

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 events in
2 deep time as a means to help understand current and future biodiversity changes (Dillon et al., 2022; Kiessling
3 et al., 2019). The use of species interactions and networks to help us understand aspects of community
4 composition has gained an interest in contemporary settings (eg Thuiller et al. (n.d.) and ??) and so it is
5 perhaps unsurprising that there has been a growing interest in using paleo food webs in a similar manner
6 (*e.g.,* Dunhill et al., 2024 looked at...; Hao et al., 2025 looked at...; Yeakel et al., 2014 looked at...). However,
7 one of the core challenges and limitations of being able to *use* food webs to answer ecological questions is
8 the challenge of *creating* them (Jordano, 2016), a challenge which is compounded when using paleo data as
9 we are limited by that which has been preserved in the fossil record. The challenges with recording species
10 interaction networks has driven the development of a large number of models and tools that can be used to
11 infer either species interactions (see *e.g.*, Morales-Castilla et al., 2015; Pichler & Hartig, 2023; Strydom et al.,
12 2021a for broader reviews) or networks (see *e.g.*, Allesina et al., 2008 (it is one of the more complete review
13 of methods IMO)), each with their own set of nuances and considerations [modify this to organically link
14 to T4T, probably something along the lines of how different network construction approaches are encoding
15 different processes]. Although the paleo food web space has seen its own development of tools that are more
16 tailored to paleo date (Fricke et al., 2022; Roopnarine, 2006; *e.g.,* Shaw et al., 2024) these tools typically
17 only predict the *feasibility* of pairwise interactions and thus the canonical paleo food web models are only
18 occupying a subset of the ‘network construction’ space. Specifically within the paleo space there is a need for
19 models that are able to generate networks that are structurally correct and do not simply represent a collation
20 of pairwise interactions. It is thus useful to identify a broader suite of methods within the contemporary
21 toolbox that can be appropriately scaled/tailored for the constraints of paleo communities (should we include
22 Yeakel et al. (2014) here as an *e.g.*, of how this is ‘possible’).

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 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 the prediction of paleo webs within the contem-**
31 **porary toolbox**

32 There is an evolving body of work that focuses on developing tools specifically for the task of predicting
33 food webs. However as highlighted in Strydom (T4T in prep) it is important that we understand what
34 assumptions are being embedded within the network as a result of the underlying philosophy which a model
35 was built on. Broadly we can think about models that are nested within two different schools of thought
36 (and thus methodological approaches, Figure 1), models that focus on assessing the *mechanistic* feasibility of
37 an interaction being able to occur between two species or models that are more closely married to specific
38 bodies of ecological *theory* - such as niche theory or foraging ecology. Broadly speaking the difference between
39 these two modelling approaches is that mechanistic models typically asses interactions at a pairwise level
40 by determining if an interaction is feasible between a species *pair* (extended e.g., here about trait-based
41 assumptions), whereas theoretical models typically use some set of assumptions to constrain the distribution
42 of links at the *community* scale (extended e.g., here probably niche model or DBM).

43 [Figure 1 about here.]

44 Models that have specifically been developed in the paleo space tend to be mechanistic models that focus on
45 using a trait-based approach to formalise feeding interactions (e.g., Shaw et al. (2024); Roopnarine (2006)),
46 are assembled by expert opinion (e.g. Dunne et al. (2014)) or make assumptions based on the evolutionary
47 signals of interactions (e.g., Fricke et al. (2022)). However, there is an argument that the theoretical models
48 that have been developed in contemporary settings should hold even for paleo communities as we expect
49 the fundamental ‘currencies of life’ to have remained constant - e.g., the energetic constraints of foraging or
50 foraging niches (is that the right way to phrase it, also I wonder is we can link to some other paleo work that
51 showcases e.g., niche/competition is something present among some of the earliest animals). Somehow close
52 this out by going from we should be able to use contemporary models we need to think about the constraints
53 that are typically placed on us by paleo data as well as the assumptions that some of these models might
54 require us to make (e.g. the niche model makes some heavy assumptions by constraining the connectance -
55 which itself is often used as a metric to understand changes or differences in network structure).

56 Additionally there are models that allow one to construct structurally sound networks that require
57 very little input data. These are methods that are amenable to the data constraints that are
58 prevalent in paleo communities in terms of both the completeness of fossil records as well as how
59 the deeper in time we move the further away we might be moving from contemporary analogs.
60 Secondly it should also be noted that different network construction approaches are encoding

61 different processes (T4T, in prep) and there is value in showcasing how the networks construct
62 models may differ.

