

Methods for Reconstructing Paleo Food Webs

Tanya Strydom ¹; Baran Karapunar ²; Andrew P. Beckerman ¹; Alexander Dunhill ²

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

23 Here we aim to provide an overview of the different models that can be used to construct food webs using
24 paleo data. Specifically we focus on identifying a suite of models that are appropriate for use with paleo data
25 that can feasibly be constructed within the limitations that are imposed by fossil data while still spanning the
26 larger network space. Additionally we use the data from Dunhill et al. (2024) as a case study to understand
27 how different models recover different networks, both in terms of structure as well as pairwise interactions and
28 establish if there are consequences for using networks that are constructed using different models in terms of
29 making inferences about the behaviour of the system by looking at how the model type influences what we
30 infer to be the dominant driver of extinctions across a mass extinction event.

³¹ **1 Constructing paleo webs**

³² **2 Challenges specific to building paleo networks**

³³ Although there has been a push for the development of tools and methods that allow us to predict species
³⁴ interactions and networks they will not all be suitable for the prediction of paleo communities. This is
³⁵ primarily due to limitations that we are faced with in terms of the information that can be inferred from
³⁶ the fossil record (such as species traits, abundances, and assemblages), which is needed as input data for the
³⁷ different models. The limited information available from the fossil record is compounded by the incomplete
³⁸ and biased preservation of species [REF], which part of a species is preserved (part vs whole), the ambiguity of
³⁹ the ‘true’ community composition [were communities conserved *in situ* or were they there owing to geological
⁴⁰ processes?; REF], as well as the availability/accessibility of different rock layers (and thus the completeness of
⁴¹ data we might have for a specific era in time). Additionally there is an increasing degree of ‘fuzziness’ around
⁴² the ecology and life histories of species the further one moves back in geological time [REF]. This is not to say
⁴³ that because we have imperfect data we should not be attempting to construct paleo food webs but rather
⁴⁴ that we need to be aware of what the uncertainties are and how these might impact the assumptions that we
⁴⁵ need to make when constructing a network (as well as how this will intersect with the intended end use of
⁴⁶ the network). This will allow us to best identify an approach that minimises the assumption and potential
⁴⁷ uncertainties within the data while still constructing a suitable network. This includes thinking about both
⁴⁸ assumptions you are making about the actual data *e.g.*, trying to extrapolate body size from fossil data but
⁴⁹ also assumptions across time *e.g.*, assuming modern trait-feeding modes are the same or that assumptions
⁵⁰ about network structure will hold across deep time.

⁵¹ **2.1 Understanding the approaches to network construction**

⁵² Broadly we can think about network construction as being nested within two different schools of thought (and
⁵³ thus methodological approaches, Figure 1), models that focus on assessing the *mechanistic* feasibility of an
⁵⁴ interaction being able to occur between two species or models that are more closely married to specific bodies
⁵⁵ of ecological *theory* - such as niche theory or foraging ecology. The former of which will construct ‘metawebs’
⁵⁶ and the latter ‘realised networks’ [Strydom et al in prep]. Models that have specifically been developed
⁵⁷ in the paleo space tend to be mechanistic in nature in that they focus on using a trait-based approach to
⁵⁸ formalise feeding interactions (*e.g.*, Shaw et al. (2024); Roopnarine (2006)), are assembled by expert opinion
⁵⁹ (*e.g.* Dunne et al. (2014)), or make assumptions based on the evolutionary signals of interactions (*e.g.*,
60 Fricke et al. (2022)). Thus paleo models typically only construct metawebs, and there is the need for the

61 intentional adoption of theoretical models if we want to realise the full potential of questions and information
 62 that we can glean from the fossil record. However, there is an argument that the fundamental ‘currencies of
 63 life’ to have remained constant - *e.g.*, the energetic constraints of foraging or foraging niches, meaning that
 64 theoretical models that have been developed and tested on contemporary food webs should still hold for paleo
 65 communities.

66 [Figure 1 about here.]

67 Here we present six different models (Table 1) that can be used to construct food webs for both this specific
 68 community but are also broadly suited to paleo network prediction. These models span all facets of the
 69 network representation space (metaweb, realised, and structural network) and are suitable for an array of
 70 different paleo communities as the data requirements fall within the limitations set by the fossil record.

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). Logit 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)

71 3 Case study: Toarcian mass extinction event

72 3.1 Dataset overview

73 3.1.1 Species occurrence

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

80 3.1.2 Defining modes of life (traits)

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

84 ($>300\text{--}500$ mm), large ($>100\text{--}300$ mm), medium ($>50\text{--}100$ mm), small ($>10\text{--}50$ mm), tiny (10 mm), for each
85 fossil species based on the ecological traits defined in the Bambach ecospace model (Bambach et al., 2007).

