

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 at the same scale. Here we present a synthesis of the different assumptions, scales, and mechanisms that are used to define the different ecological networks , leading to a revision of definitions for different types of networks. Additionally we explicitly link the different network representations to the broader methodological approaches (models) that are used to construct them. In explicitly outlining the assumptions, scales, and mechanisms of network inference allows for a formal categorisation of how to use networks to answer key ecological and conservation questions as well as defining clear 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 species richness, stability,
2 and function (Loreau & de Mazancourt, 2013). These relate to the abundance, distribution, functions, and
3 services that biodiversity provides. Network representations of biodiversity are increasingly argued to be an
4 asset to understanding and predicting the impacts of multiple, simultaneous stress on these core components
5 of biodiversity (Simmons et al., 2021). Documenting interactions between and among species is thus one
6 of the fundamental building blocks of community ecology and provide a powerful abstraction and platform
7 for mathematical and statistical modelling of biodiversity to make predictions, and to mitigate and manage
8 threats (Windsor et al., 2023).

9 However, there is a growing discourse around limitations to the interpretation and applied use of networks
10 (Blüthgen, 2010; Dormann, 2023). Against this, it is important to evaluate the value and the limitations of
11 the various network conceptualisations of biodiversity (Blüthgen & Staab, 2024). In this perspective we aim
12 to provide an overview of different **food web** representations, particularly how each representation embeds
13 assumptions about the processes that determine interactions (Section 2) about the levels of organization
14 at which this occurs (*i.e.* the biological, ecological, spatial/temporal scale) and the way in which we
15 construct the resulting networks (Section 3). The differences among this tri-partite set of assumptions
16 ultimately influence the nature and scope of inference that can be made from a given network (Proulx et al.,
17 2005).

18 Fundamentally, we are talking about an intersection of the type of data used to construct a network and
19 the underlying theory as to what drives the resolution and occurrence of interactions between species in
20 those data. We still lack a clear explanation of the different assumptions and scale dependent processes that
21 underpin network construction alongside extensive discussions about the challenges relating to data collection
22 and observation (*e.g.*, Blüthgen & Staab, 2024; Brimacombe et al., 2023, 2024; Moulatlet et al., 2024; Polis,
23 1991; Pringle & Hutchinson, 2020; Saberski et al., 2024). Such an understanding should deliver an acceleration
24 in capacity to more effectively predict the impact of multiple stressors on biodiverse communities.

25 In their recent work, Gauzens et al. (2025) showcased a 2+2 decomposition of networks around aggregated
26 versus species level resolution of nodes and around potential and realised links among the nodes. Their review
27 delivers valuable insight into the methodologies used to collect and manage data among the node and link
28 differentiation. It also delivers an overview of the scale and types of questions that are associated with each
29 category of differentiation.

30 Here we provide a complementary perspective focused on concepts, models, and theory, in contrast to the data
31 driven breakdown in Gauzens et al. (2025) (*e.g.* their Tables 1 and 2). Our approach delivers a hierarchical

32 perspective on network construction based on a gradient from feasibility, capturing the concept of metawebs
33 and Gauzen et al's 'potential' webs, through to realised webs as in Gauzens' et al. In contrast to their 2 +
34 2 decomposition (their Fig 1), our perspective showcases nested ecological scales and processes that derive
35 from shifts in the assumptions and theories embedded along this gradient. This includes classic ecological
36 'aggregations' such as functional/phylogenetic groups through to species, populations and individuals, unique
37 perspective on how space and time intersect with node and link resolution, refined insight into which networks
38 are derived by induction vs. deduction and a revealing of a core transition between assumptions about how
39 links are derived based on evolutionary vs. ecological theories.

40 In the following sections we provide a scene-setting review of nodes and edges (links) in networks before
41 aligning various processes that determine interactions with the different network representations. Ultimately,
42 we provide a unique perspective on the nested hierarchy of processes that govern transitions from meta-webs
43 to realised webs. We finish with a refined and nuanced alignment of models/representations and key questions
44 in biodiversity science in the anthropocene.

45 1 Setting the Scene: The Not So Basics of Nodes and Edges

46 Networks in ecology have multiple uses, representing an 'object' from which inferences can be made. For
47 example, a network is needed to make inference specifically about the structure of communities. The structure
48 of networks - their topology - have a long history reflecting core theory about energy flow (Lindeman, 1942),
49 function (Schneider et al., 2016) and even stability (Brose et al., 2006; Danet et al., 2024). Networks are
50 thus required as the response variable in evaluating ecological theory and statistical models of 'generative
51 processes' giving rise to such structure. Such structure is now commonly used to compare communities along
52 environmental gradients or time (Hao et al., 2025; Pecuchet et al., 2020). Networks and their topology are
53 also used as a platform for evaluating 'downstream' responses to stressors such as evaluating patterns of
54 secondary extinction (Keyes et al., 2024; Staniczenko et al., 2010). Finally, they are commonly used as a
55 platform for implementing mathematical models of community dynamics (*e.g.*, Delmas et al., 2017); delivering
56 inference about stability, function, invasive species, climate change, contaminants, and secondary extinction
57 (*e.g.*, Curtsdotter et al., 2019), to name a few applications. Against this backdrop of multiple research agendas,
58 the definition of 'edges' and 'nodes', and the levels of organisation at which they are defined, take many forms
59 (Moulatlet et al., 2024; Poisot, Stouffer, et al., 2016), each of which encode a series of assumptions within a
60 network. Here we introduce a perspective on these baseline assumptions.

