

Navigating food web prediction; assumptions, rationale, and methods

Tanya Strydom ¹; Jennifer A. Dunne ²; Timothée Poisot ^{3,4}; Andrew P. Beckerman ¹

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.

Keywords: food web, network construction

1 Although there is a growing consensus that species interaction networks are an important facet of understand-
2 ing biodiversity it is a field where we are lacking in real world data [1], and broader understanding (Eltonian
3 shortfall). Because of this overall lack of data (and extreme difficulty in generating it [2,3]) we as researchers
4 find ourselves having to predict/construct networks using a modelling approach. The problem with that is
5 that there are as many models as there are ways to define food webs and although there have been attempts
6 to compare some of the more canonical models in terms of their performance [4,5] there is a distinct lack
7 of discussion and resulting awareness of the different model families and how they are embedding different
8 philosophies.

9 It can be argued that the interaction between species (or individuals) is one of the main determinants of the
10 emergent properties that are studied in other fields of ecology, *e.g.*, the range of plant will be determined by
11 the range of its pollinator, and although the importance of species interactions and the resulting networks that
12 they form has been an acknowledged part of the ecological canon since the penning of the ‘entangled bank’
13 [6], the adoption of network ecology into other disciplines of ecology has been limited. This has primarily
14 been driven by two limitations; firstly, it is extremely challenging to actually record species interactions in
15 the field [2,3], which has resulted in a limited coverage of ‘real world’ interaction data [1], and secondly
16 has been the need to develop terminology and tools that help us to construct, conceptualise, and analyse
17 these networks. Although recording interactions in the field remains a challenge, the development of both
18 practical tools [*i.e.*, tools that help us to record or measure interactions, 7], as well as discussions around
19 the development of tools to predict or infer them [8,9], has allowed us to begin filling in these ‘global gaps’,
20 albeit in a, potentially, more synthetic manner [10]. Additionally, there has been extensive development in
21 in the ways in which we formalise networks [11,12], and the tools and language that we use to quantify the
22 structure and properties of networks [13]. All together these tools mean that, as a field, network ecology
23 can (and should) be integrated into the broader fields of ecology [*e.g.*, 14] and conservation biology [*e.g.*, 15].
24 However (as with any new tool or model), it is important that one has a firm grasp of how the underlying
25 philosophy that underpins the construction of networks (particularly synthetic ones) can have an impact on
26 the interpretation of the questions being asked. In this manuscript we will discuss three themes that should
27 help provide clarity and understanding for those wishing to take a step into network (particularly food web)
28 ecology this includes; thinking about and understanding the underlying assumptions that are made when we
29 attempt to delimit and describe a food webs, a synthesis of the different families of tools that are commonly
30 used to construct food webs, and a discussion linking network ecology to some of the outstanding questions
31 in ecology.

32 [Figure 1 about here.]

1 Why do we want to predict food webs?

Because measuring in the field is hard and sometimes we need model systems so we don't have real data. The bigger reason is that we *think* that using a network-based approach is really the answer to helping us address some of the more bending issues we toil and think about in the world.

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 inherent challenges of inventorying interactions in the field (see [8] for a more mechanistic, and [9] 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, 2024), but also how well the tool is able to retrieve the specific network or interaction properties that they desire.

2 The anatomy of a food web

Defining a food web seems simple, it is the representation of the interactions (edges) between species (nodes), however the definition of 'edges' and 'nodes', as well as the scale at which they are aggregated can take many forms. As highlighted in [16] networks can be constructed at the population (the links between individuals), community (the links between species), or metacommunity (fluxes between locations) level. Even if one were to limit their scope to thinking of interaction networks only in terms of food webs at the community-level there are still many ways to define the various components of the network, 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?). It is thus clear that the way that a network is coded (constructed) can influence the resulting observations and conclusions that are made [17,18], and it is important to have a strong grasp of what information a network is attempting to convey.

2.1 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.

2.2 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 [19] or potential [20] feeding links, or energy transfer and material flow [21]. 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 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, 22] or continuous measurements [which quantifies the effect of one species on another, 23]. 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.

[24] states that “[*Their*] approach is more like gross anatomy than like physiology... that is, the gross anatomy is frozen, rather than in motion.”.

