

# 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

**Keywords:** food web, network construction

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 Darwin’s ‘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 was primarily driven by two limitations; firstly, it is extremely challenging to actually record species interactions in the field (Jordano, 2016b, 2016a), which has resulted in a limitation in the coverage of interaction data (Poisot et al., 2021), secondly has been the need to develop a set of tools and terminology to construct, conceptualise, and analyse these networks. Although measuring interactions in the field remains a challenge, the development of both practical tools (*i.e.*, tools that help as record or measure interactions, (e.g. ref maybe Pringle & Hutchinson, 2020) although there are many) as well as predictive tools (Morales-Castilla et al., 2015; Strydom et al., 2021) is allowing us to begin filling in these ‘global gaps’. Additionally, there has been extensive development of tools that focus on quantifying the structure [ref], analysis (Dale & Fortin, 2010), properties (Delmas et al., 2019) of networks. All together these tools means that as a field network ecology can (and should) be integrated into 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 networks (particularly synthetic ones) are generated and how the underlying philosophy thereof maps onto the questions being asked. Here we provide; a discussion of 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 used to construct food webs, and a discussion linking network ecology to some of the outstanding questions in ecology.

Three themes that are aimed at: providing a standardisation of terms that are used when we are talking about both networks as well as what we mean when we are generating networks. The final theme aims to map network ecology to some of the outstanding questions in ecology

## 0.1 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.

#### 0.1.1 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 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 provide a much more

#### 0.1.2 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 a representation of the flow of a resource [ref], realised (Pringle, 2020) feeding links, potential (Dunne, 2006) feeding links, or the flow of energy (*sensu* the ADBM 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.*, although species *a* may have the ability to consume species *b* it does not mean that it will be realised ‘in the field’) will be meaningless if you are interested in understanding the flow of

energy through the system as the links are overdistributed. In addition to the various ways of defining the links between species pairs there are also a myriad of ways in which they can be quantified. Links between species are often treated as being present or absent (*i.e.*, binary) it is also possible to provide a more nuanced way to quantify them. Along with representing interactions as binary it is also possible to treat them as probabilistic [which quantifies how likely an interaction is to occur; Poisot, Cirtwill, et al. (2016)] or as a continuous measurement [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.

### 0.1.3 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 network (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. It is however clear that food webs defined in this manner fail to give any agency to the species in the community.

Talking about delimiting, the idea of aggregating over time or aggregating over space...

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

## 0.2 How do we construct ecological networks?

Arguably the need for methods and tools for constructing interaction networks 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 running further simulations (*e.g.*, extinction simulations) or understanding some higher-level process/concept (*e.g.*, understanding energy flows), importantly these networks do not require any level of species specificity *per se* and it is more the

arrangements of the nodes (species) 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 inherent challenges of inventorying interaction in the field (Morales-Castilla et al. (2015) present a more mechanistic overview, while Strydom et al. (2021) provides a more statistical overview). Of course these two categories are not distinct, mutually exclusive, groups but can rather be viewed as operating on a gradient ranging from a need for generality (*i.e.*, creating a network that, when taken in aggregate, the distribution of links (interactions) between species are ecologically plausible) to a need for specificity (*i.e.*, local-level predictions between specific species).

### 0.2.1 Predicting structure or interactions?

These two groups are they themselves made up of different tools that also 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). Thus it is important to not lose sight of the core philosophy behind the model we use and to ensure that we are using the model best suited to what we want to be accomplishing.

- Core mechanistic differences that models will work at — some are really concerned about (and thus constrained by) structure, others are more mechanistic in nature *i.e.*, species *a* has the capacity to eat species *b* because traits

### 0.2.2 Model families

Given the large number of models that have been developed it is perhaps more meaningful to group models into families with the idea that models from the same family will yield similar results because they play by similar rules. These rules referring to the underlying philosophy as to what structures either networks or the interactions within them (see Figure 1 panel A). 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 network.

[Figure 1 about here.]

[Figure 2 about here.]

**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. There is however the assumption that a network will be constrained by the number of links. 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. These two models are equivalent to the Erdos-Renyi and Configuration models (Newman, 2010) respectively (check that though).

**Neutral models:** Based on the theory that interactions occur as the result of the abundance of species (*i.e.*, the species still has no agency but its abundance does?). See 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... so not a single dimension? **TODO.** 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 statistical 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-trait 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. **TODO** Log-ratio (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 using ecological proxies (Morales-Castilla et al., 2015). 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 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:** Not so much about empirical observations but more the value of ‘local’ knowledge and having specific individuals sitting around a table and assigning 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 as opposed to binary fashion, *e.g.*, Maiorano et al. (2020) score interactions as either obligate (typical food resources) or occasional (opportunistic feeding) interactions. I feel like its worth also mentioning downfalls *a la* Brimacombe et al. (2023)...

**Data scavenging:** There are also a lot of published *interaction* data that are publicly available *e.g.*, the Global Biotic Interactions (GloBI) database (Poelen et al., 2014) and these can also be used to construct an interaction network by mining these sources 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 or absent between the two species (*e.g.*, the WebBuilder tool developed by Gray et al., 2015). It

1 is important to note that this methodology is only going to be able to infer observations that have been  
2 recorded in the field, and given the relative scarcity [*I say Poisot et al. (2021) but that's more an overview of*  
3 *complete networks but one can also get pairwise interactions from these types of data so I feel like its okay?*]  
4 and localised sampling of these types of datasets it is very likely that there will be many false negatives  
5 (missing pairwise interactions) using this approach.

