

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

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

Keywords: food web, network construction, scientific ignorance

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

11 However, the way that a network is constructed (encoded) defines an epistemology of the network concept
12 which, we argue, can influence the resulting observations and conclusions about pattern and mechanisms
13 that are made (Brimacombe et al., 2023; Proulx et al., 2005). This process of constructing networks has two
14 major pillars: the data and theory, the latter representing an expression of mechanism and process giving
15 rise to patterns that emerge from collating interactions among species. Each of these pillars carries with it
16 a set of practical, semantic and conceptual constraints that not only influence progress in making network
17 ecology more valuable and potentially predictive, but help define the spatial, temporal and evolutionary scale
18 of assumptions we make and predictions we might generate from the networks.

19 With respect to data, it is extremely challenging to actually record species interactions in the field (Jordano,
20 2016a, 2016b). Despite notable herculean efforts (**Woodward? Benguela?** Maiorano et al. (2020)), actual
21 coverage of ‘real world’ interaction data remains sparse (Poisot et al., 2021). Against this practical challenge,
22 there is additionally high variance in the terminology we use to define networks. Finally, the mathematical
23 and statistical tools we use to construct, conceptualise, analyse and predict with these networks are also
24 highly variable.

25 1. what are the underlying assumptions about nodes, edges, scale and process that are made when we
26 attempt to delimit and describe a food webs;

27 2. are there families of commonly used tools that map onto assumptions about scales and processes;

28 The provision of this detail ultimately leads to a set of insights and conclusions about whether, when and
29 under what conditions network representations of biodiversity can contribute to the advancement of ecological
30 theory and generate value in predictive ecology. Specifically, we finish this perspective with an overview of
31 fundamental questions in ecology that we think can benefit from network thinking and a proposal that such

32 thinking can accelerate our capacity to predict the impact of multiple stressors on biodiverse communities.

33 1 Setting the Scene: The Not So Basics of Nodes and Edges

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

44 1.0.1 How do we define a node?

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

53 1.0.2 What is meant by an edge?

54 At its core, links within food webs can be thought of as a representation of either feeding links between
55 species - be that realised (Pringle, 2020) or potential (Dunne, 2006), or representative of fluxes within
56 the community/system *e.g.*, energy transfer or material flow (Lindeman, 1942). How we specify links will
57 influence the resulting structure of the network - and the inferences we will make thereof. For example taking
58 a food web that consists of links representing all *potential* feeding links for a community (*i.e.*, a metaweb)
59 will be meaningless if one is interested in understanding the flow of energy through the network as the links
60 within a metaweb do not represent environmental/energetic constraints, making them poor representations

of which interactions are *realised* in a specific location (Caron et al., 2024). In addition to the various ways of defining the links between species pairs there are also a myriad of ways in which the links themselves can be quantified. Links between species are often treated as being present or absent (*i.e.*, binary) but it is also possible to use probabilities (Banville et al., 2024; which quantifies how likely an interaction is to occur, Poisot, Cirtwill, et al., 2016) or continuous measurements (which quantifies the strength of an interaction, Berlow et al., 2004).

1.0.3 Network representations

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

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

The interplay between network representation and network definition is primarily governed by the process(es) that determine the interaction between species, however these processes are also scale and context dependent.

91 Here we start by introducing the five core processes that determine either the feasibility or realisation of
92 interactions, namely: evolutionary compatibility, co-occurrence, feasibility, abundance, predator choice, and
93 non-trophic interactions; while simultaneously contextualising them within, and linking them to the different
94 network representations Figure 1; specifically if the processes captures an all-or-nothing (possibility) vs
95 context dependent (likelihood) determination of interactions between species. Of course these processes do
96 not function in a vacuum and do interact with/influence one another, but it is still beneficial to present them
97 in a categorical manner as these different processes are often the underpinning logic in the development of
98 prediction/network models, the criteria for data collection in the field, and the scale of organisation for which
99 they are relevant (species, population, or community).

100 [Figure 1 about here.]

