

# **Navigating food web prediction; assumptions, rationale, and methods**

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**Abstract:** TODO

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1 At the heart of modern biodiversity science are a set of concepts about biodiversity, community structure,  
2 productivity, and asynchrony, and how they define the stability, resilience, and dynamics of complex com-  
3 munities. The use of species interaction networks provides a powerful abstraction that one can use to help  
4 quantify, conceptualise, and understand these concepts. However, network ecology has its own nuance and  
5 idiosyncrasies that not only provide a barrier to entry but causes dissonance even within the field (Dormann,  
6 2023). This is perhaps particularly pervasive within the space of network prediction...

7 One of the fundamental challenges that we are faced when working with and studying interaction networks  
8 (and, within the context of this manuscript, specifically food webs) is that there is a scarcity of ‘real world’  
9 interaction data (Hortal et al., 2015; Poisot et al., 2021). The difficulty of recording interactions in the field  
10 (Jordano, 2016a, 2016b) has necessitated that researchers find and develop alternative means to construct  
11 and build food webs using **models** (Morales-Castilla et al., 2015; Strydom et al., 2021). Over the past  
12 decade, there has been a proliferation of tools and processes for characterising food webs, these models  
13 span a wide range of philosophies that rely on different approaches, data, and definitions, which ultimately  
14 determine how the food web is constructed and coded. Although the development of these different models  
15 have carved out the path for constructing either synthetic, ecologically plausible networks (Poisot, Gravel,  
16 et al., 2016), or providing ‘first draft’ networks that can be utilised in real world settings (Strydom et al.,  
17 2022) we are still lacking in discussions that are explicitly comparing and contrasting how the way one  
18 chooses to approach the task of constructing a food web is introducing (and ultimately embedding) specific  
19 assumptions and hypotheses (Petchey et al., 2008). Most attempts that focus on comparing and contrasting  
20 models are focused on the same group of **model families** (Pichler et al., 2020; Williams & Martinez, 2008)  
21 and only benchmark the different models as opposed to contextualising them within the bigger framework  
22 of understanding the data needs of the different models, as well as how the resulting network is defined and  
23 structured. As food webs become a more integrated part of some of the broader fields of ecology (Bhatia et  
24 al., 2023; Thuiller et al., 2024) it is critical that we review these different model families as a whole (not only  
25 in isolation), and move away from simply benchmarking the performance of these different model families.  
26 This is important because different models impose different constraints upon themselves and will not only  
27 delimit and dictate the potential questions one will be able to ask (Petchey et al., 2011) but also determine  
28 the appropriate research setting for which the model (and resulting network) can be used. For example  
29 the use of ‘structural food webs’ are useful for developing additional theory such as re-wiring of networks  
30 (Staniczenko et al., 2010) but would be meaningless if one’s intention is to produce a location-specific network  
31 [do we need an *e.g.*, ref??]. This will allow us to ensure the right models are being used to answer the right  
32 questions, particularly within the context of trying to accelerate cross-cutting research in the face of global

33 change.

34 When navigating the seas of using and constructing food webs the researcher needs to be able to clearly  
35 articulate and define the parameters that are used to define their food web(s) of interest. This will aid them  
36 in being able to select the correct model to help them to reach their goal. In order to be able to make  
37 informed decisions it is important that one has a strong grasp of exactly what it means to ‘code’/define  
38 a food web (?@sec-network-anatomy), a clear understanding of why one wants to predict a food web  
39 (?@sec-network-why), and ultimately one needs to be able to asses and evaluate which model family is  
40 going to best match up with the goal of network prediction (Section 1.2). Here we specifically aim to look  
41 at not look at only the performance of the different models but also initiate a (thus far lacking) discussion  
42 around how the interplay between the language used to define networks and the underlying theory/philosophy  
43 should also be a part of the broader discussion when it comes to the task of ‘model selection’.

## 44 1 Understanding the drivers of species interactions

- 45 • Multiple facets as to what determines interactions and the resulting food web (link here to box one and  
46 how this is going to result in potentially very different food webs)
- 47 • These different theories are shown in Figure 1 and we can see there is some element of scaling (species  
48 - population - individual)

49 [Figure 1 about here.]

### 50 1. (Co)occurrence

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

### 59 2. Feasibility

60 This is based on the idea of forbidden links introduced by Jordano (2016b), specifically that there must  
61 be some degree of *trait complementarity* that allows a predator to chase, capture, kill, and consume, its

62 prey. This is probably the level that the idea of a metaweb (Dunne, 2006) is most applicable to. Within  
63 the network prediction ‘field’ this is perhaps the most developed space. Predictive models run the gamut  
64 including mechanistic models (Morales-Castilla et al., 2015), binary classifiers (Pichler et al., 2020), and  
65 graph embedding (Strydom et al., 2023) and use either traits (or phylogeny as a proxy for the conservation  
66 thereof) as a means to ‘evaluate’ if an interaction is *possible* between two species (again not the likelihood  
67 of it happening but the likelihood of its feasibility). It is probably worth having a brief interlude here to be  
68 really clear that just because an interaction is probabilistic it does not make it weighted (at least not in the  
69 traditional sense of weighted interactions, *e.g.*, J. T. Wootton & Emmerson (2005)) - it is still ‘binary’, it  
70 just happens to be defined by a binomial distribution (*sensu* Banville, in prep).