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

Table 1: Lets make a table that gives an overview of the different model families and some of their features.  
*A column that captures naïve vs a priori knowledge of interactions/structure i.e., a 'parameter' of sorts?*

				Make ‘ <i>de novo</i> ’ predictions				
Model family	Theory	Network predicted	Links predict	(node/species identity)	Needs (minimum)	Assembly mechanism	Constraints	Interaction
null	Network structure is random	structure		no	network (species agnostic)	random	link	binary
neutral	Network structure is random, but species abundance plays a role	structure		yes	abundance, mass number of links	mass effect	link	binary



				Make ‘ <i>de novo</i> ’ predictions				
Model family	Theory	Network predicted	Links predict	(node/species identity)	Needs (minimum)	Assembly mechanism	Constraints	Interaction
resource	Networks are interval, species can be ordered on a ‘niche axis’	structure	flow of biomass (re-source?)	no	richness, connectance	‘random’	link	binary
generative	Networks are determined by their structural features	structure		no	network (species agnostic)	‘random’		binary
energetic	Interactions are determined by foraging theory (feeding links)	interactions	flow of energy	yes	body size	deterministic	energy	

		Make ‘ <i>de novo</i> ’ predictions					
		Needs		Assembly			
Model	Theory	Network	Links	(node/species identity)	(minimum)	mecha-	Constraints Interaction
family	predicted	predict				nism	
graph	Interactions	interactions	potential	yes	interactions,		probabilistic
embed-	can be		feeding		phyloge-		
ding	predicted		links		netic		
	from the				tree, list		
	latent				of target		
	traits of				species		
	networks				(species		
					pool)		
trait	Interactions	interactions	potential	yes	prior	mechanistic	trait
matching	can be		feeding		(expert)		matching
	inferred		links		knowl-		( <i>sensu</i>
	by a				edge of		forbidden
	mechanis-				trait		links in a
	tic				hierar-		way)
	frame-				chy/relationships,		
	work/relationships				traits,		
					list of		
					target		
					species		
					(species		
					pool)		

		Make ‘ <i>de novo</i> ’ predictions					
		Needs		Assembly			
Model family	Theory	Network predicted	Links predict	(node/species identity)	(mini-mum)	mecha-nism	Constraints Interaction
binary classifiers	Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors	interactions	potential feeding links	yes	interactions, traits, list of target species (species pool)	statistical	
expert knowl-edge	‘Boots on the ground’ ecological knowl-edge and observa-tions	interactions	potential feeding links	yes	list of target species (species pool)	mechanistic	forbidden links

		Make ‘ <i>de novo</i> ’ predictions					
		Needs		Assembly			
Model family	Theory	Network predicted	Links predict	(node/species identity)	(minimum)	mecha-nism	Constraints Interaction
data	Webscraping	interactions	potential	no	list of		binary
scaveng- ing	to create networks from online databases		feeding links		target species (species pool)		
co- occurrence	co- occurrence patterns arise from interac- tions so we can use these patterns to reverse engineer the inter- actions	co- occurrence links? (or am I being a bit too mean here)	association links		co- occurrence (so a species list?)		

#### 1 0.2.2.1 When to use what?

2 [Figure 3 about here.]

3 [Figure 4 about here.]

4 [Figure 5 about here.]

Source: [Article Notebook](#)

[Figure 6 about here.]

Source: [Article Notebook](#)

#### 0.2.2.2 Model benchmarking

- ‘Testing’ the performance of a model is going to depend on some of the core limitations of the model itself thus it makes sense to think of two sets benchmarking rules for network and interaction prediction models respectively (see Figure 1 panel B).
- When it comes to network models we are concerned with the ‘preservation’ of structure and distribution of links across the network. For interaction models 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))  
“As long as these predictions are not perfect, some interactions will be predicted at the ‘wrong’ position in the network; these measures cannot describe the structural effect of these mistakes. On the other hand, measures of network structure can have the same value with interactions that fall at drastically different positions; this is in part because a lot of these measures covary with connectance, and in part because as long as these values are not 0 or their respective maximum, there is a large number of network configurations that can have the same value.” - Poisot (2023)

##### 0.2.2.2.1 Benchmarking network models

- 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)  
“Possibly, the most striking caveat of the use of summary statistics is that it cannot tell us whether or not a model is able to fully replicate empirical networks.” - Allesina et al. (2008)

##### 0.2.2.2.2 Benchmarking interaction models

- Main concern with predicting interactions is that we want to test the ‘quality’ of the links we are predicting (both true positives and true negatives), but the inherent sparsity (meaning high class imbalance) means that we also need to look at the balance of these predictions.

- “Both precision and recall may be useful in cases where there is imbalanced data. However, it may be valuable to prioritize one over the other in cases where the outcome of a false positive or false negative is costly.”
- 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
- See Poisot (2023)
  - skill (ability to make the right prediction; evaluate whether low prevalence can lull us into a false sense of predictive accuracy)
  - bias (trends towards systematically over-predicting one class)
  - class imbalance (the relative number of cases representing interactions)
- “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 7 about here.]

Source: [Article Notebook](#)

I really like this way of plotting results from Pichler et al. (2020)

[Figure 8 about here.]