86 **3.1.3 Constructing networks**

87 For each paleo community (time bin) we constructed **100** networks for each model (so $6 * 100$) networks.
88 These networks were simplified so as to remove any disconnected species. In total 2 400 networks were
89 constructed. When a quantitative measure of body size is needed (ADBM, body size ratio, and l-matrix) we
90 drew a body mass for each species from a uniform distribution, with ranges being defined by the different
91 size classes *e.g.*, a species classed as ‘very large’ would have a body mass drawn from $U(300, 500)$. This was
92 repeated for each run in order to add variation to the networks constructed, however the same body sizes were
93 kept consistent for the relevant models *i.e.*, an ADBM and l-matrix network from the same replicate have
94 the same bodysizes. For both the random and niche model the desired connectance was randomly selected
95 between the range 0.07 - 0.15 for each replicate but kept consistent for both models. For each network we
96 calculated the properties listed in Table 2

97 **3.2 Models capture different network structure but in unexpected ways**

98 Broadly when we talk about quantifying the structure of a network we are interesting in capturing some aspect
99 of how the links are distributed between nodes, or alternatively about properties of the nodes. Structure
100 is useful as it is gives information as to how the interactions between species are distributed within the
101 community, informing us on *e.g.*, energy flows and fluxes [REF], propagation of stress [REF], and something
102 about trophic levels [REF]. We are also able to glean information on interaction strategies between smaller
103 interacting units in the bigger community in the form of motifs (Milo et al., 2002; Stouffer et al., 2007).
104 Motifs allow us to identify *e.g.*, the prevalence of competition, as well as smaller chains within the network.
105 Node-level properties look at the the number of links coming in to (prey) or out of (predators) a node and are
106 informative of diet specialisation.

Table 2: Network properties used fo analysis.

Metric	Definition	Scale	Reference (for maths), can make footnotes probs
Richness	Number of nodes in the network	Macro	

Metric	Definition	Scale	Reference (for maths), can make footnotes probs
Links	Normalized standard deviation of links (number of consumers plus resources per taxon)	Micro	
Connectance	L/S^2 , where S is the number of species and L the number of links	Macro	
Max trophic level	Prey-weighted trophic level averaged across taxa	Macro	Williams & Martinez (2004)
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)
Complexity	SVD complexity of a network, defined as the Pielou entropy of its singular values	Macro	Strydom et al. (2021)
Redundancy	$(L - (S - 1))/S$, where S is the number of species and L the number of links. Indicates the number of edges beyond what is needed for a minimum-connected tree	Macro	
S1	Number of linear chains, normalised	Meso	Milo et al. (2002); Stouffer et al. (2007)
S2	Number of omnivory motifs, normalised	Meso	Milo et al. (2002); Stouffer et al. (2007)

Metric	Definition	Scale	Reference (for maths), can make footnotes probs
S4	Number of apparent competition motifs, normalised	Meso	Milo et al. (2002); Stouffer et al. (2007)
S5	Number of direct competition motifs, normalised	Meso	Milo et al. (2002); Stouffer et al. (2007)
Generality	Normalized standard deviation of generality of a species standardized by L/S	Micro	Williams & Martinez (2000)
Vulnerability	Normalized standard deviation of vulnerability of a species standardized by L/S	Micro	Williams & Martinez (2000)

¹⁰⁷ In terms of wanting to assess and compare across the different models it is beneficial to approach this task
¹⁰⁸ by thinking about the different aspects of the network as well as interactions that are being predicted by
¹⁰⁹ the different models across different ‘scales’ of organisation within the network, namely macro (the entire
¹¹⁰ network), meso (smaller interacting units within the network), and micro (species-level attributes). Although
¹¹¹ there are a myriad of possible ways to ‘measure’ and analyse ecological networks (Delmas et al., 2018) we
¹¹² have selected those outlined in Table 2 as they span different scales within the network and have been shown
¹¹³ to be informative of different ecological processes.

¹¹⁴ Here we used a Multivariate Analysis Of Variance (MANOVA) to assess the differences between networks
¹¹⁵ generated by different models based on the combined information of the multiple structural network measures.

¹¹⁶ Model defined as `network structure values ~ model + time period` additionally we used a Linear Dis-
¹¹⁷ criminant Analysis (LDA) to determine if different models produced networks with differing structure. In
¹¹⁸ order to do the MANOVA and LDA we had to create within model variation for the different networks, with
¹¹⁹ the exception of the PFIM model all models have some inherent variation. In order to generate variation
¹²⁰ within the PFIM metawebs we applied a *minimal* degree of downsampling following the protocol described in

121 Roopnarine (2017). This downsampling approach uses a power law distribution to essentially ‘prune’ links
122 from the most generalist species (See SUPP MATT for a more detailed overview).

