

# T is for Topology

Tanya Strydom <sup>1</sup>; Jennifer A. Dunne <sup>2</sup>; Timothée Poisot <sup>3,4</sup>; Andrew P. Beckerman <sup>1</sup>

**Abstract:** Although it has been acknowledged that communities consist not only of co-occurring species but that they also interact being able to quantify those interactions and assemble them into interaction networks has been a limiting factor in the integration of network ecology into other fields of ecology. As the field of network ecology has matured there has been an accompanying expansion in the development of theory and tools that are centred around generating networks or predicting the interactions between species. Notably many of these tools have been developed with different underlying philosophies, ideas, and mechanisms as to what structures the interactions between species. It is thus critically important that those wanting to adopt these network generating tools be aware of how the the specific questions being asked maps to the underlying assumptions made when generating networks, as well as the limitations of how the networks/interactions are delimited. Here we provide an overview of the canonical network generating models, comparing and contrasting the underlying assumptions, data requirements, and resulting network predictions made by the different families in an attempt to provide guidance for those interested in adopting the generation of networks into their workflow. [R1. a discussion on the underlying assumptions we are making when we delimit a network]. [R2. an overview of how the different model families differ - ordination space/benchmarking]. [R3. identifying the relevant questions/bodies of theory that the networks generated by different families are suited to answer]. When choosing to construct an interaction network the researcher is faced with many assumptions and considerations that should be made and it is important to be aware of these limitations to avoid constructing (something poetic to capture the idea of falsity/false idols). Being aware of these choices is particularly important as the availability of these tools grows and network ecology starts to be adopted into other aspects of ecology and conservation biology.date: last-modified

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It can be argued that the interaction between species (or individuals) is one of the main determinants of the emergent properties that are studied in other fields of ecology, *e.g.*, the range of plant will be determined by the range of its pollinator, and although the importance of species interactions and the resulting networks that they form has been an acknowledged part of the ecological canon since the penning of the ‘entangled bank’ (Darwin, 1859) (if not even earlier, stemming from Greek Antiquity (Thanos, 1994)), the adoption of network ecology into other disciplines of ecology has been limited. This has primarily been driven by two limitations; firstly, it is extremely challenging to actually record species interactions in the field (Jordano, 2016a, 2016b), which has resulted in a limited coverage of ‘real world’ interaction data (Poisot et al., 2021), and secondly has been the need to develop terminology and tools that help us to construct, conceptualise, and analyse these networks. Although recording interactions in the field remains a challenge, the development of both practical tools (*i.e.*, tools that help us to record or measure interactions, Pringle & Hutchinson, 2020), as well as discussions around the development of tools to predict or infer them (Morales-Castilla et al., 2015; Strydom, Catchen, et al., 2021), has allowed us to begin filling in these ‘global gaps’, albeit in a, potentially, more synthetic manner (Poisot, Gravel, et al., 2016). Additionally, there has been extensive development in the ways in which we formalise networks (Dale & Fortin, 2010), and the tools and language that we use to quantify the structure and properties of networks (Delmas et al., 2019). All together these tools mean that, as a field, network ecology can (and should) be integrated into the broader fields of ecology (*e.g.*, Thuiller et al., 2024) and conservation biology. However (as with any new tool or model), it is important that one has a firm grasp of how the underlying philosophy that underpins the construction of networks (particularly synthetic ones) can have an impact on the interpretation of the questions being asked. In this manuscript we will discuss three themes that should help provide clarity and understanding for those wishing to take a step into network (particularly food web) ecology this includes; thinking about and understanding the underlying assumptions that are made when we attempt to delimit and describe a food webs, a synthesis of the different families of tools that are commonly used to construct food webs, and a discussion linking network ecology to some of the outstanding questions in ecology.

[Figure 1 about here.]

## 1 The anatomy of a food web

Although we specifically focus on food webs (interactions representing feeding links) it is beneficial to take a step back and acknowledge the diversity of form that an interaction network can encapsulate. The idea of an interaction network seems simple, it is the representation of the interactions (edges) between species (nodes), the definition of an ‘edge’ and a ‘node’, 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 between individuals), community (the links between species), or metacommunity (fluxes between locations) level. Even if we are to limit our definition of a network to represent community-level processes there are still many ways to define what is captured by the edges and nodes [insert some e.g.]. It is thus clear that the way that a network is coded (constructed) can influence the resulting observations and conclusions that are made (Brimacombe et al., 2023; Proulx et al., 2005), and it is important to have a strong grasp of what information a network is attempting to convey.

Even if one were to limit their scope to thinking of interaction networks only in terms of food webs there are still many ways to define the various components of the network, 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?, what is the spatial extent?). All these decisions will have an impact on the resultant structure and potential use-cases of the network.

## 1.1 How do we define a node?

Although this may seem an elementary question in the context of food webs — a node should represent a species, the reality is that nodes can often represent an aggregate of different (taxonomic) species - so called ‘trophic species’, and it is not uncommon that networks can have nodes that represent both taxonomic and trophic species (*e.g.*, there are many that do the basal ‘plant/phytoplankton’ node but include at least one REF). 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 [mutualism ref, at least there should be one of them], 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.

## 1.2 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) feeding links, potential (Dunne, 2006) feeding links, or energy flows[??] (Petchey et al., 2008). How we quantify 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 (*i.e.*, a ‘present’ interaction is one implies that species  $a$  has the ability to consume species  $b$  but it does not mean that this interaction is realised in the field) will be meaningless if you are interested in understanding the flow of energy through the system as the links within the network are over connected. 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 effect of one species on another, Berlow et al., 2004). Although there is a clear argument for moving away from a purely binary way of representing interactions [probabilities preprint] this of course also means that there is an additional layer to the interpretation these links.

### 1.3 Aggregating networks

Here I think we need to talk about realised vs potential links (*i.e.* the concept of a metaweb) but also the idea that we are often aggregating over time and space which makes boundaries and whatnot all a bit fuzzy

### 1.4 Putting the parts together; what does it mean?

It is clear that there are many ways to define, code, and construct food webs, however what may be less clear is understanding *why* there is such a diversity of thought. Here it may be meaningful to contextualise the different ‘types’ of food webs within the larger questions (or needs) that have been driving them. Some of the earliest work on food webs was linked to the idea of niche space, and more specifically, the idea of trophic niches and how this would influence the dimensionality of a networks (Cohen, 1977). This introduced the idea that a single dimension (the “niche axis,” Allesina et al., 2008) constrains the interactions between species; in this instance it makes sense to think of species in terms of what they consume and what they are consumed by, as they are occupying the same space in the niche axis. Networks that are defined in this way may be useful for understanding how the flow of energy (resources) are constrained between ‘species’, particularly how it moves through the trophic levels. This ‘niche-based’ way of thinking might be beneficial when thinking about networks at the structural level, and when trying to map large-scale processes [ref?] however there was also a need to develop ways of thinking that were more geared to thinking about why does species  $a$  predate species  $b$ , broadly this is the result of two things; a predator needs to have the correct traits to be able to capture, kill, and consume, its prey (a mismatch between predator and prey is termed a forbidden link, Jordano (2016b)) and it needs to be energetically feasible [feeding ecology ref]. When we think of interactions in these terms it makes sense that nodes are defined at the species level (or at least as

species that have the same traits and/or energy content), however the links between them can be quantified in different ways... [this is lazy writing]