### 0.3 Link 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)

## 0.4 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 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](#)

- Allesina, S., Alonso, D., & Pascual, M. (2008). A General Model for Food Web Structure. *Science*, 320(5876), 658–661. <https://doi.org/10.1126/science.1156269>
- Banville, F., Gravel, D., & Poisot, T. (2023). What constrains food webs? A maximum entropy framework for predicting their structure with minimal biases. *PLOS Computational Biology*, 19(9), e1011458. <https://doi.org/10.1371/journal.pcbi.1011458>
- Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16), 9383–9387. <https://doi.org/10.1073/pnas.1633576100>
- Becker, D. J., Albery, G. F., Sjödin, A. R., Poisot, T., Bergner, L. M., Chen, B., Cohen, L. E., Dallas, T. A., Eskew, E. A., Fagre, A. C., Farrell, M. J., Guth, S., Han, B. A., Simmons, N. B., Stock, M., Teeling, E. C., & Carlson, C. J. (2022). Optimising predictive models to prioritise viral discovery in zoonotic reservoirs. *The Lancet Microbe*, 3(8), e625–e637. [https://doi.org/10.1016/S2666-5247\(21\)00245-7](https://doi.org/10.1016/S2666-5247(21)00245-7)
- Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, 103(37), 13745–13749. <https://doi.org/10.1073/pnas.0603039103>
- Berlow, E. L., Brose, U., & Martinez, N. D. (2008). The “Goldilocks factor” in food webs. *Proceedings of the National Academy of Sciences*, 105(11), 4079–4080. <https://doi.org/10.1073/pnas.0800967105>
- Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., & Petchey, O. (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3), 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23(7), 1050–1063. <https://doi.org/10.1111/ele.13525>
- Brimacombe, C., Bodner, K., & Fortin, M.-J. (2024). *Applying a method before its proof-of-concept: A cautionary tale using inferred food webs*. <https://doi.org/10.13140/RG.2.2.22076.65927>
- Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T., & Fortin, M.-J. (2023). Shortcomings of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21(4),

e3002068. <https://doi.org/10.1371/journal.pbio.3002068>

Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>

Cattin, M.-F., Bersier, L.-F., Banašek-Richter, C., Baltensperger, R., & Gabriel, J.-P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427(6977), 835–839. <https://doi.org/10.1038/nature02327>

Cirtwill, A. R., Eklf, A., Roslin, T., Wootton, K., & Gravel, D. (2019). A quantitative framework for investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 0(ja). <https://doi.org/10.1111/2041-210X.13180>

Cohen, J. E. (1977). Food webs and the dimensionality of trophic niche space. *Proceedings of the National Academy of Sciences*, 74(10), 4533–4536. <https://doi.org/10.1073/pnas.74.10.4533>

Cohen, J. E., Briand, F., & Newman, C. (1990). *Community Food Webs: Data and Theory*. Springer-Verlag.

Cohen, J. E., Newman, C. M., & Steele, J. H. (1985). A stochastic theory of community food webs I. Models and aggregated data. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 224(1237), 421–448. <https://doi.org/10.1098/rspb.1985.0042>

Dale, M. R. T., & Fortin, M.-J. (2010). From Graphs to Spatial Graphs. *Annual Review of Ecology, Evolution, and Systematics*, 41, 21–38. <https://www.jstor.org/stable/27896212>

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. J. Murray.

DeAngelis, D. L., Goldstein, R. A., & O'Neill, R. V. (1975). A Model for Tropic Interaction. *Ecology*, 56(4), 881–892. <https://doi.org/10.2307/1936298>

Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães, P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019). Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brev.12433>

Desjardins-Proulx, P., Laigle, I., Poisot, T., & Gravel, D. (2017). Ecological interactions and the Netflix problem. *PeerJ*, 5, e3644. <https://doi.org/10.7717/peerj.3644>

Dunne, J. A. (2006). The Network Structure of Food Webs. In J. A. Dunne & M. Pascual (Eds.), *Ecological networks: Linking structure and dynamics* (pp. 27–86). Oxford University Press.

Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and Network Analyses of Cambrian Food Webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>

Eklöf, A., Tang, S., & Allesina, S. (2013). Secondary extinctions in food webs: A Bayesian network approach.

*Methods in Ecology and Evolution*, 4(8), 760–770. <https://doi.org/10.1111/2041-210X.12062>

Fortuna, M. A., & Bascompte, J. (2006). Habitat loss and the structure of plant-animal mutualistic networks: Mutualistic networks and habitat loss. *Ecology Letters*, 9(3), 281–286. <https://doi.org/10.1111/j.1461-0248.2005.00868.x>

Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator–prey body size relationships. *Methods in Ecology and Evolution*, 4(11), 1083–1090. <https://doi.org/10.1111/2041-210X.12103>

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

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

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

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

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

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

Newman, M. E. J. (2010). *Networks. An introduction*. Oxford University Press.