101 **2.1 The processes that determine species interactions**

102 **Evolutionary compatibility**

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

115 **(Co)occurrence**

116 Although the outright assumption that because two species are co-occurring it must mean that they are
117 interacting is inherently flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at
118 least in terms of feeding links) if they are not co-occurring in time and space. Thus co-occurrence data alone is
119 insufficient to build an accurate and ecologically meaningful representation of a food web having information
120 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 likely species are to co-occur (**dansereauSpatiallyExplicitPredictions2023?**). Additionally the interplay between the interaction between a species pair and their co-occurrence is meaningful when one is operating in the space of trying to determine the distribution of a species (Higino et al., 2023), and forms a key component of some of the next generation species distribution models *e.g.*, joint SDMs (Pollock et al., 2014).

126 Abundance

127 The abundance of the different species within the community can influence the likelihood of an interaction
128 occurring in a myriad of ways. There is the argument that networks (and the interactions that make them up)
129 are driven by only the abundance of the different species and not the characteristics (traits), *sensu* neutral
130 processes and have been formalised with the neutral model (Canard et al., 2012), as well as statistical tools
131 (Momal et al., 2020). Alternatively the abundance of species in a community can influence which interactions
132 are ultimately realised (Banville et al., 2024; Poisot et al., 2015).

133 Predator choice (energetic cost)

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

141 Indirect interactions

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

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
150 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 whose 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.

something about ‘physical’/landscape scale as well as time scale??

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 [ref] and challenging to execute in a way that captures the different processes (owing to the different time and spatial scales they may be operating at). Thus we often turn to using models to either predict the interaction between two species [ref], the structure of networks [ref], or even as a means to identify missing interactions (gap fill) within existing empirical dataset (Biton et al., 2024; 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. Different models have different underlying philosophies that often only capture one or a few of the processes discussed in Section 2, has implications for how the resulting network is defined Section 1, which will ultimately delimit and define what inferences can be made from the resulting network. Here we will introduce the three different types of network representations, 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 representation 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

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well as some species exhibiting seasonal diet shifts, these details would be lost at the scale of the metaweb an 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 [Rooney]

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...

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3.1 How do we predict food webs?

¹⁷⁷ There are many ways to predict networks as what there is to define them and along with taking into consider-

¹⁷⁸ eration the points raised in the previous section it is also beneficial to think about the context in which the

180 different models were developed - and how this will influence the networks that they produce...
181 There is a bit of a ‘point of conflict’ between those calling for ‘pixel perfect’, regional scale data (Pringle,
182 2020; Pringle & Hutchinson, 2020) and for the means to generate networks that are ecologically plausible
183 *representations* (*sensu* structural networks). This represents two challenges; one is that models that repre-
184 sent generalisations of networks often lack the ability to retrieve any species/community specificity which
185 limits their utility for real world, species-driven scenarios *e.g.*, species driven conservation efforts (Dunn et
186 al., 2009), however networks that are constructed through either (most) empirical observations or through
187 predictive means are fundamentally going to represent metawebs, *i.e.*, lack constrained links, a representation
188 of structure, or energy flow...

189 **3.1.1 Models that predict metawebs (feasible interactions)**

190 This is perhaps the most developed group of models; with a variety of approaches having been developed that
191 typically determine the feasibility of an interaction based on the trait compatibility between predator and
192 prey (*i.e.* their evolutionary compatibility) to determine ‘feeding rules’ (Morales-Castilla et al., 2015). These
193 feeding rules are broadly elucidated in two different ways; mechanistic feeding rules can be explicitly defined
194 and applied to a community (Dunne et al., 2008; *e.g.*, Shaw et al., 2024) or they are inferred from a community
195 for which there is interaction data and the ‘rules’ are then applied to a different community (Caron et al.,
196 2022; Cirtwill et al., 2019; Desjardins-Proulx et al., 2017; Eklöf et al., 2013; Llewelyn et al., 2023; Pichler et
197 al., 2020; Strydom et al., 2022; *e.g.*, Strydom et al., 2023). The fundamental difference between these two
198 model groups is that ‘mechanistic models’ rely on expert knowledge and make assumptions on trait-feeding
199 relationships, whereas the ‘pattern finding’ models are dependent on existing datasets from which to elucidate
200 feeding rules. These models are useful for determining all feasible interactions for a specific community, and
201 owing to the availability of datasets (Gray et al., 2015; *e.g.*, Poelen et al., 2014; Poisot, Baiser, et al., 2016),
202 as well as the development of model testing/benchmarking tools (Poisot, 2023), means that these models
203 can be validated and (with relative confidence) be used to construct first draft networks for communities for
204 which we have no data (Strydom et al., 2022), and are valuable for constructing prehistoric networks (Fricke
205 et al., 2022; Yeakel et al., 2014).

