

Unveiling the Complexity of Food Webs: A Comprehensive Overview of Definitions, Scales, and Mechanisms

Tanya Strydom ¹; Jennifer A. Dunne ²; Timothée Poisot ^{3,4}; Andrew P. Beckerman ¹

Abstract: Food webs are a useful abstraction and representation of the feeding links between species in a community and are used to infer many ecosystem level processes. However, the different theories, mechanisms, and criteria that underpin how a food web is defined and, ultimately, constructed means that not all food webs are representing the same ecological process. Here we present a synthesis of the different assumptions, scales and mechanisms that are used to define different ecological networks ranging from metawebs (an inventory of all potential interactions) to fully realised networks (interactions that occur within a given community over a certain timescale). Illuminating the assumptions, scales, and mechanisms of network inference allows a formal categorisation of how to use networks to answer key ecological and conservation questions and defines guidelines to prevent unintentional misuse or misinterpretation.

Keywords: food web, network construction, scientific ignorance

1 At the heart of modern biodiversity science are a set of concepts and theories about biodiversity, stability
2 and function. These relate to the abundance, distribution and services that biodiversity provides, and how
3 biodiversity – as an interconnected set of species – responds to multiple stressors. The interaction between
4 species is one of the fundamental building blocks of ecological communities, providing a powerful abstraction
5 that can help quantify, conceptualise, and understand biodiversity dynamics, and ultimately, make predic-
6 tions, mitigate change, and manage services. Such network representations of biodiversity (including within
7 species diversity) are increasingly argued to be an asset to predictive ecology, climate change mitigation
8 and resource management. Here, it is argued that characterising biodiversity in a network will allow deeper
9 capacity to understand and predict the abundance, distribution, dynamics and services provided by multiple
10 species facing multiple stressors.

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

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

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

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

40 1.0.1 How do we define a node?

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

49 1.0.2 What is meant by an edge?

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

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

63 **1.0.3 Network representations**

64 Broadly, networks can be thought of to fall into two different ‘types’; namely metawebs; traditionally defined
65 as all of the *potential* interactions for a specific species pool (Dunne, 2006), and realised networks; which
66 is the subset of interactions in a metaweb that are *realised* ‘on the ground’. The fundamental difference
67 between these two different types of networks is that a metaweb provides insight as to the viability of an
68 interaction between two species occurring and is a means to identify links that are not ecologically plausible,
69 *i.e.*, forbidden links (Jordano, 2016b), or an idea of the *complete* diet of a species (Strydom et al., 2023).
70 Although metawebs are typically ‘constrained’ to a collection of species that also co-occur, there is no reason
71 that a metaweb cannot include species that do not co-occur (although this would require some degree of
72 prediction/assumptions to identify those possible interactions). In contrast realised networks are highly
73 localised and contingent on both the co-occurrence of species as well as the influence of the environment,
74 and population and community dynamics on predator choice. In the context of definitions and semantics
75 the links that are represented by a metaweb and a realised network are different; links that are absent in a
76 metaweb can be treated as being truly absent, however links that are absent in a realised network cannot be
77 considered to be truly absent but are rather as absent due to the broader environmental/community context.
78 Importantly, a realised network is *not* simply the downscaling of a metaweb to a smaller scale (*e.g.*, moving
79 from the country to the 1x1 km² scale based on fine-scale species co-occurrence) but represents a shift towards
80 capturing the higher level processes that determine the *realisation* of an interaction. Thus, different network
81 representations are determined and constrained by different sets of assumptions as to what the processes are
82 that determine the presence/absence of an interaction between two species as well as the resulting network
83 structure.

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

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

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

[Figure 1 about here.]