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

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

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

Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M., & Hartig, F. (2020). Machine learning algorithms

to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210X.13329>

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

Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a

robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621), 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>

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

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

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

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

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

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

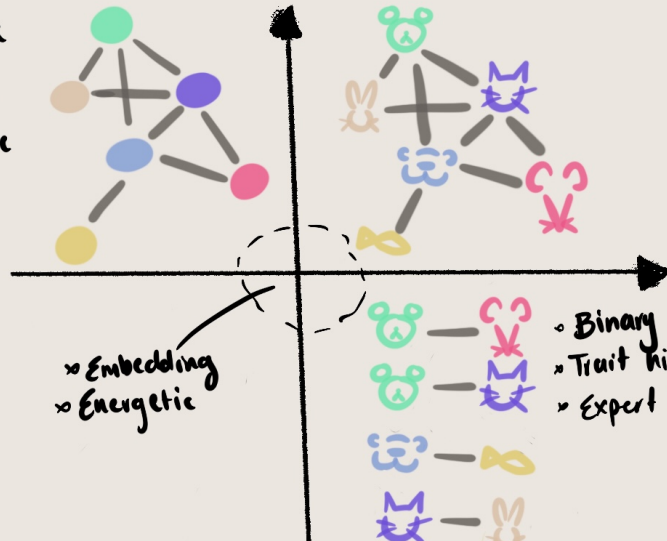
Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183. <https://doi.org/10.1038/35004572>

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

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

# A Predicting.

- Resource
- Null
- Neutral
- Generative



- Binary Classifiers
- Trait hierarchy
- Expert knowledge

# B Benchmarking

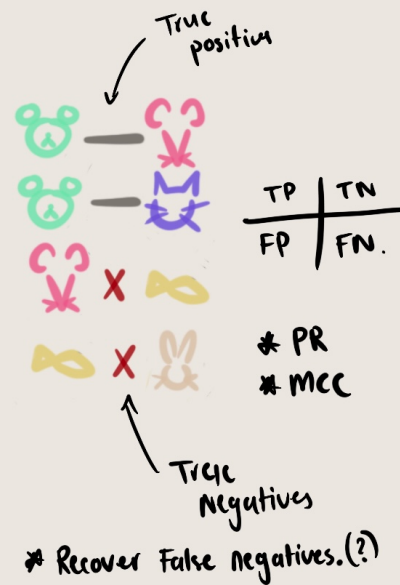
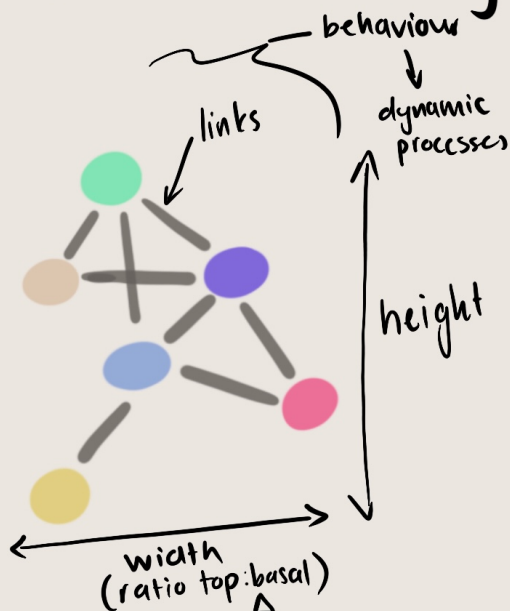


Figure 1: Conceptual figure of the 'network prediction'. Panel A shows where the model families fall in the the context of being models that predict networks or models that predict interactions space. Panel B serves to highlight the characteristics one might like to 'test'/benchmark for a model based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

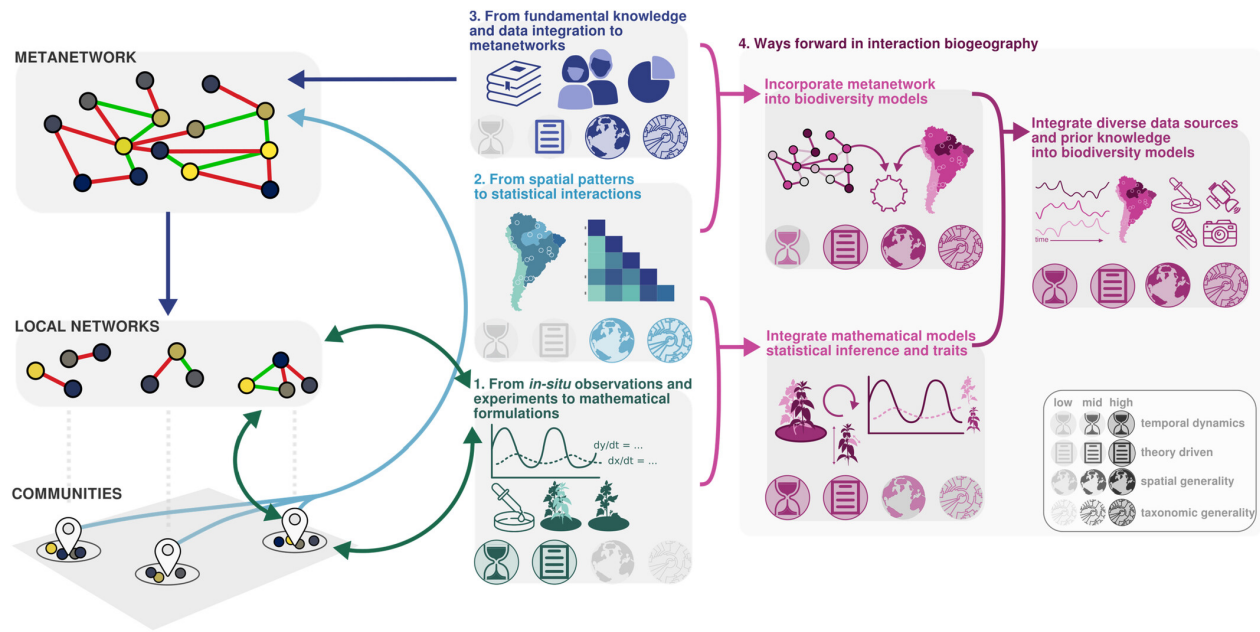


Figure 2: I like the use of the different source indicator items (not too dissimilar from Tall Tom's nature paper but also different). This is from Thuiller et al. (2024)



