

T is for Topology

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Abstract

There are many reasons one might want to generate a network and there are many tools on the market that might make that possible. However not all tools are created equally and there is reason to assume that not all networks will suit most purposes. Here the aim is to compare and contrast the different topology generating tools that are on the market and see where they shine and where they fall flat. There probably isn't one model to rule them all but it doesn't mean that we shouldn't be critical when we think about the model we want to use.

Plain Language Summary

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.

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 [ref]. And although the idea of species interactions and the resulting networks that they form has been a part of the ecological canon since the times of Darwin [ref], if not since Aristotle??? [ref], however the adoption of network ecology into other disciplines 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). The second is 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 predictions, (*e.g.* ref maybe Pringle & Hutchinson, 2020)) 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 [graph theory ref], properties [ref] 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.

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 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?).

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).

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

0.2.1 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.

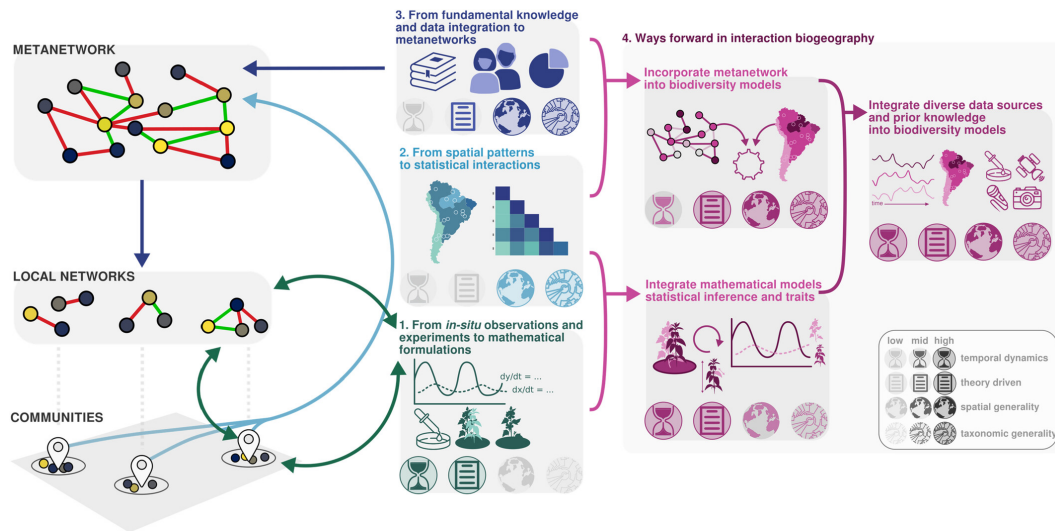


Figure 2: I like the use of the different source indicator items (not too dissimilar from Tall Tom’s nature paper but also different). This is from Thuiller et al. (2024)

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).