63 Introduce here that it is thus important to understand that not all contemporary models may actually be
64 suitable for paleo contexts as the assumptions that they make (or the data that they require) may actually
65 introduce uncertainty/errors into the resulting network rendering them of little use. Similarly not all paleo
66 methods will be suitable for all paleo communities. As a simple example the framework developed by Fricke et
67 al. (2022) uses phylogenetic relatedness as a way to infer interactions of Pleistocene mammals by looking at
68 how their extant relatives interact. Although this approach is ecologically sound (phylogenetic relatedness is
69 also used in other approaches *e.g.*, Strydom et al. (2022)) there is also an argument that the further back in
70 evolutionary time we go (and the greater the phylogenetic distance between extant and extinct communities
71 become) there is more uncertainty introduced by the phylogenetic tree than what is introduced by assuming
72 that interactions will be phylogenetically conserved. On the other side of the coin it can be very challenging
73 to determine traits from the fossil record and so it may be instead by more pragmatic to use models that that
74 are completely agnostic to the identity of the species and are instead concerned with the network structure
75 (*e.g.*, the niche model developed by Williams & Martinez (2008)). Fundamentally this means that there is a
76 trade off between the data that is available and the type of network one is interested in creating.

77 this section should be a box we can link to in the intro I think. We can also include some key
78 ‘definitions’

79 **2 Understanding how networks are different**

80 It is important to be aware that networks can be configured in different ways depending on how the interactions
81 are defined (Strydom, in prep) and that the configuration of the desired network should be informed by the
82 research question (Gauzens et al., 2025).

83 Think about the axes - trait-based/mechanistic model (metawebs) and then we have the statistical/theoretical
84 models (which have their own mini axis of regression vs full theory models... - see also Figure 1). Basically
85 we have metawebs (which represent *potential* interactions, mechanistic networks), realised networks (which
86 represent the subset of potential that are realised as a result of community and environmental context,
87 theory networks), and structural networks (species agnostic networks that are structurally informative, theory
88 networks). Here also talk about the implications of these different networks types - different uses and capturing
89 different processes. Specifically link this to models - *i.e.*, different models have been developed to construct a
90 *specific* network representation.

91 **2.0.0.1 Key Definitions**

- 92 • Metaweb:
93 • Realised Network:
94 • Structural Network:
95 • Feasible Interactions:
96 • Realised interactions:

97 **3 Challenges specific to building paleo networks**

98 Although there has been a push for the development of tools and methods that allow us to predict species
99 interactions and networks [see *e.g.*, XXX for some reviews] they will not all be suitable for the prediction of
100 paleo communities. This is primarily due to limitations that we are faced with in terms of the information
101 that can be inferred from the fossil record (such as species traits abundances, and assemblages), which is
102 needed as input data for the different models. The limited information available from the fossil record is
103 compounded by the incomplete and biased preservation of species [REF], the spatial ambiguity of fossils
104 found in a location [were species conserved *in situ* or were they there owing to geological processes; REF],
105 and an increasing degree of ‘fuzziness’ the further one moves back in geological time [our understanding
106 of both phylogenetic and functional trait space, REF]. Methodologically speaking some tools that ‘learn’
107 from contemporary communities (*e.g.*, Strydom et al. (2023), Caron et al. (2022)) will become ‘worse’ the
108 further one goes back in time since species then look very different from now but can still be useful for ‘recent’
109 communities (*e.g.*, Fricke et al. (2022)). This is not to say that it is impossible to construct paleo networks
110 but rather identify that there are a subset of models that are probably not at all suitable for constructing
111 paleo networks (*e.g.*, Null models, since there are fully driven by abundance), other methods will be better
112 suited depending on the community of interest *e.g.*, for more contemporary communities that have modern
113 analogs we can use methods rooted in phylogeny (*e.g.*, Fricke et al. (2022), Strydom et al. (2023)) or traits
114 (*e.g.*, Caron et al. (2022)), and then there is the third axis which is to think about which are the assumptions
115 that are made and there trade off of that. This includes thinking about both assumptions you are making
116 about the actual data *e.g.*, trying to extrapolate body size from fossil data but also assumptions across time
117 *e.g.*, assuming modern trait-feeding modes are the same OR that assumptions about network structure will
118 hold across deep time.

119 **3.1 Approaches to food web prediction**

120 Here we present six different models (Table 1) that can be used to construct food webs for both this specific
121 community but are also broadly suited to paleo network prediction. These models span all facets of the
122 network representation space (metaweb, realised, and structural network) and are suitable for an array of
123 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 breadth model (ADBM)	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 network	Petchey et al. (2008)

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)

124 4 Case study: Toarcian mass extinction event

125 4.1 Dataset overview

126 4.1.1 Species occurrence

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

133 4.1.2 Defining modes of life (traits)

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

¹³⁷ ($>300\text{--}500$ mm), large ($>100\text{--}300$ mm), medium ($>50\text{--}100$ mm), small ($>10\text{--}50$ mm), tiny (<10 mm), for each
¹³⁸ fossil species based on the ecological traits defined in the Bambach ecospace model (Bambach et al., 2007).