123 **Need to report the relevant effect of time in driving observed differences???**

124 [Figure 2 about here.]

125 should I report some more ‘quantitative results’ i.e. a summary table...

126 What is perhaps the most striking result in Figure 2 is that although there are clear structural differences
127 between the different models the differences are not distinct between the broader model families but rather
128 that there is a degree of overlap between them (specifically the body size ratio, PFIM, and niche models).

129 Although the log ratio and niche models are classified as different families they are built on similar ecological
130 background and theory and so it is perhaps not surprising that these networks capture a similar structure
131 (the same holds for the ADBM and l-matrix models). The fact that the random model occupies a completely
132 different space is unsurprising as it has clearly been shown that networks are non-random in nature [REF] and
133 so we expect random models to be constructing ‘ecologically illogical’ networks. What is perhaps the most
134 interesting result is that the PFIM model constructs networks that are very similar to those that are rooted
135 in niche-based processes despite the model being more mechanistic in nature. (Not sure how to articulate but
136 this is cool because there is *something* in network structure constraints that is straddling the trait-niche space
137 of ecology)

138 Although it is not possible to confidently identify the models that are predicting the ‘*correct*’ network structure
139 the fact that models from different families are able to recover similar structures is reassuring as it suggests
140 that it might be possible to substitute one model for another if the required data are not available. Although
141 it is still important that an effort is made to match the ‘best’ model/network to the question being asked.

142 It would be remiss to not think about the fact that niche models are supposed to work with trophic
143 species not taxonomic species - I wonder if we should run the niche (and possibly random) models
144 with trophic species as the starting richness and not the taxo richness...

145 **3.3 Some networks don’t share any interactions and some share a lot**

146 In addition to wanting to measure network structure researchers may also be interested in understanding
147 aspects about the diets and predators of *specific* species in a community. In this instance the interest should
148 be in understanding how the pairwise links predicted between species pairs differ between models. Here we
149 look at the interaction turnover both within and between the different models (Poisot et al., 2012). This can
150 be thought of as the equivalent of species β turnover and tells us which interactions are ‘conserved’ (shared)

151 across the networks but only between species pairs that are shared - *i.e.*, this turnover is only driven by
152 interaction and not species turnover. Here we only compared networks that we constructed for the same
153 period (as our interest is only in between model differences) and excluded the random and niche networks
154 from consideration as these two models are essentially species agnostic.

155 [Figure 3 about here.]

156 In Figure 3 it is clear that some models share a large percentage of interactions *e.g.*, between ADBM and
157 l-matrix networks and others share nothing *e.g.*, ADBM and PFIM networks. This result is unsurprising as the
158 mechanisms that determine interactions in ADBM and l-matrix (a single trait (bodysize) + parameterisation
159 of links by ecological theory) is very different from the PFIM model that makes assumptions on a trait-based,
160 mechanistic hierarchy.

161 The key takeaway that this needs to lead into is thinking about diet related questions and the model that
162 is best suited to get you there. It makes sense to contextualise this in the feasible vs realised interaction
163 spectrum - specifically that from a ‘philosophical’ basis if you are asking questions about possible diets of
164 species then it makes sense to use models that fall firmly in the ‘feasible’ space *e.g.*, PFIM model or even
165 something like the Fricke et al. (2022) model. How these results support that is that we can see the ADBM
166 and PFIM are recovering (almost) totally different pairwise links and on a conceptual basis it means that
167 we cannot use something like the ADBM to ask questions about diet breadth (note here this makes the
168 assumption that something like the PFIM is truly aligning with diet breadth, which I am inclined to say it is).

169 3.4 Model choice changes the narrative

170 3.4.0.1 Simulating Extinctions

171 Extinctions were simulated using different plausible mechanisms based on species traits (size, motility), their
172 position within the network (generality, vulnerability), as well as randomly. Each network was subjected
173 to 50 extinction runs for each extinction mechanism. The extinctions themselves were cascading in nature
174 meaning that after the target species was removed all species that no longer had any prey were also deemed
175 as extinct (secondary extinction), checking for secondary extinctions was then repeated until there were no
176 longer any species without prey. This represents one extinction event and only then would the proceeding
177 target species be removed from the network and cascading extinctions assessed again. Note that for extinction
178 simulations which use the network position of a species to determine extinction order we follow the protocol
179 from Curtsdotter et al. (2011) and reassess the vulnerability/generality of each species after each extinction
180 event to ‘redetermine’ the extinction order based on their position in the newly generated network.

