

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 etc],
49 function [REF] and even stability [REF]. Networks are thus required as the response variable in evaluating
50 ecological theory and statistical models of 'generative processes' giving rise to such structure [REF]. Such
51 structure is now commonly used to compare communities along environmental gradients [REF]. Networks and
52 their topology are also used as a platform for evaluating 'downstream' responses to stressors such as evaluating
53 patterns of secondary extinction [REF]. Finally, they are commonly used as a platform for implementing
54 mathematical models of community dynamics [REF]; delivering inference about stability, function, invasive
55 species, climate change, contaminants, and secondary extinction, to name a few applications [REF]. Against
56 this backdrop of multiple research agendas, the definition of 'edges' and 'nodes', and the levels of organisation
57 at which they are defined, take many forms (Moulatlet et al., 2024; Poisot, Stouffer, et al., 2016), each of
58 which encode a series of assumptions within a network. Here we introduce a perspective on these baseline
59 assumptions.

60 **1.1 How do we define a node?**

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

73 **1.2 What is captured by an edge?**

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

⁸⁸ 1.3 Network representations

⁸⁹ Against these definitions of nodes and edges, networks fall into two major ‘types’: metawebs, traditionally
⁹⁰ defined as all the *potential* interactions for a specific species pool (Dunne, 2006); and realised networks, which
⁹¹ is the subset of interactions in a metaweb that are *realised* for a specific community at a given time and place.
⁹² The fundamental differences between these two network representations are the spatial and temporal scale at
⁹³ which they are constructed, and the associated processes that are assumed to drive pattern at these scales.

⁹⁴ A metaweb is, at its core, a list of *feasible* interactions between pairs of species. The feasibility for a given pair
⁹⁵ is derived from the complementarity (phylogenetic relationships) of their traits, typically aligned with feeding.
⁹⁶ Feasibility can be further refined by *co-occurrence* leading to the transition from a *global* to *regional metaweb*.
⁹⁷ Metawebs thus provide a means to identify evolutionarily plausible links, regionally plausible interactions, the
⁹⁸ set of ecologically possible, *i.e.*, forbidden, links (Jordano, 2016b), and ultimately a definition of the plausible
⁹⁹ *complete* diet of a species (Strydom et al., 2023).

¹⁰⁰ In contrast, realised networks are typically more localised in space and time, and the links between species
¹⁰¹ are contingent on the co-occurrence of species, the role of the environment, and mechanisms of diet choice.
¹⁰² Fundamentally this means that the presence/absence of a link is the result of the ‘behaviour’ of the species
¹⁰³ and even when the realised network is presented as a binary matrix, the edges imply a function is available
¹⁰⁴ to define the strength of an interaction. A realised network is therefore not simply the downscaling of a
¹⁰⁵ metaweb to a smaller scale (*e.g.*, moving from the country to the 1x1 km² scale based on fine-scale species
¹⁰⁶ co-occurrence). Instead, realised webs capture processes that determine the realisation of an interaction and
¹⁰⁷ flows of energy in a community. Specifically, in realised webs, the definition of an edge shifts from being
¹⁰⁸ determined by feasibility to that of choices and consequences that centre around energy. If one were to take
¹⁰⁹ the same community of species and constructed both a metaweb and realised network the two networks might
¹¹⁰ have the same species but would be structurally different, owing to the differences in the ‘rules’ constraining
¹¹¹ the presence of links. This distinction between metawebs and realised webs leads to a further insight. Links
¹¹² that are absent in a metaweb can conceptually (although not always practically) be treated as being truly
¹¹³ absent. However, links that are absent in a realised network cannot be considered as truly absent but rather
¹¹⁴ as absent due to the broader environmental/community context.

¹¹⁵ 2 From Nodes and Edges to Process and Constraints

¹¹⁶ In the previous section we discussed how the definition of nodes and edges, representing different scales and
¹¹⁷ processes, lead to the concept of a metaweb and a realised web. The fundamental take-homes are that nodes

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

124 [Figure 1 about here.]

125 **2.1 Processes that determine the feasibility of an interaction**

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

131 **Evolutionary compatibility**

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

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

144 **(Co)occurrence**

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

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

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

155 2.2 Processes that realise networks

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

163 Abundance

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

172 Diet choice

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

¹⁷⁸ al., 2019).

