

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
3 how biodiversity – as an interconnected set of species – responds to multiple stressors. The interaction
4 between species is one of the fundamental building blocks of ecological communities, providing a powerful
5 abstraction that can help quantify, conceptualise, and understand biodiversity dynamics, and ultimately,
6 make predictions, mitigate change, and manage services (Windsor et al., 2023). Such network representations
7 of biodiversity (including within species diversity) are increasingly argued to be an asset to predictive ecology,
8 climate change mitigation and resource management, with the argument that characterising biodiversity in a
9 network will afford a deeper capacity to understand and predict the abundance, distribution, dynamics and
10 services provided by multiple species facing multiple stressors. However, there is a growing discourse around
11 limitations to the interpretation and applied use of networks (Blüthgen, 2010; Dormann, 2023), primarily as
12 the result of shortcomings regarding the conceptualisation of networks (Blüthgen & Staab, 2024).

13 An ‘interaction network’ can be defined and conceptualised in a myriad of ways, which means that different
14 networks will be embedding different processes (or determinants) of interactions, ultimately influencing the
15 patterns and mechanisms that are inferred (Proulx et al., 2005). The different ways in which a network can
16 be represented is the result of *how* the network is constructed, which itself rests on two pillars: the data used
17 to construct the network (of which there has been a plethora of discussions as to the challenges relating to
18 the scale and nature of data collection/observation *e.g.*, Blüthgen & Staab, 2024; Brimacombe et al., 2023;
19 Moulatlet et al., 2024; Polis, 1991; Pringle & Hutchinson, 2020; Saberski et al., 2024) and the underlying
20 theory as to what drives the occurrence of interactions between species. The latter represents an expression of
21 mechanism and process that gives rise to the patterns that emerge from collating interactions among species,
22 and will ultimately inform which data are deemed important in the determination of interactions occurring.
23 Each of these pillars carries with it a set of practical, semantic and conceptual constraints that not only
24 influence progress in making network ecology more valuable and potentially predictive, but help define the
25 spatial, temporal, and evolutionary scale of assumptions we make and the predictions we might generate
26 from different network representations.

27 In this perspective we aim to provide an overview of the different **food web** representations (*a note on how*
28 *there has been developments in the ‘bipartite space’ and it would be flawed to try and view them in tandem*
29 *as food webs and non-trophic webs are two very different conceptualisations*), particularly how these relate
30 to the terminology used to define a network, and how this influenced by both the processes that determine
31 networks as well as how this relates to the way in which we construct networks. The provision of this
32 detail ultimately leads to a set of insights and conclusions about whether, when, and under what conditions

33 network representations of biodiversity can contribute to the advancement of ecological theory and generate
34 value in predictive ecology. Specifically, we finish this perspective with an overview of fundamental questions
35 in ecology that we think can benefit from network thinking and a proposal that such thinking can accelerate
36 our capacity to predict the impact of multiple stressors on biodiverse communities.

37 1 Setting the Scene: The Not So Basics of Nodes and Edges

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

48 1.1 How do we define a node?

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

57 1.2 What is captured by an edge?

58 At its core, links within food webs can be thought of as a representation of either feeding links between species
59 - be that realised (Pringle, 2020) or potential (Dunne, 2006), alternative links can represent fluxes within the
60 system *e.g.*, energy transfer or material flow as the result of the feeding links between species (Lindeman,
61 1942). Fundamentally this means that the links within a network represent different ‘currencies’ (either the

62 feasibility of a link existing between two species or the energy that is moving through the system) and how the
63 links within a network are specified will influence the resulting structure of the network. For example taking
64 a food web that consists of links representing all *potential* feeding links for a community (*i.e.*, a metaweb)
65 will be meaningless if one is interested in understanding the flow of energy through the network as the links
66 within a metaweb do not represent environmental/energetic constraints, making them poor representations
67 of which interactions are *realised* in a specific location (Caron et al., 2024). In addition to the various ways
68 of defining the links between species pairs there are also a myriad of ways in which the links themselves
69 can be quantified. Links between species are often treated as being present or absent (*i.e.*, binary) but it is
70 also possible to use probabilities (Banville et al., 2024; which quantifies how likely an interaction is to occur,
71 Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of of an interaction,
72 Berlow et al., 2004).