61 1.1 How do we define a node?

62 Although this may seem elementary that a node should represent a (taxonomic) species, the reality is that
63 nodes often represents non-taxonomic units such as a trophic species (*e.g.*, Yodzis (1982); Williams & Martinez
64 (2000)), a feeding guild (*e.g.*, García-Callejas et al., 2023), or a segregation of species by life stages (*e.g.*, Clegg
65 et al., 2018). Such granularity and variation is often defined as aggregation. Such aggregation can limit the
66 ability to make species (taxonomic) specific inferences (*e.g.*, does species *a* eat species *b*?). It can also affect
67 the estimates of degree distributions and more specifically generality and vulnerability in networks (in/out
68 degree). These metrics are central to inference about the structure and complexity of networks(Beckerman
69 et al., 2006; Clegg et al., 2018). Finally, aggregation makes it challenging to use networks in ‘downstream
70 analyses’ of, for example, extinction or invasions as the identity of species and the consequences of their losses
71 can be hidden. Despite these issues, there are justifications for representing nodes as aggregated units. Most
72 prominent relates to when the distribution of the links between aggregated nodes may be more meaningful in
73 terms of understanding or making generalisations about the system **e.g.*,* tracking species extinctions across
74 feeding guilds (Dunhill et al., 2024).

75 1.2 What is captured by an edge?

76 In order to break down the definitions of an edge, it is important to introduce the concept of *potential* versus
77 *realised* links: potential links reflect feasibility while realised links are connected to flux of some currency
78 (typically energy; see below for more detail). Links within food webs are thus a representation of either
79 potential links between species Pringle (2020) or fluxes within a system *e.g.*, energy transfer or material flow
80 as the result of the feeding links between species (Lindeman, 1942; Proulx et al., 2005). Edges can thus
81 correspond to different ‘currencies’ (Gauzens et al., 2025). There is also a myriad of ways in which the links
82 themselves can be specified. Links between species can be treated as present or absent (*i.e.*, binary), may be
83 defined as probabilities (Banville et al., 2025; Poisot, Cirtwill, et al., 2016) or by continuous functions which
84 further quantify the strength of an interaction (Berlow et al., 2004). How links are specified thus requires
85 intersecting both the currency being modelled and their specification. For example, feasibility is unlikely to
86 accommodate flux, but does align with binary or probability representations. Taking a food web that consists
87 of links representing feasible interactions among a collection of species will be meaningless if one is interested
88 in understanding the flow of energy through the network as the links are not environmentally/energetically
89 constrained.

90 **1.3 Network representations**

91 Against these definitions of nodes and edges, networks fall into two major ‘types’: metawebs, traditionally
92 defined as all the *potential* interactions for a specific species pool (Dunne, 2006); and realised networks, which
93 is the subset of interactions in a metaweb that are *realised* for a specific community at a given time and place.

94 The fundamental differences between these two network representations are the spatial and temporal scale at
95 which they are constructed, and the associated processes that are assumed to drive pattern at these scales.

96 A metaweb is, at its core, a list of *feasible* interactions between pairs of species. The feasibility for a given pair
97 is derived from the complementarity of their traits, typically aligned with feeding. Feasibility can be further
98 refined by *co-occurrence* leading to the transition from a *global* to *regional metaweb*. Metawebs thus provide
99 a means to identify evolutionarily plausible links, regionally plausible interactions, the set of ecologically
100 impossible, *i.e.*, forbidden, links (Jordano, 2016b), and ultimately a definition of the plausible *complete* diet
101 of a species (Strydom et al., 2023).

102 In contrast, realised networks are typically more localised in space and time, and the links between species
103 are contingent on the co-occurrence of species, the role of the environment, and mechanisms of diet choice.

104 Fundamentally this means that the presence/absence of a link is the result of the ‘behaviour’ of the species
105 and even when the realised network is presented as a binary matrix, the edges imply a function is available
106 to define the strength of an interaction. A realised network is therefore not simply the downscaling of a
107 metaweb to a smaller scale (*e.g.*, moving from the country to the 1x1 km² scale based on fine-scale species
108 co-occurrence). Instead, realised webs capture processes that determine the realisation of an interaction and
109 flows of energy in a community. Specifically, in realised webs, the definition of an edge shifts from being
110 determined by feasibility to that of choices and consequences that centre around energy. If one were to take
111 the same community of species and construct both a metaweb and realised network the two networks might
112 have the same species but would be structurally different, owing to the differences in the ‘rules’ constraining
113 the presence of links. This distinction between metawebs and realised webs leads to a further insight. Links
114 that are absent in a metaweb can conceptually (although not always practically) be treated as being truly
115 absent. However, links that are absent in a realised network cannot be considered as truly absent but rather
116 as absent due to the broader environmental/community context.