181 As we are using Dunhill et al. (2024) as a case study we followed their approach when simulating extinctions
182 as well as assessing which extinction mechanism results in a simulated network that most closely matches the
183 real post extinction network. Extinction simulations were only run on the pre extinction networks whereby
184 species were removed until they reached the ‘target richness’, which is the richness of the post extinction
185 community. **TODO** The whole shebang about the different extinction simulation scenarios.

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

187 [Figure 4 about here.]

188 **3.4.1 Trends over time**

189 **TODO** Not sure statistically speaking what the best way to unpack this is... 2-way ANOVA/AN-
190 COVA explanation is valuable? There are intercept differences (*e.g.*, baseline average values are
191 different; are the rankings among all three response variables the same?) and there are shape
192 differences/similarities (*e.g.*, motifs are all the same shape but Co and Gen show some among
193 model differences in pattern.)

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

200 **3.4.2 Inferred extinction drivers**

201 In order to determine which extinction mechanism creates a network most similar to the post extinction
202 network we use a derivative of the true skill statistic from Gupta et al. (2022). Here we calculated both a
203 node-level TSS as well as link-level TSS, by parsing out the TSS into two components we are able to assess if
204 differences between real and simulated networks are due to node-level (the wrong species being removed) or
205 link-level (the wrong links be recovered) differences.

206 Points of discussion one will be to point to the mean absolute distance and how generally the ADBM/l-matrix
207 do really badly - high mean absolute value. And this maybe makes sense though because of how we specify
208 extinction mechanisms (trait-based) and so it sets the body-size models are not ‘talking’ the same language.
209 In terms of the TSS scores - not sure how we should unpack it. Individually by model family to see which

210 model agrees with which approach and see if different mechanisms come out stronger?

211 4 Discussion (need a catchier heading)

212 I want this section to be more about contextualising model choice within the bigger research question discussion

213 - i.e. mapping question and model choice more tightly...

214 Points to discuss:

215 • Guidelines - as a box? Can we give something concrete?? Something like Figure 5

216 • How do we synthesise these results? As in should we give clear directives or is it enough to do a bit
217 more handwaving and have the bigger message be that model choice matters?

218 [Figure 5 about here.]

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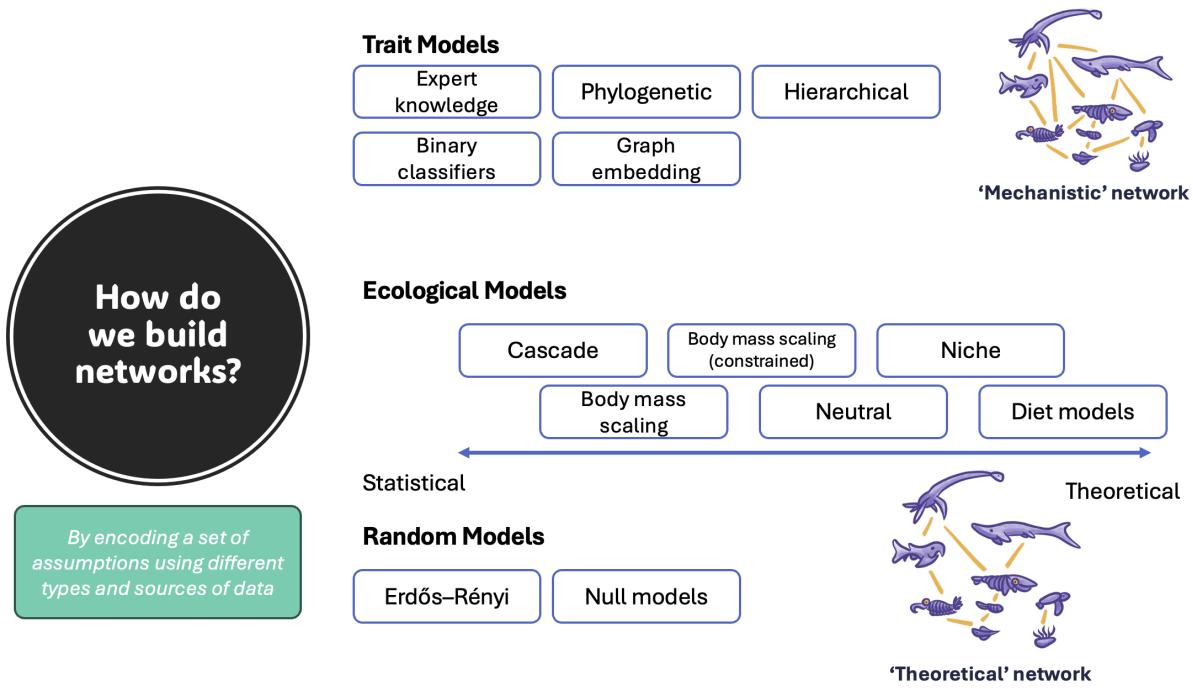


Figure 1: This obviously needs work but a variation on this to try and articulate the different approaches and broadly how they may differ.

