

Methods for Reconstructing Paleo Food Webs

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Abstract: Food webs represent the feeding relationships between species and can help infer ecosystem-level processes. Alongside the development of food web theory, methods for constructing food webs have been developed to infer species interactions when empirical data is lacking. Food web construction methods are diverse, each utilising different approaches to infer species interactions —such as the use of traits to infer mechanistic relationships vs using gut content as a proxy for species diets. These methods have distinct theories, mechanisms, and data requirements. In paleoecology, where direct evidence of feeding interactions are rare, food web construction methods are especially valuable and affords us the opportunity to make inferences about paleo communities beyond simply a record of species composition. However, the limitations of paleontological data (e.g., information of species traits is limited to that which can be preserved) restrict which methods can reliably be used. By considering both ecological theory and the constraints of what can be derived from the fossil record, we identify the methods best suited for the construction of paleo food webs. Specifically, we focus on how these methods differ in the networks they produce and what these networks can reveal about species interactions. In doing so we hope to clarify the ecological nuances of network prediction and help prevent the accidental misuse or misinterpretation of paleo food webs.

Keywords: food web, network construction

1 There has been a growing interest in looking at community responses to environmental changes across deep
2 time events as a means to help understand current and future biodiversity changes (Dillon et al., 2022; Kiessling
3 et al., 2019). Species interactions and the resulting networks have gained an interest in contemporary
4 settings as a means to help us to understand aspects of community composition and biodiversity (eg Thuiller et
5 al. (2024) and ??) and so it is perhaps unsurprising that there has been a growing interest in using paleo food
6 webs in a similar manner (*e.g., * Dunhill et al., 2024 looked at...; Hao et al., 2025 looked at...; Yeakel et al.,
7 2014 looked at...). However, one of the core challenges and limitations of being able to effectively *use* food webs
8 is the challenge of *creating* them (Jordano, 2016), although this is a challenge within contemporary settings
9 it is compounded in paleo contexts as we are dependant on the fossil record (and the inherent limitation it
10 imposes) to infer interactions from. As a way to address the challenges with recording species interactions
11 there has been the development of a large number of models and tools that can be used to infer either species
12 interactions (see *e.g.*, Morales-Castilla et al., 2015; Pichler & Hartig, 2023; Strydom et al., 2021a for broader
13 reviews) or networks (see *e.g.*, Allesina et al., 2008). Although there has been the development of models and
14 tools that are specific for inferring paleo food webs (Fricke et al., 2022; Roopnarine, 2006; *e.g., * Shaw et al.,
15 2024), it should be noted that these models only occupy a subset of the broader family of approaches that are
16 used to predict networks as they typically use only one mechanism for determining interactions (the feasibility
17 of the interaction being able to occur). Being able to only construct one ‘type’ of network means that we
18 are limited in the scope of questions that we can appropriately answer with those networks [see Strydom
19 in prep; Gauzens et al. (2025)]. However there is scope that models and tools that have been developed in
20 contemporary settings have the potential to be used for paleo settings (*e.g.*, Yeakel et al., 2014), which opens
21 the door for researchers to ask a broader and more complete range of questions about community responses
22 to environmental change.

23 Here we want to identify the differences between models that predict interactions, and models that predict
24 network structure. Specifically we want to look at 1) the structural difference between all models (*i.e.*, do we
25 see a difference in the distribution of links between networks that have the same number of nodes?) and 2)
26 the identity of pairwise links between species pairs (*i.e.*, do different models differ in which links are present
27 (or absent) between species pairs?) Additionally we want to establish if using networks that are constructed
28 using different models will change the downstream inferences that are made for this we use the work from
29 Dunhill et al. (2024) as a case study.

30 **1 Contextualising paleo web prediction within the contemporary**

31 **toolbox**

32 Although there is an evolving body of work focused on the development of food web prediction tools it is
33 important that we understand how the underlying philosophy on which a model was built will result in
34 different assumptions being embedded within the network [Strydom in prep]. Broadly we can think about
35 models that are nested within two different schools of thought (and thus methodological approaches, Figure 1),
36 models that focus on assessing the *mechanistic* feasibility of an interaction being able to occur between two
37 species or models that are more closely married to specific bodies of ecological *theory* - such as niche theory
38 or foraging ecology.

39 [Figure 1 about here.]

40 Models that have specifically been developed in the paleo space tend to be mechanistic models that focus on
41 using a trait-based approach to formalise feeding interactions (*e.g.*, Shaw et al. (2024); Roopnarine (2006)),
42 are assembled by expert opinion (*e.g.* Dunne et al. (2014)) or make assumptions based on the evolutionary
43 signals of interactions (*e.g.*, Fricke et al. (2022)). However, there is an argument that the theoretical models
44 that have been developed in contemporary settings should hold even for paleo communities as we expect
45 the fundamental ‘currencies of life’ to have remained constant - *e.g.*, the energetic constraints of foraging or
46 foraging niches. Along with constructing different Additionally there are models that allow one to construct
47 structurally sound networks that require very little input data. These are methods that are amenable to the
48 data constraints that are prevalent in paleo communities in terms of both the completeness of fossil records as
49 well as how the deeper in time we move the further away we might be moving from contemporary analogs.

