

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

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Abstract: New perspective on key aim is to showcase how the SuperTriangle represents a synthesis across scales and mechanisms, how this underpins differences in concepts and methods, and how it ultimately defines how to answer fundamental questions and at what scale+type of modelling we need to focus on to advance networks into valuable predictive ecology.

Keywords: food web, network construction, scientific ignorance

1 key ‘aim’ is to highlight how we need to think of interactions at scales and the same goes for
2 predicting. this is important because it will influence the way in which we are actually able
3 to use a network

4 At the heart of modern biodiversity science are a set of concepts and theories about biodiversity, stability
5 and function. These relate to the abundance, distribution and services that biodiversity provides, and how
6 biodiversity – as an interconnected set of species – responds to multiple stressors. The interaction between
7 species (or individuals) is one of the fundamental building blocks of ecological communities. Collecting
8 species interactions among many species (e.g. biodiversity) results in the formation of networks which are
9 long established as a canon of ecology since the penning of the ‘entangled bank’ (Darwin, 1859).

10 The use of species interaction networks provides a powerful abstraction that can help quantify, conceptualise,
11 and understand biodiversity dynamics, and ultimately, one hopes, make prediction, mitigate change and man-
12 age services. Such network representations of biodiversity (including within species diversity) are increasingly
13 argued to be an asset to predictive ecology, climate change mitigation and resource management. Here, it
14 is argued that characterising biodiversity in a network will allow deeper capacity to understand and predict
15 the abundance, distribution, dynamics and services provided by multiple species facing multiple stressors.

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

24 With respect to data, it is extremely challenging to actually record species interactions in the field (Jordano,
25 2016a, 2016b). Despite notable herculean efforts (**Woodward?** **Benguela?**), actual coverage of ‘real world’
26 interaction data is sparse (Poisot et al., 2021). Against this practical challenge, there is additionally high
27 variance in the terminology we use to define networks. Finally, the mathematical and statistical tools we use
28 to construct, conceptualise, analyse and predict with these networks are also highly variable.

- 29 1. what are the underlying assumptions about nodes, edges, scale and process that are made when we
30 attempt to delimit and describe a food webs;
- 31 2. are there families of commonly used tools that map onto assumptions about scales and processes;

32 The provision of this detail ultimately leads to a set of insights and conclusions about whether, when and
33 under what conditions network representations of biodiversity can contribute to the advancement of ecological
34 theory and generate value in predictive ecology. Specifically, we finish this perspective with an overview of
35 fundamental questions in ecology that we think can benefit from network thinking and a proposal that such
36 thinking can accelerate our capacity to predict the impact of multiple stressors on biodiverse communities.

37 1 Setting the Scene: The Not So Basics of Nodes and Edges

38 Important goal here is to introduce the idea that there are multiple facets as to what determines
39 the interaction between species and that there is some sort of ‘scale of organisation’ Figure 2. We
40 can then introduce these different scales/theories and I think some key points to highlights are the
41 *features, limits, and descriptions* of these different scales (by that I mean what rules them, what
42 finds them, and what binds them - sorry not sorry). I think it is also worth either in this section
43 or in the one where we talk about model families to discuss the idea of ‘moving between’ different
44 levels - e.g. downsampling but also feasibility - can we actually do that? ANother interesting
45 discussion here (or maybe actually something that can make its way into the concluding remarks)
46 is thinking about what determines interactions vs what determines structure...

i Box 1 -The anatomy of a food web

Defining a food web seems simple, it is the representation of the interactions (edges) between species (nodes), however the definition of ‘edges’ and ‘nodes’, as well as the scale at which they are aggregated can take many forms. As highlighted in Poisot, Stouffer, et al. (2016) networks can be constructed at the population (the links among individuals), community (the links between species), or metacommunity (fluxes between locations) level. Even if one were to limit their scope to thinking of interaction networks only in terms of food webs at the community-level there are still many ways to define the various components of the network Panel A of 1, one needs to understand the different intentions/assumptions that are made when a food web is constructed. Although the main intention of a food web is to capture and represent the feeding links between species there are many ways to define the nodes (*e.g.*, species or taxonomic group), edges (*e.g.*, **potential or realised feeding links**), the magnitude of the edges (*e.g.*, binary vs probabilistic), and even how the network itself is delimited (does it represent an aggregation of interactions over time?).