¹³⁹ 4.1.3 Constructing networks

¹⁴⁰ For each paleo community (time bin) we constructed **100** networks for each model (so $6 * 100$) networks.
¹⁴¹ These networks were ‘simplified’ to remove any disconnected species. In total 2400 networks were constructed.
¹⁴² When a quantitative measure of body size is needed (ADBM, bodymassratio, lmatrix) we drew a body mass
¹⁴³ for each species from a uniform distribution. The ranges were defined by the different size classes as discussed
¹⁴⁴ in insert cross ref to correct subsection here *e.g.*, a species classed as ‘very large’ would have a body mass
¹⁴⁵ drawn from $U(300, 500)$. This was repeated for each run in order to add variation to the networks constructed,
¹⁴⁶ however the same body sizes were kept consistent for the relevant models (adbm, bodymassratio, l-matrix)
¹⁴⁷ *i.e.*, an ADBM and bodymassratio network from the same rep number would have used the same bodysizes.
¹⁴⁸ The PFIM networks were downsampled (see relevant section is S1). For both the random and niche model
¹⁴⁹ the desired connectance was randomly selected between the range 0.07 - 0.15 for each repetition but kept
¹⁵⁰ consistent for both models. For each network we calculated the properties listed in Table 2

¹⁵¹ 4.2 Models capture different network structure but in unexpected ways

¹⁵² Why is structure important and what can it tell us? Broadly when we talk about quantifying the structure
¹⁵³ of a network we are interested in capturing some aspect of how the links are distributed between nodes, or
¹⁵⁴ alternatively about properties of the nodes (specifically in terms of the number of links coming in to (prey)
¹⁵⁵ or out of (predators) the node). What are some things we can learn/infer from network structure: energy
¹⁵⁶ flows and fluxes [REF], propagation of stress [REF], roles of species in the community [REF, think trophic
¹⁵⁷ levels]. Some closing statement about how thus there are different facets of network structure and the value
¹⁵⁸ of understanding generally how different models differ in terms of the structure that they recover - link to
¹⁵⁹ Table 2 maybe.

¹⁶⁰ In terms of wanting to assess and compare across the different models it is beneficial to approach this task by
¹⁶¹ thinking about the different aspects of the network as well as interactions that are being predicted by the
¹⁶² different models. It is perhaps beneficial to think of these across different ‘scales’ of organisation within the
¹⁶³ network, namely macro (the entire network), meso (smaller interacting units within the network), and micro
¹⁶⁴ (species-level attributes). Although there are a myriad of possible ways to ‘measure’ and analyse ecological
¹⁶⁵ networks (Delmas et al., 2018) we do still lack a clear set of guidelines for assessing how well models recover
¹⁶⁶ network structure (Allesina et al., 2008) and it is beneficial to use a small subset of metrics that can clearly

167 be tied to broader aspects of network function or capturing a ecological process.
 168 Here we used a Multivariate Analysis Of Variance (MANOVA) as it is able to capture model differences based on
 169 the combined information of the multiple structural network measures. Model defined as `network structure`
 170 `values ~ model + time period` and Linear Discriminant Analysis (LDA) to determine if different models
 171 produced networks with differing structure. **Need to report the relevant effect of time in driving**
 172 **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)

173 **4.2.1 Macro network properties**

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

182 **4.2.2 Meso network properties**

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

188 **4.2.3 Micro network properties**

189 The number of interactions established (**generality**) or received (**vulnerability**) by each species (Schoener,
190 1989), are (broadly) indicative of consumer-resource relationships and diet breadth of species [ref]. Although
191 this is usually determined at the species level the standard deviation of the generality and vulnerability of
192 species is often used when benchmarking predicted networks (Petchey et al., 2008; *e.g.*, Williams & Martinez,
193 2008).

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

196 [Figure 2 about here.]

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

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

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

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

215 4.3 Some networks don’t share any interactions and some share a lot

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

225 [Figure 3 about here.]

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

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

236 4.4 Model choice changes the narrative

237 4.4.0.1 Simulating Extinctions

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

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

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

257 [Figure 4 about here.]