*something, something, introducing that the same problem (different philosophies) is also a thing that you need to think about when aggregating interactions/generating networks.*

## 2 Constructing ecological networks

maybe a more direct link here to the fact that when working with networks its often synthetic ones *i.e.*, the product of some sort of modelling exercise; alternatively there has also been a push to develop predictive tools to create hypothetical (but plausible) networks for real world situations. Also talk about even deciding to create a network from field observations is in and of itself still a ‘model’ that has assumptions... for example decisions are made about delimiting, aggregation, and observation, the idea of aggregating over time or aggregating over space. Same can e said for different food web generating tools , they have their own underlying rules and assumptions that are made when constructing a food web, which will determine and influence the resulting structure or inferred interactions (Petchey et al., 2008)

Arguably the need for methods and tools that can be used to construct synthetic food webs arises from two different (but still aligned) places of interest within the field of network ecology. On the one side sits the researcher who is interested in generating a set of ecologically plausible networks for the purpose of understanding some higher-level process/concept (*e.g.*, understanding energy flows) in a more synthetic setting, whereby these networks do not require any level of species specificity *per se* and it is more the arrangement of the nodes and links within the context of network structure that is of value. This researcher is contrasted by one that is interested in constructing real-world, location specific, interaction data for a specific collection of species (community). This is driven by the need for researchers to find alternative ways to infer the interactions between species as a way to overcome the inherit challenges of inventorying interactions in the field (see Morales-Castilla et al. (2015) for a more mechanistic, and Strydom, Catchen, et al. (2021) for a more statistical overview of ways to approach this specific issue). Of course these two categories are not distinct, mutually exclusive, groups but can rather be viewed as operating on a continuum ranging from a need for generality (*i.e.*, creating a network that, when taken in aggregate, the distribution of links (interactions) between nodes (species) are ecologically plausible) to a need for specificity (*i.e.*, local-level predictions between specific species pairs). It is thus clear that (realistically) there will probably never be a ‘best fit’ tool that is able to construct a food web that will span the entire range of needs, and rather the

responsibility lies with the researcher to be aware of not only the underlying philosophy of the specific toolset (as this could have knock-on effects when using those networks for downstream analyses/simulations; pers. comms. Beckerman & Petchy, 2024), but also how well the tool is able to retrieve the specific network or interaction properties that they desire.

## 2.1 Model families

As there are many food web generating tools to choose from it is perhaps useful to think about these tools in terms of families, where families represent tools that have a similar methodology and (more importantly) have the same underlying philosophies and assumptions that determine the links between nodes as well as how these may be encoded, a summary of these model families are presented in Table 1 and discussed in more detail below. Although there have been efforts to compare and contrast different models (*e.g.*, Williams & Martinez, 2008 looked at ‘structural models’; and Pichler et al., 2020 looked at machine learning algorithms) there still lacks an overall synthesis as to how the different model families differ from each other - both in terms of what they are actually predicting as well as how well they are performing in the different facets of constructing a food web.

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		Network	Nodes	Links		Key
family	Theory	predicted	represent	represent	Interaction	reference
null	Network structure is random	structure	agnostic	feeding links	binary	
neutral	Network structure is random, but species abundance plays a role	structure	species	feeding links	binary	

Model		Network	Nodes	Links		Key
family	Theory	predicted	represent	represent	Interaction	reference
resource	Networks are interval, species can be ordered on a ‘niche axis’	structure	trophic species	subdivision of resource	binary	Williams & Martinez (2008)
generative	Networks are determined by their structural features	structure	agnostic	links	binary	
energetic	Interactions are determined by foraging theory (feeding links)	interactions	species	feeding links	quantitative	
graph embedding	Interactions can be predicted from the latent traits of networks	interactions	species	potential feeding links	probabilistic	Strydom et al. (2023)
trait matching	Interactions can be inferred by a mechanistic frame-work/relationships	interactions	species	feeding links	binary	Morales-Castilla et al. (2015)

Model family	Theory	Network predicted	Nodes represent	Links represent	Interaction	Key reference
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	interactions	species	feeding links	binary	Pichler et al. (2020)
expert knowledge	‘Boots on the ground’ ecological knowledge and observations	interactions	species	feeding links	binary	
data scavenging	Web scraping to create networks from online databases	interactions	species	feeding links	binary	
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	

1 **Null models:** The interactions between species occurs regardless of the identity of the species (*i.e.*, species



have no agency) and links are randomly distributed throughout the network. This family of models is often used as a way of benchmarking things... Broadly there are two different approaches; Type I (Fortuna & Bascompte, 2006), where interactions happen proportionally to connectance and Type II (Bascompte et al., 2003), where interactions happen proportionally to the joint degree of the two species involved.

**Neutral models:** Can be tied to Hubble’s (spellings but also name??) neutral theory [ref, probably mass-ratio] where it is assumed that the interactions that occur between species are due to the abundance of species within the community (Pomeranz et al., 2019).

**Resource models:** Based on the idea that networks follow a trophic hierarchy and that species interactions can be determined using a single dimension [the “niche axis”; Allesina et al. (2008)]. Essentially these models can be viewed as being based on the idea of resource partitioning (niches) along a one-dimensional resource and that the number of links scale with species richness (linear link scaling). That is, there is some sort of hierarchical feeding based on how a ‘resource’ is partitioned. Broadly this family consists of three core models; the cascade model (Cohen et al., 1990), which rests on the idea that species feed on one another in a hierarchical manner; the niche model (Williams & Martinez, 2000), broadly all species are randomly assigned a ‘feeding niche’ and all species that fall in this niche can be consumed by that species; and the nested hierarchy model (Cattin et al., 2004), which adds some component of phylogenetic clustering/signal to determine interactions. Williams & Martinez (2008) provides a broader overview of some of the variations in these models as well as comparison between them regarding their ability to retrieve elements of networks structure (see also Allesina et al. (2008)).

**Generative models:** (this is maybe a bit of a bold term to use). MaxEnt (Banville et al., 2023), (maybe) stochastic block (Xie et al., 2017).

**Feeding models:** Broadly this family of models is rooted in feeding theory and allocates the links between species based on energetics, which predicts the diet of a consumer based on energy intake. This means that the model is focused on predicting not only the number of links in a network but also the arrangement of these links based on the diet breadth of a species. The diet breadth model (Beckerman et al., 2006) as well as its allometrically scaled cousin the allometric diet breadth model (ADBM) (Petchey et al., 2008) determine links between species based on the energetic content, handling time, and density of species. See also DeAngelis et al. (1975)

Gravel et al. (2013) also poses an interesting cross-over between the adbm and niche model.