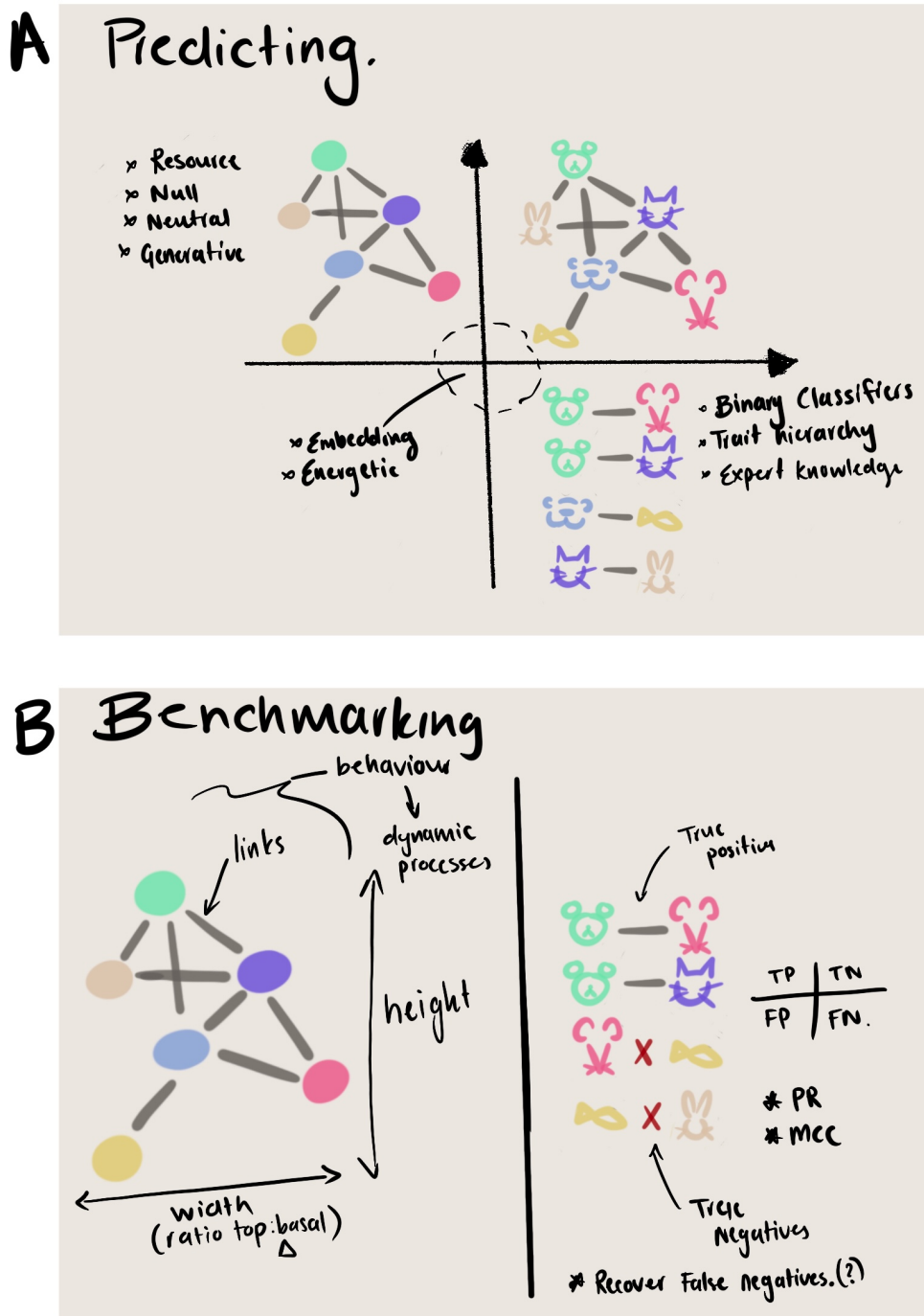


Figure 1: Conceptual figure of the ‘network prediction’. Panel A shows where the model families fall in the context of being models that predict networks or models that predict interactions space. Panel B serves to highlight the characteristics one might like to ‘test’/benchmark for a model based on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

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

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?*

Model family	Theory	Network pre-dicted	Links predict	Make ‘ <i>de novo</i> ’ predictions (node/species identity)	Needs (minimum)	Assembly mechanism	Constraint	Interaction
null	Network structure is random	structure		no	network (species agnostic)	random	link	binary

Model family	Theory	Network predicted	Links predict	Make ‘ <i>de novo</i> ’ predictions (node/species identity)	Needs (minimum)	Assembly mechanism	Constraint	Interaction
neutral	Network structure is random, but species abundance plays a role	structure		yes	abundance, number of links	mass effect	link	binary
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	

Model family	Theory	Network pre-dicted	Links predict	Make ‘ <i>de novo</i> ’ predictions (node/species identity)	Needs (minimum)	Assembly mechanism	Constraint	Interaction
graph embedding	Interactions can be pre-dicted from the latent traits of networks	interactions	potential feeding links	yes	interactions, phylogenetic tree, list of target species (species pool)			probabilistic
trait matching	Interactions can be inferred by a mechanistic framework/relationships	interactions	potential feeding links	yes	prior (expert) knowledge of trait hierarchy/relationships, list of target species (species pool)	mechanistic		trait matching (<i>sensu</i> forbidden links in a way)
binary classifiers	Interactions can be pre-dicted by learning the relationship between interactions and ecologically relevant predictors	interactions	potential feeding links	yes	interactions, traits, list of target species (species pool)	statistical		

Model family	Theory	Network predicted	Links predict	Make ‘ <i>de novo</i> ’ predictions (node/species identity)	Needs (minimum)	Assembly mechanism	Constraints	Interaction
expert knowledge	‘Boots on the ground’ ecological knowledge and observations	interactions	potential feeding links	yes	list of target species (species pool)	mechanistic	if forbidden links	
data scavenging	Web scraping to create networks from online databases	interactions	potential feeding links	no	list of target species (species pool)			binary
co-occurrence	co-occurrence patterns arise from interactions so we can use these patterns to reverse engineer the interactions	co-occurrence links? (or am I being a bit too mean here)	association links		co-occurrence (so a species list?)			