2.3 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 [25]. This introduced the idea that a single dimension [the “niche axis,” 26] 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, [3]) 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]

i Box 1 - Mechanisms that determine feeding links

Proximity

We are co-occurring in space and in time and thus we can interact

Mass-effect

Our (instantaneous) abundance in that time and space is going to influence how we interact

Complementarity

We have a set of ‘traits’ that means we can interact including:

- You as a prey item fit in my gob (I can eat you, ~~even if its small bites~~) [ref]
- You as a prey item are energetically ‘worth it’ [ref foraging ecology]
- As a predator I have the required traits that allow me to ~~kill~~ ~~unlive~~ and eat you [3]

3 How do we predict food webs?

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 [27]

Although there have been efforts to compare and contrast different models [5] 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 preforming in the different facets of constructing a food web.

3.1 Model families

As there are many food web models to choose from it is perhaps useful to think about the models in terms of model families, a summary of these families is presented in Table 1 and highlights the differences and similarities of the philosophies and assumptions that determine a network. It should be noted that although we provide some examples of specific use cases within each model family this by no means an exhaustive list of of all the different approaches ever used but rather a representative collection of some of the more canonical approaches used within each model family.

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 | Links are randomly distributed within a network | structural | agnostic | feeding links | binary | |

| Model | | Network | Nodes | Links | | Key |
|------------|---|-------------|-----------------|-------------------------|--------------|-----------|
| family | Theory | predicted | represent | represent | Interaction | reference |
| neutral | Network structure is random, but species abundance determines links between nodes | structural | species | feeding links | binary | |
| resource | Networks are interval, species can be ordered on a ‘niche axis’ | structural | trophic species | subdivision of resource | binary | [4] |
| generative | Networks are determined by their structural features | structural | agnostic | links | binary | |
| energetic | Interactions are determined by foraging theory (feeding links) | interaction | species | feeding links | quantitative | |

| Model | | Network | Nodes | Links | | Key |
|-----------------------|--|-------------|-----------|----------------------------|---------------|-----------|
| family | Theory | predicted | represent | represent | Interaction | reference |
| graph embedding | Interactions can be predicted from the latent traits of networks | interaction | species | potential feeding links | probabilistic | [28] |
| trait matching | Interactions can be inferred by a mechanistic frame- work/relationships | interaction | species | feeding links | binary | [8] |
| binary classifiers | Interactions can be predicted by learning the relationship between interactions and ecologically relevant predictors | interaction | species | feeding links | binary | [5] |
| expert knowledge | ‘Boots on the ground’ ecological knowledge and observations | interaction | species | feeding links | binary | |

| Model | | Network | Nodes | Links | | Key |
|---------------|---|---------------------------|-----------|----------------------|-------------|-----------|
| family | Theory | predicted | represent | represent | Interaction | reference |
| data | Webscraping | interaction | species | feeding links | binary | |
| scavenging | to create networks from online databases | | | | | |
| 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 | |

[Figure 2 about here.]

Source: [Model family traits](#)

3.2 Assessing model outputs

Although understanding the underlying philosophy of the different model families is beneficial it is also important to understand in what situations the different families are likely to perform well or poorly. When we are assessing the performance of the different model families it is beneficial to think of benchmarking these assessments based on a broader basis than just its ability to correctly recover network structure or pairwise interactions. When thinking about how to benchmark models it is perhaps beneficial to take a step back and once again assess what are the needs of the researcher (Section 1) and linking this back to what aspects of the network (Section 2) are of importance and assess the performance of a model within those parameters.

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 [26]. 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 [29].

3.2.0.1 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 link 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, [30]), and meso-level features (*e.g.*, motifs, [31]) of a network. This is shown in Figure 3...

- Maybe look at some of the historic papers that compare some of the ‘resource models’
- See also [26] and the likelihood function that they use for model selection
- Look at [32]

[Figure 3 about here.]

Source: [Quantitative approach to topology generators](#)

3.2.0.2 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 [9,29] but is always based off of the confusion matrix. Using the confusion matrix it is then possible to assess the ‘quality’ of the model predictions such as their accuracy or informedness. The high class imbalance (inherent sparsity) of networks means that most interactions are

absent and so a model that predicts interactions as being absent will still predict most interactions correctly [*i.e.*, getting the ‘right’ answers but for the wrong reasons, 29]

- As per [29] 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 [33].
- 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.*, introducing false negatives into the training data *sensu* what we did in [34]

[Figure 4 about here.]