73 1.3 Network representations

74 Broadly, networks can be thought of to fall into two different ‘types’; namely metawebs; traditionally defined
75 as all of the *potential* interactions for a specific species pool (Dunne, 2006), and realised networks; which
76 is the subset of interactions in a metaweb that are *realised* for a specific community at a given time and
77 place. The fundamental difference between these two different network representations is that a metaweb
78 provides insight as to the viability of an interaction between two species occurring and is a means to identify
79 links that are not ecologically plausible, *i.e.*, forbidden links (Jordano, 2016b), or provide an idea of the
80 *complete* diet of a species (Strydom et al., 2023). In contrast realised networks are highly localised and
81 the links between species are contingent on both the co-occurrence of species, the role of the environment,
82 and population and community dynamics on predator choice. In the context of definitions and semantics
83 the links that are represented by a metaweb and a realised network are different; links that are absent in a
84 metaweb can be treated as being truly absent, however links that are absent in a realised network cannot
85 be considered to be truly absent but rather as absent due to the broader environmental/community context.
86 Importantly, a realised network is *not* simply the downscaling of a metaweb to a smaller scale (*e.g.*, moving
87 from the country to the 1x1 km² scale based on fine-scale species co-occurrence) but represents a shift towards
88 capturing the higher level processes that determine the *realisation* of an interaction, *i.e.*, the definition of an
89 edges shifts from being determined by interaction feasibility to that of energetic choices/consequences. Thus,
90 different network representations are determined and constrained by different sets of assumptions as to what
91 the processes are that determine the presence/absence of an interaction between two species as well as the
92 resulting network structure.

⁹³ 2 From Nodes and Edges to Scale, Context, and Process

⁹⁴ The interplay between network representation and network (node and edge) definition is primarily governed
⁹⁵ by the process(es) that determine the interaction between species, however these processes are also scale and
⁹⁶ context dependent. Here we start by introducing the five core processes that determine either the feasibility
⁹⁷ or the realisation of interactions, namely: evolutionary compatibility, co-occurrence, abundance, predator
⁹⁸ choice, and non-trophic interactions; while simultaneously contextualising them within, and linking them
⁹⁹ to, the different network representations Figure 1. We can think of the different network representations
¹⁰⁰ to be conceptually analogous to the fundamental and realised niche, whereby the metaweb represents the
¹⁰¹ ‘fundamental diet niche’ of a species and a realised network represents the ‘realised diet’ of a species. Of
¹⁰² course these processes do not function in a vacuum and do interact with/influence one another, but it is still
¹⁰³ beneficial to present them in a categorical manner as these different processes are often the underpinning
¹⁰⁴ logic in the development of prediction/network models, the criteria for data collection in the field, and the
¹⁰⁵ scale of organisation for which they are relevant (species, population, or community).

¹⁰⁶ [Figure 1 about here.]

¹⁰⁷ 2.1 The processes that determine species interactions

¹⁰⁸ Evolutionary compatibility

¹⁰⁹ There is compelling evidence that an interaction occurring between two species is the result of their shared
¹¹⁰ (co)evolutionary history (Dalla Riva & Stouffer, 2016; Gómez et al., 2010; Segar et al., 2020) which, in the
¹¹¹ more proximal sense, is manifested as the ‘trait complementarity’ between two species (Benadi et al., 2022),
¹¹² whereby one species (the predator) has the ‘correct’ set of traits that allow it to chase, capture, kill, and
¹¹³ consume the other species (the prey). For species pairs where this condition is not met the link is deemed
¹¹⁴ to be *forbidden* (Jordano, 2016b); *i.e.*, not physically possible and will always be absent within a network.
¹¹⁵ A network constructed on the basis of evolutionary compatible links is most closely aligned with a metaweb,
¹¹⁶ although it would not be required that the species co-occur (as shown in Figure 1), and arguably makes for
¹¹⁷ a good approximation of the ‘Eltonian niche’ of species (Soberón, 2007). Finally, one should be aware that
¹¹⁸ it is possible to represent evolutionary compatible interactions as either binary (possible vs forbidden) or as
¹¹⁹ a probability (Banville et al., 2024), where the probability represents how likely the interaction between two
¹²⁰ species is to be possible.