50 Not all contemporary models may actually be suitable for paleo contexts as the assumptions that they make
51 (or the data that they require) may actually introduce uncertainty/errors into the resulting network rendering
52 them of little use. Similarly not all paleo methods will be suitable for all paleo communities. As a simple
53 example the framework developed by Fricke et al. (2022) uses phylogenetic relatedness as a way to infer
54 interactions of Pleistocene mammals by looking at how their extant relatives interact. Although this approach
55 is ecologically sound (phylogenetic relatedness is also used in other approaches *e.g.*, Strydom et al. (2022))
56 there is also an argument that the further back in evolutionary time we go (and the greater the phylogenetic
57 distance between extant and extinct communities become) there is more uncertainty introduced by the
58 phylogenetic tree than what is introduced by assuming that interactions will be phylogenetically conserved.

⁵⁹ 2 Challenges specific to building paleo networks

⁶⁰ Although there has been a push for the development of tools and methods that allow us to predict species
⁶¹ interactions and networks they will not all be suitable for the prediction of paleo communities. This is
⁶² primarily due to limitations that we are faced with in terms of the information that can be inferred from
⁶³ the fossil record (such as species traits, abundances, and assemblages), which is needed as input data for the
⁶⁴ different models. The limited information available from the fossil record is compounded by the incomplete
⁶⁵ and biased preservation of species [REF], which part of a species is preserved (part vs whole), the ambiguity of
⁶⁶ the ‘true’ community composition [were communities conserved *in situ* or were they there owing to geological
⁶⁷ processes?; REF], as well as the availability/accessibility of different rock layers (and thus the completeness of
⁶⁸ data we might have for a specific era in time). Additionally there is an increasing degree of ‘fuzziness’ around
⁶⁹ the ecology and life histories of species the further one moves back in geological time [REF]. This is not to say
⁷⁰ that because we have imperfect data we should not be attempting to construct paleo food webs but rather
⁷¹ that we need to be aware of what the uncertainties are and how these might impact the assumptions that we
⁷² need to make when constructing a network (as well as how this will intersect with the intended end use of
⁷³ the network). This will allow us to best identify an approach that minimises the assumption and potential
⁷⁴ uncertainties within the data while still constructing a suitable network. This includes thinking about both
⁷⁵ assumptions you are making about the actual data *e.g.*, trying to extrapolate body size from fossil data but
⁷⁶ also assumptions across time *e.g.*, assuming modern trait-feeding modes are the same or that assumptions
⁷⁷ about network structure will hold across deep time.

⁷⁸ 2.1 Approaches to food web prediction

⁷⁹ Here we present six different models (Table 1) that can be used to construct food webs for both this specific
⁸⁰ community but are also broadly suited to paleo network prediction. These models span all facets of the
⁸¹ network representation space (metaweb, realised, and structural network) and are suitable for an array of
⁸² different paleo communities as the data requirements are ‘paleo friendly’.

Table 1: A summary of the different families of tools that can be used to generate paleo food webs.

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference
random	Links are randomly distributed within a network	richness, number of links	parameter assumptions, species agnostic	structural network	Erdős & Rényi (1959)
niche	Networks are interval, species can be ordered on a 'niche axis'	richness, connectance	parameter assumptions, species agnostic	structural network	Williams & Martinez (2008)
allometric diet	Interactions are determined by energetic costs (foraging ecology)	body mass, biomass (abundance)	does not account for forbidden links in terms of trait compatibility, assumptions on body size and biomass (abundance) from fossil data	theoretical	Petchey et al. (2008)
breadth model (ADBM)					

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference
l-matrix	Interactions inferred using allometric rules (ratio of body sizes between predator and prey), with links being constrained by a Ricker function	body mass, number of producer species	does not account for forbidden links in terms of trait compatibility, assumptions on body size from fossil data, assumptions as to the number of producer species	theoretical network	Schneider et al. (2016)
paleo food web inference model (PFIM)	Interactions can be inferred by a mechanistic framework/relationships	feeding traits for taxa, mechanistic feeding rules	Assumption made as to the feeding mechanisms, need to elucidate traits (although this is a way smaller issue)	mechanistic web	Shaw et al. (2024)

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference
body size ratio model	Interactions inferred using allometric rules (ratio of body sizes between predator and prey). :ogit of the linking probability used to further constrain links to an 'optimal size range' for prey.	body mass	does not account for forbidden links in terms of evolutionary compatibility, assumptions on body size from fossil data	theoretical network	Rohr et al. (2010)