117 **2 From Nodes and Edges to Process and Constraints**

118 In the previous section we discussed how the definition of nodes and edges, representing different scales and
119 processes, lead to the concept of a metaweb and a realised web. The fundamental take-homes are that nodes

120 vary in their resolution, edges vary in what kind of process they represent and the intersection of these, defined
121 by meta- vs. realised webs, underpins distinct lines of inquiry and constraints on the type of inference we
122 can make with networks. Here we reveal five core constraints across evolutionary and ecological scales that
123 further delineate the transition from meta- to realised webs, exposing processes that determine the nature
124 of links among nodes: evolutionary compatibility, co-occurrence, abundance, diet choice, and non-trophic
125 interactions Figure 1.

126 [Figure 1 about here.]

127 2.1 Processes that determine the feasibility of an interaction

128 Evolutionary compatibility and co-occurrence are the two principle processes that ‘act’ at the species pair of
129 interest and define feasibility. The scale of inference and set of processes embodied in these two constraints
130 typically combine to define a ‘list’ of interactions that are viable/feasible and defined strictly as present/absent.
131 Reflecting on the previous section, nodes are typically species and rules defining edges are defined by trait
132 complementarity (phylogenetic) and/or co-occurrence. Here we provide more insight into each process.

133 Evolutionary compatibility

134 This constraint is defined by shared (co)evolutionary history between consumers and resources (Dalla Riva
135 & Stouffer, 2016; Gómez et al., 2010; Rossberg et al., 2006; Segar et al., 2020) which is manifested as ‘trait
136 complementarity’ between two species (Benadi et al., 2022). In this body of theory, the consumer has the
137 ‘correct’ set of traits that allow it to chase, capture, and consume the resource. Interactions that are not
138 compatible are defined as forbidden links (Jordano, 2016b); *i.e.*, they are not physically possible and will
139 *always* be absent within a network.

140 Networks do not properly arise from models based on this constraint. Instead, interacting species pairs are
141 defined and these are represented as binary (possible vs forbidden) or probabilistic (Banville et al., 2025). For
142 example, in the metaweb constructed by Strydom et al. (2022) probabilities are quantified as the confidence of
143 a specific interaction being *possible* between two species. A network constructed on the basis of evolutionary
144 compatibility is conceptually aligned with a ‘global metaweb’, and gives us information as to the global
145 feasibility of links between species pairs despite the fact that they do not co-occur (see Figure 1).

146 (Co)occurrence

147 The co-occurrence of species in both time and space is a fundamental requirement for an interaction between
148 two species to occur (at least in terms of feeding links). Although co-occurrence data alone is insufficient
149 for building an accurate and ecologically meaningful representation of *feeding links* (Blanchet et al., 2020),

150 it is still a critical process that determines the realisation of a feeding. Knowledge on the co-occurrence of
151 species allows us to spatially constrain a global metaweb to reflect regional metawebs (Dansereau, Barros, et
152 al., 2024). In the context of Figure 1 this would be the metawebs for regions one and two.

153 We reinforce that these two constraints don't deliver a network *per se*, but a list of feasible species pairs.
154 Although it is possible to build a network from the list of interactions generated by these constraints, it is
155 important to be aware that the structure of this network is not constrained by any community context: just
156 because species are able to interact does not mean that they will (Caron et al., 2024; Poisot et al., 2015).

157 2.2 Processes that realise networks

158 In contrast to the above, here we highlight three processes that influence the *realisation* of an interaction
159 between species and thus form the conceptual basis for realised networks. As we show in Figure 1, a ‘truly
160 realised’ network is the product of properties of the community (**abundance** and **non-trophic interactions**)
161 and the individual (**diet choice**). This represents a conceptual shift from considering the feasibility for species
162 pairwise interactions to considering the edge as a representation of energy flow. Such a transition requires
163 information about how the community, the environment and the individual *constrains* network topology as
164 defined by consumer choice (Quintero et al. (2024), Section 1.3)

165 Abundance

166 Abundance as a realising process emerges from a null model for energy acquisition: organisms feeding randomly
167 will consume resources in proportion to their abundance (Stephens & Krebs, 1986). Here, abundance of
168 different prey species influences the distribution of links in a network (Vázquez et al., 2009) by defining a
169 preference linked to individuals among species meeting (Banville et al., 2025; Poisot et al., 2015). Abundance
170 data, linked to a derived metaweb delivers a foundation ruleset that can define the distribution and strength
171 of links. Of note, however, is that such abundance constrained interactions are not necessarily contingent on
172 there being any compatibility between species (E. Canard et al., 2012; Momal et al., 2020; Pomeranz et al.,
173 2019).

174 Diet choice

175 It is well established that consumers make more active decisions than eating items in proportion to their
176 abundance (Stephens & Krebs, 1986). Ultimately, consumer choice is underpinned by an energetic cost-benefit
177 framework centered around profitability and defined by traits associated with finding, catching, killing, and
178 consuming a resource (Smith et al., 2021; Wootton et al., 2023). Energetic constraints are invoked to construct
179 networks in a myriad of ways (*e.g.*, Beckerman et al., 2006; Cherif et al., 2024; Pawar et al., 2012; Portalier et

¹⁸⁰ al., 2019).