[Figure 1 about here.]

1.0.1 How do we define a node?

Although this may seem an elementary question in the context of food webs — a node *should* represent a (taxonomic) species, the reality is that nodes can often represent an aggregation of different species - so called ‘trophic species’ or segregation of species by life stages. Representing nodes as non-taxonomic species can be useful in certain contexts (Williams & Martinez, 2000) and in cases where the adult and larval stages of a species have different diets it may make ecological sense (Clegg et al., 2018) meaning that it is not uncommon that networks often have nodes that have different definitions of a ‘species’ *e.g.* consisting of both taxonomic and trophic species. Practical implications of how we are aggregating the nodes is that the resolution may not always be ‘pixel perfect’ *i.e.*, we may be unable to assess the co-extinction risk of a species pair, however there is value in having nodes that represent an aggregation of species, as these convey a much more general overview of how the links are distributed within the community.

1.0.2 What is meant by an edge?

As discussed earlier there are many ways to define the links between species — even feeding links. At its core links within food webs can be thought of as a representation of either the flow of a resource [ref], realised (Pringle, 2020) or potential (Dunne, 2006) feeding links, or energy transfer and material flow (Lindeman, 1942). How we specify links will influence the resulting structure of the network - and the inferences we will make thereof. For example taking a food web that consists of links representing *potential* feeding links between species will be meaningless if you are interested in understanding *e.g.*, the flow of energy through the system as the links within the network are over represented. 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 (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). Moving away from a purely binary way of representing allows us to quantify a level of (un)certainty of our knowledge of interactions (*i.e.*, moving from being able to ask if they are occurring to quantifying how likely they are to occur) does add an additional level of ‘complexity’ to the construction and interpretation of networks, but ultimately it allows us to capture more information at different scales (Banville et al., 2024).

1.0.3 Putting the parts together; what does it mean?

The ingredients one uses to construct networks from nodes and edges generates a unique representation of the mechanisms (see Box 1 - Mechanisms that determine feeding links) that allow inference and reasoning about the structure, aspects of dynamics (*e.g.*, stability), and potentially the function of communities (*e.g.*, flux). It is thus beneficial to keep in mind that in the process of ‘codifying’ a network one is already embedding some sort of hypothesis as to the nature of the feeding links between species (Brimacombe et al., 2023; Proulx et al., 2005). Here it may be meaningful to contextualise the different ‘types’ of food webs within the larger research programmes (or even practical needs) that have been driving the construction of them.

Before thinking about the ways in which we can predict networks it is perhaps meaningful to take a step back and think about the different criteria that must be met in order for an interaction to be able to occur between two species, specifically thinking of this in terms of distinguishing between the feasibility versus realisation of an interaction and how these are determined (and defined by) different ‘rules’/mechanisms. If we look at this feasibility-reality continuum (Figure 2) it is clear how the different predictive approaches (methods) tend to fall within one of the broader categories identified (distinguished) in the triangle. This is not to say that this shortcoming should be viewed as a ‘bug’ but rather a ‘feature’ of the field as it allows one to engage with, as well as construct networks at different scales, which is particularly valuable if one takes into consideration the considerable ‘data cost’ of predicting well resolved, realised networks in comparison to constructing high-level metawebs. However, it is important that there is an awareness and acknowledgement of where within this feasibility-reality one is working at and how this will impact and limit the contexts in which the resulting network can be used and applied within.

49

50 2 From Nodes and Edges to Scales and Processes

51 Armed with these basics, it is now possible to review the scales and assumptions that are made by a wide
52 range of tools to assist in constructing networks against poor data with the hope of capturing important
53 processes that underpin accurate prediction. Our thesis centres on a four-tier conceptualization of networks:
54 co-occurrence, feasibility, mass effects and energetics. In the following sections we review each of these and
55 then provide a synthesis among them.

56 **2.1 Understanding the drivers of species interactions**

57 Important goal here is to introduce the idea that there are multiple facets as to what determines the interaction
58 between species and that there is some sort of ‘scale of organisation’ Figure 2. We can then introduce these
59 different scales/theories and I think some key points to highlights are the features, limits, and descriptions
60 of these different scales (by that I mean what rules them, what finds them, and what binds them - sorry not
61 sorry). I think it is also worth either in this section or in the one where we talk about model families to
62 discuss the idea of ‘moving between’ different levels - e.g. downsampling but also feasibility - can we actually
63 do that? Another interesting discussion here (or maybe actually something that can make its way into the
64 concluding remarks) is thinking about what determines interactions vs what determines structure...