258 4.4.1 Trends over time

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

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

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

270 4.4.2 Inferred extinction drivers

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

277 5 Discussion (need a catchier heading)

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

280 Points to discuss:

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

284 References

- 285 Allesina, S., Alonso, D., & Pascual, M. (2008). A general model for food web structure. *Science*, 320(5876),
286 658–661. <https://doi.org/10.1126/science.1156269>
- 287 Bambach, R. K., Bush, A. M., & Erwin, D. H. (2007). Autecology and the Filling of Ecospace: Key Metazoan

- 288 Radiations. *Palaeontology*, 50(1), 1–22. <https://doi.org/10.1111/j.1475-4983.2006.00611.x>
- 289 Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with
290 trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>
- 291 Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A., & Rall,
292 B. C. (2011). Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and
293 dynamic food webs. *Basic and Applied Ecology*, 12(7), 571–580. <https://doi.org/10.1016/j.baae.2011.09.008>
- 294 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Dalla Riva, G. V., Fortin, M.-J., Gravel, D., Guimarães, P.
295 R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2018). Analysing
296 ecological networks of species interactions. *Biological Reviews*, 112540. <https://doi.org/10.1111/brv.12433>
- 297 Dillon, E. M., Pier, J. Q., Smith, J. A., Raja, N. B., Dimitrijević, D., Austin, E. L., Cybulski, J. D., De
298 Entrambasaguas, J., Durham, S. R., Grether, C. M., Haldar, H. S., Kocáková, K., Lin, C.-H., Mazzini, I.,
299 Mychajliw, A. M., Ollendorf, A. L., Pimiento, C., Regalado Fernández, O. R., Smith, I. E., & Dietl, G. P.
300 (2022). What is conservation paleobiology? Tracking 20 years of research and development. *Frontiers in
301 Ecology and Evolution*, 10. <https://doi.org/10.3389/fevo.2022.1031483>
- 302 Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).
303 Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event. *Nature
304 Communications*, 15(1), 8599. <https://doi.org/10.1038/s41467-024-53000-2>
- 305 Dunne, J. A., Labandeira, C. C., & Williams, R. J. (2014). Highly resolved early eocene food webs show
306 development of modern trophic structure after the end-cretaceous extinction. *Proceedings of the Royal
307 Society B: Biological Sciences*, 281(1782), 20133280. <https://doi.org/10.1098/rspb.2013.3280>
- 308 Erdős, P., & Rényi, A. (1959). On random graphs. i. *Publicationes Mathematicae Debrecen*, 6(3-4), 290–297.
309 <https://doi.org/10.5486/pmd.1959.6.3-4.12>
- 310 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,
311 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene. *Science*,
312 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 313 Gauzens, B., Thouvenot, L., Srivastava, D. S., Kratina, P., Romero, G. Q., Berti, E., O’Gorman, E. J.,
314 González, A. L., Dézerald, O., Eisenhauer, N., Pires, M., Ryser, R., Farjalla, V. F., Rogy, P., Brose, U.,
315 Petermann, J. S., Geslin, B., & Hines, J. (2025). Tailoring interaction network types to answer different
316 ecological questions. *Nature Reviews Biodiversity*, 1–10. <https://doi.org/10.1038/s44358-025-00056-7>
- 317 Gupta, A., Furrer, R., & Petchey, O. L. (2022). Simultaneously estimating food web connectance and structure
318 with uncertainty. *Ecology and Evolution*, 12(3), e8643. <https://doi.org/10.1002/ece3.8643>
- 319 Hao, X., Holyoak, M., Zhang, Z., & Yan, C. (2025). Global Projection of Terrestrial Vertebrate Food
320 Webs Under Future Climate and Land-Use Changes. *Global Change Biology*, 31(2), e70061. <https://doi.org/10.1111/gcb.15811>