¹⁸¹ In contrast to metaweb ‘construction’ from a list of pairwise interactions, these methods deliver a realised web
¹⁸² directly and as an emergent property of node behaviour. We also here make a distinction, developed below,
¹⁸³ with models like the Niche Model, where diet choice is implicit in its probabilistic network generating function,
¹⁸⁴ but it is working to replicate the *expected* structure of the network and this structure does not emerge from
¹⁸⁵ node-based rules. Note that we select diet choice as a term to capture rules linked to optimal foraging (Pyke,
¹⁸⁶ 1984) and metabolic theory (Brown et al., 2004); it is a sensible ‘umbrella concept’ for capturing the energetic
¹⁸⁷ constraint on of the distribution and strength of interactions.

¹⁸⁸ Non-trophic interactions

¹⁸⁹ We include non-trophic interactions (see Miele et al., 2019) here not as a determinant of links, but a modifier
¹⁹⁰ of them - they are the community context above and beyond co-occurrence and abundance. Non-trophic
¹⁹¹ interactions include competition for space, predator interference, refuge provisioning, recruitment facilitation as
¹⁹² well as non-trophic effects that increase or decrease mortality. These interactions (Ings et al., 2009) specifically
¹⁹³ modify either the realisation or strength of trophic interactions (Golubski & Abrams, 2011; Kamaru et al.,
¹⁹⁴ 2024; Pilosof et al., 2017; Staniczenko et al., 2010) and represent direct (e.g., predator *a* outcompetes predator
¹⁹⁵ *b*) and indirect (e.g., mutualistic/facilitative interactions) mechanisms. They operate on the realisation of a
¹⁹⁶ network by altering the fine-scale distribution and abundance of species and relative contributions of direct
¹⁹⁷ and indirect effects to biomass, persistence, stability and the functioning of the communities (Buche et al.,
¹⁹⁸ 2024; Kéfi et al., 2012, 2015; Miele et al., 2019).

¹⁹⁹ 3 Network construction

²⁰⁰ The above five processes are central to understanding the assumptions inherent in building different types of
²⁰¹ networks. Each of the processes, or combinations thereof, deliver a unique set of boundary conditions on what
²⁰² a network represents and can be used for. Here we build on the introduction of these five processes to further
²⁰³ categorise the approaches to constructing networks. In doing so also introduce more detail on a variety of
²⁰⁴ methodologies used to construct networks.

²⁰⁵ 3.1 Why construct networks?

²⁰⁶ Networks are a representation of biodiversity. In a perfect world, we might know about all interactions.
²⁰⁷ However, the empirical collection of interaction data is both costly and challenging to execute (Jordano,
²⁰⁸ 2016a, 2016b; Poisot et al., 2021). In the absence of robust empirical data, we construct models that facilitate

209 interpolation and gap-filling of existing empirical datasets (*e.g.*, Biton et al., 2024; Dallas et al., 2017; Poisot
210 et al., 2023; Stock et al., 2017), predict the feasibility of interaction among pairs of species, or directly predict
211 network structure (see Strydom et al., 2021 for a broader discussion).

212 They are unique in delivering more than just estimates of species richness. As noted in the introduction, a
213 network embodies the organising structure of biodiversity and allows numerous opportunities for ‘downstream’
214 analysis, including the comparison of structures, estimation of energy flux or extinction dynamics and
215 ultimately form the structural inputs to dynamical systems models that facilitate ecological and conservation
216 relevant inference about productivity-diversity-stability-function relationships (Danet et al., 2024) in space
217 and time. But making such inferences requires careful attention to one or more of the processes discussed in
218 Section 2.

219 3.2 Construction through induction

220 Constructing feasible or realised networks can be framed as an ‘inductive reasoning’ process where insight
221 and generalisation arises from a set of observations and relationships. Inductive reasoning as a foundation
222 for network construction is implemented through node- and network levels. When applied at the node level,
223 species specific networks are created and judge by their association with expected feeding interactions. When
224 applied at the network level, networks are judged by their structural properties *per se*.

225 3.2.1 Species specific networks: construction through node level induction

226 Constructing feasible networks and facilitating the interpolation or gap-filling of existing empirical datasets on
227 sets of species interactions can be framed as an ‘inductive reasoning’ process where insight and generalisation
228 arises from a set of observations and relationships about feeding. All methods in this inference space rest on a
229 set of three assumptions: there are a set of ‘feeding rules’ that underpin interaction feasibility (Morales-Castilla
230 et al., 2015); these rules are phylogenetically conserved (Bramon Mora et al., 2018; Dalla Riva & Stouffer,
231 2016); and they can be specified by matching the traits between consumer and resource.

232 Evolutionary compatibility and co-occurrence constraints, the foundation theory for feasible networks, have
233 been critical to the construction of ‘first draft’ networks for communities for which we have no interaction data
234 (Strydom et al., 2022). They are also central to interpolation in data poor regions and predicting interactions
235 for ‘unobservable’ communities *e.g.*, prehistoric networks (Dunhill et al., 2024; Fricke et al., 2022; Yeakel et
236 al., 2014) or future, novel community assemblages (Van der Putten et al., 2010). Furthermore, they have the
237 capacity to evaluate a role of interactions among species relative to their distribution by accounting for the
238 role of the environment and the role of species interactions (Gravel et al., 2019; Higino et al., 2023; Pollock et

²³⁹ al., 2014). There are substantial data requirements for these approaches including expert knowledge, species
²⁴⁰ traits and phylogenetic relationships and/or interaction data on related species or communities.

