

# **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 km<sup>2</sup> 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.

## <sup>93</sup> 2 From Nodes and Edges to Scale, Context, and Process

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

<sup>106</sup> [Figure 1 about here.]

### <sup>107</sup> 2.1 The processes that determine species interactions

#### <sup>108</sup> Evolutionary compatibility

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

#### <sup>121</sup> (Co)occurrence

<sup>122</sup> 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 is meaningful when one is operating in the space of trying to  
129 determine the distribution of a species (Higino et al., 2023; Pollock et al., 2014), representing something of  
130 a fusion of the the Grinnellian and Eltonian niches (Gravel et al., 2019).

### 131 **Abundance**

132 The abundance of different the species within the community is thought to influence the realisation of feeding  
133 links primarily in two ways. Firstly there is the argument that that 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), be 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 while minimising handling and search time), and  
144 is well described within both optimal foraging (Pyke, 1984) and metabolic theory (Brown et al., 2004). The  
145 energetic cost of feeding is itself can be deconstructed as the energy content as well as the density (abundance)  
146 of prey (as this influences search time) and how these will influence which links are realised Figure 1, with an  
147 argument that body size represents a key trait that may capture and influence these processes (White et al.,  
148 2007; Yodzis & Innes, 1992). Additional work on on understanding the energetic cost that the environment  
149 imposes on an individual (Cherif et al., 2024) as well as the way a predator uses the landscape to search for  
150 prey (Pawar et al., 2012) is bringing us closer to accounting for the energetic cost of realising feeding links.

### 151 **Non-trophic interactions**

152 Perhaps not as intuitive when thinking about the processes that determine feeding links (trophic interac-  
153 tions) is thinking about the role of the ability of non-trophic interactions to modify either the realisation or

strength of trophic interactions (Golubski & Abrams, 2011; Pilosof et al., 2017). Non-trophic interactions can modify interactions either ‘directly’ e.g., predator *a* outcompetes predator *b* or ‘indirectly’ e.g., mutualistic/facilitative interactions will alter the fine-scale distribution and abundance of species as well as their persistence (Buche et al., 2024; Kéfi et al., 2012, 2015). The ‘unobservable’ nature of non-trophic interactions makes them a challenge to quantify, however their importance in network dynamics (Staniczenko et al., 2010) as well as cascading effects (e.g., Kamaru et al., 2024) should not be overlooked.

## 2.2 Contextualising the processes that determine species interactions

It should be self evident that the different processes discussed above are all ultimately going to influence the realisation of interactions as well as the structure of a network, however they are acting at different scales of organisation. Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of 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, 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 who’s structure is a closer approximation of reality (localised interactions) one needs to take into consideration the properties of the community as a whole and information about the individuals it is comprised of (Quintero et al., 2024), which requires more data at the community scale, such as the abundance of species.

## 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 and challenging to execute (Jordano, 2016a, 2016b), especially if one wants to capture *all* aspects of the processes discussed in Section 2 (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 network structure (Strydom et al., 2021)), or as a means to identify missing interactions (gap fill) within an existing empirical dataset (Biton et al., 2024; Dallas et al., 2017; 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. That is not to say that there is no need for empirical data collection but rather that using a model for food web prediction (or reconstruction) is a more feasible approach as it allows us to make inferences about interactions that are not happening in the ‘observable now’ (Strydom et al., 2021), with the added benefit that one is able to build some uncertainty

184 into the resulting network (Banville et al., 2024). Additionally different models have different underlying  
185 philosophies that allow us to capture one or a few of the processes discussed in Section 2, and although the  
186 delimits and defines what inferences can be made from the resulting network it also allows us to isolate and  
187 understand how different processes determine interactions (Song & Levine, 2024; Stouffer, 2019). Here we will  
188 introduce the three different types of network representations (metawebs, realised networks, and structural  
189 networks), how they link back to (and encode) the different processes determining interactions Figure 1, and  
190 broadly discuss some of the modelling approaches that are used to construct these different network types.  
191 This is paralleled by a hypothetical case study (Box 1) where we showcase the utility/applicability of the  
192 different network representations in the context of trying to understand the feeding dynamics of a seasonal  
193 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.]