83 3 Case study: Toarcian mass extinction event

84 3.1 Dataset overview

85 3.1.1 Species occurrence

86 Here we use the fossil occurrence data over an interval extends from the upper Pliensbachian (~185 Ma) to
 87 the upper Toarcian (~175 Ma) of the Cleveland Basin (see Dunhill et al., 2024 for a more comprehensive
 88 overview). The data set consists of a subset of four broad time periods (pre-extinction, post-extinction, early
 89 recovery, and late recovery). The assemblages are treated as communities of interacting organisms. Something
 90 about the total number of taxa as well as numbers per a time period? Probably also make a comment that
 91 this is a 'deep time' community we are looking at.

92 3.1.2 Defining modes of life (traits)

93 We used the modes of life (traits) as identified in Dunhill et al. (2024), who defined four traits: motility (fast,
 94 slow, facultative, non-motile), tiering (pelagic, erect, surficial, semi-infaunal, shallow infaunal, deep infaunal),
 95 feeding (predator, suspension feeder, deposit feeder, mining, grazer), and size: gigantic (>500 mm), very large

96 (>300–500 mm), large (>100–300 mm), medium (>50–100 mm), small (>10–50 mm), tiny (10 mm), for each
97 fossil species based on the ecological traits defined in the Bambach ecospace model (Bambach et al., 2007).

98 **3.1.3 Constructing networks**

99 For each paleo community (time bin) we constructed **100** networks for each model (so 6 * 100) networks.
100 These networks were ‘simplified’ to removed any disconnected species. In total 2400 networks were constructed.
101 When a quantitative measure of body size is needed (ADBM, bodymassratio, lmatrix) we drew a body mass
102 for each species from a uniform distribution. The ranges were defined by the different size classes as discussed
103 in insert cross ref to correct subsection here *e.g.*, a species classed as ‘very large’ would have a body mass
104 drawn from $U(300, 500)$. This was repeated for each run in order to add variation to the networks constructed,
105 however the same body sizes were kept consistent for the relevant models (adbm, bodymassratio, l-matrix)
106 *i.e.*, an ADBM and bodymassratio network from the same rep number would have used the same bodysizes.
107 The PFIM networks were downsampled (see relevant section is S1). For both the random and niche model
108 the desired connectance was randomly selected between the range 0.07 - 0.15 for each repetition but kep
109 consistent for both models. For each network we calculated the properties listed in Table 2

110 **3.2 Models capture different network structure but in unexpected ways**

111 Why is structure important and what can it tell us? Broadly when we talk about quantifying the structure
112 of a network we are interesting in capturing some aspect of how the links are distributed between nodes, or
113 alternatively about properties of the nodes (specifically in terms of the number of links coming in to (prey)
114 or out of (predators) the node). What are some things we can learn/infer from network structure: energy
115 flows and fluxes [REF], propagation of stress [REF], roles of species in the community [REF, think trophic
116 levels]. Some closing statement about how thus there are different facets of network structure and the value
117 of understanding generally how different models differ in terms of the structure that they recover - link to
118 Table 2 maybe.

119 In terms of wanting to asses and compare across the different models it is beneficial to approach this task by
120 thinking about the different aspects of the network as well as interactions that are being predicted by the
121 different models. It is perhaps beneficial to think of these across different ‘scales’ of organisation within the
122 network, namely macro (the entire network), meso (smaller interacting units within the network), and micro
123 (species-level attributes). Although there are a myriad of possible ways to ‘measure’ and analyse ecological
124 networks (Delmas et al., 2018) we do still lack a clear set of guidelines for assessing how well models recover
125 network structure (Allesina et al., 2008) and it is beneficial to use a small subset of metrics that can clearly

126 be tied to broader aspects of network function or capturing a ecological process.
 127 Here we used a Multivariate Analysis Of Variance (MANOVA) as it is able to capture model differences based on
 128 the combined information of the multiple structural network measures. Model defined as `network structure`
 129 `values ~ model + time period` and Linear Discriminant Analysis (LDA) to determine if different models
 130 produced networks with differing structure. **Need to report the relevant effect of time in driving**
 131 **observed differences**

Table 2: An informative caption about the different network properties

Label	Definition	Scale	Reference (for maths), can make footnotes probs
Connectance	L/S^2 , where S is the number of species and L the number of links	Macro	
GenSD	Normalized standard deviation of generality of a species standardized by L/S	Micro	Williams & Martinez (2000)
LinkSD	Normalized standard deviation of links (number of consumers plus resources per taxon)	Micro	
Richness	Number of nodes in the network	Macro	
TL	Prey-weighted trophic level averaged across taxa	Macro	Williams & Martinez (2004)
VulSD	Normalized standard deviation of vulnerability of a species standardized by L/S	Micro	Williams & Martinez (2000)