2.1 The processes that determine species interactions

Evolutionary compatibility

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

(Co)occurrence

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

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

124 **Abundance**

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

131 **Predator choice (energetic cost)**

132 Ultimately, predator choice is underpinned by the energetic cost-benefit of trying to catch, kill, and consume
133 prey (where a predator will optimise energy while minimising time), and is well described within both optimal
134 foraging [] [ref] and metabolic theory (Brown et al., 2004), which rests on the idea that the prey a predator
135 chooses to target is one that will have the greatest return on energy with the lowest energetic cost. With a
136 body of evidence that suggests that body size might be the underlying driver, and thus suitable proxy for
137 understanding these processes (Yodzis & Innes, 1992) There are additional bodies of work that attempt to
138 include the cost of movement that the environment imposes on an individual (Cherif et al., 2024) as well as
139 2D/3D search space (Pawar et al., 2012).

140 **Indirect/higher order interactions**

141 The realisation (presence/absence) or strength of trophic interactions themselves can also be modified by
142 other, indirect (non-trophic), interactions (Golubski & Abrams, 2011; Pilosof et al., 2017), this can be either
143 ‘directly’ through *e.g.*, competition or ‘indirectly’ *e.g.*, mutualistic/facilitative interactions will alter the fine-
144 scale distribution and abundance of some species (Kéfi et al., 2012, 2015) as well as persistence (Buche et al.,
145 2024).

146 **2.2 Contextualising the processes that determine species interactions**

147 It should be self evident that the different processes discussed above are all ultimately going to influence the
148 realisation of interactions as well as the structure of a network, however they are acting at different scales
149 of organisation. Both the **co-occurrence** and the **evolutionary compatibility** are valid at the scale of

the species pair of interest, that is the *possibility* of an interaction being present/absent is assessed at the pairwise level and one is left with a ‘list’ of interactions that are present/absent. Although it is possible to build a network (*i.e.*, metaweb) from this information it is important to be aware that the structure of this network is not constrained by real-world dynamics or conditions (*i.e.*, community context), and so just because species are able to interact does not mean that they will (Poisot et al., 2015). In order to construct a network who’s structure is a closer approximation of reality (localised interactions) one needs to take into consideration properties of the community as a whole and not just the two species of interest, which requires more data at the community scale, such as the abundance of species.

3 Network construction is nuanced

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

i Box 1 - Why we need to aggregate networks at different scales: A hypothetical case study

Although it might seem most prudent to be predicting, constructing, and defining networks that are the closest representation of reality there are pros and cons of constructing both realised networks as well as metawebs. Let us take for example a community across time/through seasons. In this community we expect species to be either present or absent depending on the season (*i.e.*, changes in co-occurrence) as well as some species exhibiting seasonal diet shifts, these details would be lost at the scale of the metaweb and it would be valuable to construct either smaller metawebs for the different seasonal communities (thereby capturing the changes in community diversity), or realised networks for each season (to capture diet or ecosystem process shifts). However, these small-scale networks lack the context of the bigger picture that is available at the metaweb - that is it gives us a more holistic idea of the entire diet range of a specific species, which is important when one needs to make conservation-based/applied decisions (*e.g.*, conserving the entire diet of a species and not just seasonal prey items) as well as providing information on interactions that may be possible regardless of the environmental/community context (species may have the capacity to consume certain prey items but do not do so due to local conditions).

With this in mind let us see how the different network aggregations can be used

1: A global metaweb

Knowledge of the entire diet breadth of a species is valuable especially in terms of understanding how a species will respond to changes in the community - *e.g.*, invasions/rewilding exercises (where does the new species ‘fit’ within the network?) as well as potential capacity to shift its diet. Although this might make sense across space and not time but certain species act as links across the landscape.

2: A seasonal metaweb

Knowledge at the finer scale is also valuable to understand/identify that there are in fact differences between the seasons

3: A seasonal realised network

Dynamics are useful because they are a representation of the different configurations/energy flows/ecosystem processes. Also to detect more nuanced shifts in diet - *e.g.*, seasonal diet shifts.

