Walle et al., 2023 show how incorporating prey defensive properties alongside body size  
216 improves predictions). In terms of models that do formalise these processes, diet models (Beckerman et al.,  
217 2006; Petchey et al., 2008) have been used construct networks based on both predator choice (as determined  
218 by the handling time, energy content, and predator attack rate) as well as abundance (prey density). Woottton  
219 et al. (2023) developed a model that moves the energy of the system into different modules related to the  
220 process of the predator acquiring energy from the prey *i.e.*, compartmentation in food webs (Krause et al.,  
221 2003).

222 **3.1.3 Models that predict structure (interaction agnostic)**

223 Although we identify mechanisms that determine species interactions in Section 2 not all models that are used  
224 to predict networks explicitly operate at the ‘process’ level, but rather represent the *structure* of a network  
225 based on a series of *a priori* assumptions as to the distribution of links between species (typically trophic not  
226 taxonomic species) by parametrising an aspect of the network structure, (*e.g.*, the niche model (Williams &  
227 Martinez, 2000) makes an assumption as to the expected connectance of the network, although see Allesina  
228 & Pascual (2009) for a parameter-free model) or alternatively uses structural features of an exiting *realised*  
229 network (*e.g.*, stochastic block model, Xie et al. (2017)). Importantly these structural models do not make  
230 species specific predictions (they are usually species agnostic and treat nodes as trophic species) and so cannot  
231 be used to determine if an interaction is either possible *or* realised between two species (*i.e.*, one cannot use  
232 these models to determine if species *a* eats species *b*). Although this means this suite of models are unsuitable  
233 as tools for predicting species-specific interactions, they have been shown to be sufficient tools to predict the  
234 structure of networks (Williams & Martinez, 2008), and provide a data-light (the models often only require  
235 species richness) but assumption heavy (the resulting network structure is determined by an assumption of  
236 network structure) way to construct a network.

237 **4 Making Progress with Networks**

238 **4.1 Further development of models and tools**

239 There has been a suite of models that have been developed to predict trophic links, however we are lacking in  
240 tools that are explicitly taking into consideration estimating both the feasibility as well as realisation of links,  
241 *i.e.*, both interactions and structure simultaneously (Strydom, Catchen, et al., 2021). This could be addressed  
242 either through the development of tools that do both (predict both interactions and structure), or to develop  
243 an ensemble modelling approach (Becker et al., 2022). Alternatively the development of tools that will allow  
244 for the downsampling of metawebs into realised networks (*e.g.*, Roopnarine, 2006), although deciding exactly  
245 what is driving differences between local networks and the regional metaweb might not be that simple (Saravia  
246 et al., 2022). Probably also something that aligns with trying to predict interaction strength - because that  
247 would be the gold standard (*e.g.*, Wells & O'Hara, 2013). Probably also worth just plainly stating that  
248 feasibility of developing a model that is both broadly generalisable, but also has local specificity is probably  
249 not attainable (Stouffer, 2019), and more specifically the potential use of models to untangle/identify the  
250 different processes that shape interaction networks (Song & Levine, 2024), *e.g.*, Curtsdotter et al. (2019)  
251 showcase the use of models to disentangle the drivers of community function and Strydom, Dalla Riva, et  
252 al. (2021) who identified that networks are less complex than they could be, suggesting that there are  
253 constraints on network assembly. In addition to the more intentional development of models we also need to  
254 consider the validation of these models, there have been developments and discussions for assessing how well  
255 a model recovers pairwise interactions (Poisot, 2023; Strydom, Catchen, et al., 2021), although the rate of  
256 false-negatives that may be present in the testing data still present a challenge (Catchen et al., 2023), and we  
257 still lack clear strategies for benchmarking the ability of models to recover structure (Allesina et al., 2008).

258 **4.2 At what scale should we be predicting and using networks?**

259 Look at Hutchinson et al. (2019)

260 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a  
261 'network'. Realistically most empirical networks are more aligned with metawebs as opposed to realised  
262 networks as they are often the result of some sort of aggregation of observations across time, this creates a  
263 two-fold problem. Firstly, we need to think about how this affects any sort of development of theory that sits  
264 closer to the 'realised network' side of the spectrum - how often are we trying to ask and answer questions  
265 about realised networks using feasible networks? The second is that this lack of 'direction' as to how we  
266 should define a network is (actually) probably one of the biggest barriers that is affecting the use of networks

267 in applied settings... By define I mean both delimiting the time and geographic scale at which a network is  
268 aggregated at (Estay et al., 2023). We know that space plays a role - the motility of different species will  
269 influence both the dynamics of networks but also serve to link smaller ‘subnetworks’/community (Fortin et  
270 al., 2021; Rooney et al., 2008). And so does time *e.g.*, seasonal rewiring (Brimacombe et al., 2021; Laender  
271 et al., 2010). There is also a bit of an interplay with time and data and the different scales that they may  
272 be integrated at - co-occurrence may span decades and just because two species have been recorded in the  
273 same space does not mean it was at the same timescale (Brimacombe et al., 2024).

#### 274 4.3 Feasible, realised, or sustainable?

275 When do we determine a link to be ‘real’... In the context of metawebs this is perhaps clearer - if all things  
276 were equal (*i.e.*, community context is irrelevant) would the predator be able to consume the prey. However  
277 in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction - just  
278 because an interaction is possible in the now is it able to sustain a population in the long term. And what  
279 is the scale for that long term - are we thinking at the generational scale? Because ultimately when we  
280 are constructing a network we are aggregating not only across space but also across time... This is probably  
281 again a Lokta-Volterra space question and something that the dynamic foodweb models (Curtsdotter et al.,  
282 2019; Delmas et al., 2017; Lajaaiti et al., 2024) are addressing, but again it is integrating this with the  
283 feasible/realised axis. And of course the Petchey dilemma of even what networks should we be feeding into  
284 these dynamic models.

### 285 5 The future value of networks

286 developing a dictionary of use... that helps navigate between the levels and assumptions

287 It should be clear that there is a high degree of interrelatedness and overlap between the way a network is  
288 constructed (modelled or predicted) and the process(es) it captures, these are encoded (embedded) within  
289 the network representation and ultimately influences how the network can and should be used (Berlow et  
290 al., 2008; Petchey et al., 2011). It is probably both this nuance as well as a lack of clear boundaries and  
291 guidelines as to the links between network form and function (although see Delmas et al., 2019) that has  
292 stifled the ‘productive use’ of networks beyond inventorying the interactions between species. Although,  
293 progress with using networks as a means to address questions within larger bodies of ecological theory *e.g.*,  
294 invasion biology (Hui & Richardson, 2019) and co-existence theory (García-Callejas et al., 2023) we still need  
295 to have a discussion on what the appropriate network configuration for the task at hand would be. This

<sup>296</sup> is highlighted in Box 1, and underscores that we need to evaluate exactly what process a specific network  
<sup>297</sup> representation captures as well as its suitability for the question of interest.

<sup>298</sup> The Terry & Lewis (2020) paper looks at some methods but is specifically looking at a bipartite  
<sup>299</sup> world...

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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 1: TODO.