

# **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 is one of the fundamental building blocks of ecological communities, providing a powerful abstraction  
5 that can help quantify, conceptualise, and understand biodiversity dynamics, and ultimately, make predic-  
6 tions, mitigate change, and manage services. Such network representations of biodiversity (including within  
7 species diversity) are increasingly argued to be an asset to predictive ecology, climate change mitigation  
8 and resource management. Here, it is argued that characterising biodiversity in a network will allow deeper  
9 capacity to understand and predict the abundance, distribution, dynamics and services provided by multiple  
10 species facing multiple stressors.

11 A ‘network’ can be defined and conceptualised in a myriad of ways, which means that different networks  
12 will be embedding different processes (or determinants) of interactions, ultimately influencing the patterns  
13 and mechanisms that are inferred (Brimacombe et al., 2023; Proulx et al., 2005). The different ways in  
14 which a network can be represented is the result of *how* the network is constructed, which itself rests on two  
15 pillars: the data used to construct the network and the underlying theory as to what drives the interactions  
16 between species. The latter represents an expression of mechanism and process that gives rise to the patterns  
17 that emerge from collating interactions among species, and will ultimately inform which data are deemed  
18 important in the determination of interactions occurring. Each of these pillars carries with it a set of practical,  
19 semantic and conceptual constraints that not only influence progress in making network ecology more valuable  
20 and potentially predictive, but help define the spatial, temporal, and evolutionary scale of assumptions we  
21 make and the predictions we might generate from different network representations.

22 In this perspective we aim to provide an overview of the different **food web** representations, particularly how  
23 these relate to the terminology used to define a network, and how this influenced by both the processes that  
24 determine networks as well as how this relates to the way in which we construct networks. The provision of  
25 this detail ultimately leads to a set of insights and conclusions about whether, when and under what conditions  
26 network representations of biodiversity can contribute to the advancement of ecological theory and generate  
27 value in predictive ecology. Specifically, we finish this perspective with an overview of fundamental questions  
28 in ecology that we think can benefit from network thinking and a proposal that such thinking can accelerate  
29 our capacity to predict the impact of multiple stressors on biodiverse communities.

## **30 1 Setting the Scene: The Not So Basics of Nodes and Edges**

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

### **40 1.0.1 How do we define a node?**

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

### **49 1.0.2 What is meant by an edge?**

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

60 also possible to use probabilities (Bansville et al., 2024; which quantifies how likely an interaction is to occur,  
61 Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of an interaction,  
62 Berlow et al., 2004).

63 **1.0.3 Network representations**

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

84 **2 From Nodes and Edges to Scales, Context, and Processes**

85 The interplay between network representation and network definition is primarily governed by the process(es)  
86 that determine the interaction between species, however these processes are also scale and context dependent.  
87 Here we start by introducing the five core processes that determine either the feasibility or realisation of  
88 interactions, namely: evolutionary compatibility, co-occurrence, feasibility, abundance, predator choice, and  
89 non-trophic interactions; while simultaneously contextualising them within, and linking them to the different

network representations Figure 1. We can think of the different network representations to be conceptually analogous to the fundamental and realised niche, whereby the metaweb represents the ‘fundamental diet niche’ of a species and a realised network represents the ‘realised diet’ of a species and are thus determined by different processes. Of course these processes do not function in a vacuum and do interact with/influence one another, but it is still beneficial to present them in a categorical manner as these different processes are often the underpinning logic in the development of prediction/network models, the criteria for data collection in the field, and the scale of organisation for which they are relevant (species, population, or community), which is all ultimately captured and encapsulated by the different network representations.

[Figure 1 about here.]

## 2.1 The processes that determine species interactions

### Evolutionary compatibility

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

### (Co)occurrence

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

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

#### 124 **Abundance**

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

#### 131 **Predator choice (energetic cost)**

132 Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume  
133 prey (where a predator will optimise energy while minimising time), and is well described within both optimal  
134 foraging [] [ref] and metabolic theory (Brown et al., 2004), which rests on the idea that the prey a predator  
135 chooses to target is one that will have the greatest return on energy with the lowest energetic cost. With a  
136 body of evidence that suggests that body size might be the underlying driver, and thus suitable proxy for  
137 understanding these processes (Yodzis & Innes, 1992) There are additional bodies of work that attempt to  
138 include the cost of movement that the environment imposes on an individual (Cherif et al., 2024) as well as  
139 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  
151 pairwise level and one is left with a ‘list’ of interactions that are present/absent. Although it is possible  
152 to build a network (*i.e.*, metaweb) from this information it is important to be aware that the structure of  
153 this network is not constrained by real-world dynamics or conditions (*i.e.*, community context), and so just  
154 because species are able to interact does not mean that they will (Poisot et al., 2015). In order to construct  
155 a network who’s structure is a closer approximation of reality (localised interactions) one needs to take into  
156 consideration properties of the community as a whole and not just the two species of interest, which requires  
157 more data at the community scale, such as the abundance of species.