- 321 //doi.org/10.1111/gcb.70061
- 322 Jonsson, T., Berg, S., Pimenov, A., Palmer, C., & Emmerson, M. (2015). The reliability of R50 as a
323 measure of vulnerability of food webs to sequential species deletions. *Oikos*, 124(4), 446–457. <https://doi.org/10.1111/oik.01588>
- 324
- 325 Jordano, P. (2016). Chasing Ecological Interactions. *PLOS Biology*, 14(9), e1002559. <https://doi.org/10.1371/journal.pbio.1002559>
- 326
- 327 Kiessling, W., Raja, N. B., Roden, V. J., Turvey, S. T., & Saupe, E. E. (2019). Addressing priority questions
328 of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B:
329 Biological Sciences*, 374(1788), 20190222. <https://doi.org/10.1098/rstb.2019.0222>
- 330 Martinez, N. D. (1992). Constant connectance in community food webs. *The American Naturalist*, 139(6),
331 1208–1218. <http://www.jstor.org/stable/2462337>
- 332 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple
333 building blocks of complex networks. *Science*, 298(5594), 824–827. [https://doi.org/10.1126/science.298.5594.824](https://doi.org/10.1126/science.298.
334 5594.824)
- 335 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from
336 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 337 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure.
338 *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. [https://doi.org/10.1073/pnas.0710672105](https://doi.org/10.1073/pnas.
339 0710672105)
- 340 Pichler, M., & Hartig, F. (2023). Machine learning and deep learning—A review for ecologists. *Methods in
341 Ecology and Evolution*, 14(4), 994–1016. <https://doi.org/10.1111/2041-210X.14061>
- 342 Poisot, T., Canard, E., Mouquet, N., & Hochberg, M. E. (2012). A comparative study of ecological
343 specialization estimators. *Methods in Ecology and Evolution*, 3(3), 537–544. [https://doi.org/10.1111/j.2041-210x.2011.00174.x](https://doi.org/10.1111/j.2041-
344 210x.2011.00174.x)
- 345 Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring
346 unexplained structure using latent traits. *The American Naturalist*, 176(2), 170–177. [https://doi.org/10.1086/653667](https://doi.org/10.
347 1086/653667)
- 348 Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32(1),
349 1–19. <http://www.jstor.org/stable/4096814>
- 350 Schneider, F. D., Brose, U., Rall, B. C., & Guill, C. (2016). Animal diversity and ecosystem functioning in
351 dynamic food webs. *Nature Communications*, 7(1), 12718. <https://doi.org/10.1038/ncomms12718>
- 352 Schoener, T. W. (1989). Food Webs From the Small to the Large: The Robert H. MacArthur Award Lecture.
353 *Ecology*, 70(6), 1559–1589. <https://doi.org/10.2307/1938088>

- 354 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*
355 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 356
- 357 Staniczenko, P. P. A., Kopp, J. C., & Allesina, S. (2013). The ghost of nestedness in ecological networks.
358 *Nature Communications*, 4(1), 1391. <https://doi.org/10.1038/ncomms2422>
- 359 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust
360 pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621),
361 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>
- 362 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Hemming, V.,
363 Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2022). Food web reconstruction
364 through phylogenetic transfer of low-rank network representation. *Methods in Ecology and Evolution*,
365 13(12). <https://doi.org/10.1111/2041-210X.13835>
- 366 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,
367 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer
368 learning can help predict potential species interaction networks despite data limitations. *Methods in
369 Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 370 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
371 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021b). A roadmap
372 towards predicting species interaction networks (across space and time). *Philosophical Transactions of the
373 Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 374 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
375 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021a). A roadmap
376 towards predicting species interaction networks (across space and time). *Philosophical Transactions of the
377 Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 378 Thuiller, W., Calderon-Sanou, I., Chalmandrier, L., Gaüzere, P., Ohlmann, M., Poggiato, G., & Münkemüller,
379 T. (n.d.). *Navigating the integration of Biotic Interactions in Biogeography*.
- 380 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
381 <https://doi.org/10.1038/35004572>
- 382 Williams, R. J., & Martinez, N. D. (2004). Stabilization of chaotic and non-permanent food-web dynamics.
383 *The European Physical Journal B - Condensed Matter*, 38(2), 297–303. <https://doi.org/10.1140/epjb/e2004-00122-1>
- 384
- 385 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food
386 webs. *The Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>

³⁸⁷ Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T.
³⁸⁸ (2014). Collapse of an ecological network in ancient egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>