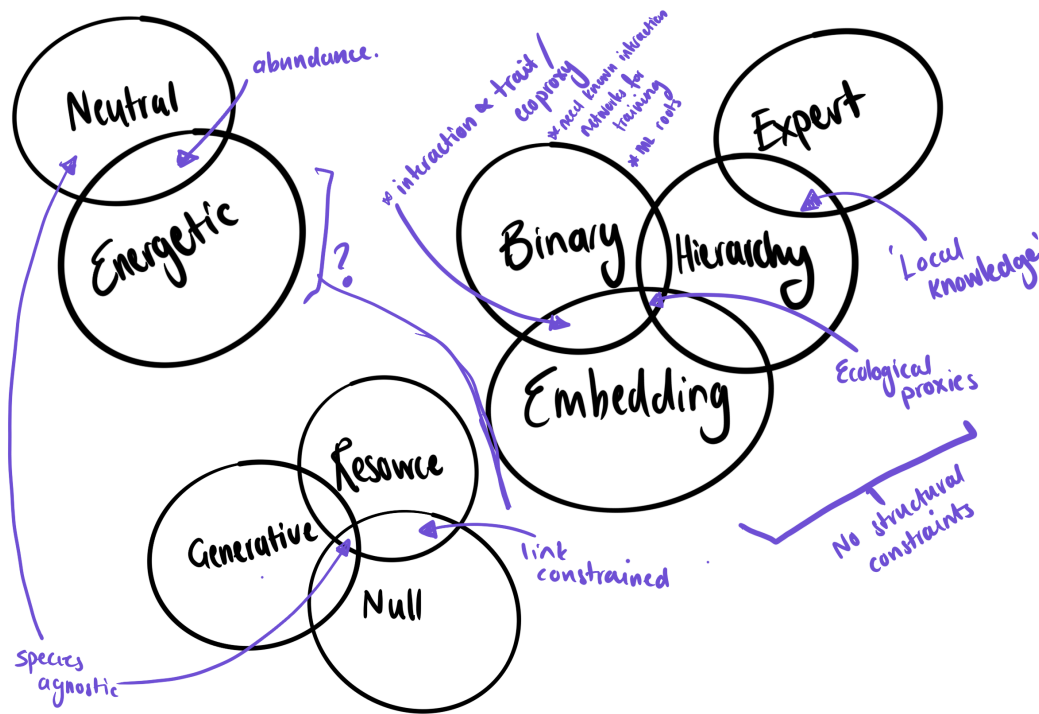


Figure 3: I still haven't given up on a sort of venn diagram idea but maybe it going to be more of a venn-flow chart hybrid...