**Binary classifiers:** The task of predicting if an interaction will occur between a species pair is treated as a binary classification task, where the task is to correlate ‘real world’ interaction data with a suitable ecological

proxy for which data is more widely available (*e.g.*, traits). Model families often used include generalised linear models (*e.g.*, Caron et al., 2022), random forest (*e.g.*, Llewelyn et al., 2023), trait-based k-NN (*e.g.*, Desjardins-Proulx et al., 2017), and Bayesian models (Cirtwill et al., 2019; *e.g.*, Eklöf et al., 2013). See Pichler et al. (2020) for a more detailed overview on the performance of machine learning and statistical approaches for inferring trait-feeding relationships.

**Graph embedding:** This family of approaches has been extensively discussed in Strydom et al. (2023) but can be broadly explained as an approach that estimates latent features from observed networks that can be used to predict interactions. Strydom et al. (2022) uses a transfer learning framework (specifically using a random dot product graph for embedding) based around the idea that interactions are evolutionarily conserved and that we can use known networks, and phylogenetic relationships, to predict interactions for a given species pool. Another approach that uses the concept of embedding is the log-ratio approach (Rohr et al., 2010)

**Trait matching:** Interactions are determined by a series of ‘feeding rules’, whereby the interaction between a species pair will only occur if all feeding rules are met. These rules are determined on an *a priori* basis using expert/ecological knowledge to determine the underlying feeding hierarchy by using ecological proxies (see Morales-Castilla et al., 2015 for a more details on the idea of using this approach). For example the Paleo Foodweb Inference Model (PFIM, Shaw et al., 2024) uses a series of rules for a set of trait categories (such as habitat and body size) to determine if an interaction can feasibly occur between a species pair. What sets this family of models apart from **expert knowledge** ones is that there is a formalisation of the feeding rules and thus there is some ability to transfer these rules to different communities.

**Expert knowledge:** This approach involves having a group of experts come together to assess and assign the likelihood of feeding interactions being able to occur for a specified community. This is done in a pairwise manner where the experts will assign a value of how confident they are that a specific species pair are likely to interact (*e.g.*, Dunne et al., 2008) This has the added advantage that interactions can be scored in a more categorical (or probabilistic) as opposed to binary fashion, *e.g.*, Maiorano et al. (2020) score interactions as either obligate (typical food resources) or occasional (opportunistic feeding) interactions.

**Data scavenging:** There are also a lot of published *interaction e.g.*, the Global Biotic Interactions (GloBI) database (Poelen et al., 2014) or *network e.g.*, Mangal (Poisot, Baiser, et al., 2016) datasets, these can be mined to look for interactions for specific species pairs. This is done by matching species pairs against those within a dataset of trophic interactions to determine if an interaction is present between the two species (*e.g.*, the WebBuilder tool developed by Gray et al., 2015). It is important to note that this methodology is only

going to be able to infer observations that have been recorded and will thus be prone to many false negatives (missing pairwise interactions) being generated using this approach.

**Co-occurrence:** Trying to infer interactions from the co-occurrence patterns of species pairs within the community *e.g.*, the geographical lasso (Ohlmann et al., 2018). This (for me) seems fundamentally flawed and Blanchet et al. (2020) seems to agree with me at least a little bit.

[Figure 2 about here.]

[Figure 3 about here.]

[Figure 4 about here.]

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## 2.2 Assessing strengths and weaknesses

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 two broader criteria, namely the ability of the model to correctly capture different elements of the structure of the network and the ability of the model to correctly retrieve 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 and linking this back to what aspects of the network (Section 1) are of importance. For example if we are concerned with being able to successfully predict pairwise interactions we want to ensure that we are able to retrieve interactions that really exist but also those that cannot exist (*sensu* forbidden links Jordano (2016b))

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).

benchmarking requires the use of empirical networks and comparing that to the predicted one

### 2.2.0.1 Benchmarking for structure

Despite structural models being some of the older model families there is a distinctive lack of clear guidelines as to how we assess the ability of these models to replicate the *entire* structure of a network. In part this may perhaps be driven by the underlying research agenda and interest in different aspects of capturing the structure of networks *e.g.*, the obsession with intervality [ref] or links distributions [ref]. However, it is still a good idea to think about the network in its entirety and to benchmark structural models in a more holistic manner. Some useful ways to assess how well the model predicts the shape (*e.g.*, the height (chain length) and...), links (*e.g.*, connectance), internal structure (*e.g.*, SVD entropy, Strydom, Dalla Riva, et al. (2021)), and meso-level features (*e.g.*, motifs, Stouffer et al. (2007)) of a network. This is shown in Figure 5...

- Maybe look at some of the historic papers that compare some of the ‘resource models’
- See also Allesina et al. (2008) and the likelihood function that they use for model selection
- Look at Vermaat et al. (2009)

[Figure 5 about here.]

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### 2.2.0.2 Benchmarking for interactions

Broadly speaking the task of assessing the ability of a model to predict interactions as being an assessment of the model’s classification ability (does it correctly predict the presence and absence of interactions?) and so we want to benchmark the model on how well it is able to correctly predict these presences and absences. This can be done in a myriad of ways (Poisot, 2023; Strydom, Catchen, et al., 2021) but is always based off of the confusion matrix [ref maybe?]. Essentially the 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). Using the confusion matrix it is then possible to assess the ‘quality’ of the model predictions such as their accuracy or informedness.

As mentioned above one of the main challenges we are faced with when trying to benchmark interaction predictions is the high class imbalance (inherit sparsity) of networks, and as highlighted by Poisot (2023) we can very easy to lull ourselves into a false sense of predictive accuracy if we use the wrong benchmarking tools — even a low skill (fails to predict interactions that are present) model can appear to do well if we

assess it on its ability to correctly predict interactions, this is because most interactions are absent and so a model that predicts interactions as being absent will still predict most interactions correctly. Another aspect of assessing these types of predictions is quantifying the bias of the model, this will give an indication if the model tends to systematically over predict one of the classes. As per Poisot (2023) the best ways to assess the classification performance of the different models is to use the Precision-Recall (PR-AUC) to assess precision [ref?], and the Matthews correlation coefficient (MCC) to assess accuracy (Matthews, 1975).

- Caveat regarding the use of real world interaction data both for training and validating predictions? *e.g.*, Poisot, Ouellet, et al. et al 2021 and Catchen et al 2023
- “These results suggest that learning from a dataset with very low connectance can be a different task than for more connected networks: it becomes increasingly important to capture the mechanisms that make an interaction exist, and therefore having a slightly more biased training dataset might be beneficial. As connectance increases, the need for biased training sets is less prominent, as learning the rules for which interactions do not exist starts gaining importance”
- Maybe also looking at how well a model can recover ‘missing links’ *i.e.*, false negatives *sensu* what we did in Strydom et al. (2022)
- Need to discuss the key differences and implications between predicting a metaweb (*sensu* Dunne (2006)) and a network realisation. Maybe also Poisot et al. (2015) that discuss how the local factors are going to play a role.