¹⁷⁹ In contrast to metaweb ‘construction’ from a list of pairwise interactions, these methods deliver a realised web
¹⁸⁰ directly and as an emergent property of node behaviour. We also here make a distinction, developed below,
¹⁸¹ with models like the Niche Model, where diet choice is implicit in its probabilistic network generating function,
¹⁸² but it is working to replicate the *expected* structure of the network and this structure does not emerge from
¹⁸³ node-based rules. Note that we select diet choice as a term to capture rules linked to optimal foraging (Pyke,
¹⁸⁴ 1984) and metabolic theory (Brown et al., 2004); it is a sensible ‘umbrella concept’ for capturing the energetic
¹⁸⁵ constraint on of the distribution and strength of interactions.

¹⁸⁶ **Non-trophic interactions**

¹⁸⁷ We include non-trophic interactions (see Miele et al., 2019) here not as a determinant of links, but a modifier
¹⁸⁸ of them - they are the community context above and beyond co-occurrence and abundance. Non-trophic
¹⁸⁹ interactions include competition for space, predator interference, refuge provisioning, recruitment facilitation as
¹⁹⁰ well as non-trophic effects that increase or decrease mortality. These interactions (Ings et al., 2009) specifically
¹⁹¹ modify either the realisation or strength of trophic interactions (Golubski & Abrams, 2011; Kamaru et al.,
¹⁹² 2024; Pilosof et al., 2017; Staniczenko et al., 2010) and represent direct (e.g., predator *a* outcompetes predator
¹⁹³ *b*) and indirect (e.g., mutualistic/facilitative interactions) mechanisms. They operate on the realisation of a
¹⁹⁴ network by altering the fine-scale distribution and abundance of species and relative contributions of direct
¹⁹⁵ and indirect effects to biomass, persistence, stability and the functioning of the communities (Buche et al.,
¹⁹⁶ 2024; Kéfi et al., 2012, 2015; Miele et al., 2019).

¹⁹⁷ **are these strictly modifiers of realised networks? - because we class them as community context**
¹⁹⁸ **with co-occurrence, a modifier of feasible networks....**

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 note 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); 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, and
233 have delivered insight in many ways. They have been critical to the construction of ‘first draft’ networks for
234 communities for which we have no interaction data (Strydom et al., 2022). They are also central to interpolation

235 in data poor regions and predicting interactions for ‘unobservable’ communities *e.g.*, prehistoric networks
236 (Dunhill et al., 2024; Fricke et al., 2022; Yeakel et al., 2014) or future, novel community assemblages (Van der
237 Putten et al., 2010). Furthermore, they have the capacity to evaluate a role of interactions among species
238 relative to their distribution by accounting for the role of the environment and the role of species interactions
239 (Gravel et al., 2019; Higino et al., 2023; Pollock et al., 2014). There are substantial data requirements for these
240 approaches including expert knowledge, species traits and phylogenetic relationships and/or interaction data
241 on related species or communities.

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

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

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

260 3.2.2 Species agnostic networks: construction through structure induction

261 Networks in this category are generated rules that create non-random networks that reflect empirical knowledge
262 of ecological network structures and evaluated by matching predictions to this *expected* structure of the
263 network(s). The determination of links between species is only implicitly linked to properties of the nodes.
264 This means these networks are usually not species specific. Although these models are data input light, often
265 requiring only species richness and an estimate of the number of expected links, they make clear assumptions

266 regarding what the expectations are for network structure. These are some of the most commonly used
267 network generation tools (e.g. the Niche model REF). There are two sub-categories of these species agnostic
268 networks.

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

279 3.3 Construction through deduction

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

290 3.3.1 Species-specific networks

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

296 by metawebs.

297 Neutral networks are built on the assumption that foraging decisions are tied *only* to the abundance of species
298 within the community (E. F. Canard et al., 2014; Krishna et al., 2008). Here links are solely determined by the
299 relative abundance of the different species in the community. Although it is highly unlikely that abundance is
300 the only determinant of interactions work by Pomeranz et al. (2019) showcases how these neutral processes
301 can be used in conjunction with inductive models to construct more refined/localised networks.

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

313 4 Making Progress with Networks

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

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

326 reveal fundamental patterns and understanding of processes in the natural world.
 327 In order to effectively use networks to aid us in answering questions about conservation/risk assessment/management
 328 and core ecological theory, we need to be mindful that we are mapping the *correct* network representation
 329 to the question of interest (Gauzens et al., 2025). Notably, there are certain questions that cannot be answered
 330 using specific network representations as the scale of the question of interest is fundamentally misaligned with
 331 either the process captured by a specific network representation Section 2.1, the underlying data that is used
 332 to construct it Section 3 or both of these factors.
 333 Here we discuss and map the different network representations shown in Figure 1 to ‘appropriate’ research
 334 questions and agendas [see also Table 1]. We also highlight some of the key methodological challenges that
 335 currently limit our conceptualisation of a ‘network’ and thus impact their effective practical application in
 336 real world settings.