3.3 The bigger picture

In addition to thinking about the ‘performance’ of a model it is also important to be aware of the ‘unseen’ costs and limitations of the different modelling families. What data do I need? Can I make *de novo* predictions? What are the related ‘sinks’ *e.g.*, computational or time? What does the network I am constructing actually represent?

3.3.1 Data need vs availability

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

3.3.2 Theory vs ‘real world’

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

networks we can use for theoretical stuffs. Need to discuss the key differences and implications between predicting a metaweb (*sensu* [20]) and a network realisation. (In a way the idea of predicting a metaweb vs realisation is what makes me hesitant to use the Mangal networks to test the structural models because do we even know what the Mangal networks represent and what the structural models are predicting...) Maybe also [35] that discuss how the local factors are going to play a role.

3.3.3 The target system?

3.3.4 Philosophy limits theory

Also need to take into consideration inherent constraints that the model imposes on itself and how it will affect our ability to test hypotheses/ask questions using the *e.g.*, from [36] - models that are constrained by connectance means that we are unable to explain connectance itself and you would need a different approach if understanding connectance is your goal. Another way of phrasing this is thinking about what is needed (input data/parameters), produced (final network characteristics), and desired (end-use).

4 Concluding remarks

- 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 [7,19], 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.
- 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).

Interestingly [4] 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.” - [7]

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)

- 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 [36] might have (and share) some thoughts on this (thanks Andrew). I feel like I need to look at [37] 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 [38]

“we highlight an interesting paradox: the models with the best performance measures are not necessarily the models with the closest reconstructed network structure.” - [29]

- *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.” - [9]

– Aligning (dove-tailing) with this the idea of ensemble modelling as presented by [39]

- 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)

4.1 Downsampling

- [40]
- “That being said, there is a compelling argument for the need to ‘combine’ these smaller functional units with larger spatial networks [41] and that we should also start thinking about the interplay of time and space [42]. Although deciding exactly what measure might actually be driving differences between local networks and the regional metaweb might not be that simple [43].”

Glossary

| Term | Definition |
|-----------------------|---|
| food web | a representation of feeding links between species |
| network generator | a model that predicts a network based on assumptions of structure, this network is species agnostic in the sense that it does not necessarily contain information at the node level |
| interaction predictor | a model that predicts species interactions, these interactions can be used to construct a network but there are no <i>a priori</i> assumptions as that will constrain the network structure |

| Term | Definition |
|------------------------|---|
| model | A tool that can be used to construct food webs, where the resulting network is a representation of a real world network. Models typically only capture specific elements of real world networks and are intended to be used in specific settings |
| model family | A family of models that share an underlying philosophy when it comes to the mapping, pragmatism, and reduction of a network. Families have the same underlying philosophies and assumptions that determine the links between nodes as well as how these may be encoded |
| metaweb | A network that represents <i>all</i> the potential links between species. Importantly these links will not necessarily all be realised in a specific location for a specific time |
| realised network | A network that represents the links between species that are occurring. These networks represent a very localised network... |
| potential feeding link | links that indicate that an interaction is ecologically feasible but not realised <i>per se</i> (a metaweb would contain potential feeding links) |
| realised feeding link | links that indicate that the interaction is realised ‘in the field’. (a realised network contains realised feeding links) |
| confusion matrix | captures the number of true positives (interaction predicted as present when it is present), false negatives (interaction predicted as absent when it is present), false positives (interaction predicted as present when it is absent), and true negatives (interaction predicted as absent when it is absent) |

1 Outstanding questions

- 2 • non-consumptive effects

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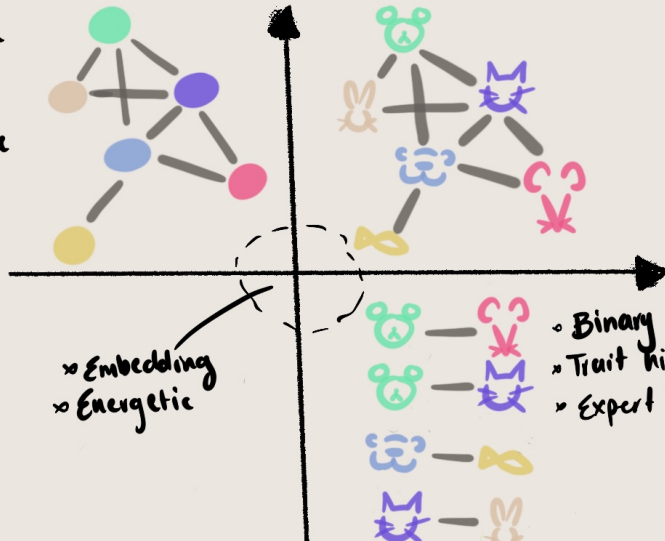
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A Predicting.