4: A structural network

Data trade off

Above we highlight the practical uses of the different network configurations but we also need to take into consideration the barriers to construction/associated data needs/cost and acknowledge them. Basically in the ideal world we would have all this information at hand but in reality we might be sitting with seasonal metawebs...

178 **3.1 Models that predict metawebs (feasible interactions)**

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

197 **3.2 Models that predict realised networks (realised interactions)**

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

209 et al. (2023) developed a model that moves the energy of the system into different modules related to the
210 process of the predator acquiring energy from the prey *i.e.*, compartmentation in food webs (Krause et al.,
211 2003).

212 3.3 Models that predict structure (interaction agnostic)

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

227 4 Making Progress with Networks

228 4.1 Further development of models and tools

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

238 feasibility of developing a model that is both broadly generalisable, but also has local specificity is probably
239 not attainable (Stouffer, 2019), and more specifically the potential use of models to untangle/identify the
240 different processes that shape interaction networks (Song & Levine, 2024), *e.g.*, Curtsdotter et al. (2019)
241 showcase the use of models to disentangle the drivers of community function and Strydom, Dalla Riva, et
242 al. (2021) who identified that networks are less complex than they could be, suggesting that there are
243 constraints on network assembly. In addition to the more intentional development of models we also need to
244 consider the validation of these models, there have been developments and discussions for assessing how well
245 a model recovers pairwise interactions (Poisot, 2023; Strydom, Catchen, et al., 2021), although the rate of
246 false-negatives that may be present in the testing data still present a challenge (Catchen et al., 2023), and we
247 still lack clear strategies for benchmarking the ability of models to recover structure (Allesina et al., 2008).

248 4.2 At what scale should we be predicting and using networks?

249 Look at Hutchinson et al. (2019)

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

264 4.3 Feasible, realised, or sustainable?

265 When do we determine a link to be ‘real’... In the context of metawebs this is perhaps clearer - if all things
266 were equal (*i.e.*, community context is irrelevant) would the predator be able to consume the prey. However
267 in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction - just

268 because an interaction is possible in the now is it able to sustain a population in the long term. And what
269 is the scale for that long term - are we thinking at the generational scale? Because ultimately when we
270 are constructing a network we are aggregating not only across space but also across time... This is probably
271 again a Lokta-Volterra space question and something that the dynamic foodweb models (Curtsdotter et al.,
272 2019; Delmas et al., 2017; Lajaaiti et al., 2024) are addressing, but again it is integrating this with the
273 feasible/realised axis. And of course the Petchey dilemma of even what networks should we be feeding into
274 these dynamic models.

275 5 The future value of networks

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

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

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

290 References

- 291 Allesina, S., Alonso, D., & Pascual, M. (2008). A General Model for Food Web Structure. *Science*, 320(5876),
292 658–661. <https://doi.org/10.1126/science.1156269>
- 293 Allesina, S., & Pascual, M. (2009). Food web models: A plea for groups. *Ecology Letters*, 12(7), 652–662.
294 <https://doi.org/10.1111/j.1461-0248.2009.01321.x>
- 295 Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas,
296 T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction*

- 297 networks. EcoEvoRxiv. <https://doi.org/10.32942/X28G8Z>
- 298 Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.
299 A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,
300 E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic
301 reservoirs. *The Lancet Microbe*, 3(8), e625–e637. [https://doi.org/10.1016/S2666-5247\(21\)00245-7](https://doi.org/10.1016/S2666-5247(21)00245-7)
- 302 Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.
303 *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- 304 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of
305 the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- 306 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,
307 V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.
308 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),
309 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 310 Biton, B., Puzis, R., & Pilosof, S. (2024). *Inductive link prediction boosts data availability and enables
311 cross-community link prediction in ecological networks*.
- 312 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.
313 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 314 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2021). Inferred seasonal interaction rewiring of a freshwater
315 stream fish network. *Ecography*, 44(2), 219–230. <https://doi.org/10.1111/ecog.05452>
- 316 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A
317 cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 318 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings
319 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),
320 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 321 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory
322 of Ecology. *Ecology*, 85(7), 1771–1789. <https://doi.org/10.1890/03-9000>
- 323 Buche, L., Bartomeus, I., & Godoy, O. (2024). Multitrophic Higher-Order Interactions Modulate Species
324 Persistence. *The American Naturalist*, 203(4), 458–472. <https://doi.org/10.1086/729222>
- 325 Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of
326 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- 327 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models
328 12