Table 1: Table Caption

Network Representation	Example Research Question
Global Metaweb	How will novel communities respond to <i>e.g.</i> extinction, turnover, invasion and rewilling
	Diet/Trait-based conservation
	Rewiring capacity of species
	Eco-Evolutionary dynamics
	Applied use potential of questions highlighted for global metawebs at the management scale <i>e.g.</i> , a protected area
Regional Metawebs	Refinement/Extension of species distribution models
	How do we allocate multiple stressors across networks
	Temperature threshold to community collapse
	Extinction and persistence after harvesting/invasion/extinction
	Stability-diversity-productivity-function
Realised webs	Ecosystem level processes
	Meta communities and the idea of meta-network-communities

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

³³⁸ **4.1.1 Global Metawebs**

³³⁹ The interactions in global metawebs are not constrained by the realisation of specific community assemblages
³⁴⁰ (or species co-occurrence). These networks provide a platform for answering questions that assume interactions
³⁴¹ *could* occur between species (feasibility) or where the potential diet breadth of species is required. Examples
³⁴² of appropriate research questions at this scale includes those about *hypothetical* or *novel* communities and
³⁴³ interactions under future climate change scenarios, or the potential ‘position’ of an invasive (or re-introduced)
³⁴⁴ species within a network (Hui & Richardson, 2019). This scale is also appropriate for a particular class of
³⁴⁵ questions related to the potential (eco-evolutionary) rewiring capacity of species, and how this may help
³⁴⁶ inform on the opportunities for persistence of species within new community assemblages (Marjakangas et
³⁴⁷ al., 2025). The implicit focus on feasibility in these examples highlights that global metawebs are linked to
³⁴⁸ strong proxies for targets and mechanisms of evolutionary change. This offers a network scale for modelling
³⁴⁹ ecological-evolutionary dynamics and the role that both the evolutionary history, natural selection, and
³⁵⁰ phenotypic plasticity shapes the diet breadth of species.

³⁵¹ **4.1.2 Regional Metawebs**

³⁵² Regional metawebs are conceptually a spatially constrained global metaweb. They make explicit the co-
³⁵³ occurrence between species. Against this backdrop, they are conceptually aligned with similar questions
³⁵⁴ to those posed above, with the added focus on a community facing, real, challenge. Additionally, regional
³⁵⁵ metawebs can and have been used to refine and constrain species distribution model predictions, giving us
³⁵⁶ more refined range maps (García-Callejas et al., 2023) or community composition under climate change
³⁵⁷ scenarios, even at global scales (Hao et al., 2025).

³⁵⁸ However we must exercise a high degree of caution when comparing structures among regional metwebs,
³⁵⁹ whether discrete collections or along environmental gradients. At this scale, where the network embeds the
³⁶⁰ assumptions of feasibility, the link distribution is not meaningfully constrained by environmental factors (see
³⁶¹ Section 1.2) and it is vital to disentangle structural change *per se* from the multiple processes that might
³⁶² determine species turnover (*e.g.*, β - diversity).

³⁶³ **4.1.3 Realised networks**

³⁶⁴ Realised network are the most representative of what comes to mind when people think of networks, and
³⁶⁵ more specifically how we can use them to help inform on larger biogeographic processes (Thuiller et al.,
³⁶⁶ 2024). This is partially because of the popularity and legacy of generative network models (like the Cascade

³⁶⁷ and Niche model) which produce realised network representations, and represent the ideal ‘currency’ for
³⁶⁸ which to understand the constraints placed on interactions/network structure by the broader community
³⁶⁹ and environmental context. This change in currency and context affords us the opportunity to ask questions
³⁷⁰ that revolve around major ecological theory - *e.g.*, community stability and resilience, biodiversity dynamics,
³⁷¹ ecosystem function, structure-function relationships - and around major conservation and climate change global
³⁷² challenges - *e.g.*, temperature change, extinction dynamics, invasion impacts and reintroductions/rewilding.

³⁷³ Something something about how we can asks questions here about nodes but instead of it being limited to
³⁷⁴ the fesibility space (e.g. rewiring capacity or diet breadth).

³⁷⁵ Realised networks embody an explicit focus on the link between network structure to ecosystem function.
³⁷⁶ Because the structure of realised webs are isolated from turnover processes they allow us to think about the
³⁷⁷ propagation of change (across both time and space) which allows us to ask questions about the persistence of
³⁷⁸ communities and how they respond to perturbations or stressors (at both the level of the node as well as the
³⁷⁹ modification of links).