Label	Definition	Scale	Reference (for maths), can make footnotes probs
Diameter	Diameter can also be measured as the average of the distances between each pair of nodes in the network	Macro	Delmas et al. (2018)
ρ	Spectral radius is a conceptual analog to nestedness (and more appropriate for unipartite networks). It is defined as the absolute value of the largest real part of the eigenvalues of the <i>undirected</i> adjacency matrix	Macro	Staniczenko et al. (2013)
Complexity	SVD complexity of a network, defined as the Pielou entropy of its singular values	Macro	Strydom et al. (2021a)
S1	Number of linear chains	Meso	Milo et al. (2002); Stouffer et al. (2007)
S2	Number of omnivory motifs	Meso	Milo et al. (2002); Stouffer et al. (2007)
S4	Number of apparent competition motifs	Meso	Milo et al. (2002); Stouffer et al. (2007)
S5	Number of direct competition motifs	Meso	Milo et al. (2002); Stouffer et al. (2007)

132 **3.2.1 Macro network properties**

133 **Connectance** (Martinez, 1992) has been shown to be the feature of networks that underpin a series of other
134 properties and function (Strydom et al., 2021b) and so it is perhaps the most important structural attribute for
135 a model to be able to retrieve correctly. Additionally we consider the **complexity** of networks by calculating
136 their SVD entropy (this gives us an estimate of the physical as opposed to behavioural complexity of networks;
137 Strydom et al. (2021a)), we could also look at the rank/rank deficiency of networks which (theoretically)
138 represents the number fo unique interaction strategies in the network (Strydom et al., 2021a), which may be
139 specifically interesting in terms of looking at pre and post extinction but also as a way to unpack ‘functional
140 redundancy’ that some models may introduce.

141 **3.2.2 Meso network properties**

142 Motifs represent smaller subset of interactions between three species, and are argued to capture dynamics
143 that are likely to be ecologically relevant (Milo et al., 2002; Stouffer et al., 2007). Here we specifically look at
144 the number of **linear chains**, **omnivory**, **apparent competition**, and **direct competition** motifs. In
145 the broader context the ability of a model in being able to capture these smaller motifs will inform as to its
146 suitability of use understanding the more dynamic component of network ecology.

147 **3.2.3 Micro network properties**

148 The number of interactions established (**generality**) or received (**vulnerability**) by each species (Schoener,
149 1989), are (broadly) indicative of consumer-resource relationships and diet breadth of species [ref]. Although
150 this is usually determined at the species level the standard deviation of the generality and vulnerability of
151 species is often used when benchmarking predicted networks (Petchey et al., 2008; *e.g.*, Williams & Martinez,
152 2008).

153 The **specificity** of species in a network is measured as a function of the proportion of resources they effectively
154 use (Poisot et al., 2012)

155 [Figure 2 about here.]

156 What is perhaps the most striking result in Figure 2 is that although there are clear structural differences
157 between the different models the differences are not distinct between the broader model families but rather
158 that there is a degree of overlap between them (specifically the log ratio, PFIM, and niche models). Although
159 the log ratio and niche models are classified as different families they are built on similar ecological background
160 and theory and so it is perhaps not surprising that these networks capture a similar structure (the same holds

for the ADBM and l-matrix models). The fact that the random model occupies a completely different space is unsurprising as it has clearly been shown that networks are non-random in nature [REF] and so we expect random models to be constructing ecologically illogical networks. What is perhaps the most interesting result is that the PFIM model constructs networks that are very similar to those that are rooted in niche-based processes despite the model being more mechanistic in nature. Not sure how to articulate but this is cool because the is *something* in network structure constraints that is straddling the trait-niche space of ecology - but also see my next point about it being ‘correct’ is still up for debate

Although it is not possible to confidently identify the models that are predicting the ‘*correct*’ network structure the fact that a models from different families are able to recover similar structures is reassuring as it suggests that it might be possible to substitute one model for another if the input data is insufficient.

TODO Is it sound to try and unpack the ‘pairwise differences’ between the different structural metrics as well (or some) as this will allow us to say e.g. Niche and PFIM might recover the same connectance but differ in vulnerability.

3.3 Some networks don’t share any interactions and some share a lot

In addition to wanting to measure network structure researchers may also be interested in understanding aspects about the diets and predators of *specific* species in a community. In this instance the interest should be in understanding how the pairwise links predicted between species pairs differ between models. Here we look at the interaction turnover (Poisot et al., 2012) both within and between the different models. This can be thought of as the equivalent of species β turnover and tells us which interactions are ‘conserved’ (shared) across the networks but only between species pairs that are shared - *i.e.*, this turnover is only driven by interaction and not species turnover. Here we only compared networks that we constructed for the same period (as our interest is only in between model differences) and excluded the random and niche networks from consideration as these two models are essentially species agnostic.