- 65 • These different theories are shown in Figure 2 and we can see there is some element of scaling (species
66 - population - individual)

67 [Figure 2 about here.]

68 **1. (Co)occurrence**

69 Although the outright assumption that because two species are co-occurring it must mean that they are
70 interacting is inherently flawed (Blanchet et al., 2020), it is of course impossible for two species to interact (at
71 least in terms of feeding links) if they are not co-occurring in time and space. Hence it is of course important
72 to take into consideration the co-occurrence of both the resource and the consumer. An example of this
73 would be the work from Dansereau et al. (2023), where a metaweb (feasibility network) is downsampled into
74 smaller realisations based on better data/knowledge as to which species are occurring at a specific location
75 - however arguably these are still firmly in the space of feasible interactions for the specific location but are
76 approaching a better approximation of ‘reality’...

77 **2. Feasibility**

78 This is based on the idea of forbidden links introduced by Jordano (2016b), specifically that there must
79 be some degree of *trait complementarity* that allows a predator to chase, capture, kill, and consume, its
80 prey. This is probably the level that the idea of a metaweb (Dunne, 2006) is most applicable to. Within
81 the network prediction ‘field’ this is perhaps the most developed space. Predictive models run the gamut
82 including mechanistic models (Morales-Castilla et al., 2015), binary classifiers (Pichler et al., 2020), and
83 graph embedding (Strydom et al., 2023) and use either traits (or phylogeny as a proxy for the conservation
84 thereof) as a means to ‘evaluate’ if an interaction is *possible* between two species (again not the likelihood
85 of it happening but the likelihood of its feasibility). It is probably worth having a brief interlude here to be
86 really clear that just because an interaction is probabilistic it does not make it weighted (at least not in the

⁸⁷ traditional sense of weighted interactions, *e.g.*, J. T. Wootton & Emmerson (2005)) - it is still ‘binary’, it
⁸⁸ just happens to be defined by a binomial distribution (*sensu* Banville et al. (2024)).

⁸⁹ **3. Mass effect**

⁹⁰ Not sure if there are models that ‘only’ consider abundance (barring the neutral model) and that it is rather
⁹¹ more of a building block in some of the models that are more relevant to the next steps. Maybe there is an
⁹² argument that this ‘rule’ is ‘irrelevant’ in the context of how I am presenting network prediction and more
⁹³ so a data parameter one needs... maybe...

⁹⁴ This is probably the point where we start to shift from a *potential* (presence/absence) way of defining
⁹⁵ interactions and start moving into the ‘qualitative’/weighted interaction space - we are not ‘determining’ if
⁹⁶ the interaction is feasible but rather making an assumption on prey selection based on the species’ likelihood
⁹⁷ of ‘meeting’, although Banville et al. (2024) presents a compelling case that this could still be considered
⁹⁸ something that falls under the ‘feasibility’ and not ‘reality’ side of the spectrum... (well at least past Tanya
⁹⁹ seemed to think so)

¹⁰⁰ **4. Energetics**

¹⁰¹ This is where we begin to move into the foraging ecology space - specifically consumption rate and how that
¹⁰² pertains to energy acquisition *i.e.*, optimal foraging theory. In the loosest sense I think this is the ‘prey choice’
¹⁰³ space - but specifically in the context of how prey choice as informed by energetic cost (not just purely based
¹⁰⁴ on *e.g.*, the most abundant species). If we think about ways that people have approached this there are the
¹⁰⁵ diet models of (Beckerman et al., 2006) and (Petchey et al., 2008) as well as the ‘trait’ framework developed
¹⁰⁶ by K. L. Wootton et al. (2023) that moves the ‘energy’ into different ‘modules’ related to the process of
¹⁰⁷ the consumer acquiring energy from the resource (however there is a disregard for the ‘Rule 1’ requirement
¹⁰⁸ of forbidden links, again not bad just pointing it out). The idea of the consumer search space developed
¹⁰⁹ by Pawar et al. (2012) is also an interesting consideration. Finally the environment itself is also imposing
¹¹⁰ energy costs on the predator. Basically the ideas presented in Cherif et al. (2024), which is essentially a
¹¹¹ take on movement ecology? What it boils down to is being able to quantify the cost of movement *i.e.*, the
¹¹² physical constraints that the environment imposes on a species... Maybe we can also think of it more in terms
¹¹³ of metabolic rate?