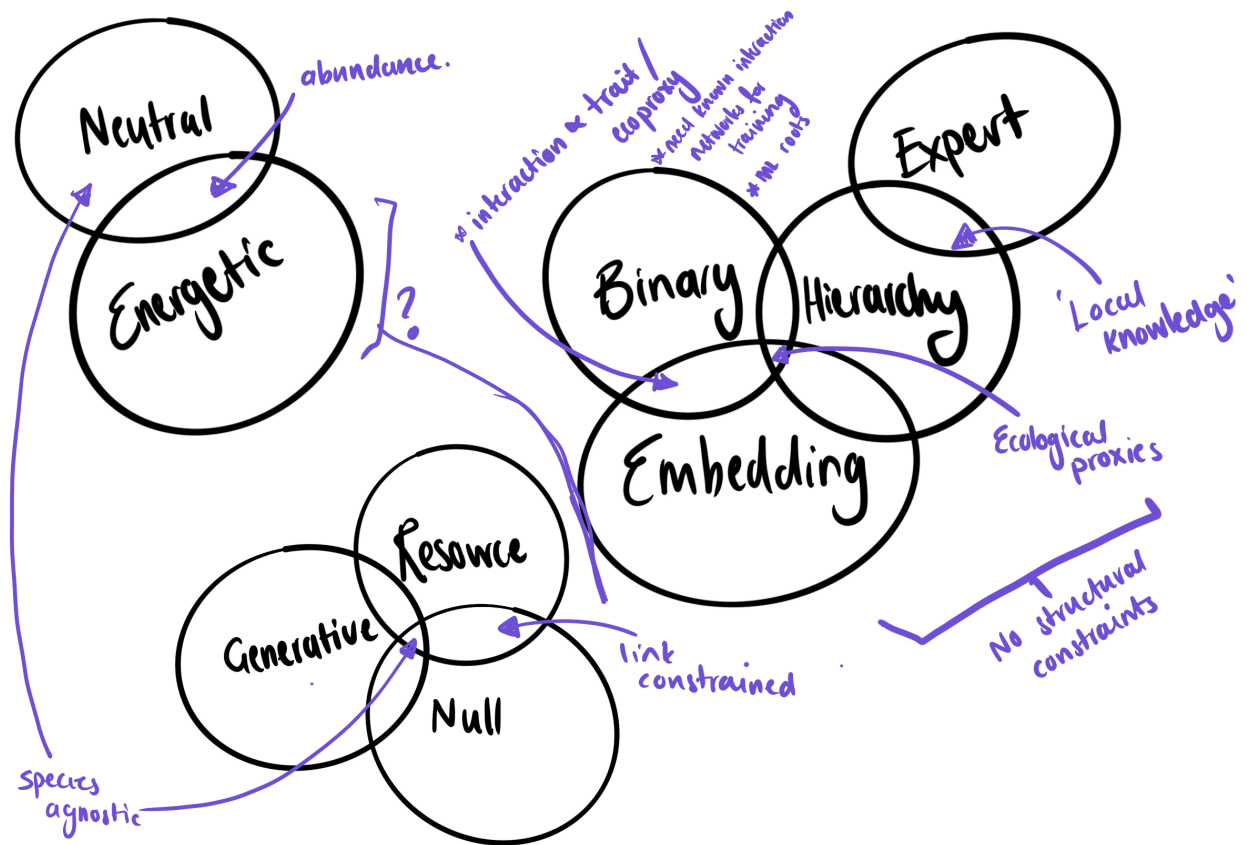


Figure 3: I still haven't given up on a sort of venn diagram idea but maybe it going to be more of a venn-flow chart hybrid...