¹²¹ (Co)occurrence

¹²² Although the outright assumption that because two species are co-occurring it must mean that they are

123 interacting is flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at least in
124 terms of feeding links) if they are not co-occurring in time and space. Thus, although co-occurrence data
125 alone is insufficient to build an accurate and ecologically meaningful representation of *feeding links* it is still
126 a critical process that determines the realisation of feeding links and allows us to constrain a global metaweb
127 to only consider ‘realised’ communities (Dansereau et al., 2024) and an understanding of the intersection of
128 species interactions and their co-occurrence (*sensu* a fusion of the the Grinnellian and Eltonian niches niche,
129 Gravel et al. (2019)) is meaningful when one is operating in the space of trying to determine the distribution
130 of a species (Higino et al., 2023; Pollock et al., 2014).

131 **Abundance**

132 The abundance of the different species within the community is thought to influence the realisation of feeding
133 links primarily in two ways. Firstly there is the argument that the structure of networks (and the interactions
134 that they are composed of) are driven *only* by the abundance of the different species and that interactions
135 are not contingent on there being any compatibility (trait matching) between them, *sensu* neutral processes
136 (Canard et al., 2012; Momal et al., 2020). However, a more ecologically sound assumption would be that
137 the abundance of different prey species will influence the distribution of links in a network (Vázquez et al.,
138 2009), by influencing which prey are targeted or preferred by the predator as abundance influences factors
139 such as the likelihood of two species (individuals) meeting (Banville et al., 2024; Poisot et al., 2015), or in
140 the dynamic sense will influence the persistence of viable populations.

141 **Profitability (energetics)**

142 Ultimately, predator choice is underpinned by the energetic cost-benefit (profitability) of trying to catch, kill,
143 and consume prey (where a predator will optimise energy intake while minimising handling and search time
144 (energy cost)), and is well described within both optimal foraging (Pyke, 1984) and metabolic theory (Brown
145 et al., 2004). The energetic cost of feeding is determined by both the energy content as well as the density
146 (abundance) of prey (as this influences search time), and a predator will opt to select the prey type that will
147 be most profitable. Additional work on on understanding the energetic cost that the environment imposes on
148 an individual (Cherif et al., 2024) as well as the way a predator uses the landscape to search for prey (Pawar
149 et al., 2012) brings us closer to accounting for the energetic cost of realising feeding links.

150 **Non-trophic interactions**

151 Perhaps not as intuitive when thinking about the processes that determine feeding links is accounting for
152 the ability of non-trophic interactions (such as competition) to modify either the realisation or strength of
153 trophic interactions (Golubski & Abrams, 2011; Pilosof et al., 2017). Non-trophic interactions can modify in-

154 interactions either ‘directly’ *e.g.*, predator *a* outcompetes predator *b* or ‘indirectly’ *e.g.*, mutualistic/facilitative
155 interactions will alter the fine-scale distribution and abundance of species as well as their persistence (Buche
156 et al., 2024; Kéfi et al., 2012, 2015). The ‘unobservable’ nature of non-trophic interactions makes them a
157 challenge to quantify, however their importance in network dynamics (Staniczenko et al., 2010) as well as
158 cascading effects (*e.g.*, Kamaru et al., 2024) should not be overlooked.