¹¹⁴ 3 Network prediction is scale dependent

¹¹⁵ The way in which we predict a network is driven by the underlying theory Figure 2 which con-
¹¹⁶ strains or informs the assumptions we make (this of course also has implications with regards
¹¹⁷ to how the resulting network is defined (Box 1)). We can then spend a moment introducing
¹¹⁸ the different model families Table 1. I think a clear messaging here might be that models can
¹¹⁹ share a similar underlying theory but use different methods to get there (*e.g.*, using ecological
¹²⁰ rules (explicit), ecological expectations (pattern finders), or mathematical models (assumptions
¹²¹ on the structure of the matrix - maybe even network)). Importantly different models will also
¹²² have different ‘limits’ to them - this is probably a product of both where they are found within
¹²³ the ‘theory space’ Figure 2 as well as the definition of the network (Box 1) space. Should we
¹²⁴ also maybe revisit the idea of interaction vs structure predictors... I think it is still a point that
¹²⁵ is worth raising but no longer the framework on which we hang the different model families...

- ¹²⁶ • The way in which we predict networks is ‘constrained’/informed by the different theories shown in
¹²⁷ Figure 2
- ¹²⁸ • Need to be aware of this and be aware how/what we can use the networks - Petchey dilemma
- ¹²⁹ • The ‘scale’ that a network is constructed should be a determinant of what we can learn about a system
¹³⁰ *e.g.*, can’t use a feasibility network to learn something about energy flows. This is because they are
¹³¹ capturing different processes
- ¹³² • Link the ‘model families’ to the different scales/theories
- ¹³³ • Data...

¹³⁴ As discussed in Box 1 there are many ways to define a food web, meaning that there are equally as many
¹³⁵ reasons one might be interested in predicting a food web. However we may think of two primary drivers
¹³⁶ for wanting to predict networks (Panel B Figure 1), namely an interest in generating a set of ecologically
¹³⁷ plausible networks (*i.e.*, being able to describe networks using a model) or being able to recover (predict)
¹³⁸ location specific, ‘realised’, interactions for a specific species community (*i.e.*, being able to predict/infer the
¹³⁹ interactions between species). Of course these two categories are not distinct, mutually exclusive, groups but
¹⁴⁰ can rather be viewed as operating on a continuum ranging from a need for generality (*i.e.*, creating a network
¹⁴¹ that, when taken in aggregate, the distribution of links (interactions) between nodes (species) are ecologically
¹⁴² plausible) to a need for specificity (*i.e.*, local-level predictions between specific species pairs). Although the
¹⁴³ ability to predict ‘real-world’ interactions (and the resulting food webs) can have more intuitive ‘real world’

¹⁴⁴ applications *e.g.*, being able to ‘recover’ food webs that have since gone extinct (Dunne et al., 2008; Yeakel
¹⁴⁵ et al., 2014), using pairwise interactions to understand species distributions (Pollock et al., 2014) or even
¹⁴⁶ co-extinction risk (Dunn et al., 2009), a more structural approach to network construction affords one an
¹⁴⁷ opportunity to interrogate some of the more high-level mechanisms that are structuring networks (Box 1).

¹⁴⁸ It is perhaps more important that when one is talking about ‘why’ they want to predict networks to articulate
¹⁴⁹ exactly what anatomical part of the food web we are interested in scrutinising.

¹⁵⁰ 3.1 How do we predict food webs?