[Figure 6 about here.]

### 3 Linking network ecology to the outstanding questions in ecology

- Bring up the fact that delimiting a network is in and of itself fuzzy - we tend to think of them in terms of snapshots but in reality the final (empirical) network is often the result of aggregation over multiple timescales.
- Also the fact that *some* people are concerned about the taxonomic resolution and cascading effects those might have on our understanding of network structure (Pringle, 2020; Pringle & Hutchinson, 2020), we are at risk of losing our ability to distinguish the wood from the tree - are we not (at least at times) concerned more with understanding ecosystem level processes than with needing to understand things *perfectly* at the species level.
  - I don’t think these ‘rare’/nuanced links (e.g. carnivorous hippos) are going to rock the boat when

we think about networks at the structural level. To say this in a different way maybe it comes down to thinking about the scale of organisation within a network... The classical levels of organisation within ecology (population, community, ...) are also relevant when we think about a networks.

- Brief history of the development of tools within the context of the two different fields? Sort of where the theory/body of work was based and how that has changed?
- In certain situations structure is ‘enough’ but there may be use cases where we are really interested in the node-level interactions *i.e.*, species identity is a thing we care about and need to be able to retrieve specific interactions at specific nodes correctly.
- What is the purpose of generating a network? Is it an element of a bigger question we are asking, *e.g.*, I want to generate a series of networks to do some extinction simulations/bioenergetic stuff OR are we looking for a ‘final product’ network that is relevant to a specific location? (this can still be broad in geographic scope).

Cohen et al. (1985) states that “[*Their*] approach is more like gross anatomy than like physiology... that is, the gross anatomy is frozen, rather than in motion.”.

Interestingly Williams & Martinez (2008) also explicitly talk about *structural* food-web models in their introduction... so how I see it that means that there has always been this inherent acknowledgement that models are functioning at a specific ‘network level’.

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

“It makes no sense to describe the interaction structure of nodes which in themselves are poorly defined.” — Roslin et al. (2013, p. 2)

## 4 Discussion

- I think a big take home will (hopefully) be how different approaches do better in different situations and so you as an end user need to take this into consideration and pick accordingly. I think Petchey et

al. (2011) might have (and share) some thoughts on this (thanks Andrew). I feel like I need to look at Berlow et al. (2008) but maybe not exactly in this context but vaguely adjacent.

- An interesting thing to also think about (and arguably it will be addressed based on some of the other thoughts and ideas) is data dependant and data independent ‘parametrisation’ of the models...
- Why do interaction models do so badly at predicting structure? Nuance of metaweb vs realisation but also time? At the core of it interaction models are trained on existing interaction data; this is data that are most likely closer to a metaweb than a local realisation even if they are being inventoried at a small scale.

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

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

- *Do we need network models to predict interactions and interaction models to predict structure?* (lets not think about that too hard or I might just have to sit in silence for a while...)

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

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

- It will be interesting to bring up the idea that if a model is missing a specific pairwise link but doing well at the structural level then when does it matter?
- Close out with a call to action that we have models that predict networks very well and models that predict interactions very well but nothing that is doing well at predicting both - this is where we should be focusing our attention when it comes to furthering model development. (we need models that will fill the space in the top right quadrant of panel A in Figure 1)

## References

Source: [Article Notebook](#)

- 1 Allesina, S., Alonso, D., & Pascual, M. (2008). A General Model for Food Web Structure. *Science*, 320(5876),  
2 658–661. <https://doi.org/10.1126/science.1156269>
- 3 Banville, F., Gravel, D., & Poisot, T. (2023). What constrains food webs? A maximum entropy framework  
4 for predicting their structure with minimal biases. *PLOS Computational Biology*, 19(9), e1011458. <https://doi.org/10.1371/journal.pcbi.1011458>
- 5 Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal  
6 mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16), 9383–9387. <https://doi.org/10.1073/pnas.1633576100>
- 7 Becker, D. J., Albery, G. F., Sjödin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T.  
8 A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling,  
9 E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic  
10 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)
- 11 Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity.  
12 *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- 13 Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of*  
14 *the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- 15 Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen,  
16 V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O.  
17 (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3),  
18 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- 19 Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.  
20 *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- 21 Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A*  
22 *cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- 23 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings  
24 of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),  
25 e3002068. <https://doi.org/10.1371/journal.pbio.3002068>
- 26 Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with  
27 trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>
- 28 Cattin, M.-F., Bersier, L.-F., Banašek-Richter, C., Baltensperger, R., & Gabriel, J.-P. (2004). Phylogenetic  
29 constraints and adaptation explain food-web structure. *Nature*, 427(6977), 835–839. <https://doi.org/10.1038/nature02327>
- 30  
31  
32  
33



- 1 Cirtwill, A. R., Eklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for  
2 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 0(ja).  
3 <https://doi.org/10.1111/2041-210X.13180>
- 4 Cohen, J. E. (1977). Food webs and the dimensionality of trophic niche space. *Proceedings of the National*  
5 *Academy of Sciences*, 74(10), 4533–4536. <https://doi.org/10.1073/pnas.74.10.4533>
- 6 Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag.
- 7 Cohen, J. E., Newman, C. M., & Steele, J. H. (1985). A stochastic theory of community food webs I. Models  
8 and aggregated data. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 224(1237),  
9 421–448. <https://doi.org/10.1098/rspb.1985.0042>
- 10 Dale, M. R. T., & Fortin, M.-J. (2010). From Graphs to Spatial Graphs. *Annual Review of Ecology, Evolution,*  
11 *and Systematics*, 41, 21–38. <https://www.jstor.org/stable/27896212>
- 12 Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured*  
13 *Races in the Struggle for Life*. J. Murray.
- 14 DeAngelis, D. L., Goldstein, R. A., & O'Neill, R. V. (1975). A Model for Tropic Interaction. *Ecology*, 56(4),  
15 881–892. <https://doi.org/10.2307/1936298>
- 16 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,  
17 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).  
18 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. [https://doi.org/](https://doi.org/10.1111/brv.12433)  
19 [10.1111/brv.12433](https://doi.org/10.1111/brv.12433)
- 20 Desjardins-Proulx, P., Laigle, I., Poisot, T., & Gravel, D. (2017). Ecological interactions and the Netflix  
21 problem. *PeerJ*, 5, e3644. <https://doi.org/10.7717/peerj.3644>
- 22 Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological*  
23 *networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.
- 24 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and  
25 Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. [https://doi.org/10.1371/journal.](https://doi.org/10.1371/journal.pbio.0060102)  
26 [pbio.0060102](https://doi.org/10.1371/journal.pbio.0060102)
- 27 Eklöf, A., Tang, S., & Allesina, S. (2013). Secondary extinctions in food webs: A Bayesian network approach.  
28 *Methods in Ecology and Evolution*, 4(8), 760–770. <https://doi.org/10.1111/2041-210X.12062>
- 29 Fortuna, M. A., & Bascompte, J. (2006). Habitat loss and the structure of plant-animal mutualistic networks:  
30 Mutualistic networks and habitat loss. *Ecology Letters*, 9(3), 281–286. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2005.00868.x)  
31 [0248.2005.00868.x](https://doi.org/10.1111/j.1461-0248.2005.00868.x)
- 32 Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from  
33 predator–prey body size relationships. *Methods in Ecology and Evolution*, 4(11), 1083–1090. <https://doi.org/10.1111/2041-210X.12062>