194

195 **3.1 Models that predict metawebs (feasible interactions)**

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

217 **3.2 Models that predict realised networks (realised interactions)**

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

show how incorporating prey defensive properties alongside body size improves predictions). In terms of constructing realised networks, diet models (Beckerman et al., 2006; Petchey et al., 2008) have been used to construct networks based on both predator choice (as determined by the handling time, energy content, and predator attack rate) as well as abundance (prey density) and progress has also been made in understanding the compartmentation of energy in networks and how this influences energy acquisition (Krause et al., 2003; Wootton et al., 2023). As realised networks are built on the concept of dynamic processes (the abundance of species will always be in flux) these networks are valuable for understanding the behaviour of networks over time or their response to change (Curtsdotter et al., 2019; Delmas et al., 2017; Lajaaiti et al., 2024). However, they are ‘costly’ to construct (requiring data about the entire community as it is the behaviour of the system that determines the behaviour of the part) and also lack the larger diet niche context afforded by metawebs.

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

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

252 **4 Making Progress with Networks**

253 **4.1 Further development of models and tools**

254 There has been a suite of models that have been developed to predict feeding links, however we are lacking  
255 in tools that are explicitly taking into consideration estimating both the feasibility as well as realisation of  
256 links, *i.e.*, both interactions and structure simultaneously (Strydom et al., 2021). This could be addressed  
257 either through the development of tools that do both (predict both interactions and structure), or to develop  
258 an ensemble modelling approach (Becker et al., 2022; Terry & Lewis, 2020) or tools that will allow for the  
259 downsampling of metawebs into realised networks (*e.g.*, Roopnarine, 2006). Additionally although realised  
260 networks are more closely aligned with capturing interaction strength we lack models that allow us to quantify  
261 this (Strydom et al., 2021; Wells & O’Hara, 2013). In addition to the more intentional development of models  
262 we also need to consider the validation of these models, there have been developments and discussions for  
263 assessing how well a model recovers pairwise interactions (Poisot, 2023; Strydom et al., 2021), although the  
264 rate of false-negatives that may be present in the testing data still present a challenge (Catchen et al., 2023),  
265 and we still lack clear set of guidelines for benchmarking the ability of models to recover structure (Allesina  
266 et al., 2008).

267 **4.2 At what scale should we be predicting and using networks?**

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

281 **5 The future value of networks**

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

283 It should be clear that there is a high degree of interrelatedness and overlap between the way a network is  
284 constructed (modelled or predicted) and the process(es) it captures, these are encoded (embedded) within  
285 the network representation and ultimately influences how the network can and should be used (Berlow et  
286 al., 2008; Petchey et al., 2011), with different network representations yielding different interpretations of  
287 processes (Keyes et al., 2024). It is probably both this nuance as well as a lack of clear boundaries and  
288 guidelines as to the links between network form and function (although see Delmas et al., 2019) that has  
289 stifled the ‘productive use’ of networks beyond inventorying the interactions between species. Although,  
290 progress with using networks as a means to address questions within larger bodies of ecological theory *e.g.*,  
291 invasion biology (Hui & Richardson, 2019) and co-existence theory (García-Callejas et al., 2023), has been  
292 made we still need to have a discussion on what the appropriate network representation for the task at hand  
293 would be. This is highlighted in Box 1, and underscores that we need to evaluate exactly what process a  
294 specific network representation captures as well as its suitability for the question of interest.

295 **5.1 How will novel communities interact?**

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

298 **5.2 How will changes in the community influence ecosystem processes?**

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

302 **5.3 How do species persist/co-exist?**

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

305 [Figure 3 about here.]

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
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??

## 306 References

- 307 Allesina, S., Alonso, D., & Pascual, M. (2008). A General Model for Food Web Structure. *Science*, 320(5876),  
 308 658–661. <https://doi.org/10.1126/science.1156269>
- 309 Allesina, S., & Pascual, M. (2009). Food web models: A plea for groups. *Ecology Letters*, 12(7), 652–662.  
 310 <https://doi.org/10.1111/j.1461-0248.2009.01321.x>