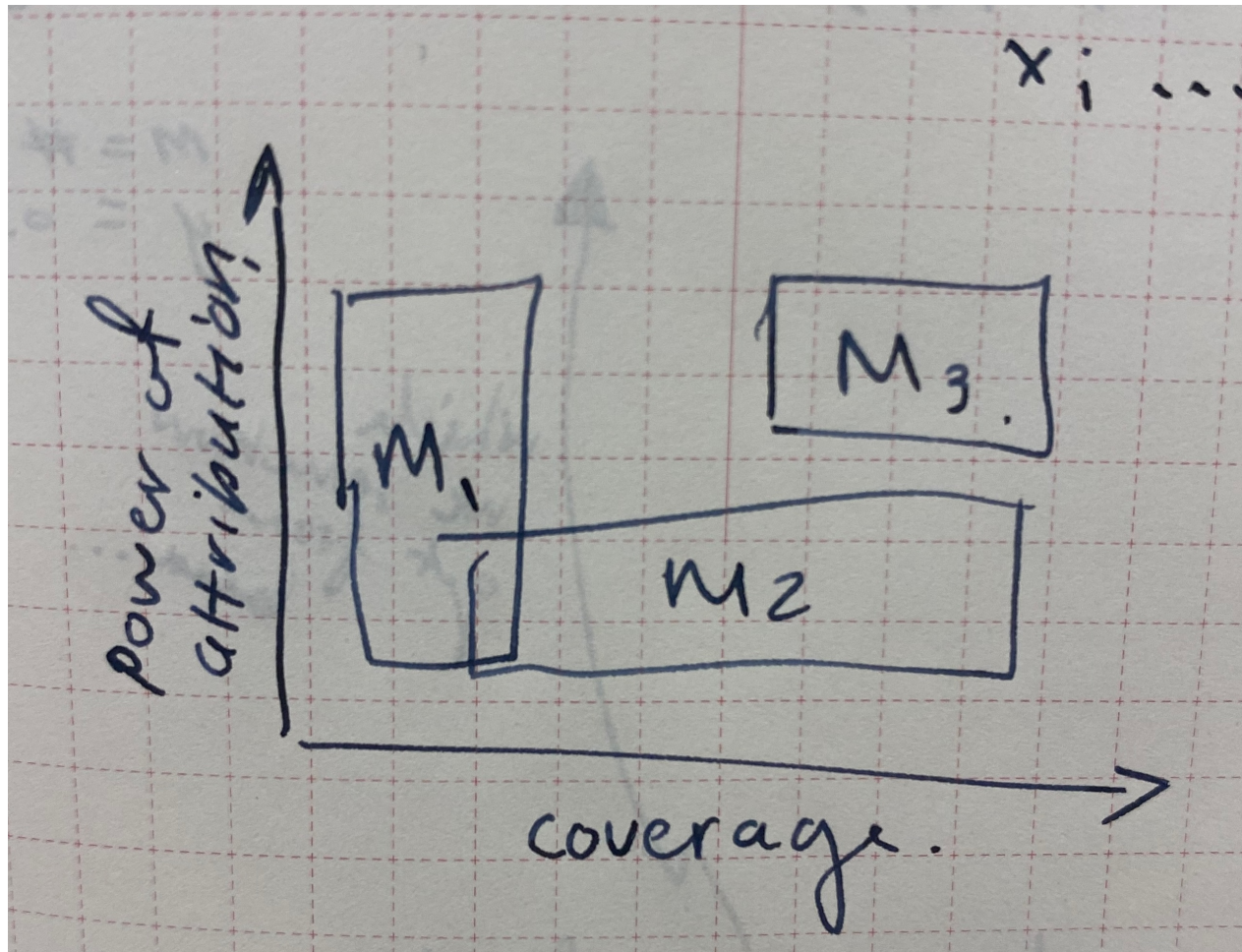


Figure 4: I like these schematics that Charlie Outhwaite presented at the EEB seminar (there was a series of them).