²⁴¹ Feeding rules are defined in multiple ways. The determination of the feeding rules can be defined *a priori*
²⁴² based expert knowledge opinions. Typically this is done on a ‘trait matching’ basis. An example are the paleo
²⁴³ food web models of Shaw et al. (2024) and Roopnarine (2017) that specify a series of rules for a set of traits
²⁴⁴ and interactions are deemed feasible if all conditions are met. Alternatively the body size ratio between the
²⁴⁵ consumer and resource is often used (*e.g.*, Gravel et al., 2013; Rohr et al., 2010), with the idea that consumers
²⁴⁶ will only utilise a resource with a body size less than or equal to their own. However, work from Van De
²⁴⁷ Walle et al. (2023) seems to suggest that adding morphological traits in addition to body size ratio improves
²⁴⁸ model performance.

²⁴⁹ Rules are also defined by correlating real world interaction data with suitable ecological proxies for which
²⁵⁰ data is more widely available (*e.g.*, traits) using some sort of binary classifier (see Pichler et al. (2020) for an
²⁵¹ overview). These include generalised linear models (*e.g.*, Caron et al., 2022), random forest (*e.g.*, Llewelyn et
²⁵² al., 2023), trait-based k-NN (*e.g.*, Desjardins-Proulx et al., 2017), and Bayesian models (Cirtwill et al., 2019;
²⁵³ *e.g.*, Eklöf et al., 2013).

²⁵⁴ Finally, graph embedding uses the structural features of a known network to infer the position of species in an
²⁵⁵ unknown network through the decomposition of the interaction onto the embedding space. This decomposition
²⁵⁶ relies on a combination of ecological proxies (*e.g.*, traits) in conjunction with known interactions to infer the
²⁵⁷ latent values of species, which can then be mapped onto decomposition of a known network. See Strydom et
²⁵⁸ al. (2023) for a detailed review of methods and Strydom et al. (2022) for a specific example.

²⁵⁹ **3.2.2 Species agnostic networks: construction through structure induction**

²⁶⁰ Networks in this category are generated rules that create non-random networks that reflect empirical knowledge
²⁶¹ of ecological network structures and evaluated by matching predictions to this *expected* structure of the
²⁶² network(s). The determination of links between species is only implicitly linked to properties of the nodes.
²⁶³ This means these networks are usually not species specific. Although these models are data input light, often
²⁶⁴ requiring only species richness and an estimate of the number of expected links, they make clear assumptions
²⁶⁵ regarding what the expectations are for network structure. These are some of the most commonly used
²⁶⁶ network generation tools (*e.g.* the Niche model; Williams & Martinez (2008)). There are two sub-categories of
²⁶⁷ these species agnostic networks.

²⁶⁸ Stochastic network models use a probabilistic rule-set about diet choice and niche breadth to reflect fundamental

269 ideas of foraging biology. These models that are based on the compartmentalisation and acquisition of energy
270 for species at different trophic levels (Allesina & Pascual, 2009; Krause et al., 2003) and that network structure
271 can be determined by distributing interactions along single dimension [the ‘niche axis’; Allesina et al. (2008)].
272 Typically these models parametrise some aspect of the network structure (although see Allesina & Pascual,
273 2009 for a parameter-free model). These models include the most commonly used network generator, the
274 Niche model (Williams & Martinez, 2000), as well as the original Cascade model (Cohen et al., 1990) and the
275 derived Nested hierarchy model (Cattin et al., 2004). These models often form the basis for dynamic models
276 e.g., the allometric trophic network (Brose et al., 2006; Schneider et al., 2016) and bioenergetic food web
277 models (Delmas et al., 2017).

278 3.3 Construction through deduction

279 In contrast to the above approaches centered on feasibility, realised networks via methods reflecting abundance
280 and diet choice typically rely on deductive reasoning and have a unique agenda to those above. In contrast to
281 the inductive methods, inference about a realised network follows from a set of premises defining generative
282 processes, often referred to as mechanisms. Typically, models that embed abundance and diet choice constraints
283 reference theory that allows inference about the distribution and strength of interactions. Such models are
284 ‘network topology generators’ and have a strong representation in research comparing network structures
285 along environmental gradients and delivering inference about extinctions and energy flux. They also provide
286 the structural backbone for dynamical systems modelling to address questions about stability-structure-
287 productivity-function relationships, secondary extinction dynamics, species invasion and climate change.
288 There are two broad group of models in this deductive category.

289 3.3.1 Species-specific networks

290 These models capture the behaviour of the nodes by explicitly taking into account the properties of the
291 different species in the community. Which means that there is a degree of variance in which links are predicted
292 between species unlike the more ‘static’ predictions made by inductive models. However, these networks are
293 ‘costly’ to construct in real world settings (requiring data about the entire community, as it is the behaviour
294 of the system that determines the behaviour of the part) and also lack the larger diet niche context afforded
295 by metawebs.