- 330 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,
331 33(4), e13807. <https://doi.org/10.1111/geb.13807>
- 332 Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with
333 trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>
- 334 Catchen, M. D., Poisot, T., Pollock, L. J., & Gonzalez, A. (2023). *The missing link: Discerning true from*
335 *false negatives when sampling species interaction networks.*
- 336 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,
337 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The
338 environment to the rescue: Can physics help predict predator–prey interactions? *Biological Reviews*,
339 n/a(n/a). <https://doi.org/10.1111/brv.13105>
- 340 Cirtwill, A. R., Eklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for
341 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10(6),
342 902–911. <https://doi.org/10.1111/2041-210X.13180>
- 343 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.
344 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 345 Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., Traugott, M., &
346 Bommarco, R. (2019). Ecosystem function in predator–prey food webs—confronting dynamic models with
347 empirical data. *Journal of Animal Ecology*, 88(2), 196–210. <https://doi.org/10.1111/1365-2656.12892>
- 348 Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones
349 using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>
- 350 Dallas, T., Park, A. W., & Drake, J. M. (2017). Predicting cryptic links in host-parasite networks. *PLOS*
351 *Computational Biology*, 13(5), e1005557. <https://doi.org/10.1371/journal.pcbi.1005557>
- 352 Dansereau, G., Barros, C., & Poisot, T. (2024). Spatially explicit predictions of food web structure from
353 regional-level data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 379(1909).
354 <https://doi.org/10.1098/rstb.2023.0166>
- 355 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,
356 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).
357 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brv.12433>
- 359 Delmas, E., Brose, U., Gravel, D., Stouffer, D. B., & Poisot, T. (2017). Simulations of biomass dynamics in
360 community food webs. *Methods in Ecology and Evolution*, 8(7), 881–886. <https://doi.org/10.1111/2041-210X.12713>
- 362 Desjardins-Proulx, P., Laigle, I., Poisot, T., & Gravel, D. (2017). Ecological interactions and the Netflix

- 363 problem. *PeerJ*, 5, e3644. <https://doi.org/10.7717/peerj.3644>
- 364 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological*
365 *networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 366 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and
367 Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 368
- 369 Eklöf, A., Tang, S., & Allesina, S. (2013). Secondary extinctions in food webs: A Bayesian network approach.
370 *Methods in Ecology and Evolution*, 4(8), 760–770. <https://doi.org/10.1111/2041-210X.12062>
- 371 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks
372 over space. *Frontiers in Ecology and Evolution*, 11.
- 373 Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings*
374 *of the Royal Society B: Biological Sciences*, 288(1949), rspb.2020.1889, 20201889. <https://doi.org/10.1098/rspb.2020.1889>
- 375
- 376 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,
377 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.
378 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 379 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., Gravel, D., & Montoya,
380 J. M. (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, 2(5),
381 782–790. <https://doi.org/10.1038/s41559-018-0517-3>
- 382 García-Callejas, D., Godoy, O., Buche, L., Hurtado, M., Lanuza, J. B., Allen-Perkins, A., & Bartomeus, I.
383 (2023). Non-random interactions within and across guilds shape the potential to coexist in multi-trophic
384 ecological communities. *Ecology Letters*, 26(6), 831–842. <https://doi.org/10.1111/ele.14206>
- 385 Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions
386 interact? *Journal of Animal Ecology*, 80(5), 1097–1108. <https://doi.org/10.1111/j.1365-2656.2011.01852.x>
- 387
- 388 Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across
389 the entire tree of life. *Nature*, 465(7300), 918–921. <https://doi.org/10.1038/nature09113>
- 390 Gray, C., Figueroa, D. H., Hudson, L. N., Ma, A., Perkins, D., & Woodward, G. (2015). Joining the dots:
391 An automated method for constructing food webs from compendia of published interactions. *Food Webs*,
392 5, 11–20. <https://doi.org/10.1016/j.fooweb.2015.09.001>
- 393 Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch
394 between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*,
395 11, e14620. <https://doi.org/10.7717/peerj.14620>