- 311 Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas,  
312 T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction*  
313 *networks*. EcoEvoRxiv. <https://doi.org/10.32942/X28G8Z>
- 314 Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.  
315 A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,  
316 E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic  
317 reservoirs. *The Lancet Microbe*, 3(8), e625–e637. [https://doi.org/10.1016/S2666-5247\(21\)00245-7](https://doi.org/10.1016/S2666-5247(21)00245-7)
- 318 Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.  
319 *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- 320 Benadi, G., Dormann, C. F., Fründ, J., Stephan, R., & Vázquez, D. P. (2022). Quantitative Prediction of  
321 Interactions in Bipartite Networks Based on Traits, Abundances, and Phylogeny. *The American Naturalist*,  
322 199(6), 841–854. <https://doi.org/10.1086/714420>
- 323 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of  
324 the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- 325 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,  
326 V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.  
327 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),  
328 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 329 Biton, B., Puzis, R., & Pilosof, S. (2024). *Inductive link prediction boosts data availability and enables  
330 cross-community link prediction in ecological networks*.
- 331 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.  
332 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 333 Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: A critique and an  
334 ecologist’s guide. *Basic and Applied Ecology*, 11(3), 185–195. <https://doi.org/10.1016/j.baae.2010.01.001>
- 335 Blüthgen, N., & Staab, M. (2021). Ecology: Mammals, interaction networks and the relevance of scale.  
336 *Current Biology*, 31(13), R850–R853. <https://doi.org/10.1016/j.cub.2021.05.032>
- 337 Blüthgen, N., & Staab, M. (2024). A Critical Evaluation of Network Approaches for Studying Species  
338 Interactions. *Annual Review of Ecology, Evolution, and Systematics*, 55(1), 65–88. <https://doi.org/10.1146/annurev-ecolsys-102722-021904>
- 339 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2021). Inferred seasonal interaction rewiring of a freshwater  
340 stream fish network. *Ecography*, 44(2), 219–230. <https://doi.org/10.1111/ecog.05452>
- 341 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A*

- 344 cautionary tale using inferred food webs. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 345 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings  
346 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),  
347 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 348 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory  
349 of Ecology. *Ecology*, 85(7), 1771–1789. <https://doi.org/10.1890/03-9000>
- 350 Buche, L., Bartomeus, I., & Godoy, O. (2024). Multitrophic Higher-Order Interactions Modulate Species  
351 Persistence. *The American Naturalist*, 203(4), 458–472. <https://doi.org/10.1086/729222>
- 352 Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of  
353 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- 354 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models  
355 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,  
356 33(4), e13807. <https://doi.org/10.1111/geb.13807>
- 357 Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with  
358 trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>
- 360 Catchen, M. D., Poisot, T., Pollock, L. J., & Gonzalez, A. (2023). *The missing link: Discerning true from  
361 false negatives when sampling species interaction networks.*
- 362 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,  
363 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The  
364 environment to the rescue: Can physics help predict predator–prey interactions? *Biological Reviews*,  
365 138(n/a). <https://doi.org/10.1111/brv.13105>
- 366 Cirtwill, A. R., Ekklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for  
367 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10(6),  
368 902–911. <https://doi.org/10.1111/2041-210X.13180>
- 369 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.  
370 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 371 Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., Traugott, M., &  
372 Bommarco, R. (2019). Ecosystem function in predator–prey food webs—confronting dynamic models with  
373 empirical data. *Journal of Animal Ecology*, 88(2), 196–210. <https://doi.org/10.1111/1365-2656.12892>
- 374 Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones  
375 using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>
- 376 Dallas, T., Park, A. W., & Drake, J. M. (2017). Predicting cryptic links in host-parasite networks. *PLOS*