296 Neutral networks are built on the assumption that foraging decisions are tied *only* to the abundance of species
297 within the community (E. F. Canard et al., 2014; Krishna et al., 2008). Here links are solely determined by the
298 relative abundance of the different species in the community. Although it is highly unlikely that abundance is

299 the only determinant of interactions work by Pomeranz et al. (2019) showcases how these neutral processes
300 can be used in conjunction with inductive models to construct more refined/localised networks.

301 There is a broader group of models that focus on determining interactions in terms of energetic constraints
302 on diet breadth, often using the ratio of consumer-resource bodysize as a proxy for capturing the energetic
303 constraints of feeding. Models such as those developed by Portalier et al. (2019) and Wootton et al. (2023)
304 are similar to the mechanistic approaches discussed in Section 3.2, however instead of determining interactions
305 based on mechanistic feasibility it is rather constrained by the energetic cost of predation. Note that although
306 these models do not place any explicit constraints on the expected structure of the network, the links should
307 still be considered as ‘realised’ owing to the energetic constraint placed on links. A different subset of diet
308 models (*e.g.*, Beckerman et al., 2006; Petchey et al., 2008) use a diet choice approach, however similar to the
309 stochastic network models they also embed assumptions on network structure. Thus these models predict
310 both interactions and network structure simultaneously, although they would benefit in being refined by more
311 explicitly accounting for trait-based (*i.e.*, feasibility) parameterisation (Curtsdotter et al., 2019).

312 4 Making Progress with Networks

313 The motivation to leverage network ecology in conservation ecology, environmental risk assessment and natural
314 resource management stems from a shift away from species/population specific measures of the effects of
315 stress and disturbance to community level metrics of these impacts. These metrics, such as resilience and
316 more generally stability, ecosystem function and biodiversity *per se*, are natural properties of networks. This
317 suggests that modern conservation, risk assessment and resource management requires robust network tools
318 to support decision making.

319 This is also true in the disciplines of ecology and environmental science and their focus on abundance,
320 distribution, functions and services that biodiversity provides (Loreau & de Mazancourt, 2013). Major
321 questions remain, for example, about stability-diversity-productivity relationships, the impacts of extinctions
322 and invasions and the impacts of multiple stressors operating at multiple ecological scales. A network approach
323 to answering these types of questions specifically allows us to evaluate how environmental gradients and
324 anthropogenic stress map through direct and indirect effects among species in a complex community and
325 reveal fundamental patterns and understanding of processes in the natural world.

326 In order to effectively use networks to aid us in answering questions about conservation/risk assessment/management
327 and core ecological theory, we need to be mindful that we are mapping the *correct* network representation
328 to the question of interest (Gauzens et al., 2025). Notably, there are certain questions that cannot be answered

329 using specific network representations as the scale of the question of interest is fundamentally misaligned with
330 either the process captured by a specific network representation Section 2.1, the underlying data that is used
331 to construct it Section 3 or both of these factors.

332 Here we discuss and map the different network representations shown in Figure 1 to ‘appropriate’ research
333 questions and agendas see also 1. We also highlight some of the key methodological challenges that currently
334 limit our conceptualisation of a ‘network’ and thus impact their effective practical application in real world
335 settings.

Table 1: Showcasing some of the broader avenues of inquiry, specifically how they map to the different network representations

Network Representation	Example Research Question
Global Metaweb	How will novel communities respond to <i>e.g.</i> , extinction, turnover, invasion and rewilding
	Diet-based conservation focusing not only on the target species but the species it might depend on for food resources
	Rewiring capacity/potential of species by looking at the <i>entire</i> diets of species
	Eco-Evolutionary dynamics and how they relate to the conservation and origination of feeding strategies
Regional Metawebs	Applied use potential of questions highlighted for global metawebs at the management scale <i>e.g.</i> , a protected area
	Refinement/extension of species distribution models by incorporating co-occurrence and species associations <i>e.g.</i> , predator and prey
Realised webs	The allocation of multiple stressors across networks
	Temperature threshold to community collapse
	Extinction and persistence after harvesting/invasion/extinction
	Stability-diversity-productivity-function

Network Representation	Example Research Question
	Explicitly tying ecosystem level processes and nutrient flows to networks
	Meta communities and the idea of meta-network-communities

³³⁶ **4.1 Key Eco-Evo-Conservation Questions**

³³⁷ **4.1.1 Global Metawebs**

³³⁸ The interactions in global metawebs are not constrained by the realisation of specific community assemblages
³³⁹ (or species co-occurrence). These networks provide a platform for answering questions that assume interactions
³⁴⁰ *could* occur between species (feasibility) or where the potential diet breadth of species is required. Examples
³⁴¹ of appropriate research questions at this scale includes those about *hypothetical* or *novel* communities and
³⁴² interactions under future climate change scenarios, or the potential ‘position’ of an invasive (or re-introduced)
³⁴³ species within a network (Hui & Richardson, 2019). This scale is also appropriate for a particular class of
³⁴⁴ questions related to the potential (eco-evolutionary) rewiring capacity of species, and how this may help
³⁴⁵ inform on the opportunities for persistence of species within new community assemblages (Marjakangas et
³⁴⁶ al., 2025). The implicit focus on feasibility in these examples highlights that global metawebs are linked to
³⁴⁷ strong proxies for targets and mechanisms of evolutionary change. This offers a network scale for modelling
³⁴⁸ ecological-evolutionary dynamics and the role that both the evolutionary history, natural selection, and
³⁴⁹ phenotypic plasticity shapes the diet breadth of species.