- 396 Hui, C., & Richardson, D. M. (2019). How to Invade an Ecological Network. *Trends in Ecology & Evolution*,
397 34(2), 121–131. <https://doi.org/10.1016/j.tree.2018.11.003>
- 398 Hutchinson, M. C., Bramon Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., Jordano, P., &
399 Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community
400 ecology. *Functional Ecology*, 33(2), 206–217. <https://doi.org/10.1111/1365-2435.13237>
- 401 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 402 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 403 Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015).
404 Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky
405 shores. *Ecology*, 96(1), 291–303. <https://doi.org/10.1890/13-1424.1>
- 406 Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N.,
407 Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., & Brose,
408 U. (2012). More than a meal... integrating non-feeding interactions into food webs: More than a meal
409 *Ecology Letters*, 15(4), 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- 410 Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments
411 revealed in food-web structure. *Nature*, 426(6964), 282–285. <https://doi.org/10.1038/nature02115>
- 412 Laender, F. D., Oevelen, D. V., Soetaert, K., & Middelburg, J. J. (2010). Carbon transfer in a herbivore-
413 and microbial loop-dominated pelagic food webs in the southern Barents Sea during spring and summer.
414 *Marine Ecology Progress Series*, 398, 93–107. <https://doi.org/10.3354/meps08335>
- 415 Lajaaiti, I., Bonnici, I., Kéfi, S., Mayall, H., Danet, A., Beckerman, A. P., Malpas, T., & Delmas, E. (2024).
416 *EcologicalNetworksDynamics.jl A Julia package to simulate the temporal dynamics of complex ecological*
417 *networks* (p. 2024.03.20.585899). bioRxiv. <https://doi.org/10.1101/2024.03.20.585899>
- 418 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 419 Llewelyn, J., Strona, G., Dickman, C. R., Greenville, A. C., Wardle, G. M., Lee, M. S. Y., Doherty, S.,
420 Shabani, F., Saltré, F., & Bradshaw, C. J. A. (2023). Predicting predator-prey interactions in terrestrial
421 endotherms using random forest. *Ecography*, 2023(9), e06619. <https://doi.org/10.1111/ecog.06619>
- 422 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from
423 abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.13380>
- 424 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from

- 429 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 430 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic
431 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 432 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web
433 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 434 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some
435 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 436 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms
437 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and
438 Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- 439 Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks.
440 *Nature Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 441 Poelen, J. H., Simons, J. D., & Mungall, C. J. (2014). Global biotic interactions: An open infrastructure to
442 share and analyze species-interaction datasets. *Ecological Informatics*, 24, 148–159. <https://doi.org/10.1016/j.ecoinf.2014.08.005>
- 443 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods
444 in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 445 Poisot, T., Baiser, B., Dunne, J., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T. N., Stouffer, D. B., Wood, S.
446 A., & Gravel, D. (2016). Mangal – making ecological network analysis simple. *Ecography*, 39(4), 384–390.
447 <https://doi.org/10.1111/ecog.00976>
- 448 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of
449 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/mec.12420>
- 450 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
451 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 452 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks
453 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 454 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., &
455 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint
456 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/10.1111/2041-210X.12180>
- 457 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton
458 University Press.
- 459
- 460