- 377 *Computational Biology*, 13(5), e1005557. <https://doi.org/10.1371/journal.pcbi.1005557>
- 378 Dansereau, G., Barros, C., & Poisot, T. (2024). Spatially explicit predictions of food web structure from  
379 regional-level data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 379(1909).  
380 <https://doi.org/10.1098/rstb.2023.0166>
- 381 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,  
382 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).  
383 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brv.12433>
- 384
- 385 Delmas, E., Brose, U., Gravel, D., Stouffer, D. B., & Poisot, T. (2017). Simulations of biomass dynamics in  
386 community food webs. *Methods in Ecology and Evolution*, 8(7), 881–886. <https://doi.org/10.1111/2041-210X.12713>
- 387
- 388 Desjardins-Proulx, P., Laigle, I., Poisot, T., & Gravel, D. (2017). Ecological interactions and the Netflix  
389 problem. *PeerJ*, 5, e3644. <https://doi.org/10.7717/peerj.3644>
- 390 Dormann, C. F. (2023). The rise, and possible fall, of network ecology. In *Defining Agroecology – A Festschrift  
391 for Teja Tscharntke* (pp. 143–159.). Tredition.
- 392 Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).  
393 Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event. *Nature  
394 Communications*, 15(1), 8599. <https://doi.org/10.1038/s41467-024-53000-2>
- 395 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological  
396 networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 397 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and  
398 Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. [https://doi.org/10.1371/journal.pbio.0060102](https://doi.org/10.1371/journal.<br/>399 pbio.0060102)
- 400 Eklöf, A., Tang, S., & Allesina, S. (2013). Secondary extinctions in food webs: A Bayesian network approach.  
401 *Methods in Ecology and Evolution*, 4(8), 760–770. <https://doi.org/10.1111/2041-210X.12062>
- 402 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks  
403 over space. *Frontiers in Ecology and Evolution*, 11.
- 404 Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings  
405 of the Royal Society B: Biological Sciences*, 288(1949), rspb.2020.1889, 20201889. <https://doi.org/10.1098/rspb.2020.1889>
- 406
- 407 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,  
408 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.  
409 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>

- 410 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., Gravel, D., & Montoya,  
411 J. M. (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, 2(5),  
412 782–790. <https://doi.org/10.1038/s41559-018-0517-3>
- 413 García-Callejas, D., Godoy, O., Buche, L., Hurtado, M., Lanuza, J. B., Allen-Perkins, A., & Bartomeus, I.  
414 (2023). Non-random interactions within and across guilds shape the potential to coexist in multi-trophic  
415 ecological communities. *Ecology Letters*, 26(6), 831–842. <https://doi.org/10.1111/ele.14206>
- 416 Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions  
417 interact? *Journal of Animal Ecology*, 80(5), 1097–1108. <https://doi.org/10.1111/j.1365-2656.2011.01852.x>
- 418 x
- 419 Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across  
420 the entire tree of life. *Nature*, 465(7300), 918–921. <https://doi.org/10.1038/nature09113>
- 421 Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B.,  
422 Tylianakis, J. M., Wood, S. A., & Roslin, T. (2019). Bringing Elton and Grinnell together: A quantitative  
423 framework to represent the biogeography of ecological interaction networks. *Ecography*, 42(3), 401–415.  
424 <https://doi.org/10.1111/ecog.04006>
- 425 Gray, C., Figueroa, D. H., Hudson, L. N., Ma, A., Perkins, D., & Woodward, G. (2015). Joining the dots:  
426 An automated method for constructing food webs from compendia of published interactions. *Food Webs*,  
427 5, 11–20. <https://doi.org/10.1016/j.fooweb.2015.09.001>
- 428 Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch  
429 between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*,  
430 11, e14620. <https://doi.org/10.7717/peerj.14620>
- 431 Hui, C., & Richardson, D. M. (2019). How to Invade an Ecological Network. *Trends in Ecology & Evolution*,  
432 34(2), 121–131. <https://doi.org/10.1016/j.tree.2018.11.003>
- 433 Hutchinson, M. C., Bramon Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., Jordano, P., &  
434 Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community  
435 ecology. *Functional Ecology*, 33(2), 206–217. <https://doi.org/10.1111/1365-2435.13237>
- 436 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 437 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 438 Kamaru, D. N., Palmer, T. M., Riginos, C., Ford, A. T., Belnap, J., Chira, R. M., Githaiga, J. M., Gituku,  
439 B. C., Hays, B. R., Kavwele, C. M., Kibungei, A. K., Lamb, C. T., Maiyo, N. J., Milligan, P. D., Mutisya,  
440 S., Ng'weno, C. C., Ongutu, M., Pietrek, A. G., Wildt, B. T., & Goheen, J. R. (2024). Disruption of