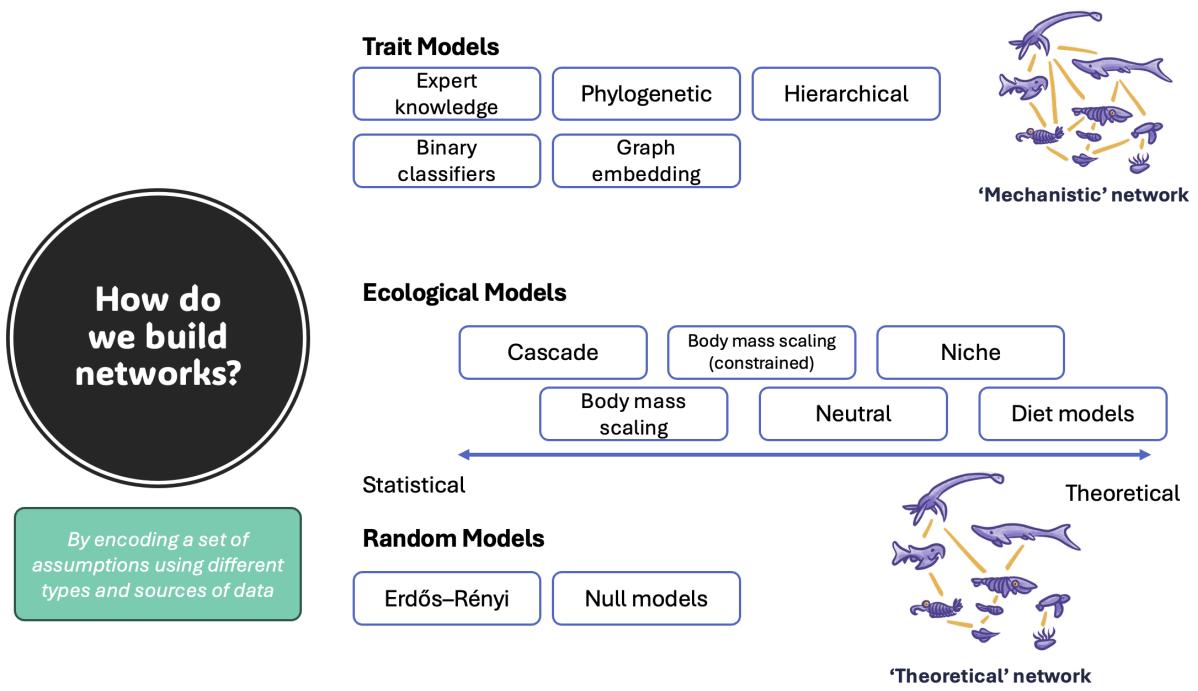


Figure 1: This obviously needs work but a variation on this to try and articulate the different approaches and broadly how they may differ.