- Resource
- Null
- Neutral
- Generative



- Binary Classifiers
- Trait hierarchy
- Expert knowledge

B Benchmarking

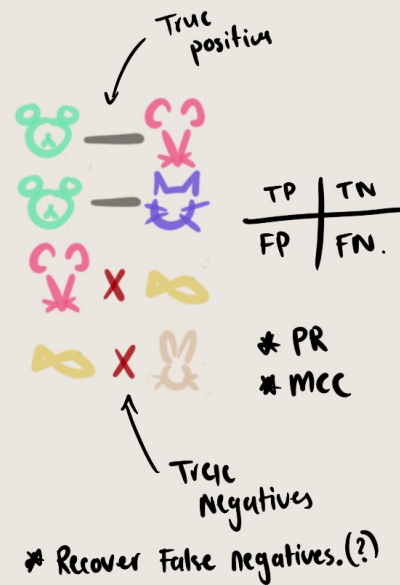
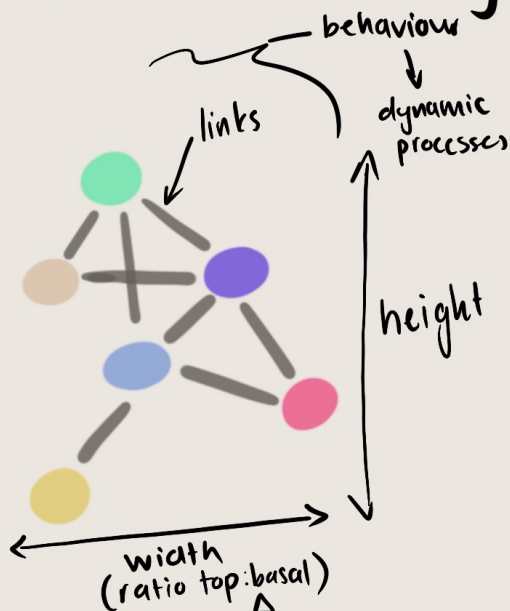


Figure 1: Conceptual figure of the ‘network prediction’. Panel A shows where the model families fall in the the context of being models that predict networks or models that predict interactions space. Panel B serves to highlight the characteristics one might like to ‘test’/benchmark for a model based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