1 [//doi.org/10.1111/2041-210X.12103](https://doi.org/10.1111/2041-210X.12103)

2 Gray, C., Figueroa, D. H., Hudson, L. N., Ma, A., Perkins, D., & Woodward, G. (2015). Joining the dots:  
3 An automated method for constructing food webs from compendia of published interactions. *Food Webs*,  
4 5, 11–20. <https://doi.org/10.1016/j.fooweb.2015.09.001>

5 Jordano, P. (2016a). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>

6 Jordano, P. (2016b). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>

9 Llewelyn, J., Strona, G., Dickman, C. R., Greenville, A. C., Wardle, G. M., Lee, M. S. Y., Doherty, S.,  
10 Shabani, F., Saltr , F., & Bradshaw, C. J. A. (2023). Predicting predator–prey interactions in terrestrial  
11 endotherms using random forest. *Ecography*, 2023(9), e06619. <https://doi.org/10.1111/ecog.06619>

12 Maiorano, L., Montemaggiori, A., Ficetola, G. F., O'Connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A  
13 species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, 29(9), 1452–1457.  
14 <https://doi.org/10.1111/geb.13138>

15 Matthews, B. W. (1975). Comparison of the predicted and observed secondary structure of T4 phage  
16 lysozyme. *Biochimica Et Biophysica Acta (BBA) - Protein Structure*, 405(2), 442–451. [https://doi.org/10.1016/0005-2795\(75\)90109-9](https://doi.org/10.1016/0005-2795(75)90109-9)

18 Morales-Castilla, I., Matias, M. G., Gravel, D., & Ara jo, M. B. (2015). Inferring biotic interactions from  
19 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>

20 Ohlmann, M., Mazel, F., Chalmandrier, L., Bec, S., Coissac, E., Gielly, L., Pansu, J., Schilling, V., Taberlet,  
21 P., Zinger, L., Chave, J., & Thuiller, W. (2018). Mapping the imprint of biotic interactions on  $\beta$ -diversity.  
22 *Ecology Letters*, 21(11), 1660–1669. <https://doi.org/10.1111/ele.13143>

23 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web  
24 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>

26 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some  
27 thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>

29 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms  
30 to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and*  
31 *Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>

32 Poelen, J. H., Simons, J. D., & Mungall, C. J. (2014). Global biotic interactions: An open infrastructure to  
33 share and analyze species-interaction datasets. *Ecological Informatics*, 24, 148–159. <https://doi.org/10.1016/j.ecoinf.2014.05.001>

1016/j.ecoinf.2014.08.005

- Poisot, T. (2023). Guidelines for the prediction of species interactions through binary classification. *Methods in Ecology and Evolution*, 14(5), 1333–1345. <https://doi.org/10.1111/2041-210X.14071>
- Poisot, T., Baiser, B., Dunne, J., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T. N., Stouffer, D. B., Wood, S. A., & Gravel, D. (2016). Mangal – making ecological network analysis simple. *Ecography*, 39(4), 384–390. <https://doi.org/10.1111/ecog.00976>
- Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., & Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*, n/a(n/a). <https://doi.org/10.1111/jbi.14127>
- Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/2041-210X.13125>
- Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B., & Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological hypotheses. *Ecography*, 39(4), 402–408. <https://doi.org/10.1111/ecog.01941>
- Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks in ecology? *Functional Ecology*, 30(12), 1878–1882. <https://www.jstor.org/stable/48582345>
- Pomeranz, J. P. F., Thompson, R. M., Poisot, T., & Harding, J. S. (2019). Inferring predator–prey interactions in food webs. *Methods in Ecology and Evolution*, 10(3), 356–367. <https://doi.org/10.1111/2041-210X.13125>
- Pringle, R. M. (2020). Untangling Food Webs. In *Untangling Food Webs* (pp. 225–238). Princeton University Press. <https://doi.org/10.1515/9780691195322-020>
- Pringle, R. M., & Hutchinson, M. C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology, Evolution and Systematics*, 51(Volume 51, 2020), 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>
- Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, 20(6), 345–353. <https://doi.org/10.1016/j.tree.2005.04.004>
- Rohr, R. P., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling Food Webs: Exploring Unexplained Structure Using Latent Traits. *The American Naturalist*, 176(2), 170–177. <https://doi.org/10.1086/653667>
- Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). A framework for reconstructing ancient food webs using functional trait data (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>

1 [//doi.org/10.1101/2024.01.30.578036](https://doi.org/10.1101/2024.01.30.578036)

2 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a  
3 robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*,  
4 274(1621), 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>

5 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,  
6 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction  
7 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,  
8 13(12), 2838–2849. <https://doi.org/10.1111/2041-210X.13835>

9 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,  
10 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer  
11 learning can help predict potential species interaction networks despite data limitations. *Methods in*  
12 *Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>

13 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
14 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
15 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*  
16 *the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>

17 Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD Entropy Reveals the High Complexity of Ecological  
18 Networks. *Frontiers in Ecology and Evolution*, 9. <https://doi.org/10.3389/fevo.2021.623141>

19 Thanos, C. A. (1994). Aristotle and Theophrastus on plant-animal interactions. In M. Arianoutsou &  
20 R. H. Groves (Eds.), *Plant-animal interactions in Mediterranean-type ecosystems* (pp. 3–11). Springer  
21 Netherlands. [https://doi.org/10.1007/978-94-011-0908-6\\_1](https://doi.org/10.1007/978-94-011-0908-6_1)

22 Thuiller, W., Calderón-Sanou, I., Chalmandrier, L., Gaüzère, P., O'Connor, L. M. J., Ohlmann, M., Poggiato,  
23 G., & Münkemüller, T. (2024). Navigating the integration of biotic interactions in biogeography. *Journal*  
24 *of Biogeography*, 51(4), 550–559. <https://doi.org/10.1111/jbi.14734>

25 Vermaat, J. E., Dunne, J. A., & Gilbert, A. J. (2009). Major dimensions in food-web structure properties.  
26 *Ecology*, 90(1), 278–282. <https://www.ncbi.nlm.nih.gov/pubmed/19294932>