159 **2.2 Contextualising the processes that determine species interactions**

160 It should be self evident that the different processes discussed above will ultimately influence the realisation
161 of interactions as well as the structure of a network, however they are acting at different scales of organisation.
162 Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of the species pair of
163 interest, that is the *possibility* of an interaction being present/absent is assessed at the pairwise level and
164 one is left with a ‘list’ of interactions that are present/absent. Although it is possible to build a network
165 (*i.e.*, metaweb) from this information it is important to be aware that the structure of this network is not
166 constrained by real-world dynamics or conditions (*i.e.*, the community context), and so just because species
167 are able to interact does not mean that they will (Poisot et al., 2015). In order to construct a network who’s
168 structure is a closer approximation of reality (localised interactions) one needs to take into consideration the
169 properties of the community as a whole and information about the individuals it is comprised of (Quintero
170 et al., 2024), which requires more data at the community scale, such as the abundance of species.

171 **3 Network construction is nuanced**

172 The act of constructing a ‘real world’ network will ultimately be delimited by its intended use, however the
173 reality is that the empirical collection of interaction data is both costly and challenging to execute (Jordano,
174 2016a, 2016b), especially if one wants to capture *all* aspects of the processes discussed in Section 2 (owing
175 to the different time and spatial scales they may be operating at). Thus we often turn to models to either
176 predict networks (be that the interaction between two species, or network structure (Strydom et al., 2021)),
177 or as a means to identify missing interactions (gap fill) within an existing empirical dataset (Biton et al.,
178 2024; Dallas et al., 2017; Stock, 2021), and so for the purpose of this discussion network construction will
179 be synonymous with using a model as a means to represent or predict a network. That is not to say that
180 there is no need for empirical data collection, but rather that using a model for food web prediction (or
181 reconstruction) is a more feasible approach as it allows us to make inferences about interactions that are
182 not happening in the ‘observable now’ (Strydom et al., 2021), and has the added benefit that one is able
183 to explicitly account for uncertainty within the network construction process (Banville et al., 2024). Most

184 importantly different models have different underlying philosophies, this allows isolate and operate within
185 one (or a few) of the processes discussed in Section 2, and better sets us up to understand how different
186 processes determine interactions (Song & Levine, 2024; Stouffer, 2019). Here we will introduce the three
187 different types of network representations (metawebs, realised networks, and structural networks), how they
188 link back to (and encode) the different processes determining interactions Figure 1, and broadly discuss some
189 of the modelling approaches that are used to construct these different network types. This is paralleled
190 by a hypothetical case study (Box 1) where we showcase the utility/applicability of the different network
191 representations 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

note I am using a figure for layout experimentation purposes

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 that experiences a degree of species turnover between 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 shifts in their diets (be that due to changes in species occurrence or predator choice). If one were to construct a metaweb that disregards these season shifts ('global metaweb') these details would be lost 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 *e.g.*, Schwarz et al. (2020)). 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

[Figure 2 about here.]

192

193 3.1 Models that predict metawebs (feasible interactions)

194 This is perhaps the most developed group of models; with a variety of approaches having been developed
195 that typically determine the feasibility of an interaction using the trait compatibility between predator and

196 prey (*i.e.* their evolutionary compatibility) to determine ‘feeding rules’ (Morales-Castilla et al., 2015). These
197 feeding rules are broadly elucidated in two different ways; mechanistic feeding rules can be explicitly defined
198 and applied to a community (Dunne et al., 2008; Roopnarine, 2017; *e.g.*, Shaw et al., 2024) or they are
199 inferred from a community for which there are interaction data and the ‘rules’ are then applied to a different
200 community (Caron et al., 2022; Cirtwill et al., 2019; Desjardins-Proulx et al., 2017; Eklöf et al., 2013;
201 Llewelyn et al., 2023; Pichler et al., 2020; Strydom et al., 2022; *e.g.*, Strydom et al., 2023). The fundamental
202 difference between these two model groups is that ‘mechanistic models’ rely on expert knowledge and make
203 explicit assumptions on trait-feeding relationships, whereas the ‘pattern finding’ models are dependent on
204 existing datasets from which to elucidate feeding rules. These models are useful for determining all feasible
205 interactions for a specific community, and owing to the availability of empirical interaction datasets (Gray
206 et al., 2015; *e.g.*, Poelen et al., 2014; Poisot, Baiser, et al., 2016), as well as the development of model
207 testing/benchmarking tools (Poisot, 2023), means that these models can be validated and (with relative
208 confidence) be used to construct first draft networks for communities for which we have no interaction data
209 (Strydom et al., 2022), and are valuable not only in data poor regions but also for predicting interactions
210 for ‘unobservable’ communities *e.g.*, prehistoric networks (Dunhill et al., 2024; Fricke et al., 2022; Yeakel et
211 al., 2014) or future, novel community assemblages. Importantly metawebs are inherently ‘static’ in the sense
212 that they are *not* able to capture dynamic processes (since the notion of feasibility is all or nothing), however
213 they provide a bigger picture context (*e.g.*, understanding the *entire* diet breadth of a species) and often
214 require little data to construct.