- 443 an ant-plant mutualism shapes interactions between lions and their primary prey. *Science*, 383(6681),  
444 433–438. <https://doi.org/10.1126/science.adg1464>
- 445 Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015).  
446 Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky  
447 shores. *Ecology*, 96(1), 291–303. <https://doi.org/10.1890/13-1424.1>
- 448 Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N.,  
449 Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., & Brose,  
450 U. (2012). More than a meal... integrating non-feeding interactions into food webs: More than a meal ....  
451 *Ecology Letters*, 15(4), 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- 452 Keyes, A. A., Barner, A. K., & Dee, L. E. (2024). Synthesising the Relationships Between Food Web Structure  
453 and Robustness. *Ecology Letters*, 27(10), e14533. <https://doi.org/10.1111/ele.14533>
- 454 Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments  
455 revealed in food-web structure. *Nature*, 426(6964), 282–285. <https://doi.org/10.1038/nature02115>
- 456 Laender, F. D., Oevelen, D. V., Soetaert, K., & Middelburg, J. J. (2010). Carbon transfer in a herbivore-  
457 and microbial loop-dominated pelagic food webs in the southern Barents Sea during spring and summer.  
458 *Marine Ecology Progress Series*, 398, 93–107. <https://doi.org/10.3354/meps08335>
- 459 Lajaaiti, I., Bonnici, I., Kéfi, S., Mayall, H., Danet, A., Beckerman, A. P., Malpas, T., & Delmas, E. (2024).  
460 *EcologicalNetworksDynamics.jl* A Julia package to simulate the temporal dynamics of complex ecological  
461 networks (p. 2024.03.20.585899). bioRxiv. <https://doi.org/10.1101/2024.03.20.585899>
- 462 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 463 Llewelyn, J., Strona, G., Dickman, C. R., Greenville, A. C., Wardle, G. M., Lee, M. S. Y., Doherty, S.,  
464 Shabani, F., Saltré, F., & Bradshaw, C. J. A. (2023). Predicting predator–prey interactions in terrestrial  
465 endotherms using random forest. *Ecography*, 2023(9), e06619. <https://doi.org/10.1111/ecog.06619>
- 466 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from  
467 abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.13380>
- 468 Morales, J. M., & Vázquez, D. P. (2008). The effect of space in plant–animal mutualistic networks: Insights  
469 from a simulation study. *Oikos*, 117(9), 1362–1370. <https://doi.org/10.1111/j.0030-1299.2008.16737.x>
- 470 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from  
471 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 472 Moulatlet, G., Luna, P., Dattilo, W., & Villalobos, F. (2024). *The scaling of trophic specialization in  
473 interaction networks across levels of organization*. Authorea. <https://doi.org/10.22541/au.172977303>.

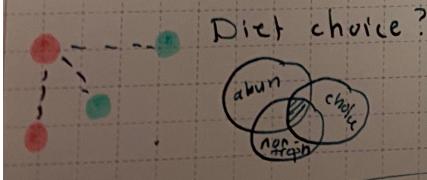
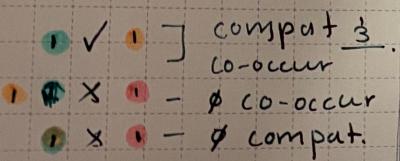
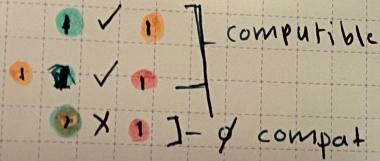
- 476 33335171/v1
- 477 Olivier, P., Frelat, R., Bonsdorff, E., Kortsch, S., Kröncke, I., Möllmann, C., Neumann, H., Sell, A. F., &  
478 Nordström, M. C. (2019). Exploring the temporal variability of a food web using long-term biomonitoring  
479 data. *Ecography*, 42(12), 2107–2121. <https://doi.org/10.1111/ecog.04461>
- 480 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic  
481 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 482 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web  
483 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 484 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some  
485 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 486 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms  
487 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and  
488 Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- 489 Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks.  
490 *Nature Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 491 Poelen, J. H., Simons, J. D., & Mungall, C. J. (2014). Global biotic interactions: An open infrastructure to  
492 share and analyze species-interaction datasets. *Ecological Informatics*, 24, 148–159. <https://doi.org/10.1016/j.ecoinf.2014.08.005>
- 493 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods  
494 in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 495 Poisot, T., Baiser, B., Dunne, J., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T. N., Stouffer, D. B., Wood, S.  
496 A., & Gravel, D. (2016). Mangal – making ecological network analysis simple. *Ecography*, 39(4), 384–390.  
497 <https://doi.org/10.1111/ecog.00976>
- 498 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of  
499 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/2041-210X.12471>
- 500 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
501 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 502 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks  
503 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 504 Polis, G. A. (1991). Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory.  
505 *The American Naturalist*, 138(1), 123–155. <https://doi.org/10.1086/285208>