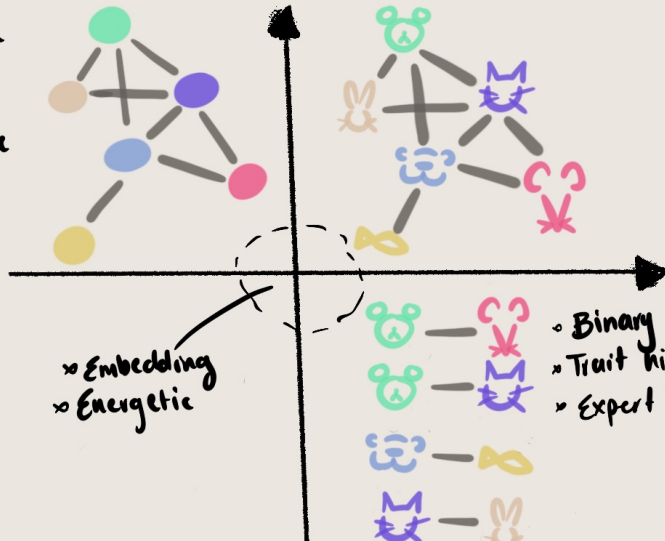
27 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.  
28 <https://doi.org/10.1038/35004572>

29 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food  
30 webs. *Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>

31 Xie, J.-R., Zhang, P., Zhang, H.-F., & Wang, B.-H. (2017). Completeness of Community Structure in  
32 Networks. *Scientific Reports*, 7(1), 5269. <https://doi.org/10.1038/s41598-017-05585-6>

# A Predicting.

- Resource
- Null
- Neutral
- Generative



- Embedding
- Energetic

- Binary Classifiers
- Trait hierarchy
- Expert knowledge

# B Benchmarking

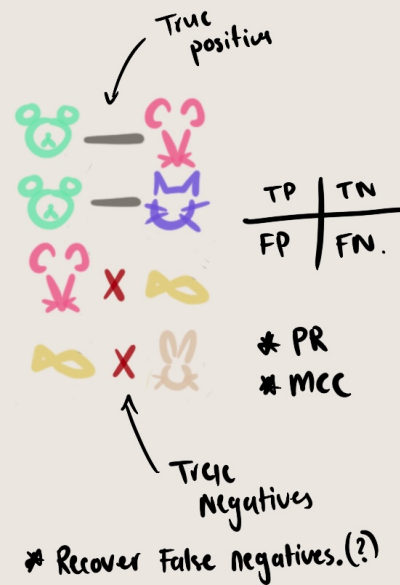
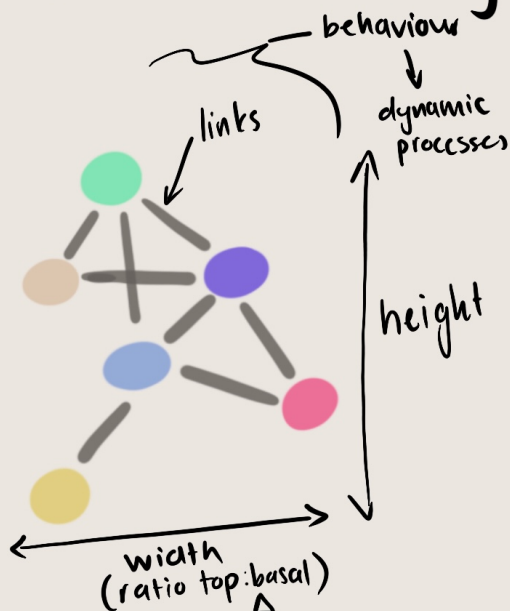


Figure 1: Conceptual figure of the 'network prediction'. Panel A shows where the model families fall in the the context of being models that predict networks or models that predict interactions space. Panel B serves to highlight the characteristics one might like to 'test'/benchmark for a model based on it being either a network or interaction predicting model

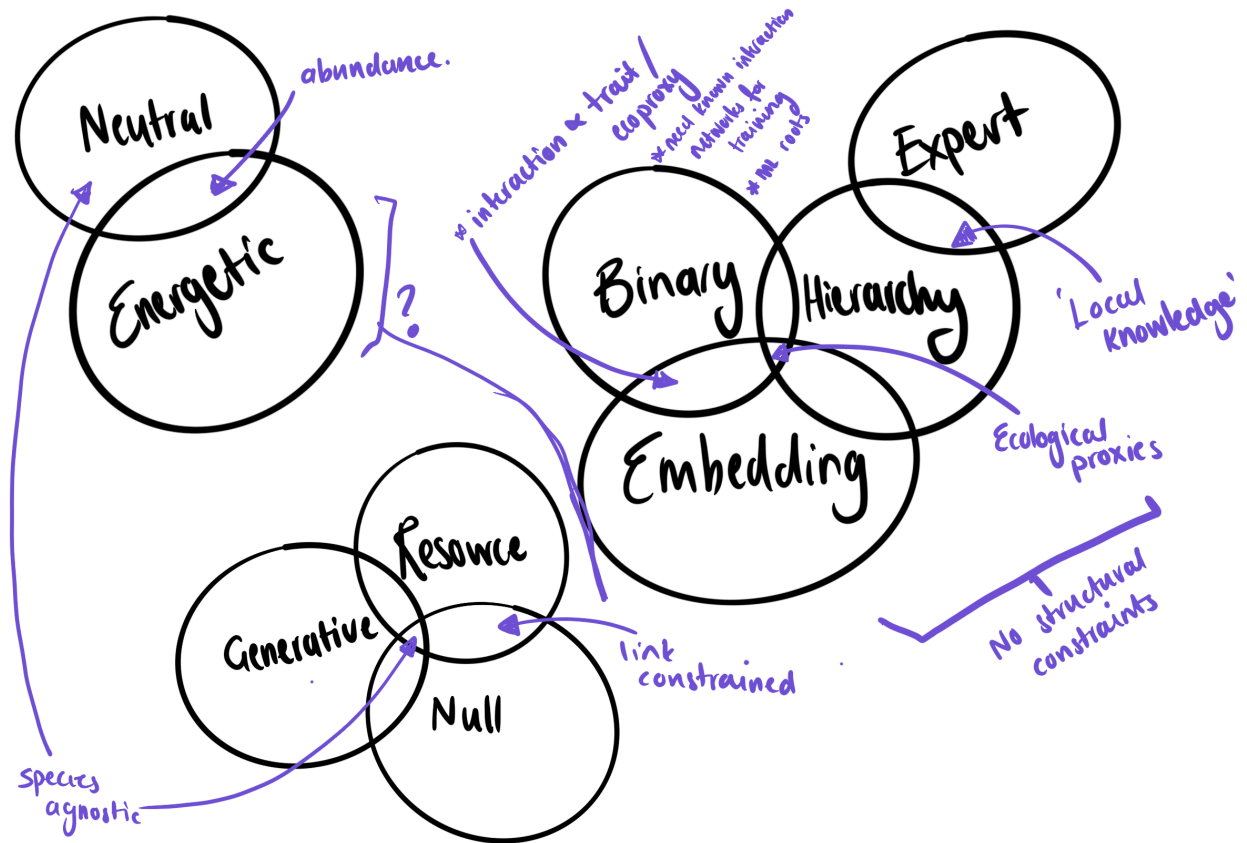


Figure 2: I still haven't given up on a sort of venn diagram idea but maybe it going to be more of a venn-flow chart hybrid...