[Figure 3 about here.]

In Figure 3 it is clear that some models share a large percentage of interactions *e.g.*, between ADBM and l-matrix networks and others share nothing *e.g.*, ADBM and PFIM networks. This result is unsurprising as the mechanisms that determine interactions in ADBM and l-matrix (a single trait (bodysize) + some ecological theory) is very different from the PFIM model that makes assumptions on a trait-based hierarchy. The key takeaway that this needs to lead into is thinking about diet related questions and the model that is best suited to get you there. It makes sense to contextualise this in the feasible vs realised interaction

191 spectrum - specifically that from a ‘philosophical’ basis if you are asking questions about possible diets of
192 species then it makes sense to use models that fall firmly in the ‘feasible’ space *e.g.*, PFIM model or even
193 something like the Fricke et al. (2022) model. How these results support that is that we can see the ADBM
194 and PFIM are recovering (almost) totally different pairwise links.

195 **3.4 Model choice changes the narrative**

196 **3.4.0.1 Simulating Extinctions**

197 Extinctions were simulated using different plausible mechanisms based on both species traits (size, motility),
198 their position within the network (generality, vulnerability), as well as randomly. Each network was subjected
199 to **50** extinction runs for each extinction mechanisms. The extinctions themselves were cascading in nature
200 meaning that after the target species was removed all species that no longer had any prey were also deemed
201 as extinct (secondary extinction), checking for secondary extinctions was then repeated until there were no
202 longer any species without prey. This represents one extinction event and only then would the proceeding
203 target species be removed from the network and cascading extinctions assessed again. Note that for extinction
204 simulations which use the network position of a species to determine extinction order we follow the protocol
205 from Curtsdotter et al. (2011) and reassess the vulnerability/generality of each species after each extinction
206 event to ‘redetermine’ the extinction order.

207 As we are using Dunhill et al. (2024) as a case study we followed their approach when simulating extinctions
208 as well as assessing which extinction mechanism results in a simulated network that most closely matches the
209 real post extinction network. Extinction simulations were only run on the pre extinction networks whereby
210 species were removed until they reached the ‘target richness’, which is the richness of the post extinction
211 community. In order to determine which extinction mechanism creates a network most similar to the post
212 extinction network we used the (get full name of score) TSS (Gupta et al., 2022) to assess how different the
213 pairwise interactions are between ‘simulated’ and ‘real’ post extinction communities as well as looking at the
214 absolute differences in network structure metrics.

215 **TODO** not sure if we also want to unpack/showcase robustness R_{50} (Jonsson et al., 2015)

216 [Figure 4 about here.]

217 **3.4.1 Trends over time**

218 **TODO** Not sure statistically speaking what the best way to unpack this is... 2-way ANOVA/AN-
219 COVA explanation is valuable? There are intercept differences (*e.g.*, baseline average values are

220 different; are the rankings among all three response variables the same?) and there are shape
221 differences/similarities (e.g., motifs are all the same shape but Co and Gen show some among
222 model differences in pattern.)

223 Visual take-away seems to suggest that we see that the values (intercepts) of the different summary statistics
224 are different but (broadly) they are capturing the same trends. This might suggest that although we observe
225 differences in structure (Figure 2) the general patterns still remain the same. This is good news because it
226 means that at least the models that we have used here tend to tell us the same general story - which is worth
227 contextualising in the space of 'right' vs 'wrong' and as long as we are not fixated on the point value but
228 rather on understanding the trends.

229 3.4.2 Inferred extinction drivers

230 Points of discussion one will be to point to the mean absolute distance and how generally the ADBM/l-matrix
231 do really badly - high mean absolute value. And this maybe makes sense though because of how we specify
232 extinction mechanisms (trait-based) and so it sets the body-size models are not 'talking' the same language.
233 In terms of the TSS scores - not sure how we should unpack it. Individually by model family to see which
234 model agrees with which approach and see if different mechanisms come out stronger? **TODO** still need to
235 sanity check the TSS anyway...

236 4 Discussion (need a catchier heading)

237 I want this section to be more about contextualising model choice within the bigger research question discussion
238 - i.e. mapping question and model choice more tightly...

239 Points to discuss:

- 240 • Guidelines - as a box? Can we give something concrete??
241 • How to we synthesise these results? As in should we give clear directives or is it enough to do a bit
242 more handwaving and have the bigger message be that model choice matters?