- 509 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., &  
510 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint  
511 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/10.1111/2041-210X.12180>
- 512
- 513 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton  
514 University Press. <https://doi.org/10.1515/9780691195322-020>
- 515 Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology,*  
516 *Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>
- 517
- 518 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.  
519 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 520 Pyke, G. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology, Evolution and*  
521 *Systematic*, 15, 523–575. <https://doi.org/10.1146/annurev.ecolsys.15.1.523>
- 522 Quintero, E., Arroyo-Correa, B., Isla, J., Rodríguez-Sánchez, F., & Jordano, P. (2024). *Downscaling mu-*  
523 *tualistic networks from species to individuals reveals consistent interaction niches and roles within plant*  
524 *populations* (p. 2024.02.02.578595). bioRxiv. <https://doi.org/10.1101/2024.02.02.578595>
- 525 Rooney, N., McCann, K. S., & Moore, J. C. (2008). A landscape theory for food web architecture. *Ecology*  
526 *Letters*, 11(8), 867–881. <https://doi.org/10.1111/j.1461-0248.2008.01193.x>
- 527 Roopnarine, P. D. (2006). Extinction Cascades and Catastrophe in Ancient Food Webs. *Paleobiology*, 32(1),  
528 1–19. <https://www.jstor.org/stable/4096814>
- 529 Roopnarine, P. D. (2017). Ecological Modelling of Paleocommunity Food Webs. In *Conservation Paleobiology:*  
530 *Using the Past to Manage for the Future* (pp. 201–226). University of Chicago Press.
- 531 Saberski, E., Lorimer, T., Carpenter, D., Deyle, E., Merz, E., Park, J., Pao, G. M., & Sugihara, G. (2024).  
532 The impact of data resolution on dynamic causal inference in multiscale ecological networks. *Communi-*  
533 *cations Biology*, 7(1), 1–10. <https://doi.org/10.1038/s42003-024-07054-z>
- 534 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network  
535 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),  
536 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 537 Schwarz, B., Vázquez, D. P., CaraDonna, P. J., Knight, T. M., Benadi, G., Dormann, C. F., Gauzens, B.,  
538 Motivans, E., Resasco, J., Blüthgen, N., Burkle, L. A., Fang, Q., Kaiser-Bunbury, C. N., Alarcón, R.,  
539 Bain, J. A., Chacoff, N. P., Huang, S.-Q., LeBuhn, G., MacLeod, M., ... Fründ, J. (2020). Temporal scale-  
540 dependence of plant–pollinator networks. *Oikos*, 129(9), 1289–1302. <https://doi.org/10.1111/oik.07303>
- 541 Segar, S. T., Fayle, T. M., Srivastava, D. S., Lewinsohn, T. M., Lewis, O. T., Novotny, V., Kitching, R. L.,

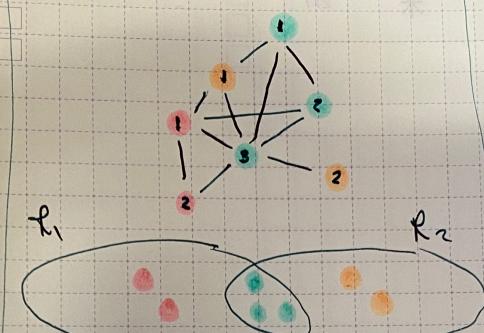
- 542 & Maunsell, S. C. (2020). The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology &*  
543 *Evolution*, 35(5), 454–466. <https://doi.org/10.1016/j.tree.2020.01.004>
- 544 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*  
545 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 546 Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*,  
547 10(12), 1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- 548 Song, C., & Levine, J. M. (2024). *Rigorous (in)validation of ecological models* (p. 2024.09.19.613075). bioRxiv.  
549 <https://doi.org/10.1101/2024.09.19.613075>
- 550 Staniczenko, P. P. A., Lewis, O. T., Jones, N. S., & Reed-Tsochas, F. (2010). Structural dynamics and  
551 robustness of food webs. *Ecology Letters*, 13(7), 891–899. <https://doi.org/10.1111/j.1461-0248.2010.01485.x>
- 552 Stock, M. (2021). Pairwise learning for predicting pollination interactions based on traits and phylogeny.  
553 *Ecological Modelling*, 14.
- 554 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*,  
555 88(2), 192–195. <https://doi.org/10.1111/1365-2656.12949>
- 556 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,  
557 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction  
558 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,  
559 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- 560 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,  
561 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer  
562 learning can help predict potential species interaction networks despite data limitations. *Methods in*  
563 *Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 564 Strydom, T., Catchen, M. D., Banville, F., Barros, C., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
565 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
566 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*  
567 *the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 568 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.  
569 <https://doi.org/10.1002/ecy.3047>
- 570 Valdovinos, F. S., Hale, K. R. S., Dritz, S., Glaum, P. R., McCann, K. S., Simon, S. M., Thébault, E., Wetzel,  
571 W. C., Wootton, K. L., & Yeakel, J. D. (2023). A bioenergetic framework for aboveground terrestrial  
572 food webs. *Trends in Ecology & Evolution*, 38(3), 301–312. <https://doi.org/10.1016/j.tree.2022.11.004>