³⁵⁰ **4.1.2 Regional Metawebs**

³⁵¹ Regional metawebs are conceptually a spatially constrained global metaweb. They make explicit the co-
³⁵² occurrence between species. Against this backdrop, they are conceptually aligned with similar questions to
³⁵³ those posed above, with the added focus on a community facing, real-world, challenge. Additionally, regional
³⁵⁴ metawebs can and have been used to refine and constrain species distribution model predictions, giving us
³⁵⁵ more refined range maps (García-Callejas et al., 2023) or community composition under climate change
³⁵⁶ scenarios, even at global scales (Hao et al., 2025).

³⁵⁷ However we must exercise a high degree of caution when comparing structures among regional metawebs,
³⁵⁸ whether discrete collections or along environmental gradients. At this scale, where the network embeds the
³⁵⁹ assumptions of feasibility, the link distribution is not meaningfully constrained by environmental factors (see

360 Section 1.2) and it is vital to disentangle structural change *per se* from the multiple processes that might
361 determine species turnover (*e.g.*, β - diversity).

362 **4.1.3 Realised networks**

363 Realised network are the most representative of what comes to mind when people think of networks, and
364 more specifically how we can use them to help inform on larger biogeographic processes (Thuiller et al.,
365 2024). This is partially because of the popularity and legacy of generative network models (like the Cascade
366 and Niche model) which produce realised network representations, and represent the ideal ‘currency’ for
367 which to understand the constraints placed on interactions/network structure by the broader community
368 and environmental context. This change in currency and context affords us the opportunity to ask questions
369 that revolve around major ecological theory - *e.g.*, community stability and resilience, biodiversity dynamics,
370 ecosystem function, structure-function relationships - and around major conservation and climate change global
371 challenges - *e.g.*, temperature change, extinction dynamics, invasion impacts and reintroductions/rewilding.

372 Realised networks embody an explicit focus on the link between network structure to ecosystem function.
373 Because the structure of realised webs are isolated from turnover processes they allow us to think about the
374 propagation of change (across both time and space) which allows us to ask questions about the persistence of
375 communities and how they respond to perturbations or stressors (at both the level of the node as well as the
376 modification of links). For example in Section 4.1.1 we discuss how global metawebs can inform as to the
377 rewiring *capacity* of a species, a realised network however would be better suited to capture the rewiring of
378 networks over time as a response to changes in the environment or community.

379 Although the recent boom in the availability of long-term observation data is allowing us to unpack decades
380 of insights for stability-diversity-productivity relationships for more complex communities (Danet et al., 2024)
381 or to evaluate the impacts and efficacy of re-introductions (Wooster et al., 2024), we need to be mindful that
382 empirical interaction data is typically accumulated over time and so it compresses the transient nature of the
383 interactions between species (Polis, 1991). Thus we need to apply a degree of caution when using empirical
384 data to construct realised networks - although there is scope to think about developing methods that will
385 allow us to modify metawebs in such a way that their structures become more aligned with realised webs (see
386 the next section).

387 **4.2 Key methodological challenges**

388 As noted above, the three types of networks help highlight longstanding methodological challenges that affect
389 our ability to increase both precision and accuracy of inference derived from the questions we highlight above.

390 Here we review some of these challenges and opportunities that are arising to mitigate them.

391 **Understanding what empirical data represents:** Ultimately, knowing what is right/precise/correct in an
392 ecological network requires robust data. What does it mean when we ‘observe’ an interaction be that directly
393 (predator actively feeding on prey) or indirectly via *e.g.*, gut or isotope analysis. A network constructed with
394 empirical data will most likely still represent an ‘accumulation’ of feeding data making it conceptually more
395 closely aligned with idea of a metaweb.

396 **The validation of network structure:** Progress has been made in the development of tools and approaches
397 of assessing how well a model recovers pairwise interactions (Poisot, 2023; Strydom et al., 2021), but we
398 still lack a clear set of guidelines for benchmarking the ability of models to recover structure (Allesina et al.,
399 2008). This makes it challenging to assess if models are capturing network structure accurately, especially
400 if one wants to use empirical data as the ‘testing set’. Specifically, can we use a network constructed using
401 long-term interaction observation data (*i.e.*, conceptually a metaweb) to assess the accuracy of a modelled (*I*
402 *don’t know how I feel about this word*), realised network? Additionally one needs to think about *what* aspect
403 of accurate/precise network construction is the most important - is it the structure or ability to correctly
404 predict pairwise links? In the case of attempting to construct a metaweb it is important that one is accurately
405 recovering both links that are truly present and absent, however in the case of realised webs it is perhaps not
406 that clear. Is it sufficient to correctly recover structure *e.g.*, connectance or do the pairwise links also need to
407 be correct?