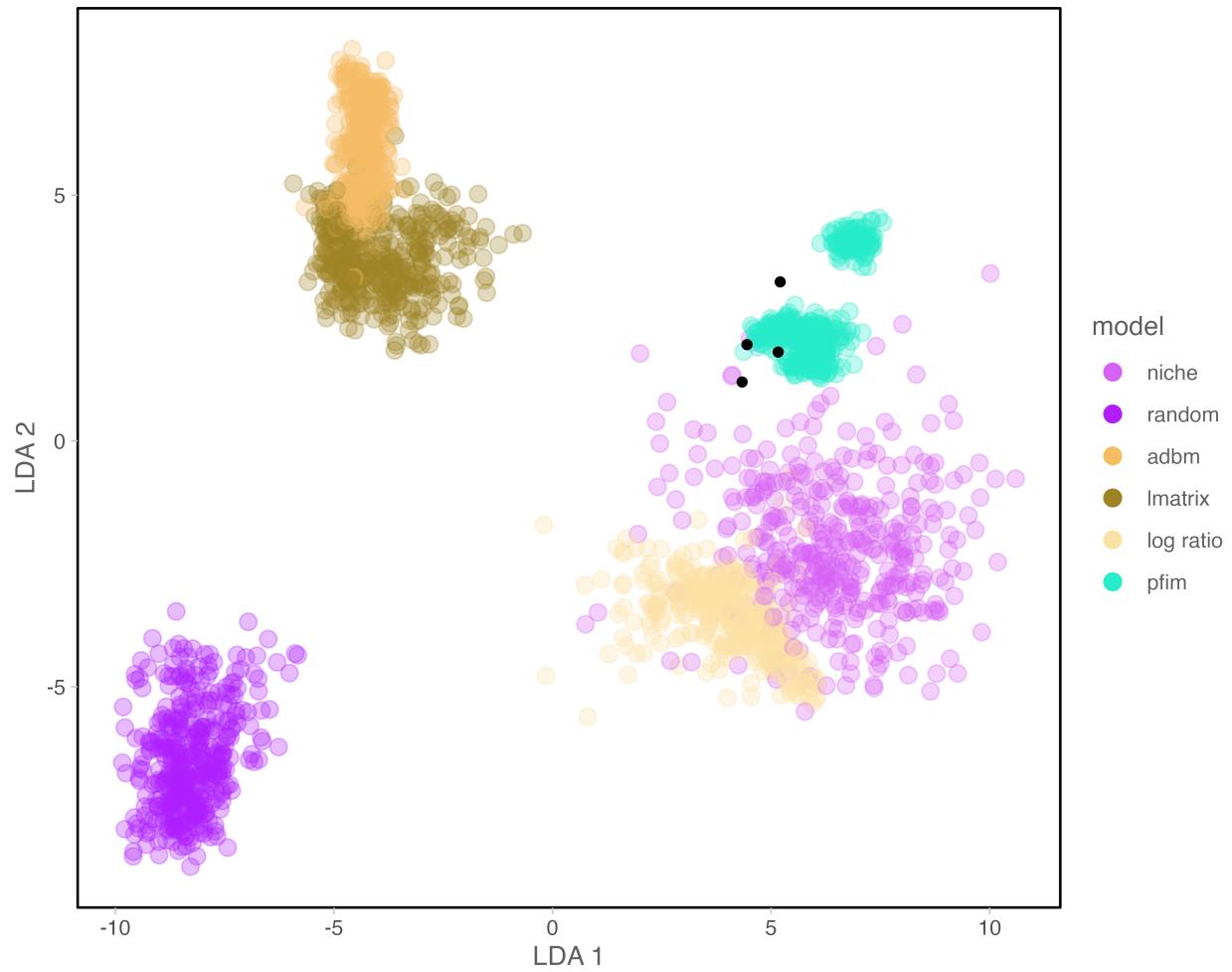


Figure 2: stuff...

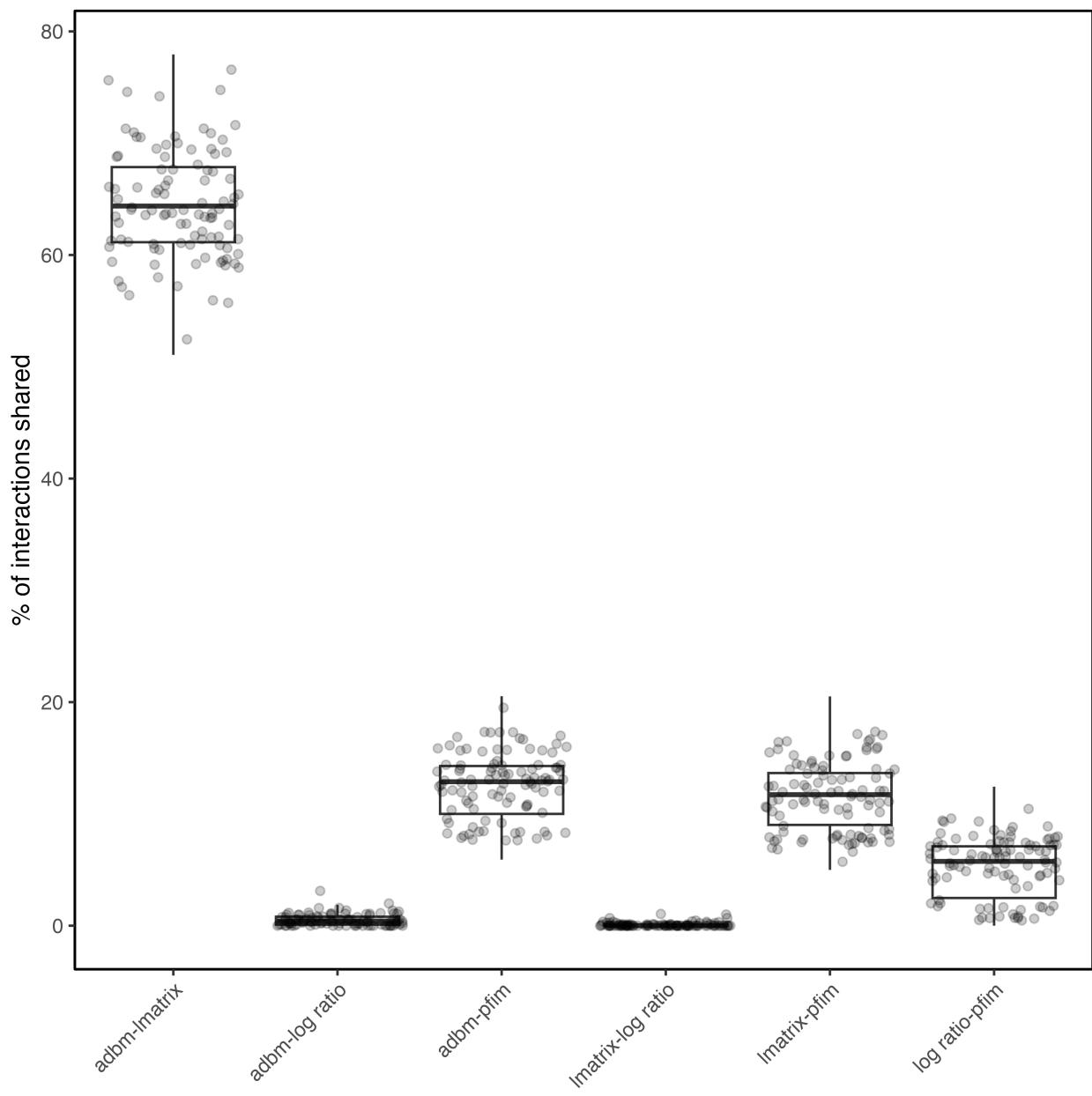


Figure 3: stuff... % interaction shared is calculated as number shared interactions / ((number interactions left - shared interactions) + (number interactions right - shared interactions) + shared interactions). Additionally niche and random models are excluded as it is illogical since both of these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