### 71 **3. Mass effect**

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

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

### 82 **4. Energetics**

83 This is where we begin to move into the foraging ecology space - specifically consumption rate and how that  
84 pertains to energy acquisition *i.e.*, optimal foraging theory. In the loosest sense I think this is the ‘prey choice’  
85 space - but specifically in the context of how prey choice as informed by energetic cost (not just purely based  
86 on *e.g.*, the most abundant species). If we think about ways that people have approached this there are the  
87 diet models of (Beckerman et al., 2006) and (Petchey et al., 2008) as well as the ‘trait’ framework developed  
88 by K. L. Wootton et al. (2023) that moves the ‘energy’ into different ‘modules’ related to the process of the  
89 consumer acquiring energy from the resource (however there is a disregard for the ‘Rule 1’ requirement of  
90 forbidden links, again not bad just pointing it out). The idea of the consumer search space developed by  
91 Pawar et al. (2012) is also an interesting consideration.

92 I think this should be its own rule since its really more about the idea of how the environment is imposing

93 energy costs on the predator as opposed the energetic costs (and gain) of consuming the prey. Basically the  
94 ideas presented in Cherif et al. (2024), which is essentially a take on movement ecology? What it boils down  
95 to is being able to quantify the cost of movement *i.e.*, the physical constraints that the environment imposes  
96 on a species... Maybe we can also think of it more in terms of metabolic rate?

### **i** Box 1 -The anatomy of a food web

Important goal of this box is to highlight the different terminology that is used to describe a food web but especially in the context of the ‘feasibility’ vs ‘realised’ food webs

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 2, 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 2 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, in prep).

### 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 1) 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.

99

## 100 1.1 Network prediction is scale dependant

- 101 • The way in which we predict networks is ‘constrained’/informed by the different theories shown in  
102 Figure 1
- 103 • Need to be aware of this and be aware how/what we can use the networks - Petchy dilemma
- 104 • The ‘scale’ that a network is constructed should be a determinant of what we can learn about a system  
105 e.g., can’t use a feasibility network to learn something about energy flows. This is because they are  
106 capturing different processes
- 107 • Link the ‘model families’ to the different scales/theories
- 108 • Data...

109 As discussed in Box 1 there are many ways to define a food web, meaning that there are equally as many  
110 reasons one might be interested in predicting a food web. However we may think of two primary drivers  
111 for wanting to predict networks (Panel B Figure 2), namely an interest in generating a set of ecologically  
112 plausible networks (*i.e.*, being able to describe networks using a model) or being able to recover (predict)  
113 location specific, ‘realised’, interactions for a specific species community (*i.e.*, being able to predict/infer the  
114 interactions between species). Of course these two categories are not distinct, mutually exclusive, groups but  
115 can rather be viewed as operating on a continuum ranging from a need for generality (*i.e.*, creating a network  
116 that, when taken in aggregate, the distribution of links (interactions) between nodes (species) are ecologically  
117 plausible) to a need for specificity (*i.e.*, local-level predictions between specific species pairs). Although the

ability to predict ‘real-world’ interactions (and the resulting food webs) can have more intuitive ‘real world’ applications *e.g.*, being able to ‘recover’ food webs that have since gone extinct (Dunne et al., 2008; Yeakel et al., 2014), using pairwise interactions to understand species distributions (Pollock et al., 2014) or even co-extinction risk (Dunn et al., 2009), a more structural approach to network construction affords one an opportunity to interrogate some of the more high-level mechanisms that are structuring networks (Box 1). It is perhaps more important that when one is talking about ‘why’ they want to predict networks to articulate exactly what anatomical part of the food web we are interested in scrutinising.