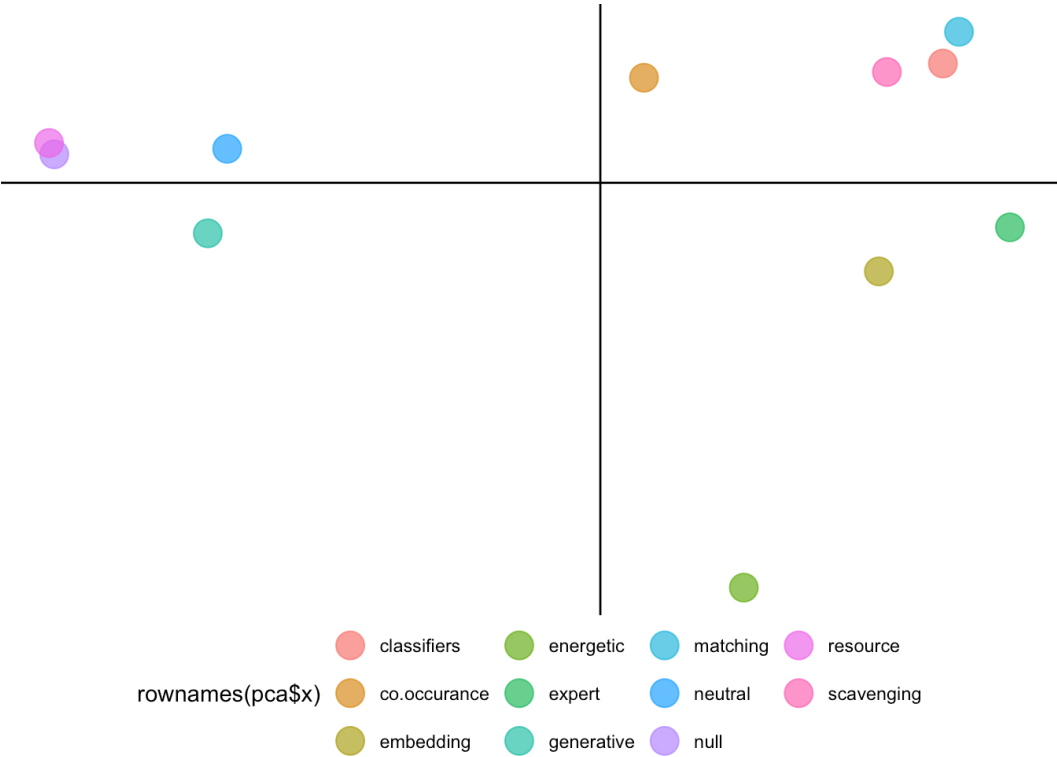


Figure 5: PCA of the trait table

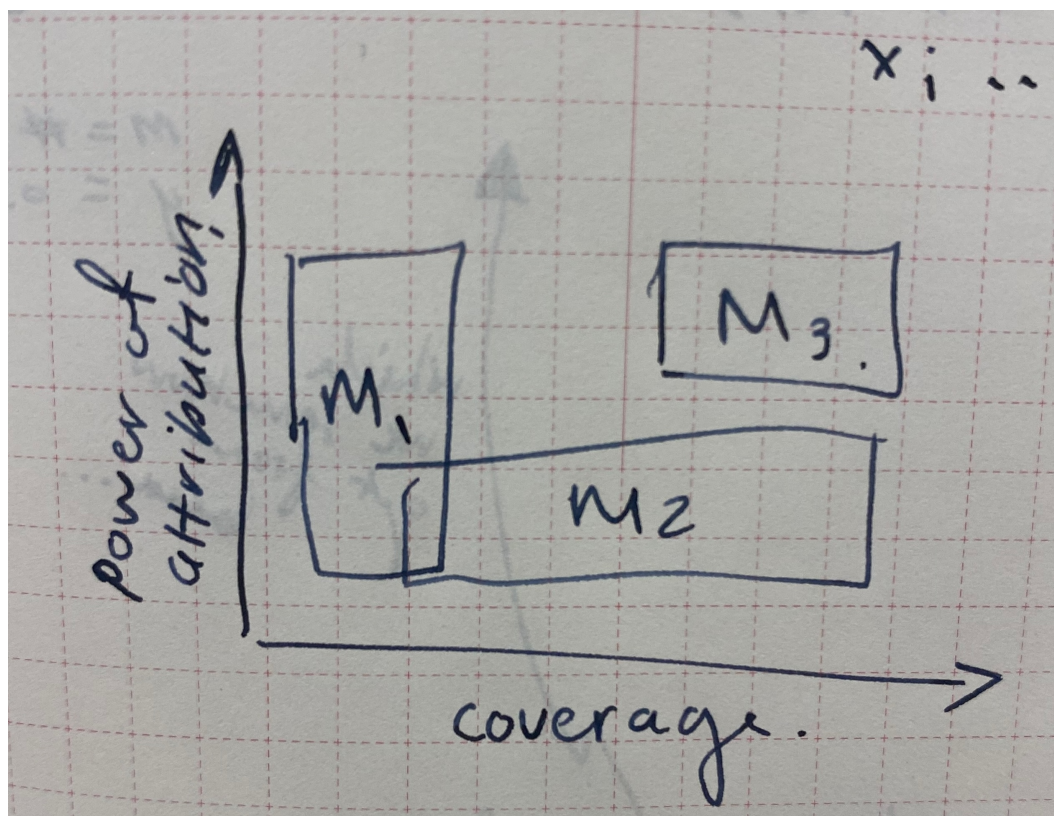


Figure 4: I like these schematics that Charlie Outhwaite presented at the EEB seminar (there was a series of them).