206 **3.1.2 Models that predict realised networks (realised interactions)**

207 In order to construct realised networks models need to incorporate *both* the feasibility of interactions (*i.e.*,
208 determine the entire diet breadth of a species) as well as then determine which interactions are realised (*i.e.*,
209 incorporate the ‘cost’ of interactions). As far as we are aware there is no model that explicitly accounts

for the feasibility (evolutionary compatibility) between species and rather *only* accounts for processes that determine the realisation of an interaction (*i.e.*, abundance, predator choice, or non-trophic interactions). Although the use of allometric scaling *i.e.*, body size (Beckerman et al., 2006; *e.g.*, Valdovinos et al., 2023) may represent a first step in capturing evolutionary compatibility one still needs to account for other feeding traits. In terms of models that do formalise these processes, diet models (Beckerman et al., 2006; Petchey et al., 2008) have been used construct networks based on both predator choice (as determined by the handling time, energy content, and predator attack rate) as well as abundance (prey density). Wootton et al. (2023) developed a model that moves the energy of the system into different modules related to the process of the predator acquiring energy from the prey *i.e.*, compartmentation in food webs (Krause et al., 2003).

3.1.3 Models that predict structure (interaction agnostic)

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

4 Making Progress with Networks: Why Definitions matter

4.1 Further development of models and tools

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

²³⁹ either through the development of tools that do both (predict both interactions and structure), or it might
²⁴⁰ be possible to do a ensemble modelling approach (Becker et al., 2022). Alternatively the development of
²⁴¹ tools that will allow for the downsampling of metawebs into realised networks (*e.g.*, Roopnarine, 2006),
²⁴² although deciding exactly what is driving differences between local networks and the regional metaweb
²⁴³ might not be that simple (Saravia et al., 2022). Probably also something that aligns with trying to predict
²⁴⁴ interaction strength - because that would be the gold standard. Probably also worth just plainly stating that
²⁴⁵ feasibility of developing a model that is both broadly generalisable, but also cas local specificity is probably
²⁴⁶ not attainable (Stouffer, 2019), and more specifically the potential use un models untangling/identifying the
²⁴⁷ different processes (Song & Levine, 2024)

²⁴⁸ 4.2 At what scale should we be predicting/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 defne I mean both delimiting the time and geographic scale at which a network is
²⁵⁸ aggregated at (Estay et al., 2023). This is important because it can influence the inferences made, *e.g.*, the
²⁵⁹ large body of work (landscape theory for food web architecture) that showcases how different species use the
²⁶⁰ landscape will influence network dynamics (Rooney et al., 2008). 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 teh same space does not mean it was at the same timescale
²⁶³ (Brimacombe et al., 2024)

²⁶⁴ 4.3 How should we use different networks?

²⁶⁵ What for and how we can use networks is perhaps one of the biggest ‘gaps’ we have in network ecology
²⁶⁶ (Tim’s EBV ms), and there is a serious need to start drawing clear, ecological links between network form
²⁶⁷ and function (although see Delmas et al., 2019). That being said one of the most important things we can
²⁶⁸ do is to be aware of the parameter space that is possible given a specific definition of a network and operate

269 within those parameters. And we should use this in how we also evaluate/benchmark the performance of the
270 different models as well; Poisot (2023) presents a set of guidelines for assessing how well a model recovers
271 pairwise interactions but we lack any clear strategies for benchmarking structure.