## 1.2 How do we predict food webs?

Selecting a model for the task of network prediction should come down to two things; what *aspect* of a food web one is interested in predicting, and what data are available, necessary, and sufficient. As shown in panel B of Figure 2 the interest in a network is (usually) at either the ‘structural’ or ‘interaction’ level and the development of models for the task of network prediction often focus on high fidelity (performance) at one of these scales. With this in mind it is beneficial to think of the different model families relative to these two different goals; here we refer to models that are used to predict the structure of a network as **topology generators** and models developed to infer the interactions for a given species pool as **interaction predictors**. It is meaningful to make this distinction because although it is possible to construct a food web given using an *interaction predictor* the models themselves lack any sort of parametrisation of the network structure and so the resulting network is a poor reflection of the actual network structure (Caron et al., 2024). This is primarily because *interaction predictors* are models that evaluate the feasibility of an interaction between species pairs and not in the context of feasibility at the community level. Models themselves are a reflection of the different goals and intentions of the research program from which they are developed and are often ‘described’ by a specific mechanism that will determine the resulting structure or interactions (Box 1). Models such as the niche (Williams & Martinez, 2000) or cascade (Cohen et al., 1990) were developed with the intent of being used to understand the *structural* aspects of food webs, specifically how links are distributed amongst species in the community, whereas bayesian (Cirtwill et al., 2019) or trait hierarchy (Shaw et al., 2024) models have been developed on the basis that the traits of a species are the underlying mechanism in determining the feasibility of interactions (*i.e.*, species *a* has the capacity to eat species *b*). Along with predicting different anatomical parts of a food web the different models have varying degrees of data that are needed to ‘parametrise’ the network. Once these two limitations are assessed and addressed it is then possible to select the model (or model family) that will best be able to capture food web feature that the researcher is most interested in (see Box 2 - Assessing model outputs). It is thus clear that

149 (realistically) there will probably never be a ‘best fit’ tool that is able to construct a food web that will span  
150 the entire range of needs, and rather the responsibility lies with the researcher to be aware of not only the  
151 underlying philosophy of the specific toolset (as this could have knock-on effects when using those networks  
152 for downstream analyses/simulations; pers. comms. Beckerman, 2024), but also how well the tool is able to  
153 retrieve the specific network or interaction properties that is of interest.

154 In order for a model to formalise a ‘complete’ food web it is necessary to formalise two aspects  
155 of the network, ‘who eats whom’ (to determine the links between nodes) as well as the structure  
156 of the network (to limit the distribution of links), however most models are inclined to focus on  
157 one of the two aspects panel B of [2](#).

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

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

### 166 1.2.1 Model families

167 As there are many food web models to choose from it is perhaps useful to think about the models in terms  
168 of model families, a summary of these families is presented in [Table 1](#) and along with [Figure 3](#) highlights the  
169 differences and similarities of the philosophies and assumptions that determine a network. A more extensive  
170 overview of the different models that fall with in the different model families can be found in [SuppMat 1](#) and  
171 for a more detailed 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, this includes a brief description of the underlying philosophy of the family as well as how the different elements (nodes and edges) of the generated network represents.

Model family	Theory	Network predicted	Nodes represent	Links represent	Interaction	Key reference
null	Links are randomly distributed within a network	structural	agnostic	feeding links	binary	
neutral	Network structure is random, but species abundance determines links between nodes	structural	species	feeding links	binary	
resource	Networks are interval, species can be ordered on a ‘niche axis’	structural	trophic species	subdivision of resource	binary	Williams & Martinez (2008)
generative	Networks are determined by their structural features	structural	agnostic	links	binary	

Model family	Theory	Network predicted	Nodes represent	Links represent	Interaction	Key reference
energetic	Interactions are determined by foraging theory (feeding links)	interaction	species	feeding links	quantitative	
graph embedding	Interactions can be predicted from the latent traits of networks	interaction	species	potential feeding links	probabilistic	Strydom et al. (2023)
trait matching	Interactions can be inferred by a mechanistic frame-work/relationships	interaction	species	feeding links	binary	Morales-Castilla et al. (2015)
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	interaction	species	feeding links	binary	Pichler et al. (2020)

Model family	Theory	Network predicted	Nodes represent	Links represent	Interaction	Key reference
expert knowledge	'Boots on the ground'	interaction ecological knowledge and observations	species	feeding links	binary	
data scavenging	Webscraping to create networks from online databases	interaction	species	feeding links	binary	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 patterns	species	association links	binary	Kusch et al. (2023) (although more plant-plant <i>i.e.</i> non-trophic...)

172

[Figure 3 about here.]

### **i** Box 2 - Assessing model outputs

we could possibly still keep this box but alter the framing so that it is more about the fact that benchmarking is also going to require you to think about the type of network you have and maybe that we need to develop more detailed protocols for how we benchmark different networks (especially when it comes to benchmarking structure). The Caron 2024 paper

173

shows that retrieving interactions correctly isn't going to mean you retrieve interactions correctly.

Although understanding the underlying philosophy of the different model families is beneficial it is also important to understand in what situations the different families are likely to perform well or poorly. When we are assessing the performance of the different model families it is beneficial to think of benchmarking these assessments based on a broader basis than just its ability to correctly recover network structure or pairwise interactions. When thinking about how to benchmark models it is perhaps beneficial to take a step back and once again assess what are the needs of the researcher ([?@sec-network-why](#)) and linking this back to what aspects of the network ([?@sec-network-anatomy](#)) are of importance and assess the performance of a model within those parameters.