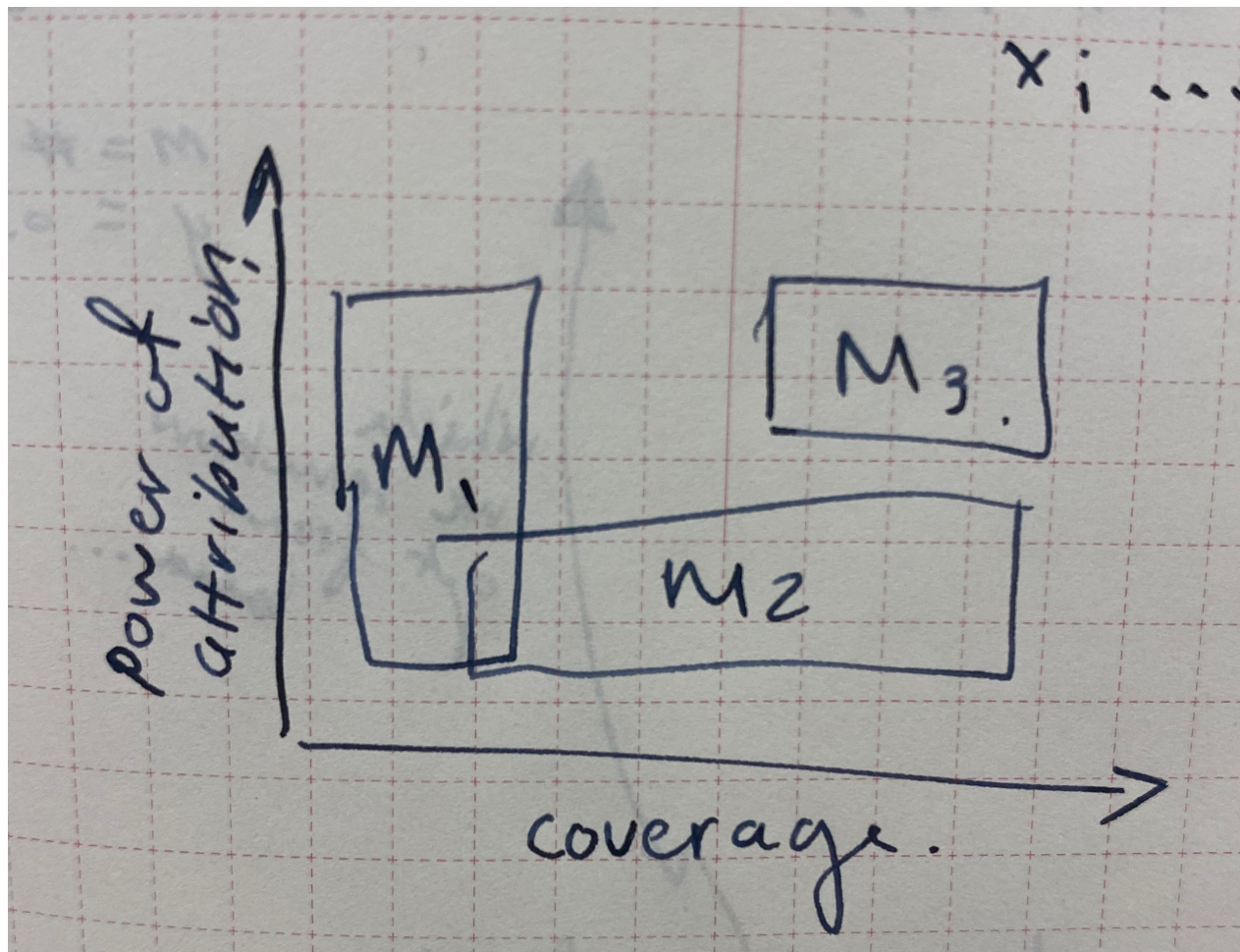


Figure 3: I like these schematics that Charlie Outhwaite presented at the EEB seminar (there was a series of them).