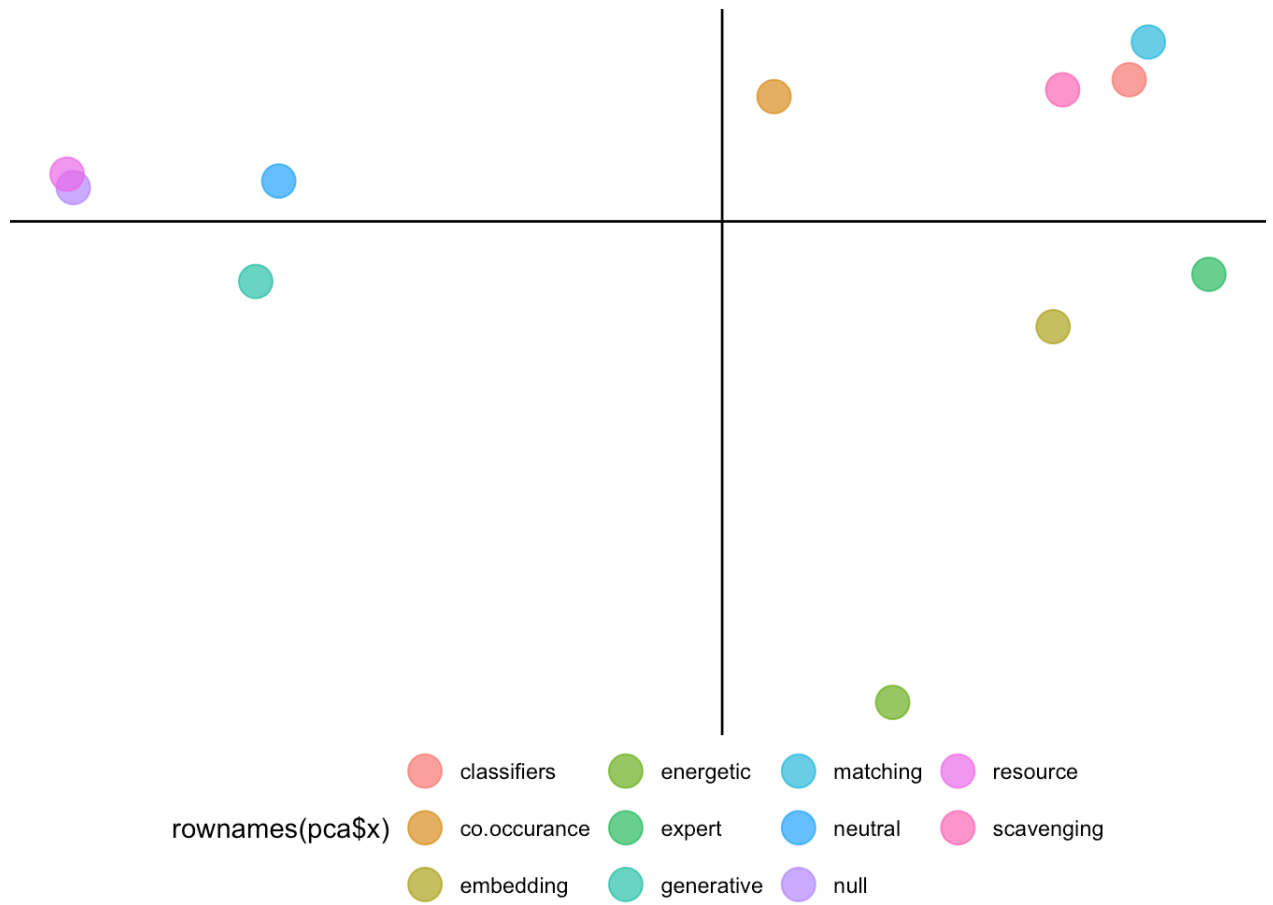


Figure 5: PCA of the trait table

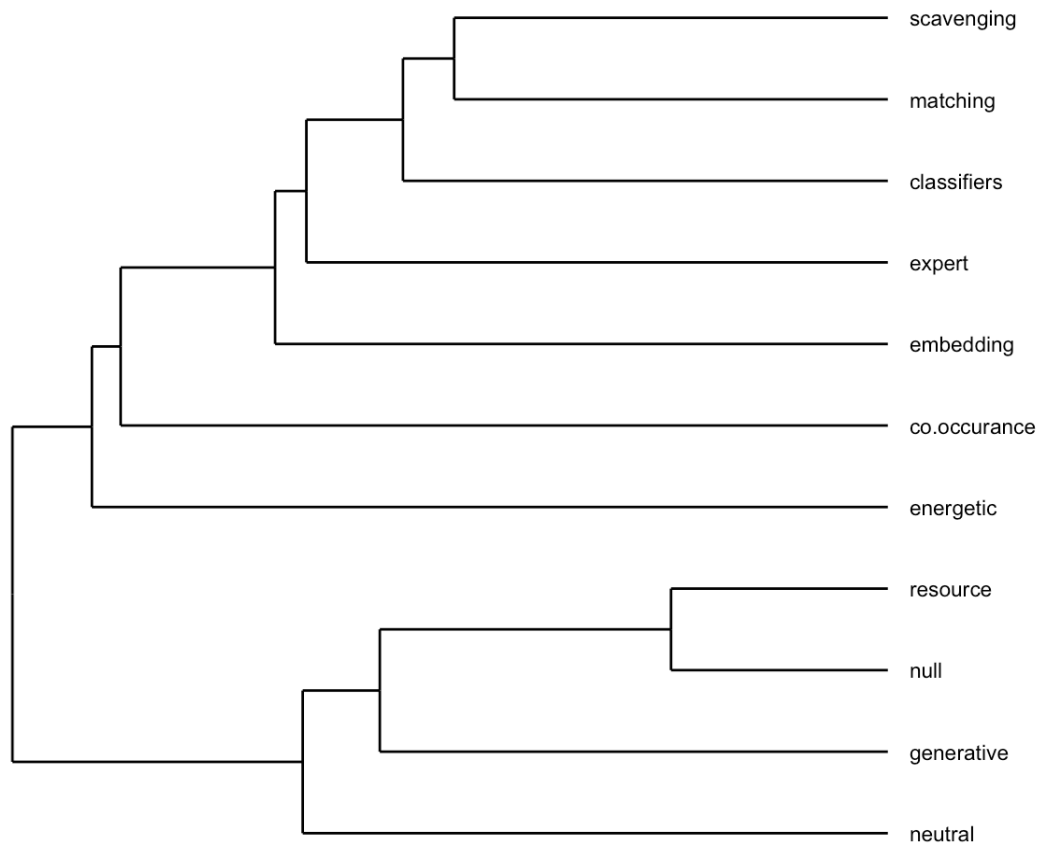


Figure 6: Dendrogram of the trait table

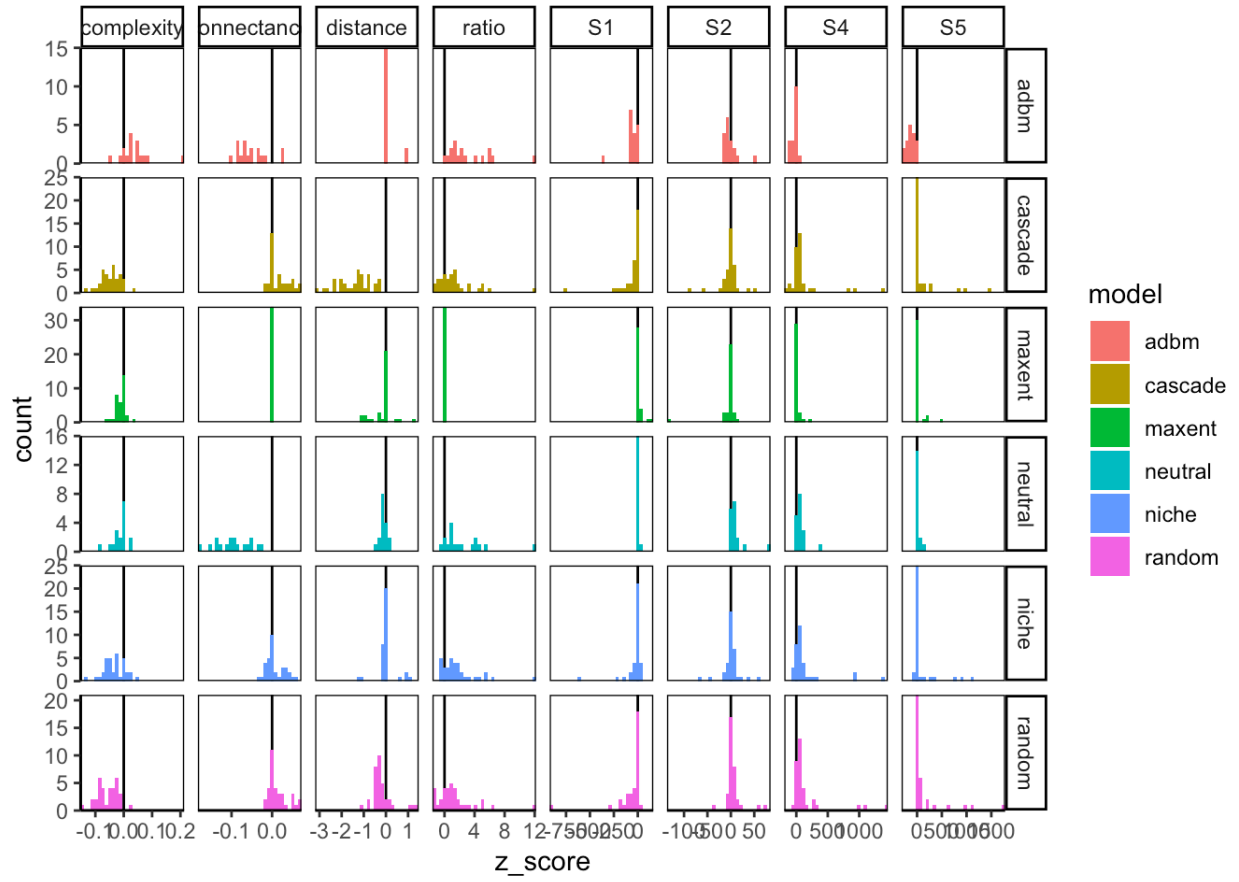