### Benchmarking

Benchmarking how well a model is doing to capture the desired elements of a network is also a task that required some thought and contemplation. Even if we think about the predicting the structure of a network it is possible that two networks may have the same number of nodes and links but that those links may be distributed in very different ways. Thus it is important to think critically about the suite of summary statistics that are used to assess a model, since there is no one 'silver bullet' summary statistic that will be able to assess if a model is able to fully replicate an empirical network (Allesina et al., 2008). One of the main challenges when assessing the ability to retrieve pairwise interactions is that food webs are sparse (that means that there are few links given the number of species) and it is important that we are able to discern between a model that is able to correctly predict interactions that do (true positives) and not (true negatives) occur and one that is simply predicting a lack of interactions (Poisot, 2023). For more detailed methods as to how benchmarking was done refer to [SuppMat 3](#)

[Figure 4 about here.]

### Data cost

This includes thinking about the need for additional data sources (such as trait or phylogenetic data), the computational cost, as well as the time it might take to generate a network, *e.g.*, binary classifiers require an (often times) extensive list of additional trait data for the model training process, which limits predictions to communities for which you do have the relevant auxiliary data available.

### Philosophical constraints

Probably mentioned elsewhere but basically are we constructing networks because we want to make real-world, case-specific predictions *e.g.*, for a conservation area or do we want to just have a set of ecologically plausible networks we can use for theoretical stuffs. Need to discuss the key differences

and implications between predicting a **metaweb** (*sensu* Dunne (2006)) and a network realisation. (In a way the idea of predicting a metaweb vs realisation is what makes me hesitant to use the Mangal networks to test the structural models because do we even know what the Mangal networks represent and what the structural models are predicting...) Maybe also Poisot et al. (2015) that discuss how the local factors are going to play a role.

Also need to take into consideration inherent constraints that the model imposes on itself and how it will affect our ability to test hypotheses/ask questions using the *e.g.*, from Petchey et al. (2011) - models that are constrained by connectance means that we are unable to explain connectance itself and you would need a different approach if understanding connectance is your goal. Another way of phrasing this is thinking about what is needed (input data/parameters), produced (final network characteristics), and desired (end-use).

An interesting thing to also think about is data dependant and data independent ‘parametrisation’ of the models...

175

### 176 1.3 Concluding remarks

- 177 • As discussion about the different model families and in what areas they do/do not do well. This will  
178 depend probably a fair bit on how Figure 4 end up looking... But it will also be important to tie in  
179 some of the other considerations/constraints that are listed in what is currently Box 2
  - 180 – In certain situations structure is ‘enough’ but there may be use cases where we are really interested  
181 in the node-level interactions *i.e.*, species identity is a thing we care about and need to be able to  
182 retrieve specific interactions at specific nodes correctly.
  - 183 • Why do interaction models do so badly at predicting structure? Nuance of metaweb vs realisation but  
184 also time? At the core of it interaction models are trained on existing interaction data; this is data  
185 that are most likely closer to a metaweb than a local realisation even if they are being inventoried at a  
186 small scale...
    - 187 – We can briefly shoehorn downsampling here maybe??
  - 188 • It will be interesting to bring up the idea that if a model is missing a specific pairwise link but doing  
189 well overall then when does it matter?
    - 190 – The fact that *some* people are concerned about the taxonomic resolution and cascading effects  
191 those might have on our understanding of network structure (Pringle, 2020; Pringle & Hutchinson,  
192 2020), but that puts us in a place where we are at risk of losing our ability to distinguish the wood

193 from the tree - are we not (at least at times) concerned more with understanding ecosystem level  
194 processes than with needing to understand things *perfectly* at the species level.

- 195 – I don't think these 'rare'/nuanced links (e.g. carnivorous hippos) are going to rock the boat when  
196 we think about networks at the structural level.

197 "The resolution of food-web data is demonic because it can radically change network topology  
198 and associated biological inferences in ways that are unknowable in the absence of better data." -  
199 Pringle & Hutchinson (2020) The counter to this is that structural models are often not working  
200 at the species level and thus the structure remains 'unchanged' when you increase the resolution  
201 - I don't think that people are that concerned with the structure of real world networks barring  
202 connectance and since that scales with species richness anyway your final proportion will probably  
203 still remain the same...

- 204 • I think a big take home will (hopefully) be how different approaches do better in different situations  
205 and so you as an end user need to take this into consideration and pick accordingly. I think Petchey  
206 et al. (2011) might have (and share) some thoughts on this. I feel like I need to look at Berlow et al.  
207 (2008) but maybe not exactly in this context but vaguely adjacent.

208 – I think this is sort of the crux of the argument presented in Brimacombe et al. (2024) as well.

209 "we highlight an interesting paradox: the models with the best performance measures are not  
210 necessarily the models with the closest reconstructed network structure." - Poisot (2023)

- 211 • Do we need network models to predict interactions and interaction models to predict structure?