272 **4.4 Feasible, realised, or sustainable?**

273 When do we determine a link to be ‘real’... In the context of feasible networks this is perhaps clearer - if
274 all things were equal (*i.e.*, community context is irrelevant) would the predator be able to consume the
275 prey. However in the realised space there is also the question of the long term ‘energetic feasibility’ of an
276 interaction - just because an interaction is possible in the now is it able to sustain a population in the long
277 term. And what is the scale for that long term - are we thinking at the generational scale? Because ultimately
278 when we are constructing a network we are aggregating not only across space but also across time... This is
279 probably again a Lokta-Volterra space question and something that the dynamic foodweb model (Curtsdotter
280 et al., 2019; Delmas et al., 2017; Lajaaiti et al., 2024) is addressing, but again it is integrating this with the
281 feasible/realised axis.

282 **5 Concluding remarks**

283 I think a big take home will (hopefully) be how different approaches do better in different situations and so
284 you as an end user need to take this into consideration and pick accordingly. I think Petchey et al. (2011)
285 might have (and share) some thoughts on this. I feel like I need to look at Berlow et al. (2008) but maybe
286 not exactly in this context but vaguely adjacent. This is sort of the crux of the argument presented in
287 Brimacombe et al. (2024) as well.

288 Do we expect there to be differences when thinking about unipartite vs bipartite networks? Is there underlying
289 ecology/theory that would assume that different mechanisms (and thus models) are relevant in these two
290 ‘systems’.

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

292 **References**

- 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>
- 305 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of
306 the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- 307 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,
308 V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.
309 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),
310 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 311 Biton, B., Puzis, R., & Pilosof, S. (2024). *Inductive link prediction boosts data availability and enables
312 cross-community link prediction in ecological networks*.
- 313 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.
314 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 315 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A
316 cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 317 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings
318 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),
319 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 320 Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of
321 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- 323 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models
324 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,
325 33(4), e13807. <https://doi.org/10.1111/geb.13807>
- 326 Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with
327 trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>
- 328 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,

- 329 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The
330 environment to the rescue: Can physics help predict predator–prey interactions? *Biological Reviews*,
331 n/a(n/a). <https://doi.org/10.1111/brv.13105>
- 332 Cirtwill, A. R., Eklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for
333 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10(6),
334 902–911. <https://doi.org/10.1111/2041-210X.13180>
- 335 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.
336 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 337 Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., Traugott, M., &
338 Bommarco, R. (2019). Ecosystem function in predator–prey food webs—confronting dynamic models with
339 empirical data. *Journal of Animal Ecology*, 88(2), 196–210. <https://doi.org/10.1111/1365-2656.12892>
- 340 Dalla Riva, G. V., & Stouffer, D. B. (2016). Exploring the evolutionary signature of food webs' backbones
341 using functional traits. *Oikos*, 125(4), 446–456. <https://doi.org/10.1111/oik.02305>
- 342 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,
343 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).
344 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brv.12433>
- 345 Delmas, E., Brose, U., Gravel, D., Stouffer, D. B., & Poisot, T. (2017). Simulations of biomass dynamics in
346 community food webs. *Methods in Ecology and Evolution*, 8(7), 881–886. <https://doi.org/10.1111/2041-210X.12713>
- 349 Desjardins-Proulx, P., Laigle, I., Poisot, T., & Gravel, D. (2017). Ecological interactions and the Netflix
350 problem. *PeerJ*, 5, e3644. <https://doi.org/10.7717/peerj.3644>
- 351 Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction:
352 Are most endangered species parasites and mutualists? *Proceedings. Biological Sciences*, 276(1670),
353 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- 354 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological
355 networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 356 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and
357 Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 359 Eklöf, A., Tang, S., & Allesina, S. (2013). Secondary extinctions in food webs: A Bayesian network approach.
360 *Methods in Ecology and Evolution*, 4(8), 760–770. <https://doi.org/10.1111/2041-210X.12062>
- 361 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks

- 362 over space. *Frontiers in Ecology and Evolution*, 11.
- 363 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,
364 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.
365 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 366 Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: What happens when interspecific interactions
367 interact? *Journal of Animal Ecology*, 80(5), 1097–1108. <https://doi.org/10.1111/j.1365-2656.2011.01852.x>
- 368 x
- 369 Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across
370 the entire tree of life. *Nature*, 465(7300), 918–921. <https://doi.org/10.1038/nature09113>
- 371 Gray, C., Figueroa, D. H., Hudson, L. N., Ma, A., Perkins, D., & Woodward, G. (2015). Joining the dots:
372 An automated method for constructing food webs from compendia of published interactions. *Food Webs*,
373 5, 11–20. <https://doi.org/10.1016/j.fooweb.2015.09.001>
- 374 Higino, G. T., Banville, F., Dansereau, G., Muñoz, N. R. F., Windsor, F., & Poisot, T. (2023). Mismatch
375 between IUCN range maps and species interactions data illustrated using the Serengeti food web. *PeerJ*,
376 11, e14620. <https://doi.org/10.7717/peerj.14620>
- 377 Hutchinson, M. C., Bramon Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., Jordano, P., &
378 Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community
379 ecology. *Functional Ecology*, 33(2), 206–217. <https://doi.org/10.1111/1365-2435.13237>
- 380 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 381 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 382 Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015).
383 Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky
384 shores. *Ecology*, 96(1), 291–303. <https://doi.org/10.1890/13-1424.1>
- 385 Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., Boit, A., Joppa, L. N.,
386 Lafferty, K. D., Williams, R. J., Martinez, N. D., Menge, B. A., Blanchette, C. A., Iles, A. C., & Brose,
387 U. (2012). More than a meal... integrating non-feeding interactions into food webs: More than a meal
388 *Ecology Letters*, 15(4), 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- 389 Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments
390 revealed in food-web structure. *Nature*, 426(6964), 282–285. <https://doi.org/10.1038/nature02115>
- 391 Lajaaiti, I., Bonnici, I., Kéfi, S., Mayall, H., Danet, A., Beckerman, A. P., Malpas, T., & Delmas, E. (2024).
392 *EcologicalNetworksDynamics.jl* A Julia package to simulate the temporal dynamics of complex ecological
393

- 395 networks (p. 2024.03.20.585899). bioRxiv. <https://doi.org/10.1101/2024.03.20.585899>
- 396 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 397
- 398 Llewelyn, J., Strona, G., Dickman, C. R., Greenville, A. C., Wardle, G. M., Lee, M. S. Y., Doherty, S.,
399 Shabani, F., Saltré, F., & Bradshaw, C. J. A. (2023). Predicting predator-prey interactions in terrestrial
400 endotherms using random forest. *Ecography*, 2023(9), e06619. <https://doi.org/10.1111/ecog.06619>
- 401 Maiorano, L., Montemaggiore, A., Ficetola, G. F., O'Connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A
402 species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, 29(9), 1452–1457.
403 <https://doi.org/10.1111/geb.13138>
- 404 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from
405 abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.13380>
- 406
- 407 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from
408 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 409 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic
410 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 411 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web
412 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 413
- 414 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some
415 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 416
- 417 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms
418 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and
419 Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>
- 420 Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks.
421 *Nature Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 422 Poelen, J. H., Simons, J. D., & Mungall, C. J. (2014). Global biotic interactions: An open infrastructure to
423 share and analyze species-interaction datasets. *Ecological Informatics*, 24, 148–159. <https://doi.org/10.1016/j.ecoinf.2014.08.005>
- 424
- 425 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods
426 in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 427 Poisot, T., Baiser, B., Dunne, J., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T. N., Stouffer, D. B., Wood, S.