Figure 7: Difference between real and model network property. S1 - S5 represent the different motif structures identified in Stouffer et al. (2007).

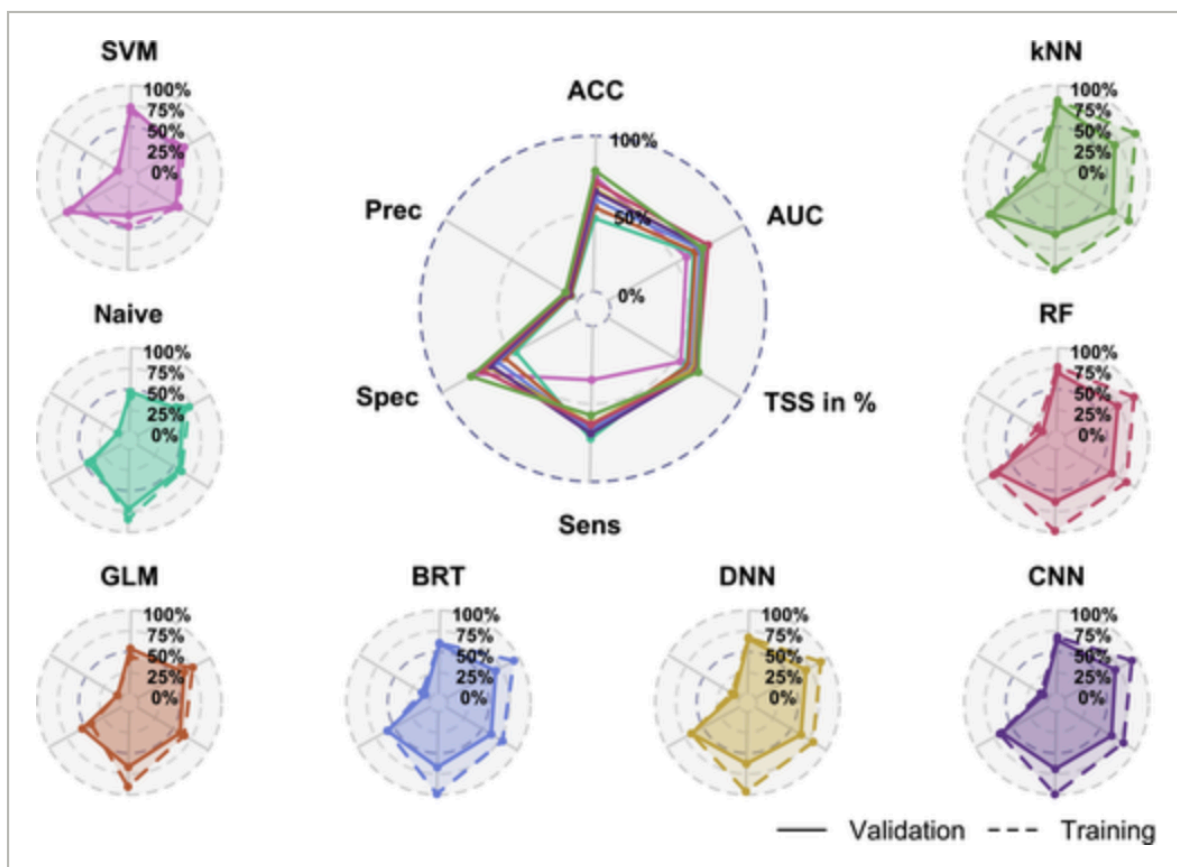


Figure 8: Cool way to conceptualise results from Pichler et al. (2020)