212 – "Another argument for the joint prediction of networks and interactions is to reduce circularity  
213 and biases in the predictions. As an example, models like linear filtering generate probabilities of  
214 non-observed interactions existing, but do so based on measured network properties." - Strydom  
215 et al. (2021)

216 – Aligning (dove-tailing) with this the idea of ensemble modelling as presented by Becker et al.  
217 (2022)

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

- 221 • Do we expect there to be differences when thinking about unipartite vs bipartite networks? Is there  
222 underlying ecology/theory that would assume that different mechanisms (and thus models) are relevant

223 in these two ‘systems’.

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

226 **1.3.1 DownSampling**

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

229 • Dansereau et al. (2023)

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

235 **1.3.2 Time**

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

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

250 **Glossary**

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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)

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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)

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251 **Outstanding questions**

- 252     • non-consumptive effects
- 253     • how do we define the spatial and temporal ‘boundaries’ of a network?
- 254     • how do we define a ‘real’ network?

255 **References**

- 256     Allesina, S., Alonso, D., & Pascual, M. (2008). A General Model for Food Web Structure. *Science*, 320(5876),  
257         658–661. <https://doi.org/10.1126/science.1156269>
- 258     Becker, D. J., Albery, G. F., Sjodin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.  
259         A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,  
260         E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic  
261         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)
- 262     Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.  
263         *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- 265     Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of  
266         the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- 267     Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,  
268         V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.

- 269 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),  
270 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 271 Bhatia, U., Dubey, S., Gouhier, T. C., & Ganguly, A. R. (2023). Network-based restoration strategies  
272 maximize ecosystem recovery. *Communications Biology*, 6(1), 1–10. <https://doi.org/10.1038/s42003-023-05622-3>
- 273
- 274 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.  
275 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 276 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A  
277 cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 278 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings  
279 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),  
280 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 281 Caron, D., Brose, U., Lurgi, M., Blanchet, F. G., Gravel, D., & Pollock, L. J. (2024). Trait-matching models  
282 predict pairwise interactions across regions, not food web properties. *Global Ecology and Biogeography*,  
283 33(4), e13807. <https://doi.org/10.1111/geb.13807>
- 284 Cherif, M., Brose, U., Hirt, M. R., Ryser, R., Silve, V., Albert, G., Arnott, R., Berti, E., Cirtwill, A.,  
285 Dyer, A., Gauzens, B., Gupta, A., Ho, H.-C., Portalier, S. M. J., Wain, D., & Wootton, K. (2024). The  
286 environment to the rescue: Can physics help predict predator–prey interactions? *Biological Reviews*,  
287 n/a(n/a). <https://doi.org/10.1111/brv.13105>
- 288 Cirtwill, A. R., Ekklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for  
289 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10(6),  
290 902–911. <https://doi.org/10.1111/2041-210X.13180>
- 291 Clegg, T., Ali, M., & Beckerman, A. P. (2018). The impact of intraspecific variation on food web structure.  
292 *Ecology*, 99(12), 2712–2720. <https://doi.org/10.1002/ecy.2523>
- 293 Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag.
- 294 Dansereau, G., Barros, C., & Poisot, T. (2023). *Spatially explicit predictions of food web structure from  
295 regional level data*.
- 296 Dormann, C. F. (2023). The rise, and possible fall, of network ecology. In *Defining Agroecology – A Festschrift  
297 for Teja Tscharntke* (pp. 143–159.). Tredition.
- 298 Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction:  
299 Are most endangered species parasites and mutualists? *Proceedings. Biological Sciences*, 276(1670),  
300 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- 301 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological*

- 302 networks: *Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 303 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and  
304 Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 305
- 306 Estay, S. A., Fortin, M.-J., & López, D. N. (2023). Editorial: Patterns and processes in ecological networks  
307 over space. *Frontiers in Ecology and Evolution*, 11.
- 308 Fortin, M.-J., Dale, M. R. T., & Brimacombe, C. (2021). Network ecology in dynamic landscapes. *Proceedings  
309 of the Royal Society B: Biological Sciences*, 288(1949), rspb.2020.1889, 20201889. <https://doi.org/10.1098/rspb.2020.1889>
- 310
- 311 Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven  
312 Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annual Review of Ecology, Evolution, and  
313 Systematics*, 46(1), 523–549. <https://doi.org/10.1146/annurev-ecolsys-112414-054400>
- 314 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 315
- 316 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 317
- 318 Kusch, E., Bimler, M., Lutz, J. A., & Ordonez, A. (2023). *Ecological network inference is not consistent  
319 across scales or approaches* (p. 2023.07.13.548816). bioRxiv. <https://doi.org/10.1101/2023.07.13.548816>
- 320 Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417. <https://doi.org/10.2307/1930126>
- 321
- 322 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from  
323 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 324 Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic  
325 interaction strengths. *Nature*, 486(7404), 485–489. <https://doi.org/10.1038/nature11131>
- 326 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web  
327 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 328
- 329 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some  
330 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 331
- 332 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms  
333 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and  
334 Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>