### 158 3 Network construction is nuanced

159 The act of constructing a ‘real world’ network will ultimately be delimited by its intended use, however  
160 the reality is that the empirical collection of interaction data is both costly and challenging to execute  
161 (Jordano, 2016a, 2016b), especially if one wants to capture *all* aspects of the processes discussed in Section 2  
162 (owing to the different time and spatial scales they may be operating at). Thus we often turn to models  
163 to either predict networks (be that the interaction between two species, or its structure (Strydom et al.,  
164 2021)), or as a means to identify missing interactions (gap fill) within an existing empirical dataset (Biton  
165 et al., 2024; Dallas et al., 2017; Stock, 2021), and so for the purpose of this discussion network construction  
166 will be synonymous with using a model as a means to represent or predict a network. That is not to say  
167 that there is no need for empirical data collection but rather that using a model for food web prediction  
168 (or reconstruction) is a more feasible approach as it allows us to make inferences about interactions that  
169 are not happening in the ‘observable now’ (Strydom et al., 2021), with the added benefit that one is able  
170 to build some uncertainty into the resulting network (Banville et al., 2024), as well as explicitly designing  
171 models that allow us to isolate and understand how different processes determine interactions (Song & Levine,  
172 2024; Stouffer, 2019). Additionally different models have different underlying philosophies that allow us to  
173 capture one or a few of the processes discussed in Section 2, which ultimately delimits and defines what  
174 inferences can be made from the resulting network. Here we will introduce the three different types of  
175 network representations (metawebs, realised networks, and structural networks), how they link back to the  
176 different processes determining interactions Figure 1, and broadly discuss some of the modelling approaches  
177 that are used to construct these different network types. This is paralleled by a hypothetical case study (Box  
178 1) where we showcase the utility/applicability of the different network representations in the context of trying  
179 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.

#### **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...

181 **3.1 Models that predict metawebs (feasible interactions)**

182 This is perhaps the most developed group of models; with a variety of approaches having been developed  
183 that typically determine the feasibility of an interaction based on the trait compatibility between predator  
184 and prey (*i.e.* their evolutionary compatibility) to determine ‘feeding rules’ (Morales-Castilla et al., 2015).  
185 These feeding rules are broadly elucidated in two different ways; mechanistic feeding rules can be explicitly  
186 defined and applied to a community (Dunne et al., 2008; *e.g.*, Shaw et al., 2024) or they are inferred from  
187 a community for which there is interaction data and the ‘rules’ are then applied to a different community  
188 (Caron et al., 2022; Cirtwill et al., 2019; Desjardins-Proulx et al., 2017; Eklöf et al., 2013; Llewelyn et  
189 al., 2023; Pichler et al., 2020; Strydom et al., 2022; *e.g.*, Strydom et al., 2023). The fundamental difference  
190 between these two model groups is that ‘mechanistic models’ rely on expert knowledge and make assumptions  
191 on trait-feeding relationships, whereas the ‘pattern finding’ models are dependent on existing datasets from  
192 which to elucidate feeding rules. These models are useful for determining all feasible interactions for a specific  
193 community, and owing to the availability of empirical interaction datasets (Gray et al., 2015; *e.g.*, Poelen  
194 et al., 2014; Poisot, Baiser, et al., 2016), as well as the development of model testing/benchmarking tools  
195 (Poisot, 2023), means that these models can be validated and (with relative confidence) be used to construct  
196 first draft networks for communities for which we have no data (Strydom et al., 2022), and are valuable  
197 for constructing networks where we lack any interaction data *e.g.*, prehistoric networks (Fricke et al., 2022;  
198 Yeakel et al., 2014) or even to predict interactions for contemporary species that do not currently co-occur  
199 and thus we have no way of empirically evaluating if the interaction is feasible or not.

200 **3.2 Models that predict realised networks (realised interactions)**

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

212 et al. (2023) developed a model that moves the energy of the system into different modules related to the  
213 process of the predator acquiring energy from the prey *i.e.*, compartmentation in food webs (Krause et al.,  
214 2003).