³⁸⁰ Although the recent boom in the availability of long-term observation data is allowing us to unpack decades
³⁸¹ of insights for stability-diversity-productivity relationships for more complex communities (Danet et al., 2024)
³⁸² or to evaluate the impacts and efficacy of re-introductions (Wooster et al., 2024), we need to be mindful that
³⁸³ empirical interaction data is typically accumulated over time and so it compresses the transient nature of the
³⁸⁴ interactions between species (Polis, 1991). Thus we need to apply a degree of caution when using empirical
³⁸⁵ data to construct realised networks - although there is scope to think about developing methods that will
³⁸⁶ allow us to modify metawebs in such a way that their structures become more aligned with realised webs (see
³⁸⁷ the next section).

³⁸⁸ 4.2 Key methodological challenges

³⁸⁹ As noted above, the three types of networks help highlight longstanding methodological challenges that affect
³⁹⁰ our abiloty to increase both precision and accuracy of inference derived from the questions we highlight above.
³⁹¹ Here we review some of these challenges and opportunities that are arising to mitigate them.

³⁹² **Understanding what emperical data represents:** Ultimately, knowing what is right/precise/correct in an
³⁹³ ecological network requires robust data. What does it mean when we ‘observe’ an interaction be that directly
³⁹⁴ (predator actively feeding on prey) or indirectly via *e.g.*, gut or isotope analysis. A netwrok constructued
³⁹⁵ with emperical data will most likley still represent an ‘accumulation’ of feeding data making it conceptually
³⁹⁶ more closely aligned with idea of a metaweb.

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

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

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

418 *What about the eco-evolutionary space? What does Louille and Loreau’s model represent?*

419 **Making networks more tractable in applied spaces:** There is a disconnect when it comes to effectively
420 using networks in applied spaces (Dansereau, Braga, et al., 2024). **WHY - need three reasons...**

421 We need to make an effort to more efficiently map the from (structure) of a network to its function as well as
422 identify how this can effectively be integrated into policy to make it meaningful and actionable. Additionally
423 we also need a firmer grasp as to what defines a ‘network’ as a unit, are the logical (environmental) boundaries
424 between networks and how do these relate to ‘management’ units and scales (Fortin et al., 2021).

425 **5 Concluding remarks**

426 Having a clear understanding of the interplay between network representations and the processes that they
427 are capable of encoding is critical if we are to understand exactly which networks can be used to answer which
428 questions. As we highlight in Box 1 the different network representations have different potential uses and it
429 should be clear that there is no ‘best’ network representation but rather a network representation that is
430 best suited to its intended purpose. In providing a formalisation regards to the assumptions and mechanisms
431 that need to be explicitly taken into consideration when deciding to use (and construct) networks we hope to
432 prevent the unintentional misuse or misinterpretation of networks as well as provide a starting point from
433 which we can develop a better framework for the applied use of networks to answer questions that are not
434 only pressing within the field but also within broader biodiversity science.

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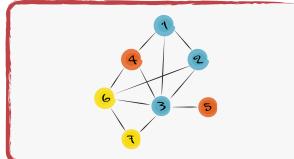
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REPRESENTATION

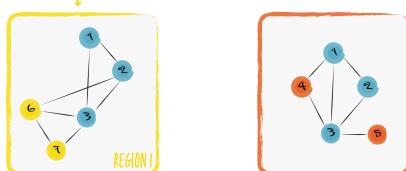
GLOBAL METAWEB

All feasible interactions for a collection of species



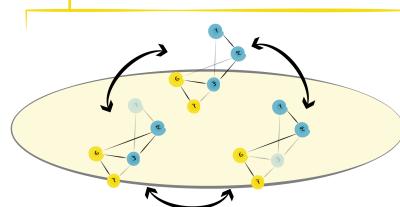
REGIONAL METAWEB

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

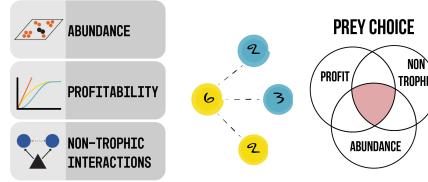
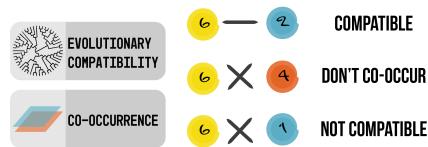
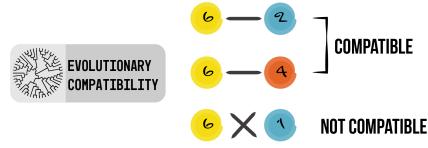


REALISED NETWORKS

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 accounting for the co-occurrence of the difference 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.