- 335 Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods*  
336 in *Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- 337 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &  
338 Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,  
339 48(7), 1552–1563. <https://doi.org/10.1111/jbi.14127>
- 340 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of  
341 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10>
- 342 Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B.,  
343 & Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological  
344 hypotheses. *EcoGraphy*, 39(4), 402–408. <https://doi.org/10.1111/ecog.01941>
- 345 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
346 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 347 Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks  
348 in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- 349 Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O’Hara, R. B., Parris, K. M., Vesk, P. A., &  
350 McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint  
351 Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/>  
352 [10.1111/2041-210X.12180](https://doi.org/10.1111/2041-210X.12180)
- 353 Pringle, R. M. (2020). Untangling Food Webs. In *Unsolved Problems in Ecology* (pp. 225–238). Princeton  
354 University Press. <https://doi.org/10.1515/9780691195322-020>
- 355 Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology,*  
356 *Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>
- 357 Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution.  
358 *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- 359 Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network  
360 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3),  
361 630–642. <https://doi.org/10.1111/1365-2656.13652>
- 362 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*  
363 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 364 Staniczenko, P. P. A., Lewis, O. T., Jones, N. S., & Reed-Tsochas, F. (2010). Structural dynamics and  
365 robustness of food webs. *Ecology Letters*, 13(7), 891–899. <https://doi.org/10.1111/j.1461-0248.2010.0248.0248.x>
- 366
- 367

- 368 01485.x
- 369 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a  
370 robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*,  
371 274(1621), 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>
- 372 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,  
373 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction  
374 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,  
375 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>
- 376 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,  
377 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer  
378 learning can help predict potential species interaction networks despite data limitations. *Methods in  
379 Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 380 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
381 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
382 towards predicting species interaction networks (across space and time). *Philosophical Transactions of  
383 the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 384 Terry, J. C. D., & Lewis, O. T. (2020). Finding missing links in interaction networks. *Ecology*, 101(7), e03047.  
385 <https://doi.org/10.1002/ecy.3047>
- 386 Thuiller, W., Calderón-Sanou, I., Chalmandrier, L., Gaüzère, P., O'Connor, L. M. J., Ohlmann, M., Poggiato,  
387 G., & Münkemüller, T. (2024). Navigating the integration of biotic interactions in biogeography. *Journal  
388 of Biogeography*, 51(4), 550–559. <https://doi.org/10.1111/jbi.14734>
- 389 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.  
390 <https://doi.org/10.1038/35004572>
- 391 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food  
392 webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 393 Wootton, J. T., & Emmerson, M. (2005). Measurement of Interaction Strength in Nature. *Annual Review of  
394 Ecology, Evolution, and Systematics*, 36(1), 419–444. <https://doi.org/10.1146/annurev.ecolsys.36.091704.175535>
- 396 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory  
397 of trophic interactions. *Functional Ecology*, 37(1), 26–43. <https://doi.org/10.1111/1365-2435.13954>
- 398 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).  
399 Collapse of an ecological network in Ancient Egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>

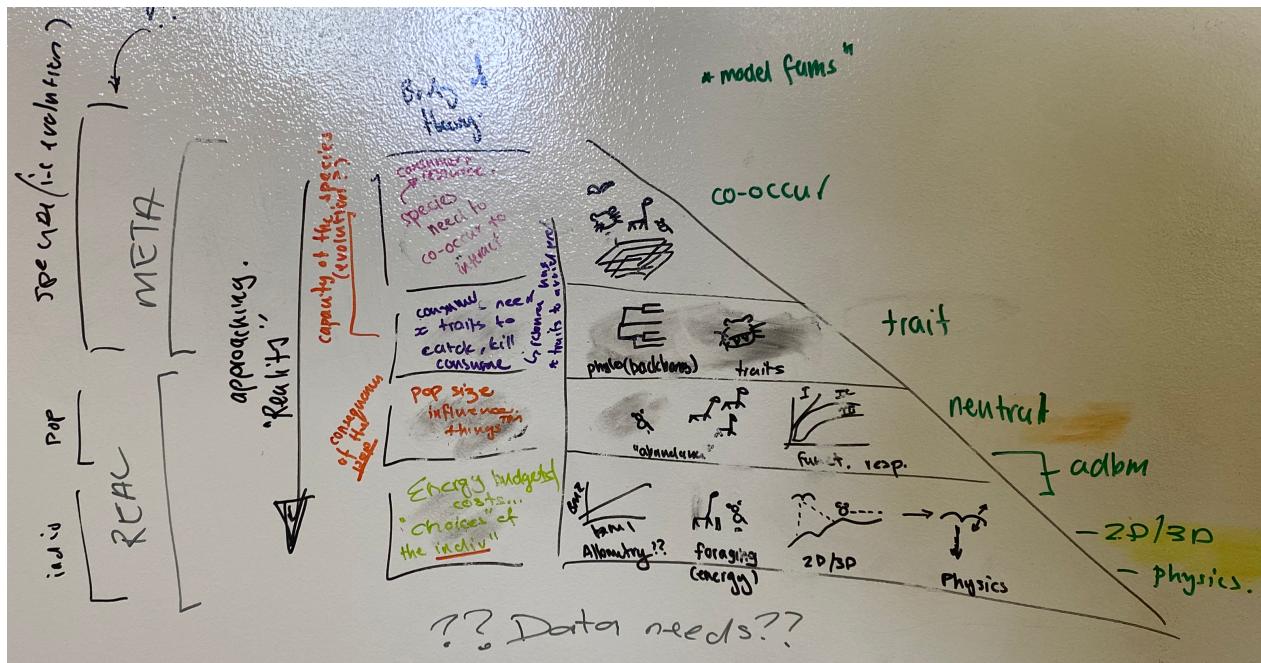
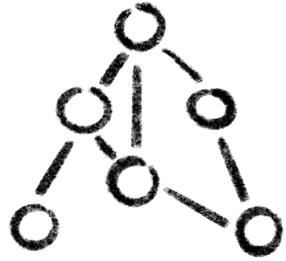