215 3.2 Models that predict realised networks (realised interactions)

216 In order to construct realised networks models need to incorporate *both* the feasibility of interactions (*i.e.*,
217 determine the entire diet breadth of a species) as well as then determine which interactions are realised (*i.e.*,
218 incorporate the ‘cost’ of interactions). As far as we are aware there is no model that explicitly accounts for
219 both of these ‘rules’ (although see Olivier et al. (2019)) and rather *only* account for processes that determine
220 the realisation of an interaction (*i.e.*, abundance, predator choice, or non-trophic interactions). Although
221 the use of allometry *i.e.*, body size (Beckerman et al., 2006; *e.g.*, Valdovinos et al., 2023; White et al., 2007;
222 Yodzis & Innes, 1992) may represent a first step in capturing ‘evolutionary compatibility’ alongside more
223 energy (predator choice) driven processes we still need to account for other traits that determine feeding
224 compatibility (*e.g.*, Van De Walle et al., 2023 show how incorporating prey defensive properties alongside
225 body size improves predictions). In terms of constructing realised networks, diet models (Beckerman et al.,
226 2006; Petchey et al., 2008) have been used construct networks based on both predator choice (as determined

227 by the handling time, energy content, and predator attack rate) as well as abundance (prey density) and
228 progress has also been made in understanding the compartmentation of energy in networks and how this
229 influences energy acquisition (Krause et al., 2003; Wootton et al., 2023). As realised networks are build
230 on the concept of dynamic processes (the abundance of species will always be in flux) these networks are
231 valuable for understanding the behaviour of networks over time or their response to change (Curtsdotter et
232 al., 2019; Delmas et al., 2017; Lajaaiti et al., 2024). However, they are ‘costly’ to construct (requiring data
233 about the entire community as it is the behaviour of the system that determines the behaviour of the part)
234 and also lack the larger diet niche context afforded by metawebs.

235 **3.3 Models that predict structure (interaction agnostic)**

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

250 **4 Making Progress with Networks**

251 **4.1 Further development of models and tools**

252 There has been a suite of models that have been developed to predict feeding links, however we are lacking
253 in tools that are explicitly taking into consideration estimating both the feasibility as well as realisation of
254 links, *i.e.*, both interactions and structure simultaneously (Strydom et al., 2021). This could be addressed
255 either through the development of tools that do both (predict both interactions and structure), or to develop

256 an ensemble modelling approach (Becker et al., 2022; Terry & Lewis, 2020) or tools that will allow for the
257 downsampling of metawebs into realised networks (*e.g.*, Roopnarine, 2006). Additionally, although realised
258 networks are more closely aligned with capturing interaction strength we lack models that allow us to quantify
259 this (Strydom et al., 2021; Wells & O'Hara, 2013). In addition to the more intentional development of models
260 we also need to consider the validation of these models, there have been developments and discussions for
261 assessing how well a model recovers pairwise interactions (Poisot, 2023; Strydom et al., 2021), although their
262 are still challenges related to the completeness of the datasets used for validation, specifically the challenge of
263 dealing with false-negatives (Catchen et al., 2023). In terms of validating the predicted structure of networks,
264 we still lack clear set of guidelines for benchmarking the ability of models to recover structure (Allesina et
265 al., 2008).