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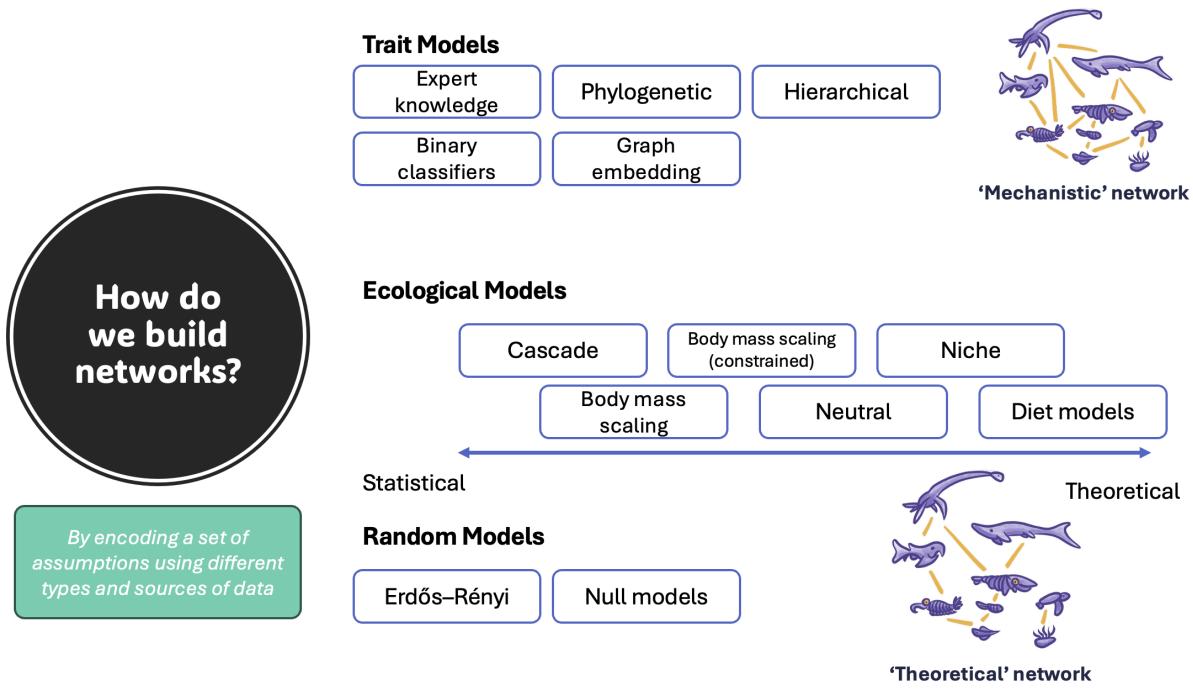


Figure 1: This obviously needs work but a variation on this to try and articulate the different approaches and broadly how they may differ.