Figure 1: TODO.

## A: ANATOMY



## Network

$\text{I}^3$  - scale       $\text{O}$  - time  
 $\text{O}$  - location

B:

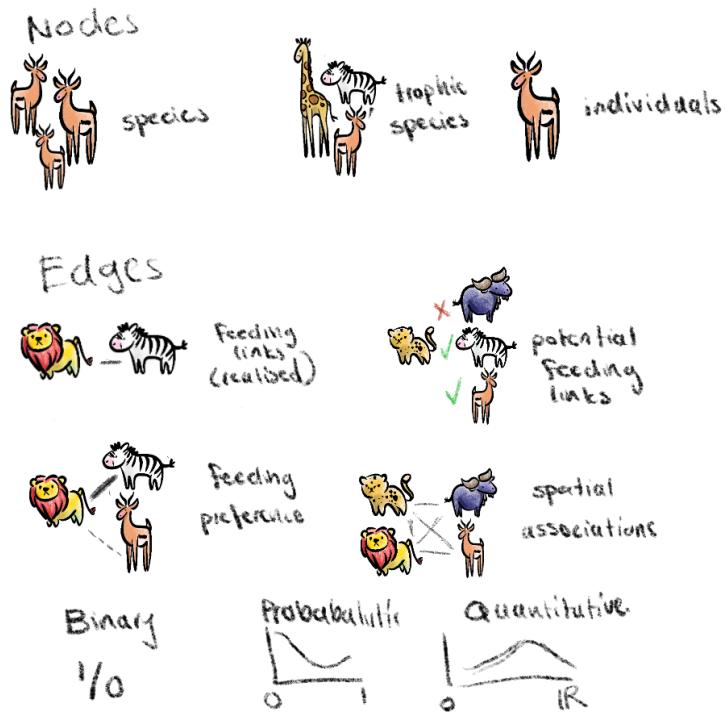


Figure 2: The many ways in which a food web can be defined and described at the node, edge, and even network level.