266 **4.2 At what scale should we be predicting and using networks?**

267 The appropriate level of aggregation for a ‘network’ is an emerging discussion within the field (Estay et al.,
268 2023; Moulatlet et al., 2024; Saberski et al., 2024), and perhaps presents the biggest challenge if we want
269 to understand how different processes determine interactions (Saravia et al., 2022), as well as identify the
270 appropriate networks for different research questions Figure 3. Thus we need an understanding of not only
271 how time and scale influence the interpretation of networks (Blüthgen & Staab, 2021; Morales & Vázquez,
272 2008), but how this is in turn influenced by the type of network representations used. Space influences both
273 network properties (Galiana et al., 2018), as well as dynamics (Fortin et al., 2021; Rooney et al., 2008), and
274 time has implications when it comes to accounting for seasonal turnover in communities (Brimacombe et al.,
275 2021; Laender et al., 2010) as well as thinking about co-occurrence, particularly the records that are used
276 to determine co-occurrence (Brimacombe et al., 2024). Although multilayer networks may allow us to encode
277 the nuances of space and time (Hutchinson et al., 2019) we still need to understand the implications of *e.g.*,
278 constructing networks that are not at ecologically but rather politically relevant scales (Strydom et al., 2022)
279 and what the implications of this disconnect may be.

280 **4.3 Making use of the different network representations**

281 It should be clear that there is a high degree of interrelatedness and overlap between the way in which
282 a network is constructed (modelled or predicted) and the process(es) that it captures Figure 1, these are
283 encoded (embedded) within the network representation and ultimately influences how the network can and
284 should be used (Berlow et al., 2008; Petchey et al., 2011), with different network representations yielding
285 different interpretations of processes (Keyes et al., 2024). It is probably both this nuance as well as a lack of

286 clear boundaries and guidelines as to the links between network form and function (although see Delmas et
287 al., 2019) that has stifled the ‘productive use’ of networks beyond the inventorying the interactions between
288 species. Although progress with using networks as a means to address questions within larger bodies of
289 ecological theory *e.g.*, invasion biology (Hui & Richardson, 2019) and co-existence theory (García-Callejas et
290 al., 2023) has been made we still lack explicit guidelines as to what the appropriate network representation
291 for the task at hand would be, and as highlighted in Box 1, underscores the need to evaluate exactly what
292 process a specific network representation captures as well as its suitability for the question of interest. In
293 Figure 3 we present a mapping of what we believe are some of the key questions for which interaction networks
294 can be used to the different networks representations that are most suitable, as well as highlight some of the
295 methodological challenges that still need to be improved upon.

296 4.4 How will novel communities interact?

297 Here we can talk about the effects of range shifts and invasions and how this will result in new/novel
298 community assemblages. And then also the intentional changes of species compositions through rewilding.

299 4.5 How will changes in the community influence ecosystem processes?

300 Linking to dynamic networks and how this lets us build spatially/temporally explicit networks which can be
301 used to infer form and function. Also bring in the discussion on the suitable aggregation (and the fact that
302 we don’t know)

303 4.6 How do species persist/co-exist?

304 Specific sub points to consider here is persistence, especially persistence to perturbation. Again, dynamic
305 networks and network/community assembly and finally extinctions (Dunhill et al., 2024).

306 [Figure 3 about here.]

Table 1: This table represents an alternative approach to try and think about mapping questions to network representations.

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’

Question (broad)	Question (specific)	Network representation
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
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 A affect pop B?	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??