¹⁵¹ Selecting a model for the task of network prediction should come down to two things; what *aspect* of a
¹⁵² food web one is interested in predicting, and what data are available, necessary, and sufficient. As shown
¹⁵³ in panel B of Figure 1 the interest in a network is (usually) at either the ‘structural’ or ‘interaction’ level
¹⁵⁴ and the development of models for the task of network prediction often focus on high fidelity (performance)
¹⁵⁵ at one of these scales. With this in mind it is beneficial to think of the different model families relative
¹⁵⁶ to these two different goals; here we refer to models that are used to predict the structure of a network as
¹⁵⁷ **topology generators** and models developed to infer the interactions for a given species pool as **interaction**
¹⁵⁸ **predictors**. It is meaningful to make this distinction because although it is possible to construct a food
¹⁵⁹ web given using an *interaction predictor* the models themselves lack any sort of parametrisation of the
¹⁶⁰ network structure and so the resulting network is a poor reflection of the actual network structure (Caron
¹⁶¹ et al., 2024). This is primarily because *interaction predictors* are models that evaluate the feasibility of
¹⁶² an interaction between species pairs and not in the context of feasibility at the community level. Models
¹⁶³ themselves are a reflection of the different goals and intentions of the research program from which they are
¹⁶⁴ developed and are often ‘described’ by a specific mechanism that will determine the resulting structure or
¹⁶⁵ interactions (Box 1). Models such as the niche (Williams & Martinez, 2000) or cascade (Cohen et al., 1990)
¹⁶⁶ were developed with the intent of being used to understand the *structural* aspects of food webs, specifically
¹⁶⁷ how links are distributed amongst species in the community, whereas bayesian (Cirtwill et al., 2019) or trait
¹⁶⁸ hierarchy (Shaw et al., 2024) models have been developed on the basis that the traits of a species are the
¹⁶⁹ underlying mechanism in determining the feasibility of interactions (*i.e.*, species *a* has the capacity to eat
¹⁷⁰ species *b*). Along with predicting different anatomical parts of a food web the different models have varying
¹⁷¹ degrees of data that are needed to ‘parametrise’ the network. Once these two limitations are assessed and
¹⁷² addressed it is then possible to select the model (or model family) that will best be able to capture food
¹⁷³ web feature that the researcher is most interested in (see Box 2 - Assessing model outputs). It is thus clear
¹⁷⁴ that (realistically) there will probably never be a ‘best fit’ tool that is able to construct a food web that

175 will span the entire range of needs, and rather the responsibility lies with the researcher to be aware of not
176 only the underlying philosophy of the specific toolset (as this could have knock-on effects when using those
177 networks for downstream analyses/simulations; pers. comms. Beckerman, 2024), but also how well the tool
178 can retrieve the specific network or interaction properties that is of interest.

179 In order for a model to formalise a ‘complete’ food web it is necessary to formalise two aspects
180 of the network, ‘who eats whom’ (to determine the links between nodes) as well as the structure
181 of the network (to limit the distribution of links), however most models are inclined to focus on
182 one of the two aspects panel B of 1.

183 Crucially most topology generators lack some key data on the interaction between species (this
184 can be because of how the model itself defines species or the way in which links are assigned in
185 the network) and interaction predictors lack some sort of parametrisation of network structure
186 (just because two species can interact it does not mean that they will, Poisot et al., 2015).

187 What is the purpose of generating a network? Is it an element of a bigger question we are asking,
188 e.g., I want to generate a series of networks to do some extinction simulations/bioenergetic stuff
189 OR are we looking for a ‘final product’ network that is relevant to a specific location? (this can
190 still be broad in geographic scope).

191 3.2 Categorizing Model Families

192 NEED A TRANSITION PARAGRAPH

193 As there are many food web models to choose from it is perhaps useful to think about the models in terms of
194 model families, a summary of these families is presented in Table 1 highlights the differences and similarities
195 of the philosophies and assumptions that determine a network. A more extensive overview of the different
196 models that fall with in the different model families can be found in SuppMat 1 and for a more detailed
197 breakdown of the different ‘traits’ of the model families refer to SuppMat 2.

Table 1: A summary of the different families of tools that can be used to generate food webs. Here ‘type’ leans on the ideas from Momal et al. (2020) in terms of reconstructing networks from other known (observed) interactions and inferring interactions without relying on observed interactions.