226 Source: [Article Notebook](#)

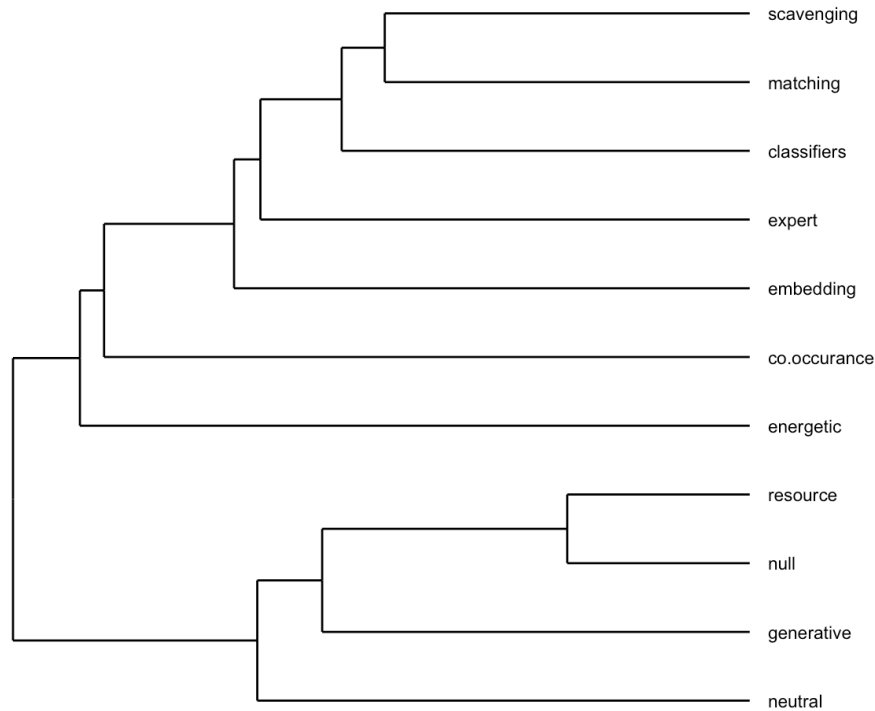


Figure 6: Dendrogram of the trait table

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228 *0.2.1.2 Model benchmarking*

- 229 • ‘Testing’ the performance of a model is going to depend on some of the core
230 limitations of the model itself thus it makes sense to think of two sets bench-
231 marking rules for network and interaction prediction models respectively (see
232 Figure 1 panel B).
- 233 • When it comes to network models we are concerned with the ‘preservation’ of
234 structure and distribution of links across the network. For interaction models
235 we want to ensure that we are able to retrieve interactions that really exist
236 but also those that cannot exist (*sensu* forbidden links Jordano (2016b))

237 “As long as these predictions are not perfect, some interactions will be pre-
238 dicted at the ‘wrong’ position in the network; these measures cannot describe
239 the structural effect of these mistakes. On the other hand, measures of net-
240 work structure can have the same value with interactions that fall at drasti-
241 cally different positions; this is in part because a lot of these measures covary
242 with connectance, and in part because as long as these values are not 0 or
243 their respective maximum, there is a large number of network configurations
244 that can have the same value.” - Poisot (2023)

245 *0.2.1.2.1 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)

0.2.1.2.2 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 inherit 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* Jennifer A. Dunne (2006)) and a network realisation. Maybe also Poisot et al. (2015) that discuss how the local factors are going to play a role.