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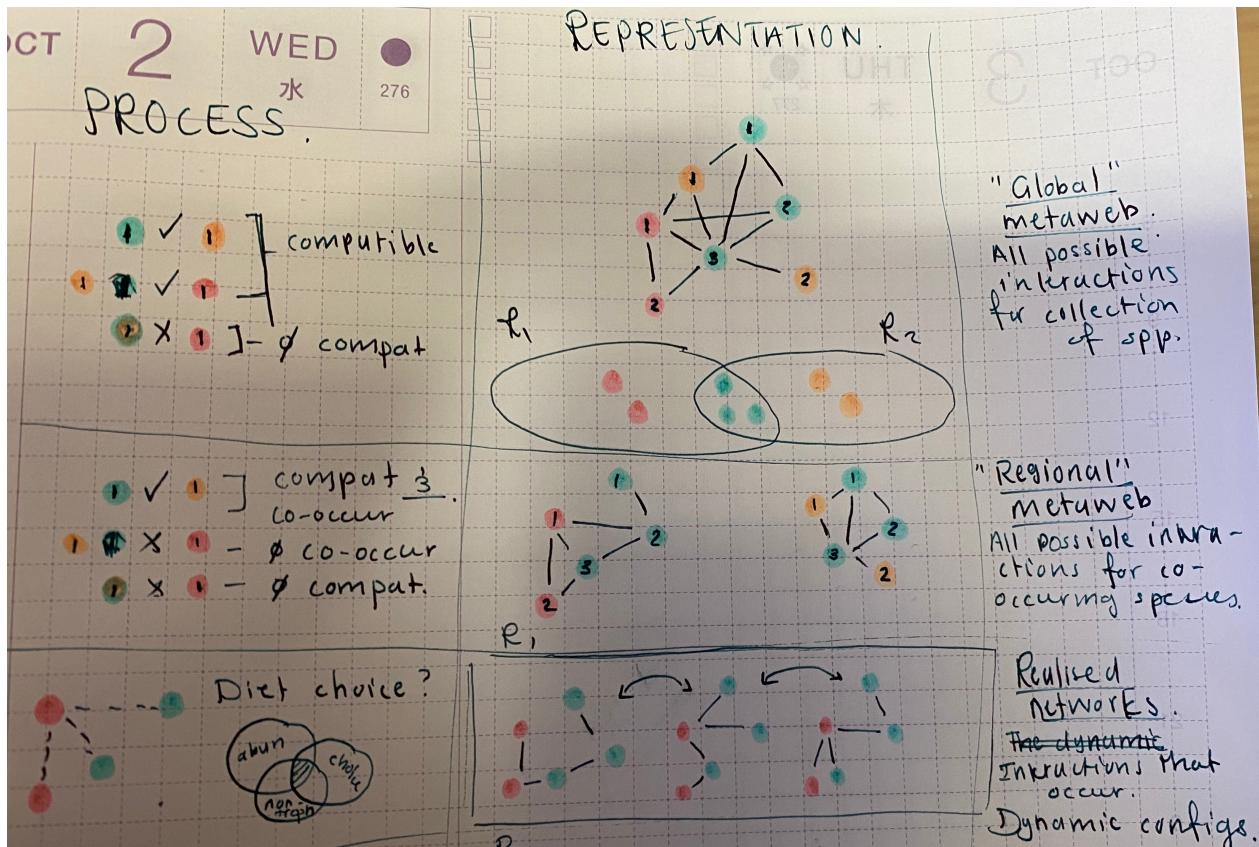
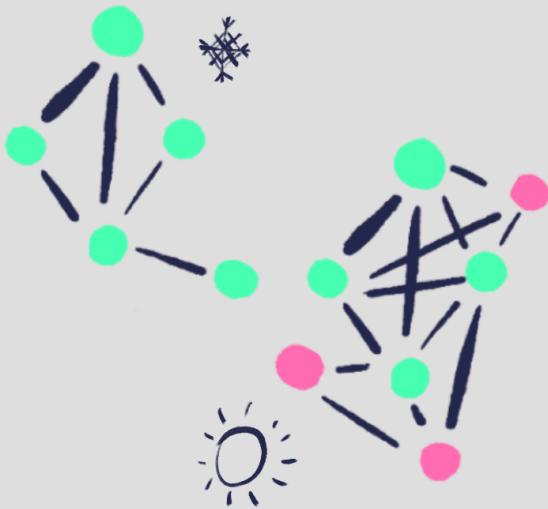


Figure 1: Aligning the various processes that determine interactions with the different network representations. First we start with a ‘global metaweb’ this network which captures all possible interactions for an arbitrary collection of species, we can further refine this network by taking in to consideration 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.