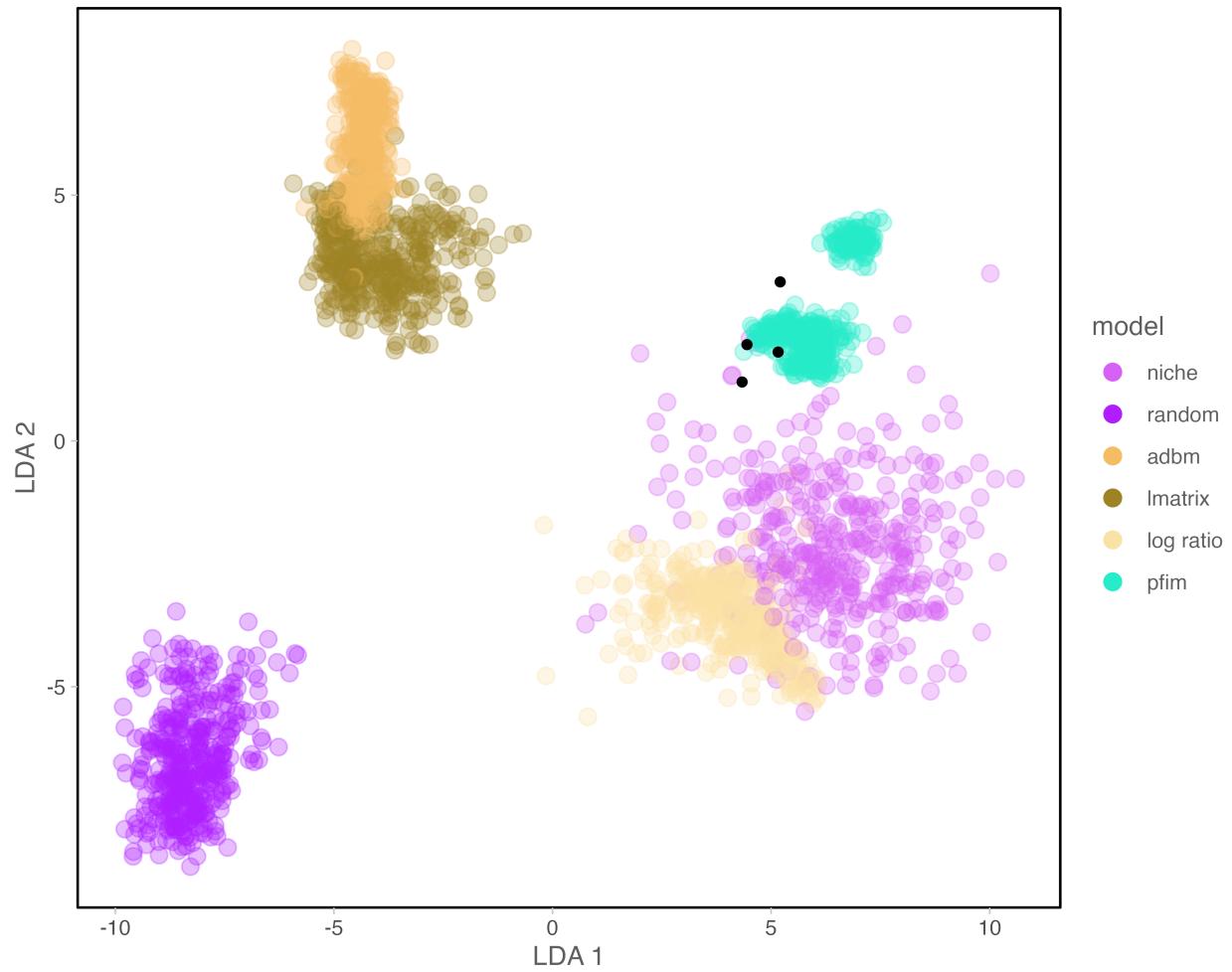


Figure 2: stuff...