- 428 A., & Gravel, D. (2016). Mangal – making ecological network analysis simple. *Ecography*, 39(4), 384–390.
- 429 <https://doi.org/10.1111/ecog.00976>
- 430 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
- 431 Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,
- 432 48(7), 1552–1563. <https://doi.org/10.1111/jbi.14127>
- 433 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of
- 434 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/mee.12500>
- 435 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
- 436 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 437 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks
- 438 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 439 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., &
- 440 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint
- 441 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/10.1111/2041-210X.12180>
- 442 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton
- 443 University Press. <https://doi.org/10.1515/9780691195322-020>
- 444 Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology,*
- 445 *Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>
- 446 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.
- 447 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 448 Rooney, N., McCann, K. S., & Moore, J. C. (2008). A landscape theory for food web architecture. *Ecology*
- 449 *Letters*, 11(8), 867–881. <https://doi.org/10.1111/j.1461-0248.2008.01193.x>
- 450 Roopnarine, P. D. (2006). Extinction Cascades and Catastrophe in Ancient Food Webs. *Paleobiology*, 32(1),
- 451 1–19. <https://www.jstor.org/stable/4096814>
- 452 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network
- 453 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),
- 454 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 455 Segar, S. T., Fayle, T. M., Srivastava, D. S., Lewinson, T. M., Lewis, O. T., Novotny, V., Kitching, R. L.,
- 456 & Maunsell, S. C. (2020). The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology &*
- 457 *Evolution*, 35(5), 454–466. <https://doi.org/10.1016/j.tree.2020.01.004>
- 458 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*
- 459 *Ecological Network Analysis*. <https://doi.org/10.1111/9781119990100.0001>
- 460

- 461 reconstructing ancient food webs using functional trait data (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 462
- 463 Song, C., & Levine, J. M. (2024). Rigorous (in)validation of ecological models (p. 2024.09.19.613075). bioRxiv. <https://doi.org/10.1101/2024.09.19.613075>
- 464
- 465 Stock, M. (2021). Pairwise learning for predicting pollination interactions based on traits and phylogeny. *Ecological Modelling*, 14.
- 466
- 467 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*, 88(2), 192–195. <https://doi.org/10.1111/1365-2656.12949>
- 468
- 469 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*, 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- 470
- 471
- 472
- 473 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer learning can help predict potential species interaction networks despite data limitations. *Methods in Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 474
- 475
- 476
- 477 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz, N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap towards predicting species interaction networks (across space and time). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 478
- 479
- 480
- 481 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047. <https://doi.org/10.1002/ecy.3047>
- 482
- 483 Valdovinos, F. S., Hale, K. R. S., Dritz, S., Glaum, P. R., McCann, K. S., Simon, S. M., Thébault, E., Wetzel, W. C., Wootton, K. L., & Yeakel, J. D. (2023). A bioenergetic framework for aboveground terrestrial food webs. *Trends in Ecology & Evolution*, 38(3), 301–312. <https://doi.org/10.1016/j.tree.2022.11.004>
- 484
- 485
- 486 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183. <https://doi.org/10.1038/35004572>
- 487
- 488 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 489
- 490 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 491
- 492 Xie, J.-R., Zhang, P., Zhang, H.-F., & Wang, B.-H. (2017). Completeness of Community Structure in Networks. *Scientific Reports*, 7(1), 5269. <https://doi.org/10.1038/s41598-017-05585-6>
- 493

- 494 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).
- 495 Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>
- 496
- 497 Yodzis, P. (1982). The Compartmentation of Real and Assembled Ecosystems. *The American Naturalist*,
- 498 120(5), 551–570. <https://doi.org/10.1086/284013>
- 499 Yodzis, P., & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*,
- 500 139(6), 1151–1175. <https://doi.org/10.1086/285380>

the "driver" of the interaction
≠ the underlying theory (1:1) & the
'way' we get to the answer is diff
e.g. co-occurrence is about sharing
space/time but we use niche theory/
env. filtering as the means to determine
co-occurrence.

JUN 27		THU 木	179
		(mechanism)	
		what determines interaction	
6	level of obj.	Body of theory	
15	Species	fund. niche/ env. filter	co- occurrence
21	pop.	backgrounds (mora) truit-match	"capacity"
0	indiv.	neutral. funct. resp.	pop size/ dynamics
3		"physicw" 2D 3D prey choice	energy

?? allometric scaling ??

: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS)
BETWEEN SPECIES

Figure 1: TODO.