### 215 3.3 Models that predict structure (interaction agnostic)

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

## 230 4 Making Progress with Networks

### 231 4.1 Further development of models and tools

232 There has been a suite of models that have been developed to predict trophic links, however we are lacking  
233 in tools that are explicitly taking into consideration estimating both the feasibility as well as realisation of  
234 links, *i.e.*, both interactions and structure simultaneously (Strydom et al., 2021). This could be addressed  
235 either through the development of tools that do both (predict both interactions and structure), or to develop  
236 an ensemble modelling approach (Becker et al., 2022). Alternatively the development of tools that will allow  
237 for the downsampling of metawebs into realised networks (*e.g.*, Roopnarine, 2006), although deciding exactly  
238 what is driving differences between local networks and the regional metaweb might not be that simple (Saravia  
239 et al., 2022). Probably also something that aligns with trying to predict interaction strength - because that  
240 would be the gold standard (*e.g.*, Wells & O’Hara, 2013). In addition to the more intentional development of

241 models we also need to consider the validation of these models, there have been developments and discussions  
242 for assessing how well a model recovers pairwise interactions (Poisot, 2023; Strydom et al., 2021), although  
243 the rate of false-negatives that may be present in the testing data still present a challenge (Catchen et al.,  
244 2023), and we still lack clear strategies for benchmarking the ability of models to recover structure (Allesina  
245 et al., 2008).

## 246 4.2 At what scale should we be predicting and using networks?

247 Look at Hutchinson et al. (2019)

248 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a  
249 ‘network’. Realistically most empirical networks are more aligned with metawebs as opposed to realised  
250 networks as they are often the result of some sort of aggregation of observations across time, this creates a  
251 two-fold problem. Firstly, we need to think about how this affects any sort of development of theory that sits  
252 closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer questions  
253 about realised networks using feasible networks? The second is that this lack of ‘direction’ as to how we  
254 should define a network is (actually) probably one of the biggest barriers that is affecting the use of networks  
255 in applied settings... By define I mean both delimiting the time and geographic scale at which a network  
256 is aggregated at (Estay et al., 2023). We know that space plays a role influence both network properties  
257 (Galiana et al., 2018), as well as dynamics (Fortin et al., 2021; Rooney et al., 2008). And so does time *e.g.*,  
258 seasonal rewiring (Brimacombe et al., 2021; Laender et al., 2010). There is also a bit of an interplay with  
259 time and data and the different scales that they may be integrated at - co-occurrence may span decades and  
260 just because two species have been recorded in the same space does not mean it was at the same timescale  
261 (Brimacombe et al., 2024).

## 262 4.3 Feasible, realised, or sustainable?

263 When do we determine a link to be ‘real’... In the context of metawebs this is perhaps clearer - if all things  
264 were equal (*i.e.*, community context is irrelevant) would the predator be able to consume the prey. However  
265 in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction - just  
266 because an interaction is possible in the now is it able to sustain a population in the long term. And what  
267 is the scale for that long term - are we thinking at the generational scale? Because ultimately when we  
268 are constructing a network we are aggregating not only across space but also across time... This is probably  
269 again a Lokta-Volterra space question and something that the dynamic foodweb models (Curtsdotter et al.,  
270 2019; Delmas et al., 2017; Lajaaiti et al., 2024) are addressing, but again it is integrating this with the

271 feasible/realised axis. And of course the Petchey dilemma of even what networks should we be feeding into  
272 these dynamic models.

## 273 5 The future value of networks

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

275 It should be clear that there is a high degree of interrelatedness and overlap between the way a network is  
276 constructed (modelled or predicted) and the process(es) it captures, these are encoded (embedded) within  
277 the network representation and ultimately influences how the network can and should be used (Berlow et al.,  
278 2008; Petchey et al., 2011). It is probably both this nuance as well as a lack of clear boundaries and guidelines  
279 as to the links between network form and function (although see Delmas et al., 2019) that has stifled the  
280 ‘productive use’ of networks beyond inventorying the interactions between species. Although, progress with  
281 using networks as a means to address questions within larger bodies of ecological theory *e.g.*, invasion biology  
282 (Hui & Richardson, 2019) and co-existence theory (García-Callejas et al., 2023), has been made we still need  
283 to have a discussion on what the appropriate network representation for the task at hand would be. This  
284 is highlighted in Box 1, and underscores that we need to evaluate exactly what process a specific network  
285 representation captures as well as its suitability for the question of interest.

Table 1: An informative table

Question (broad)	Question (specific)	Network representation
Species invasions	What species will the invading species interact with?	Regional metaweb but need to derive information from a global metaweb since these are interactions that are ‘novel’
Species invasions	How does the invading species alter network dynamics and function?	Realised network (after having moved through the global metaweb to understand which interactions are feasible)
Range shifts and novel communities	Under global change how will novel community assemblages interact?	Global metaweb, need context of broader community

Question (broad)	Question (specific)	Network representation
Extinctions	Cascading effect of the loss of a species from the network	Regional metaweb - need to account for entire diet, a realised network will exclude the entire diet but will allow to elucidate the final structure
Species/community persistence	Dynamics over time. Stability/resilience. How does a change in pop <i>A</i> affect pop <i>B</i> ?	Realised networks - but dynamic!
Synthetic networks	Creating ecologically plausible communities for synthetic analyses	Structural networks - data light!
Practical use	What is both attainable (data constraints) but also of practical use to 'real world' decision making. So moving from theory to applied	??Regional metawebs??