- 462 University Press. <https://doi.org/10.1515/9780691195322-020>
- 463 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.
464 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 465 Rooney, N., McCann, K. S., & Moore, J. C. (2008). A landscape theory for food web architecture. *Ecology*
466 *Letters*, 11(8), 867–881. <https://doi.org/10.1111/j.1461-0248.2008.01193.x>
- 467 Roopnarine, P. D. (2006). Extinction Cascades and Catastrophe in Ancient Food Webs. *Paleobiology*, 32(1),
468 1–19. <https://www.jstor.org/stable/4096814>
- 469 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network
470 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),
471 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 472 Segar, S. T., Fayle, T. M., Srivastava, D. S., Lewinsohn, T. M., Lewis, O. T., Novotny, V., Kitching, R. L.,
473 & Maunsell, S. C. (2020). The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology &*
474 *Evolution*, 35(5), 454–466. <https://doi.org/10.1016/j.tree.2020.01.004>
- 475 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*
476 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 477
- 478 Song, C., & Levine, J. M. (2024). *Rigorous (in)validation of ecological models* (p. 2024.09.19.613075). bioRxiv.
479 <https://doi.org/10.1101/2024.09.19.613075>
- 480 Stock, M. (2021). Pairwise learning for predicting pollination interactions based on traits and phylogeny.
481 *Ecological Modelling*, 14.
- 482 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*,
483 88(2), 192–195. <https://doi.org/10.1111/1365-2656.12949>
- 484 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,
485 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction
486 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,
487 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- 488 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,
489 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer
490 learning can help predict potential species interaction networks despite data limitations. *Methods in*
491 *Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 492 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
493 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap
494 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*

- 495 *the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 496 Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD Entropy Reveals the High Complexity of Ecological
497 Networks. *Frontiers in Ecology and Evolution*, 9. <https://doi.org/10.3389/fevo.2021.623141>
- 498 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.
499 <https://doi.org/10.1002/ecy.3047>
- 500 Valdovinos, F. S., Hale, K. R. S., Dritz, S., Glaum, P. R., McCann, K. S., Simon, S. M., Thébault, E., Wetzel,
501 W. C., Wootton, K. L., & Yeakel, J. D. (2023). A bioenergetic framework for aboveground terrestrial
502 food webs. *Trends in Ecology & Evolution*, 38(3), 301–312. <https://doi.org/10.1016/j.tree.2022.11.004>
- 503 Van De Walle, R., Logghe, G., Haas, N., Massol, F., Vandegehuchte, M. L., & Bonte, D. (2023). Arthro-
504 pod food webs predicted from body size ratios are improved by incorporating prey defensive properties.
505 *Journal of Animal Ecology*, 92(4), 913–924. <https://doi.org/10.1111/1365-2656.13905>
- 506 Wells, K., & O'Hara, R. B. (2013). Species interactions: Estimating per-individual interaction strength and
507 covariates before simplifying data into per-species ecological networks. *Methods in Ecology and Evolution*,
508 4(1), 1–8. <https://doi.org/10.1111/j.2041-210x.2012.00249.x>
- 509 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
510 <https://doi.org/10.1038/35004572>
- 511 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food
512 webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 513 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory
514 of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 515 Xie, J.-R., Zhang, P., Zhang, H.-F., & Wang, B.-H. (2017). Completeness of Community Structure in
516 Networks. *Scientific Reports*, 7(1), 5269. <https://doi.org/10.1038/s41598-017-05585-6>
- 517 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).
518 Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>
- 519
- 520 Yodzis, P. (1982). The Compartmentation of Real and Assembled Ecosystems. *The American Naturalist*,
521 120(5), 551–570. <https://doi.org/10.1086/284013>
- 522 Yodzis, P., & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*,
523 139(6), 1151–1175. <https://doi.org/10.1086/285380>