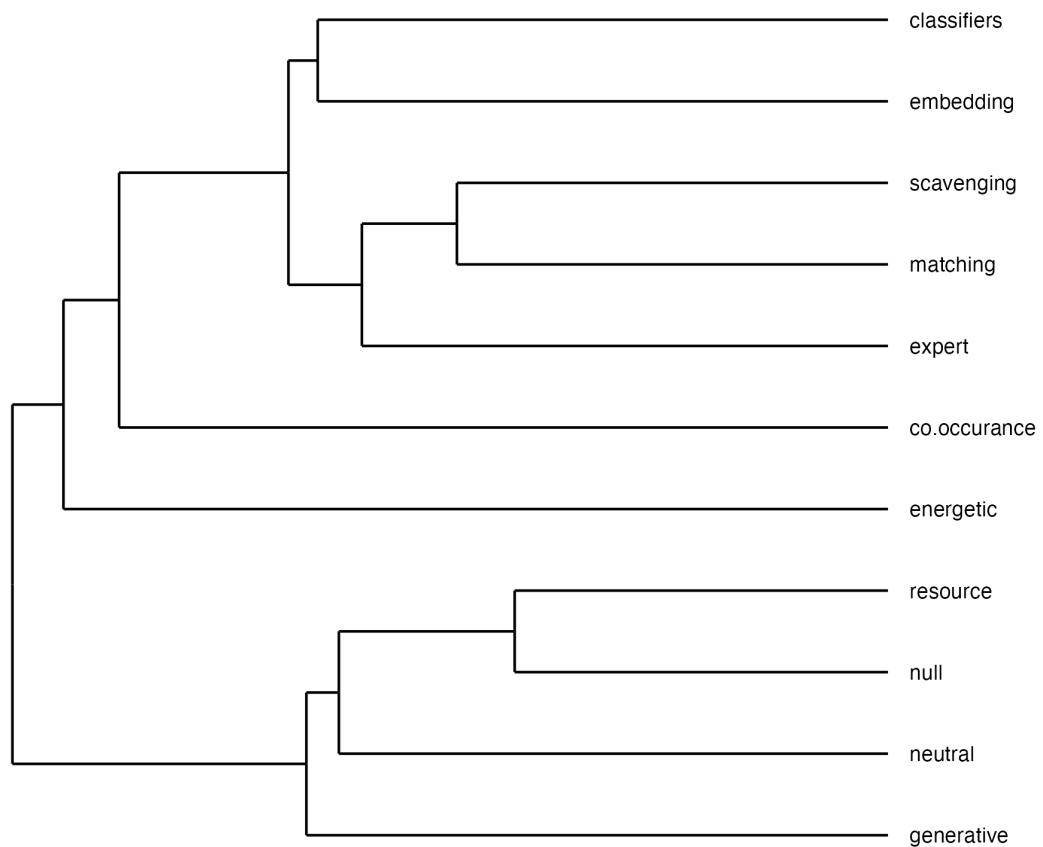


Figure 3: Dendrogram of the trait table using a hierarchical clustering model, This is based off of the traits table in SuppMat 2)

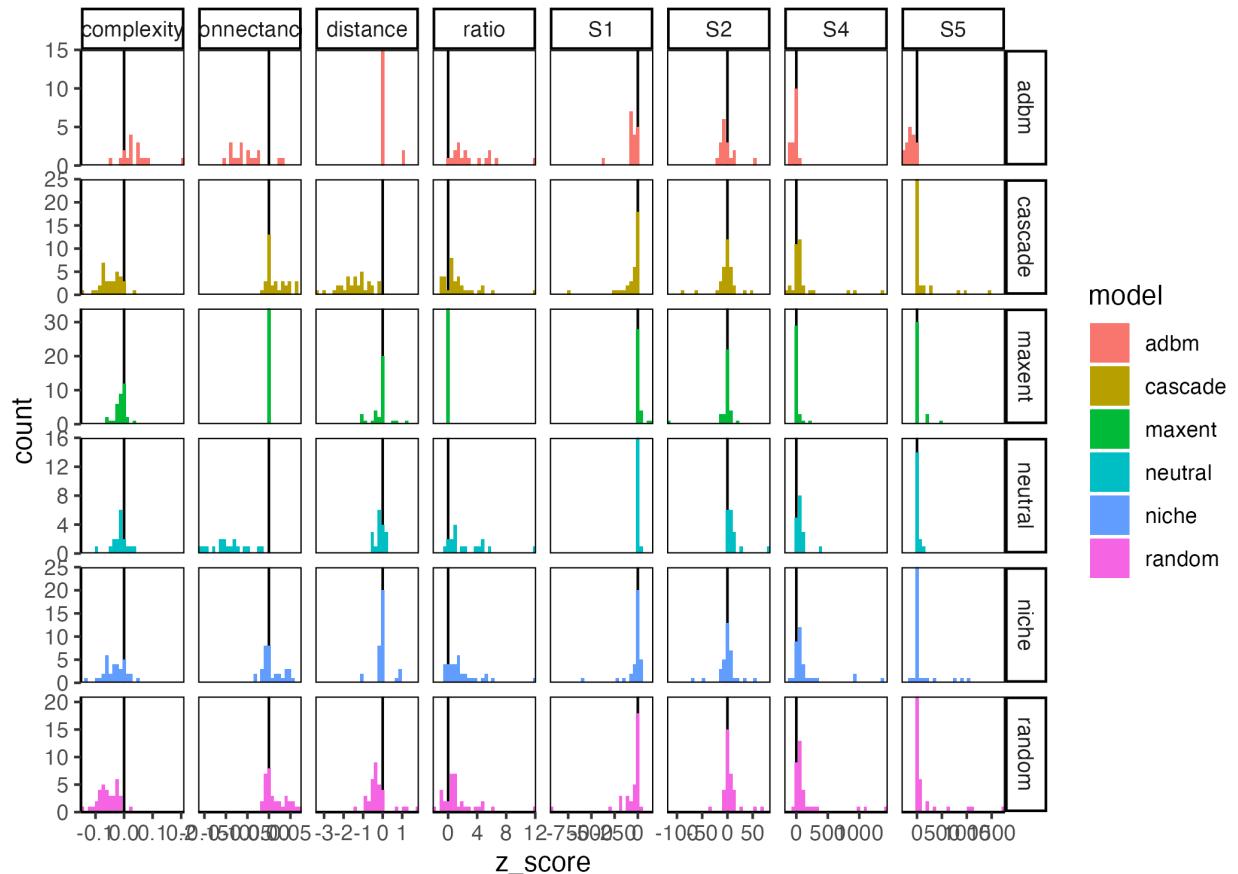


Figure 4: Difference between real and model network property. S1 - S5 represent the different motif structures identified in Stouffer et al. (2007) which are S1: Number of linear chains, S2: Number of omnivory motifs, S4: Number of apparent competition motifs, and S5: Number of direct competition motifs