Model family	Assumption	Theory	Type	Key reference
null	Links are randomly distributed within a network		network inference	

Model family	Assumption	Theory	Type	Key reference
neutral	Network structure is random, but species abundance determines links between nodes	abundance	network inference	Canard et al. (2012)
resource	Networks are interval, species can be ordered on a ‘niche axis’		network inference	Williams & Martinez (2008)
generative	Networks are determined by their structural features		network reconstruction	
energetic	Interactions are determined by energetic costs	abundance + energy	network reconstruction	
graph embedding	Interactions can be predicted from the latent traits of networks	feasibility	network reconstruction	Strydom et al. (2023)
trait matching	Interactions can be inferred by a mechanistic framework/relationships	feasibility	network reconstruction	Morales-Castilla et al. (2015)
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	feasibility	network reconstruction	Pichler et al. (2020)
expert knowledge	‘Boots on the ground’ ecological knowledge and observations	feasibility	network reconstruction	
data scavenging	Webscraping to create networks from online databases		network reconstruction	Poisot, Gravel, et al. (2016) (f you squint?)
co-occurrence	co-occurrence patterns arise from interactions so we can use these patterns to reverse engineer the interactions	co-occurrence	network inference	

¹⁹⁸ 4 Making Progress with Networks

¹⁹⁹ In this section I want to highlight that we don't actually have any clear guidelines as to how we can 'use'
²⁰⁰ networks - which probably stems from both the fact that when I am talking about a network and when
²⁰¹ someone else is talking about a network we may actually be talking about two very different conceptualisations
²⁰² of 'a network' (this should actually be a selling point in the intro - may have just found my *raison d'être*) as
²⁰³ well as that a lot of the ideas that we have about networks are not really tied to any sort of tangible function
²⁰⁴ (i.e. Tim's GeoBon ms thing-y). However we can maybe at least try to present some guidelines - but I think
²⁰⁵ specifically within the sort of Petchy dilemma space and clearly tied to the ideas we discuss in the ms. This
²⁰⁶ includes: understanding the limits of how a network is defined and how the underlying theory impacts the use
²⁰⁷ as well as data?? IDK we need to shoehorn data in here somehow... We can also use this as a gap identifying
²⁰⁸ space and I think the framing can still rest under the limits concept particularly time, space, and boundaries
²⁰⁹ - which will all probably fall under some aspect of biological scale... We can also raise the idea of trust - as in
²¹⁰ which methods have more support/trust than others. Also what even a 'real' network entails (and this links
²¹¹ again back to Tim's stuff) as well as a subtle jab at Pringles notion that the most critical issue in the world
²¹² of food webs is being able to identify every. single. link. even though there is no real discussion as to what
²¹³ is an 'opportunistic' link vs a link that represents a sustainable energy source for a population (or would it
²¹⁴ be an individual)...

²¹⁵ We need to be aware of the parameter space that is possible given a specific definition of a network and
²¹⁶ operate within those parameters.

²¹⁷ 5 Concluding remarks

²¹⁸ I think the idea of time and how we are aggregating networks across that should be a prominent feature
²¹⁹ here...

²²⁰ • In certain situations structure is 'enough' but there may be use cases where we are really interested in
²²¹ the node-level interactions *i.e.*, species identity is a thing we care about and need to be able to retrieve
²²² specific interactions at specific nodes correctly.

²²³ • Why do interaction models do so badly at predicting structure? Nuance of metaweb vs realisation but
²²⁴ also time? At the core of it interaction models are trained on existing interaction data; this is data
²²⁵ that are most likely closer to a metaweb than a local realisation even if they are being inventoried at a
²²⁶ small scale...

- 227 – We can briefly shoehorn downsampling here maybe??
- 228 • It will be interesting to bring up the idea that if a model is missing a specific pairwise link but doing
229 well overall then when does it matter?
- 230 – The fact that *some* people are concerned about the taxonomic resolution and cascading effects
231 those might have on our understanding of network structure (Pringle, 2020; Pringle & Hutchinson,
232 2020), but that puts us in a place where we are at risk of losing our ability to distinguish the wood
233 from the tree - are we not (at least at times) concerned more with understanding ecosystem level
234 processes than with needing to understand things *perfectly* at the species level.
- 235 – I don't think these 'rare'/nuanced links (e.g. carnivorous hippos) are going to rock the boat when
236 we think about networks at the structural level.
- 237 “The resolution of food-web data is demonic because it can radically change network topology
238 and associated biological inferences in ways that are unknowable in the absence of better data.” -
239 Pringle & Hutchinson (2020) The counter to this is that structural models are often not working
240 at the species level and thus the structure remains ‘unchanged’ when you increase the resolution
241 - I don't think that people are that concerned with the structure of real world networks barring
242 connectance and since that scales with species richness anyway your final proportion will probably
243 still remain the same...
- 244 • I think a big take home will (hopefully) be how different approaches do better in different situations
245 and so you as an end user need to take this into consideration and pick accordingly. I think Petchey
246 et al. (2011) might have (and share) some thoughts on this. I feel like I need to look at Berlow et al.
247 (2008) but maybe not exactly in this context but vaguely adjacent.
- 248 – I think this is sort of the crux of the argument presented in Brimacombe et al. (2024) as well.
- 249 “we highlight an interesting paradox: the models with the best performance measures are not
250 necessarily the models with the closest reconstructed network structure.” - Poisot (2023)
- 251 • Do we need network models to predict interactions and interaction models to predict structure?
- 252 – “Another argument for the joint prediction of networks and interactions is to reduce circularity
253 and biases in the predictions. As an example, models like linear filtering generate probabilities of
254 non-observed interactions existing, but do so based on measured network properties.” - Strydom
255 et al. (2021)
- 256 – Aligning (dove-tailing) with this the idea of ensemble modelling as presented by Becker et al.