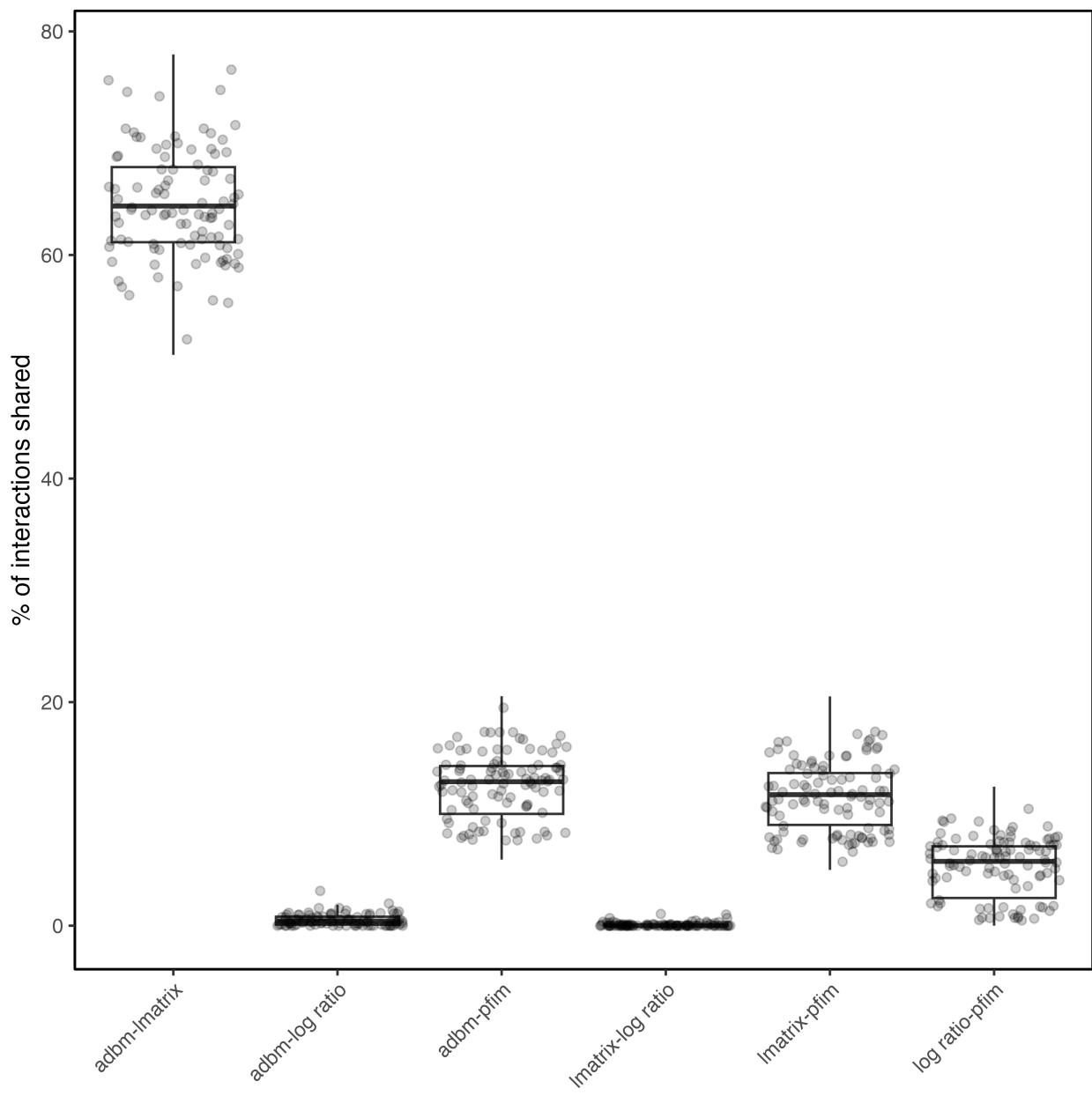


Figure 3: stuff... % interaction shared is calculated as number shared interactions / ((number interactions left - shared interactions) + (number interactions right - shared interactions) + shared interactions). Additionally niche and random models are excluded as it is illogical since both of these models are fundamentally species agnostic

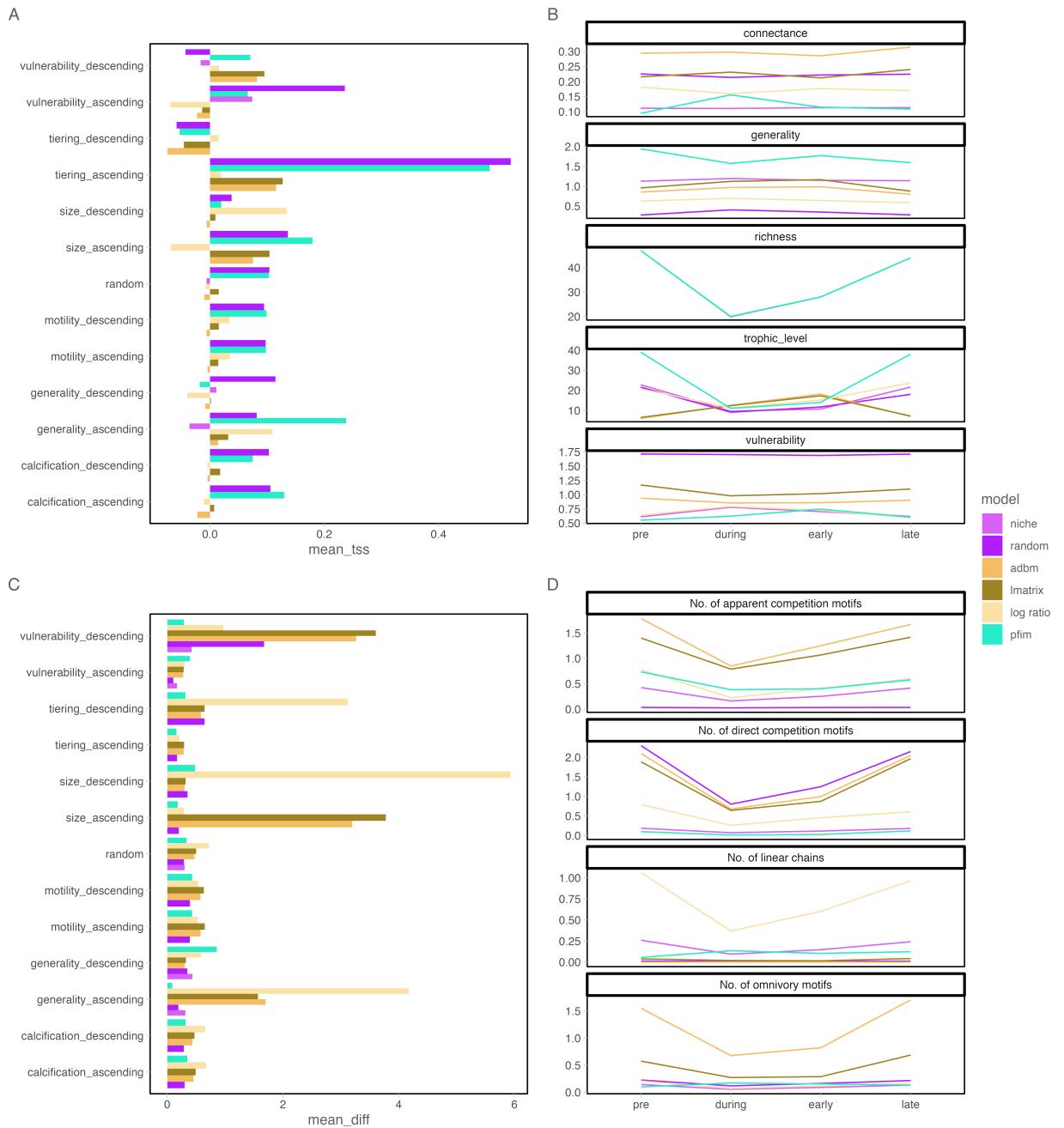


Figure 4: stuff... Recreation of the figure from Dunhill 2024. Note not 100% sold on the TSS and absolute mean calculations...