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

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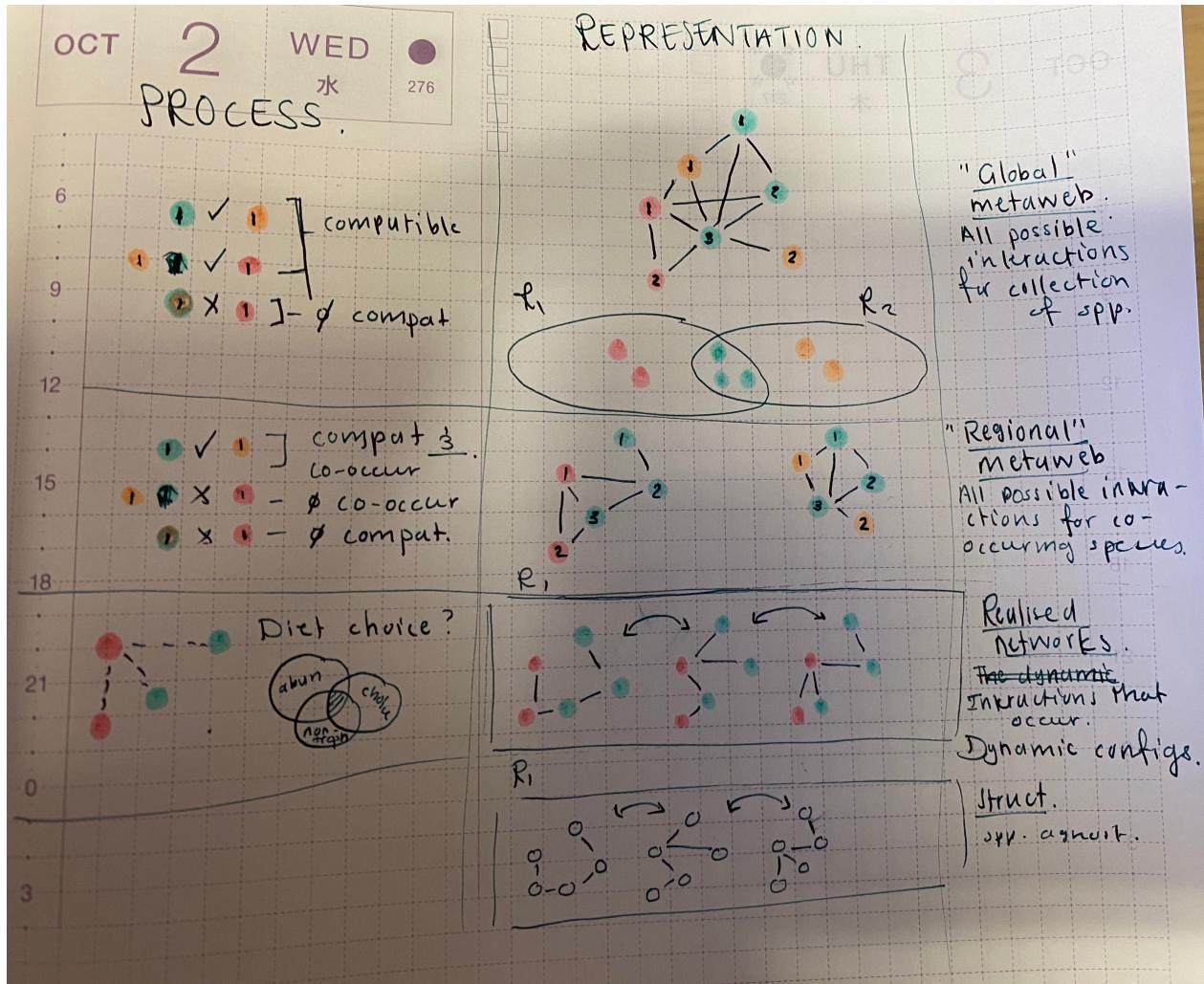


Figure 1: Aligning the various processes that determine interactions with the different network representations. First we start with a ‘global metaweb’ this network which captures all possible interactions for an arbitrary collection of species, we can further refine this network by taking in to consideration the co-occurrence of these difference species - as shown here we have two regions with some species (blue) that are found in both regions and others endemic to either region one (pink) or region two (orange). These regional metawebs to capture all possible interactions, however it only considers species that co-occur. However even within a region we do not expect all interactions to be realised but rather that there are multiple configurations of the regional metaweb over both space and time. The ‘state’ of the different network realisations are ultimately influenced not just by the co-occurrence of a species pair but rather the larger community context such as the abundance of different species, maximising energy gain, or indirect/higher order interactions.