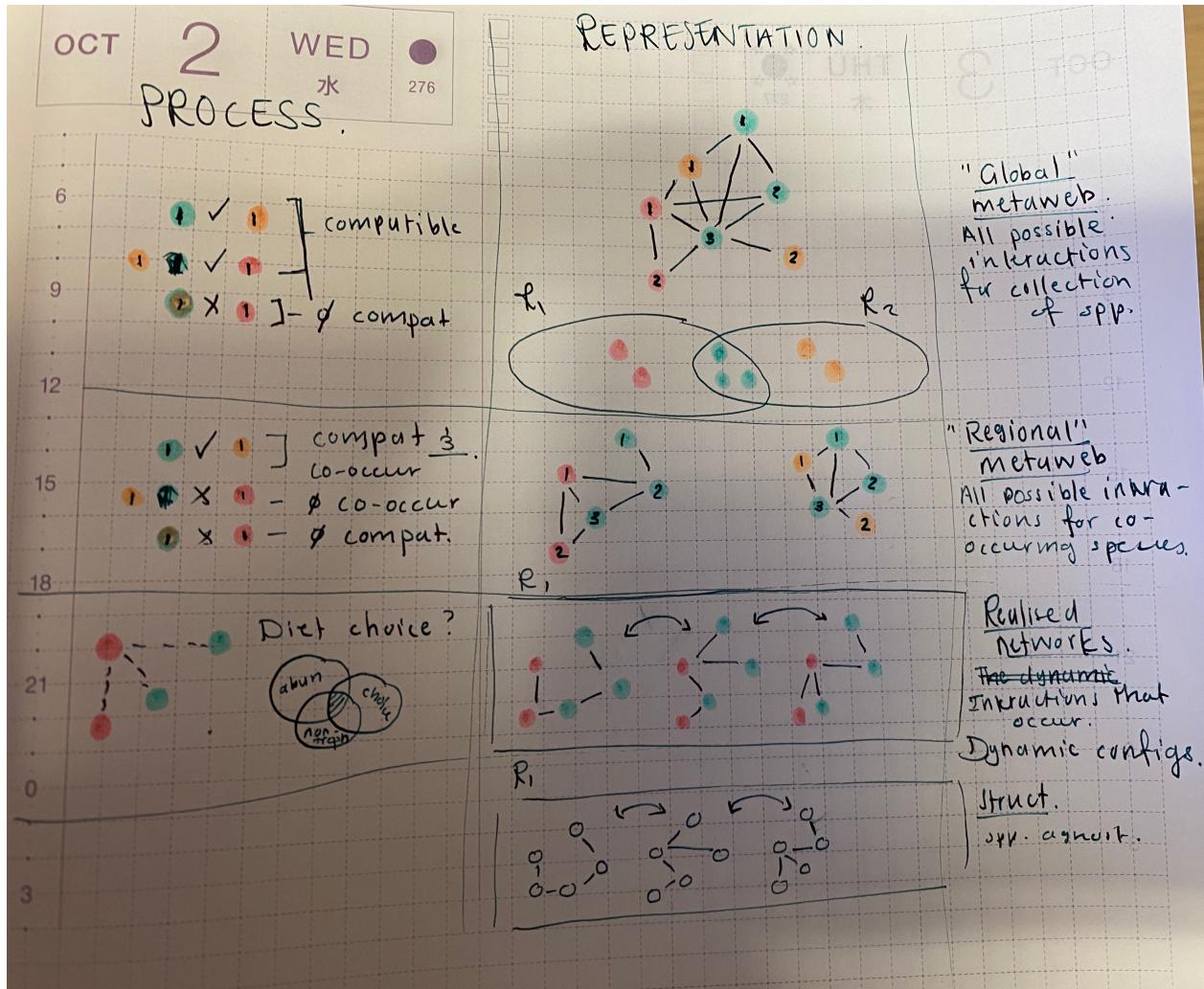


Figure 1: Aligning the various processes that determine interactions with the different network representations. First we start with a ‘global metaweb’ this network which captures all possible interactions for an arbitrary collection of species, we can further refine this network by taking in to consideration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