257 (2022)

258 • Close out with a call to action that we have models that predict networks very well and models that
259 predict interactions very well but nothing that is doing well at predicting both - this is where we should
260 be focusing our attention when it comes to furthering model development...

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

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

266 do we bring this up? this could be a box... if we have the ‘finances’ for it... otherwise it should go to the
267 outstanding questions fur sure

268 “That being said, there is a compelling argument for the need to ‘combine’ these smaller functional units
269 with larger spatial networks (Fortin et al., 2021) and that we should also start thinking about the interplay
270 of time and space (Estay et al., 2023). Although deciding exactly what measure might actually be driving
271 differences between local networks and the regional metaweb might not be that simple (Saravia et al., 2022).”

272 5.1 Time

273 We lack a clear agenda (and conceptualisation) as to what the appropriate level of aggregation is for a
274 ‘network’. Realistically most empirical networks are more aligned with ‘feasibility networks’ as opposed to
275 ‘realised networks’ as they are often the result of some sort of aggregation of observations across time. This
276 ‘problem’ is two-fold. Firstly we need to think about how this affects any sort of development of theory
277 that sits closer to the ‘realised network’ side of the spectrum - how often are we trying to ask and answer
278 questions about realised networks using feasible networks? The second is that this lack of ‘direction’ as to
279 how we should define a network is (actually) probably one of the biggest barriers that is affecting the use of
280 networks in applied settings...

281 Another time perspective question is when do we determine a link to be ‘real’... In the context of feasible
282 networks this is perhaps clearer - all things equal would the predator be bale to consume the prey. However
283 in the realised space there is also the question of the long term ‘energetic feasibility’ of an interaction - just
284 because an interaction is possible in the now is it able to sustain a population in the long term. And what
285 is the scale for that long term - are we thinking at the generational scale? Because ultimately when we are
286 constructing a network we are aggregating not only across space but also across time.

287 **Glossary**

Term	Definition
food web	a representation of feeding links between species
topology generator	a model that predicts a network based on assumptions of structure, this network is species agnostic in the sense that it does not necessarily contain information at the node level
interaction predictor	a model that predicts species interactions, these interactions can be used to construct a network but there are no <i>a priori</i> assumptions as that will constrain the network structure
model	A tool that can be used to construct food webs, where the resulting network is a representation of a real world network. Models typically only capture specific elements of real world networks and are intended to be used in specific settings
model family	A family of models that share an underlying philosophy when it comes to the mapping, pragmatism, and reduction of a network. Families have the same underlying philosophies and assumptions that determine the links between nodes as well as how these may be encoded
metaweb	A network that represents <i>all</i> the potential links between species. Importantly these links will not necessarily all be realised in a specific location for a specific time
realised network	A network that represents the links between species that are occurring. These networks represent a very localised network...
potential feeding link	links that indicate that an interaction is ecologically feasible but not realised <i>per se</i> (a metaweb would contain potential feeding links)

Term	Definition
realised feeding link	links that indicate that the interaction is realised ‘in the field’. (a realised network contains realised feeding links)
confusion matrix	captures the number of true positives (interaction predicted as present when it is present), false negatives (interaction predicted as absent when it is present), false positives (interaction predicted as present when it is absent), and true negatives (interaction predicted as absent when it is absent)

²⁸⁸ Outstanding questions

- ²⁸⁹ • non-consumptive effects
- ²⁹⁰ • how do we define the spatial and temporal ‘boundaries’ of a network?
- ²⁹¹ • how do we define a ‘real’ network?