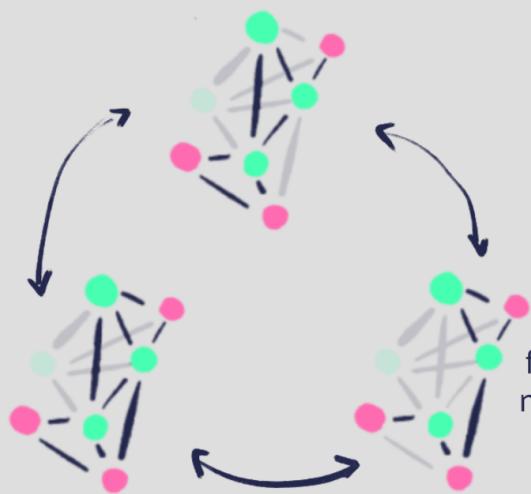
1. A 'global' metaweb

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. Seasonal metawebs

- Knowledge at the finer scale is also valuable to understand/identify that there are in fact differences between the seasons
- Information of seasonal diet of species



3. Seasonal (rellised networks)

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.

- Structurally informative
- can be @ even finer scale & time / space

Figure 2

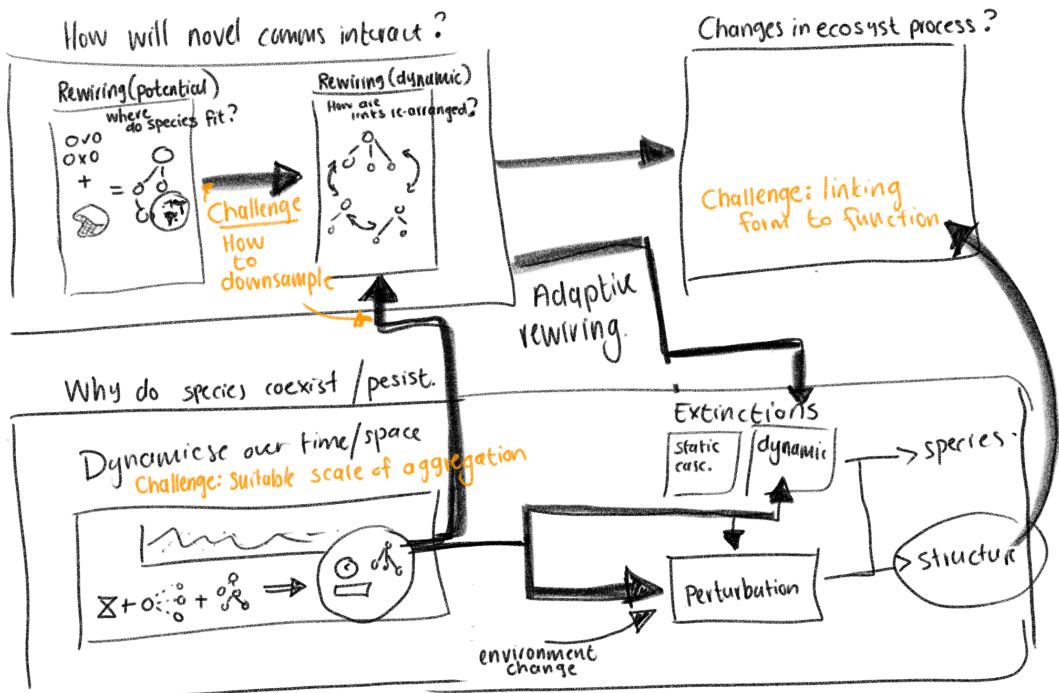


Figure 3: An attempt to try and visualise a way to map the different scales of network representations to the way in which we can interrogate/ask questions about them?