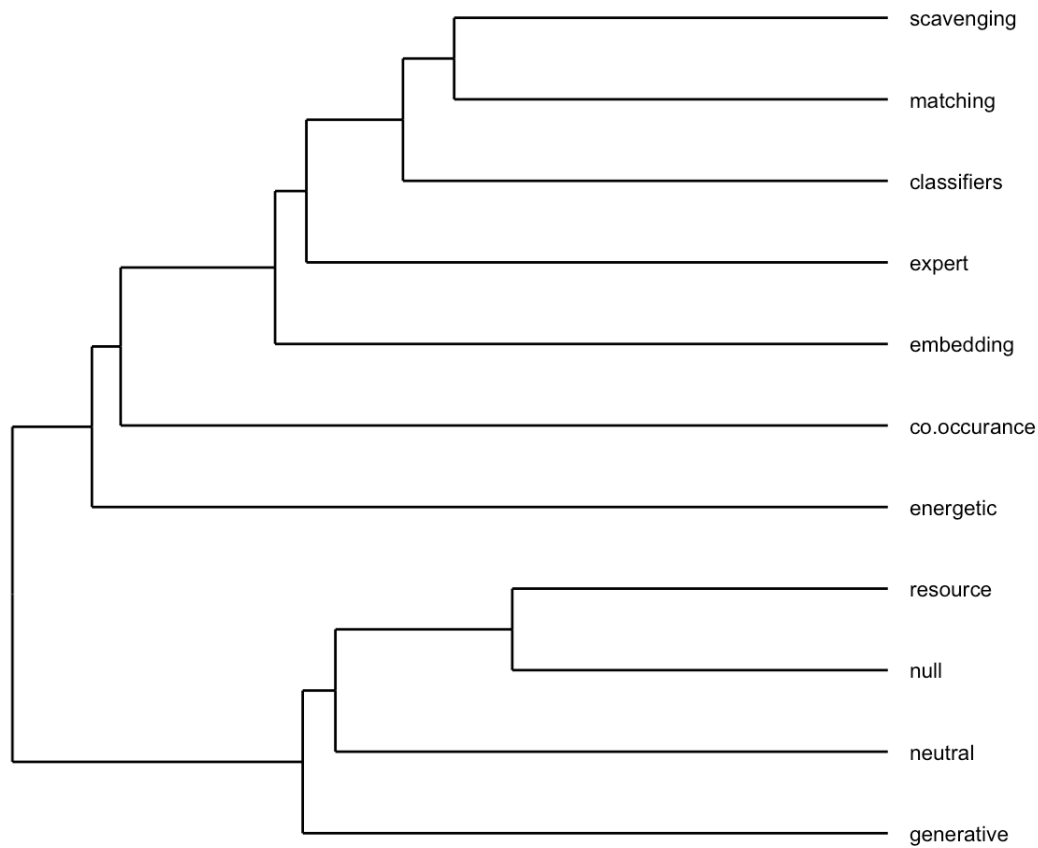


Figure 4: Dendrogram of the trait table



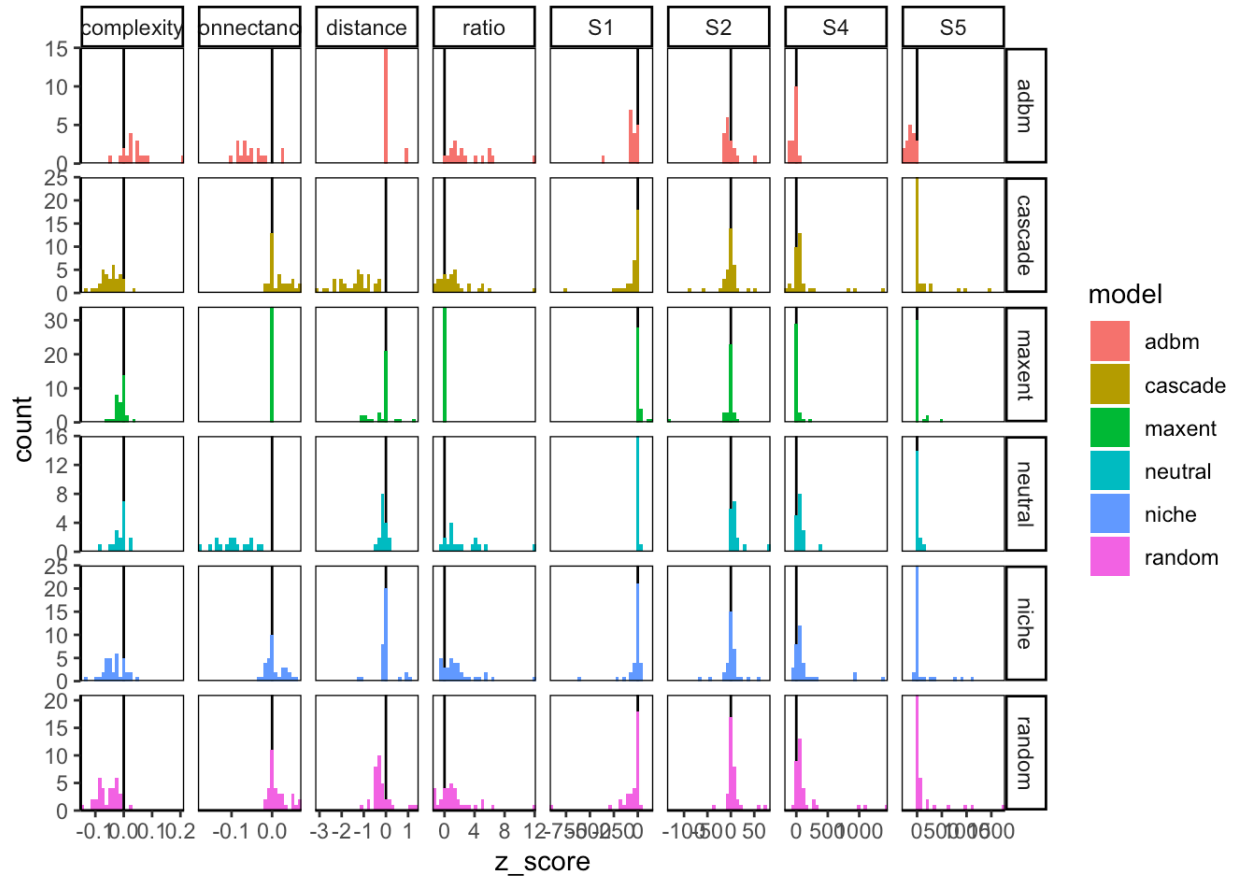


Figure 5: Difference between real and model network property. S1 - S5 represent the different motif structures identified in Stouffer et al. (2007).

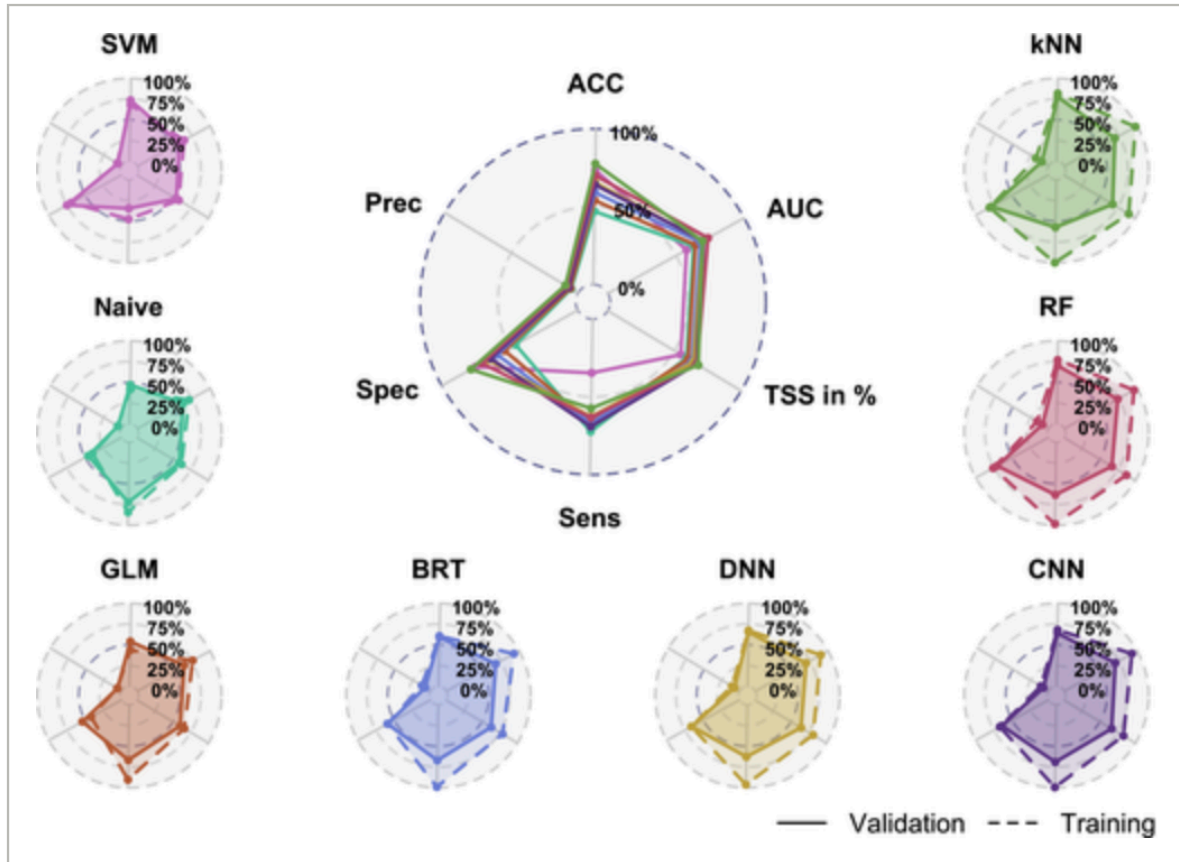


Figure 6: Moc result from Pichler et al. (2020)