²⁹² References

- ²⁹³ Banville, F., Strydom, T., Blyth, P., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas, T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2024). *Deciphering probabilistic species interaction networks*. EcoEvoRxiv. <https://doi.org/10.32942/X28G8Z>
- ²⁹⁶ Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T. A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling, E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic 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)
- ³⁰⁰ Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- ³⁰³ Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>

- 305 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,
306 V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.
307 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),
308 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 309 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.
310 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 311 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A
312 cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 313 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings
314 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),
315 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 316 Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of
317 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7(8), e38295. <https://doi.org/10.1371/journal.pone.0038295>
- 318 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models
319 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,
320 33(4), e13807. <https://doi.org/10.1111/geb.13807>
- 321 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,
322 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The
323 environment to the rescue: Can physics help predict predator-prey interactions? *Biological Reviews*,
324 n/a(n/a). <https://doi.org/10.1111/brv.13105>
- 325 Cirtwill, A. R., Ekklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for
326 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10(6),
327 902–911. <https://doi.org/10.1111/2041-210X.13180>
- 328 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.
329 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 330 Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag.
- 331 Dansereau, G., Barros, C., & Poisot, T. (2023). *Spatially explicit predictions of food web structure from
332 regional level data*.
- 333 Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured
334 Races in the Struggle for Life*. J. Murray.
- 335 Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction:
336 Are most endangered species parasites and mutualists? *Proceedings. Biological Sciences*, 276(1670),

- 338 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- 339 340 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 341 342 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 343 344 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks over space. *Frontiers in Ecology and Evolution*, 11.
- 345 346 347 Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 288(1949), rspb.2020.1889, 20201889. <https://doi.org/10.1098/rspb.2020.1889>
- 348 349 350 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 351 352 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 353 354 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 355 356 357 Momal, R., Robin, S., & Ambroise, C. (2020). Tree-based inference of species interaction networks from abundance data. *Methods in Ecology and Evolution*, 11(5), 621–632. <https://doi.org/10.1111/2041-210X.13380>
- 358 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 360 361 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 362 363 364 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 365 366 367 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 368 369 370 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>

- 371 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods*
372 in *Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 373 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
374 Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,
375 48(7), 1552–1563. <https://doi.org/10.1111/jbi.14127>
- 376 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of
377 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10>
- 378 Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B.,
379 & Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological
380 hypotheses. *Ecography*, 39(4), 402–408. <https://doi.org/10.1111/ecog.01941>
- 381 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
382 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 383 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks
384 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 385 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O’Hara, R. B., Parris, K. M., Vesk, P. A., &
386 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint
387 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/>
388 [10.1111/2041-210X.12180](https://doi.org/10.1111/2041-210X.12180)
- 389 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton
390 University Press. <https://doi.org/10.1515/9780691195322-020>
- 391 Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology,*
392 *Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>
- 394 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.
395 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 396 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network
397 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),
398 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 399 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*
400 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 402 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,
403 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer

- 404 learning can help predict potential species interaction networks despite data limitations. *Methods in*
405 *Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 406 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
407 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap
408 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*
409 *the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 410 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.
411 <https://doi.org/10.1002/ecy.3047>
- 412 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
413 <https://doi.org/10.1038/35004572>
- 414 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food
415 webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 416 Wootton, J. T., & Emmerson, M. (2005). Measurement of Interaction Strength in Nature. *Annual Review of*
417 *Ecology, Evolution, and Systematics*, 36(1), 419–444. <https://doi.org/10.1146/annurev.ecolsys.36.091704.175535>
- 419 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory
420 of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 421 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).
422 Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>



Figure 1: The many ways in which a food web can be defined and described at the node, edge, and even network level.

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.

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			(mechanism)	
			what determines	
			interaction	
6		Body of theory		
15	Species	fund. niches env. filter	co- occurrence	
21		buck bones (mora)	"capacity"	
0	pop.	truit-match		
3	indiv.	neutral. funct. resp.	pop size / dynamics	
?? allometric scaling ??				
				: THEORY OF WHAT DETERMINES FEEDING LINKS (INTERACTIONS) BETWEEN SPECIES

Figure 2: TODO.