- 575 Van De Walle, R., Logghe, G., Haas, N., Massol, F., Vandegehuchte, M. L., & Bonte, D. (2023). Arthro-  
576 pod food webs predicted from body size ratios are improved by incorporating prey defensive properties.  
577 *Journal of Animal Ecology*, 92(4), 913–924. <https://doi.org/10.1111/1365-2656.13905>
- 578 Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant–  
579 animal mutualistic networks: A review. *Annals of Botany*, 103(9), 1445–1457. <https://doi.org/10.1093/aob/mcp057>
- 580 Wells, K., & O'Hara, R. B. (2013). Species interactions: Estimating per-individual interaction strength and  
581 covariates before simplifying data into per-species ecological networks. *Methods in Ecology and Evolution*,  
582 4(1), 1–8. <https://doi.org/10.1111/j.2041-210x.2012.00249.x>
- 583 White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size  
584 and abundance in ecology. *Trends in Ecology & Evolution*, 22(6), 323–330. <https://doi.org/10.1016/j.tree.2007.03.007>
- 585 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.  
586 <https://doi.org/10.1038/35004572>
- 587 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food  
588 webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 589 Windsor, F. M., van den Hoogen, J., Crowther, T. W., & Evans, D. M. (2023). Using ecological networks  
590 to answer questions in global biogeography and ecology. *Journal of Biogeography*, 50(1), 57–69. <https://doi.org/10.1111/jbi.14447>
- 591 Woottton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory  
592 of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 593 Xie, J.-R., Zhang, P., Zhang, H.-F., & Wang, B.-H. (2017). Completeness of Community Structure in  
594 Networks. *Scientific Reports*, 7(1), 5269. <https://doi.org/10.1038/s41598-017-05585-6>
- 595 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).  
596 Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>
- 597 Yodzis, P. (1982). The Compartmentation of Real and Assembled Ecosystems. *The American Naturalist*,  
598 120(5), 551–570. <https://doi.org/10.1086/284013>
- 599 Yodzis, P., & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*,  
600 139(6), 1151–1175. <https://doi.org/10.1086/285380>

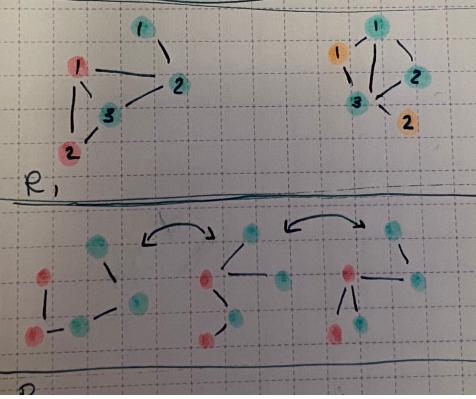
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## REPRESENTATION



"Global" metaweb.  
All possible interactions for collection of spp.



"Regional" metaweb.  
All possible interactions for co-occurring species.



Realised networks.  
The dynamic interactions that occur.  
Dynamic config.