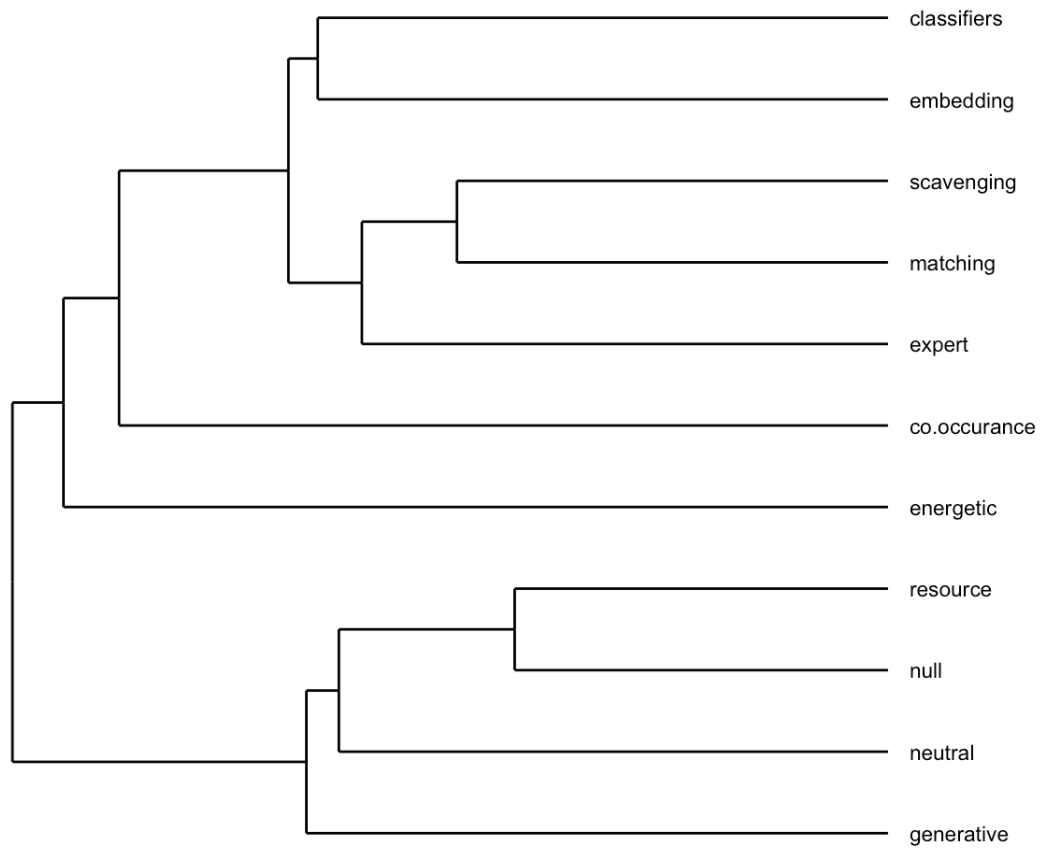


Figure 2: Dendrogram of the trait table

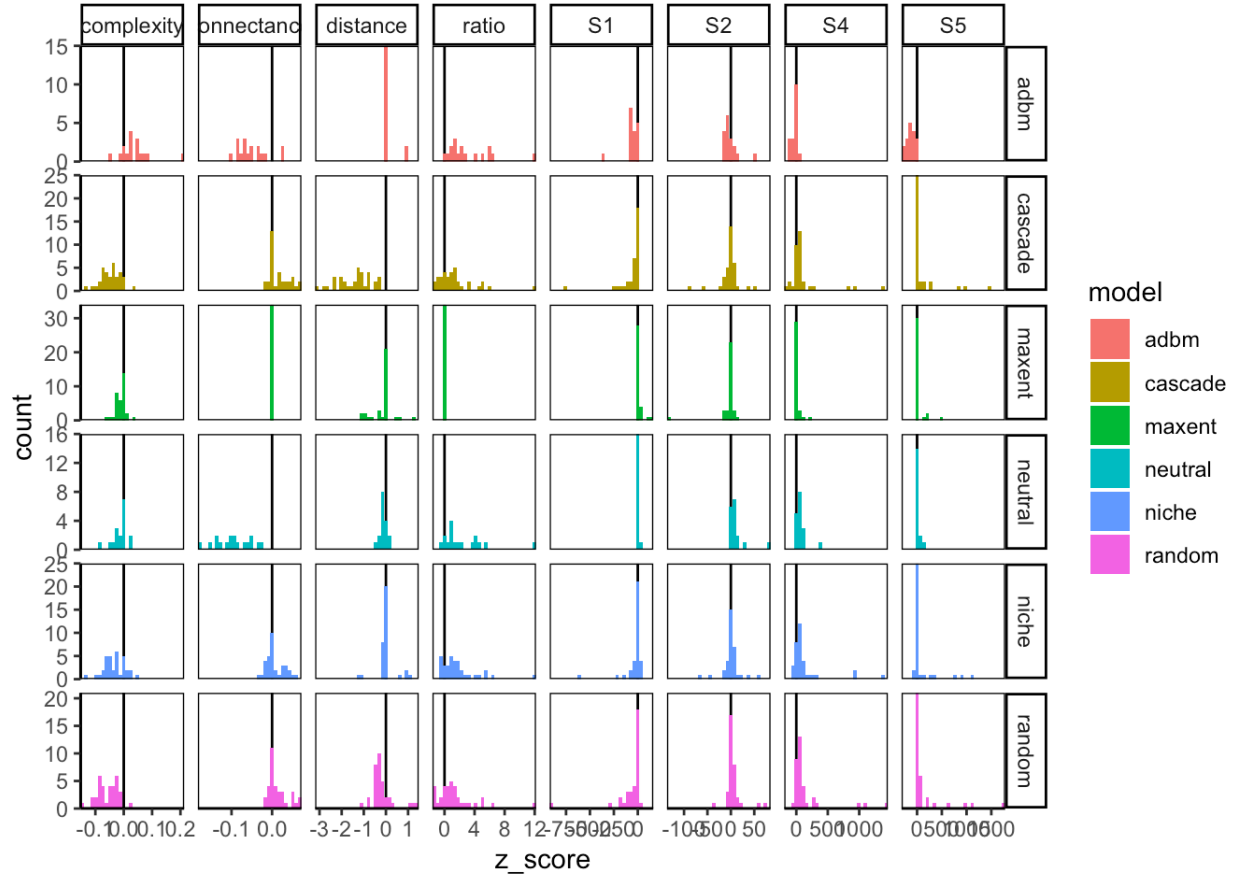


Figure 3: Difference between real and