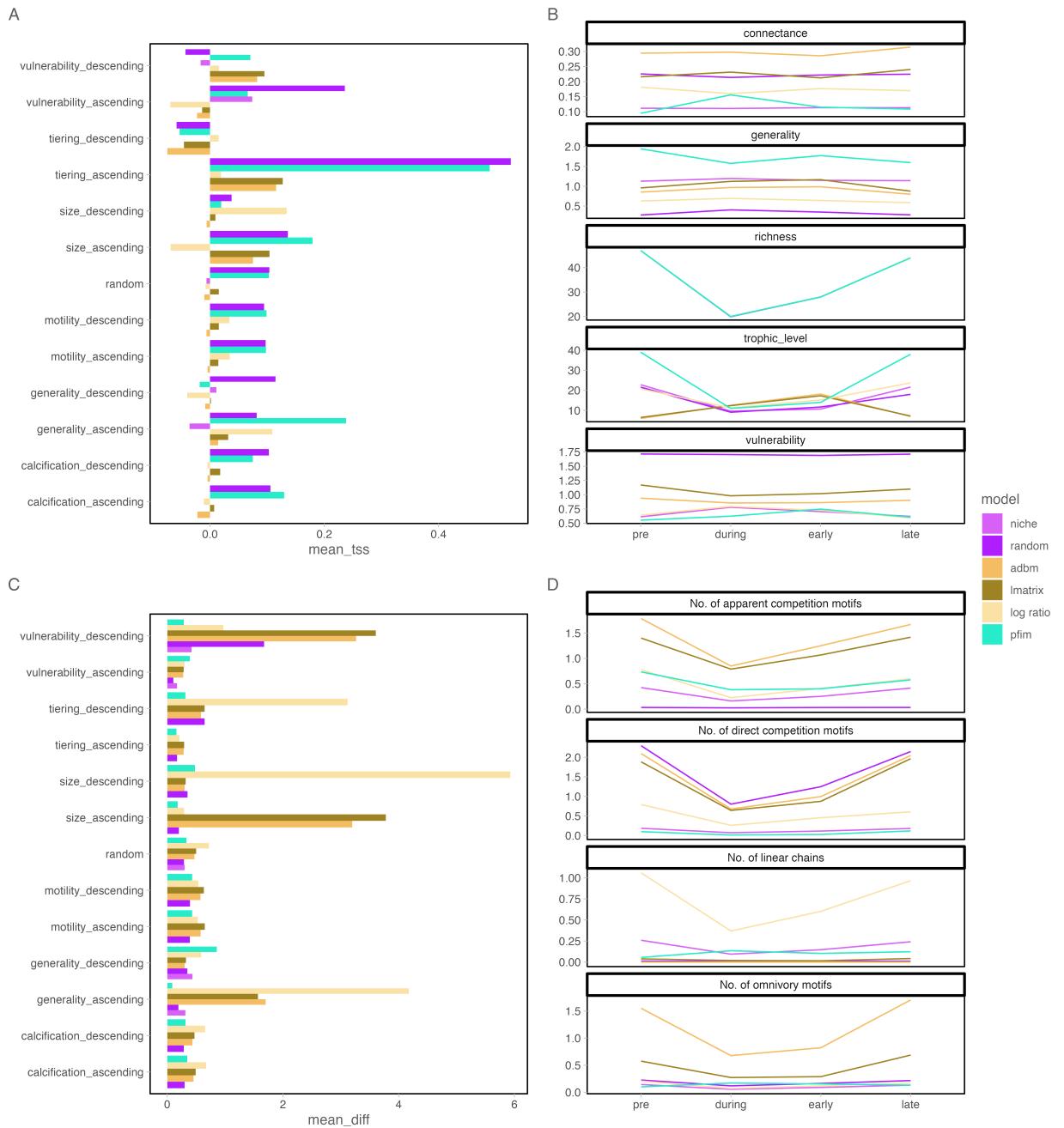


Figure 4: stuff... Recreation of the figure from Dunhill 2024. Note not 100% sold on the TSS and absolute mean calculations...