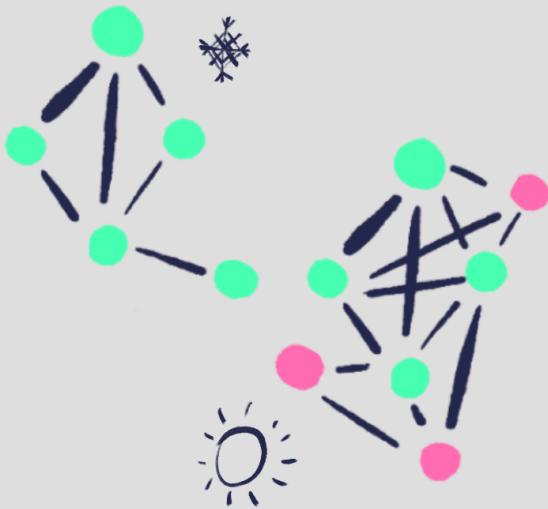
Figure 1: Aligning the various processes that determine interactions with the different network representations. First we start with a 'global metaweb' this network which captures all possible interactions for an arbitrary collection of species, we can further refine this network by taking in to consideration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





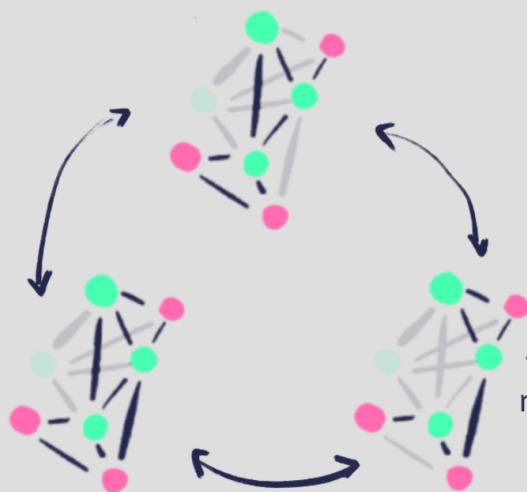
### 1. A 'global' metaweb

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 (reutilised 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

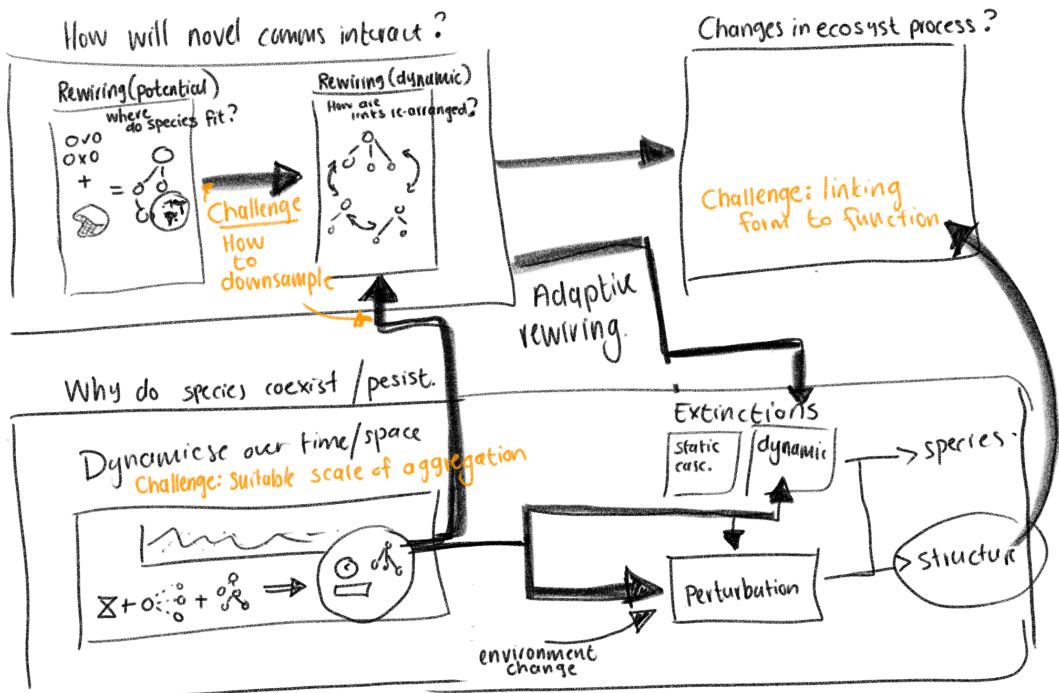


Figure 3: An attempt to try and visualise a way to map the different scales of network representations to the way in which we can interrogate/ask questions about them?