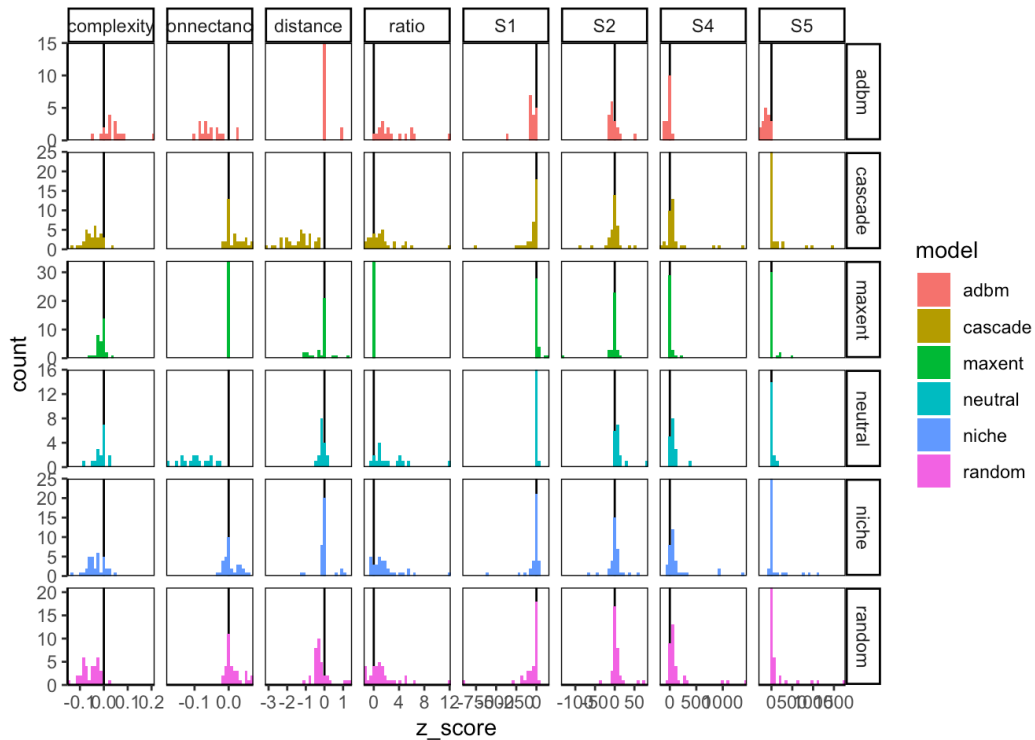


Figure 7: Difference between real and model network property. S1 - S5 represent the different motif structures identified in Stouffer et al. (2007).

Source: [Article Notebook](#)

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

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?

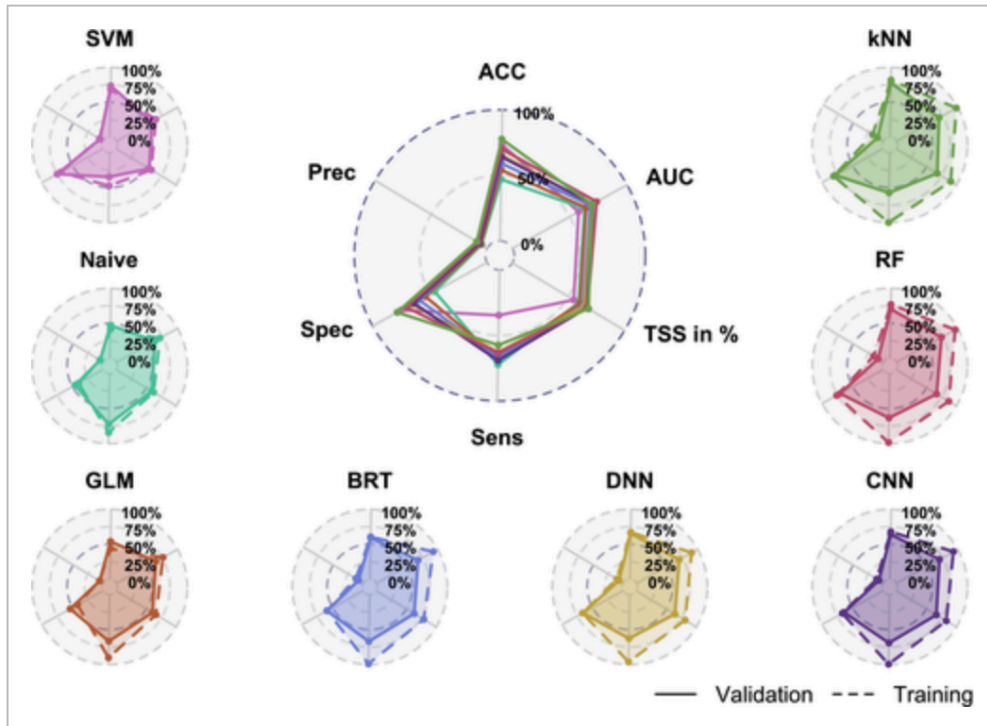


Figure 8: Cool way to conceptualise results from Pichler et al. (2020)

- 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).

Joel E. 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)

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Source: [Article Notebook](#)

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