model network property. S1 - S5 represent the different motif structures identified in [31].

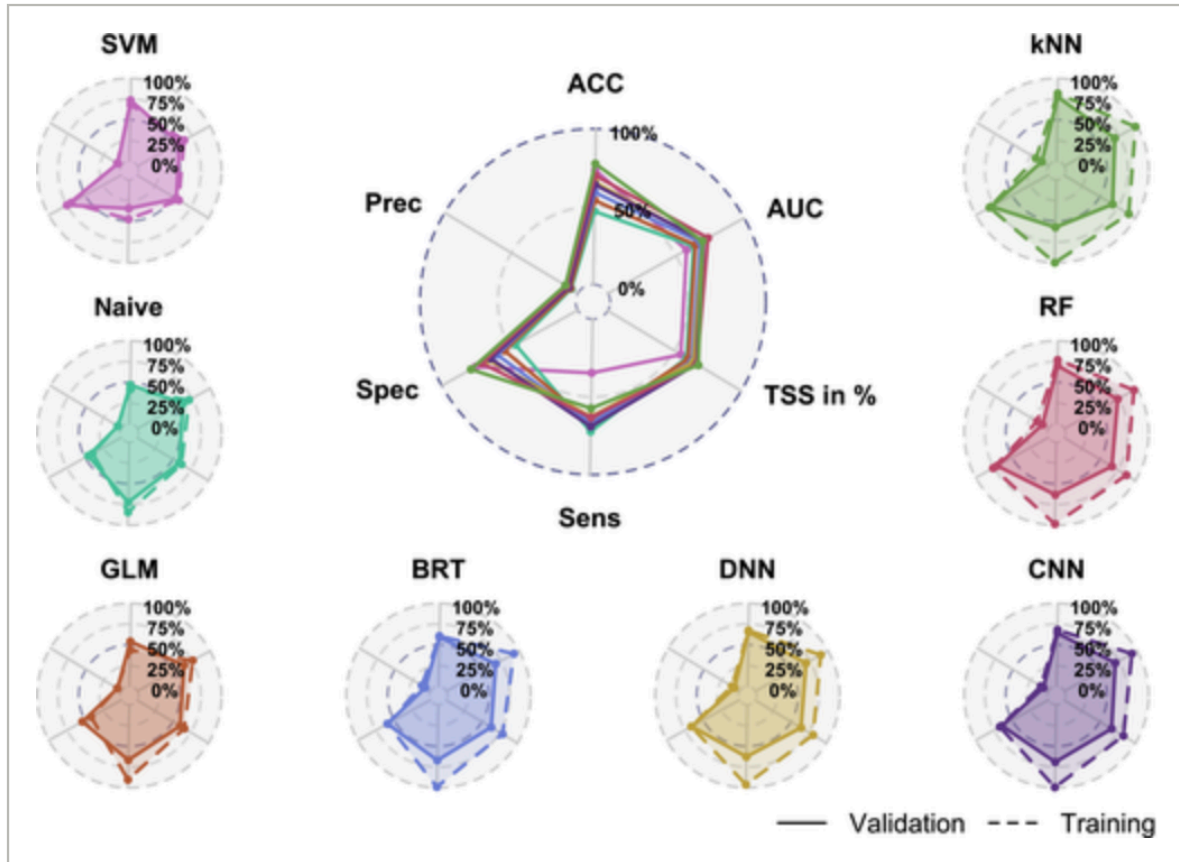


Figure 4: Moc result from [5]