408 **Transitioning between metawebs and realised webs:** Currently most approaches to modelling realised
409 networks fail to explicitly account for any form of evolutionary constraint (although see Van De Walle et al.
410 (2023) and Wootton et al. (2023)) and we need to develop either an ensemble modelling approach (Becker
411 et al., 2022; Terry & Lewis, 2020) or tools that will allow for the downsampling of metawebs into realised
412 networks, (*e.g.*, Roopnarine, 2006).

413 Importantly we need to think critically how the creation of either an ‘ensemble network’ or downsampled
414 metaweb might change the underlying ‘currency’ of a network and thus the underling definition of the edge
415 *e.g.* the downsampling approach developed by Roopnarine (2006) structurally constrains the network to
416 structurally look like a realised web, but the links to not represent prey choice *per se*.

417 Having a well developed framework as well as ‘fluidity’ to allow us to scale up between meta- and realised
418 food webs lays the groundwork for us to actively begin the integration of food webs into the classical
419 metacommunity-metaccosystem space (Massol et al., 2011) as well as ecosystem level processes (Liu et al.,
420 2025). The being said developments in the community-ecosystem space should be intentional about articulating

⁴²¹ a firm distinction as to what defines a ‘network’ as a unit, as well as defining the logical (spatial and temporal)
⁴²² boundaries between networks (Fortin et al., 2021).

⁴²³ **Making networks more tractable in applied spaces:** There is a disconnect when it comes to effectively
⁴²⁴ using networks in applied spaces. This is probably at least in part related to the challenges with delineating
⁴²⁵ ‘boundaries’ between networks, and specifically how these relate to ‘management units’ and scales in addition to
⁴²⁶ a limited interpretability of network metrics, specifically how this can be applied to conservation targets/indices
⁴²⁷ (Dansereau, Braga, et al., 2024). In order to address these shortcomings we need to make an effort to more
⁴²⁸ efficiently map the form (structure) of a network to its function in order to identify how this can effectively
⁴²⁹ be integrated into policy to make it meaningful and actionable (O’Connor et al., 2025), all while remaining
⁴³⁰ mindful to ensure that we identify the appropriate network representation.

⁴³¹ 5 Concluding remarks

⁴³² Having a clear understanding of the interplay between network representations and the processes that they
⁴³³ are capable of encoding is critical if we are to understand exactly which networks can be used to answer which
⁴³⁴ questions. As we highlight in Section 4 the different network representations have different potential uses and
⁴³⁵ it should be clear that there is no ‘best’ network representation but rather a network representation that is
⁴³⁶ best suited to its intended purpose. In providing a formalisation regards to the assumptions and mechanisms
⁴³⁷ that need to be explicitly taken into consideration when deciding to use (and construct) networks we hope to
⁴³⁸ prevent the unintentional misuse or misinterpretation of networks as well as provide a starting point from
⁴³⁹ which we can develop a better framework for the applied use of networks to answer questions that are not
⁴⁴⁰ only pressing within the field but also within broader biodiversity science.

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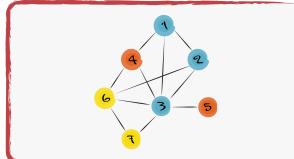
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REPRESENTATION

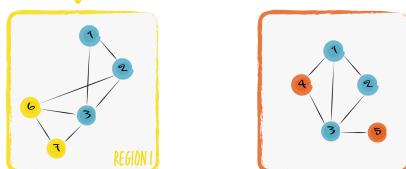
GLOBAL METAWEB

All feasible interactions for a collection of species



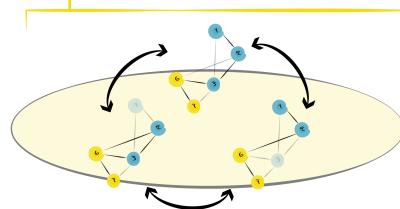
REGIONAL METAWEB

All feasible interactions for a co-occurring collection of species (i.e., interactions for a specific community)

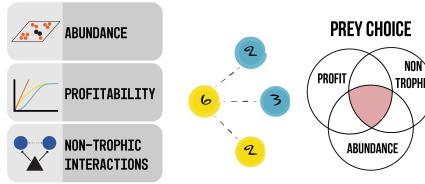
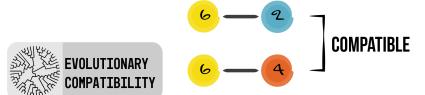


REALISED NETWORKS

Interactions that occur within a community for a given time and place. These networks represent the dynamics between species in the communities



PROCESS



WHAT DETERMINES THE PRESENCE OF LINKS?

WHAT DETERMINES THE DISTRIBUTION OF LINKS?

Figure 1: Aligning the various processes that determine interactions (right column) with the different network representations (left column). First, we start with a **global metaweb** this network captures all possible interactions for a collection of species in the global context. However, within the global environment different species occur in different regions (region one = yellow and region 2 = orange), and it is possible to construct two different metawebs (**regional metawebs**) for each region by taking account for the co-occurrence of the different species - as shown here we have two regions with some species that are found in both regions (blue) and others endemic to either region one (yellow) or region two (orange). 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 **realised networks** is 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, maximisation of energy gain, or indirect/higher order interactions.