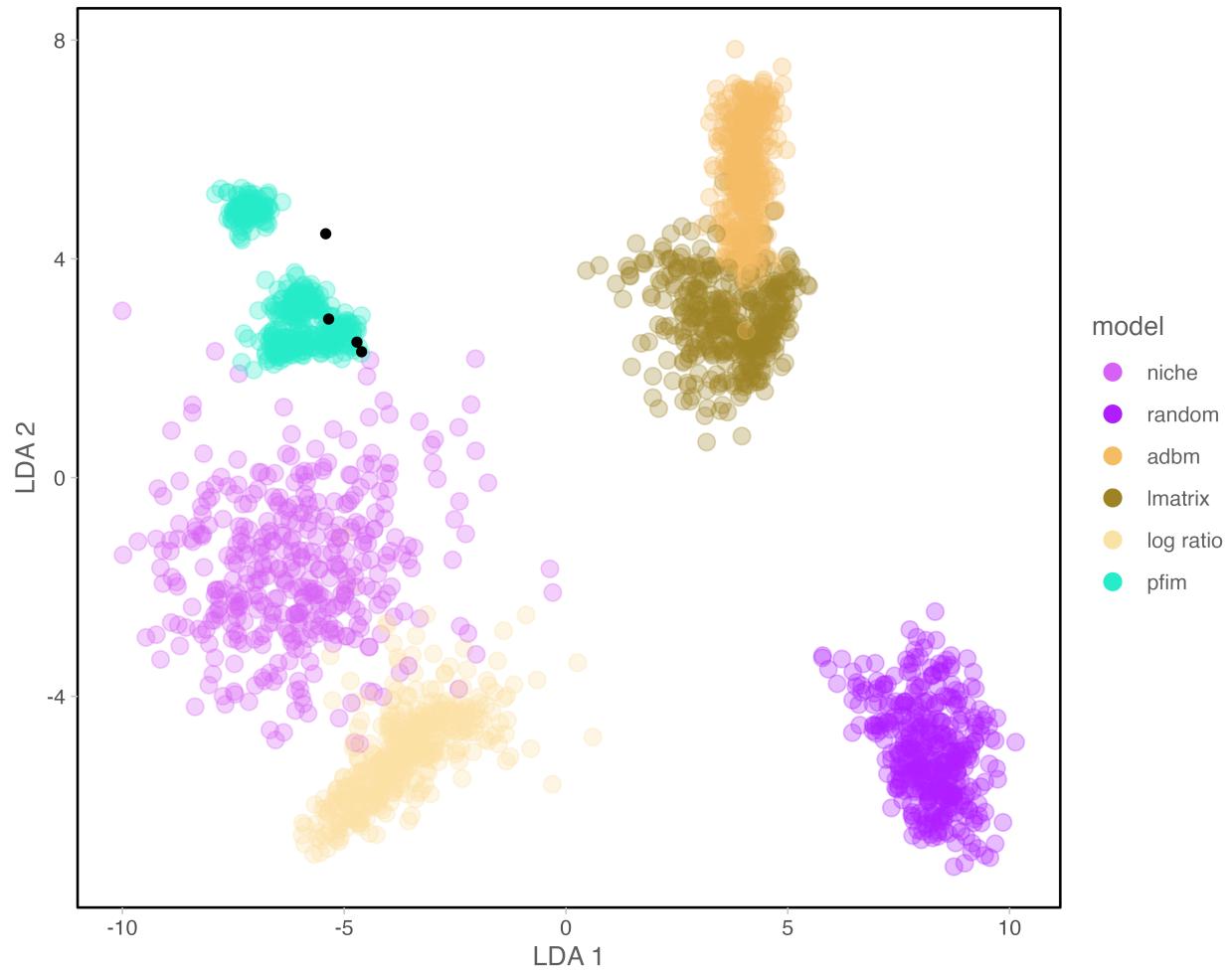


Figure 2: Linear Discriminant Analysis using thirteen different metrics of network structure. The colours represent the different models. The black points represent the predicted metaweb co-ordinates for the four different time periods.

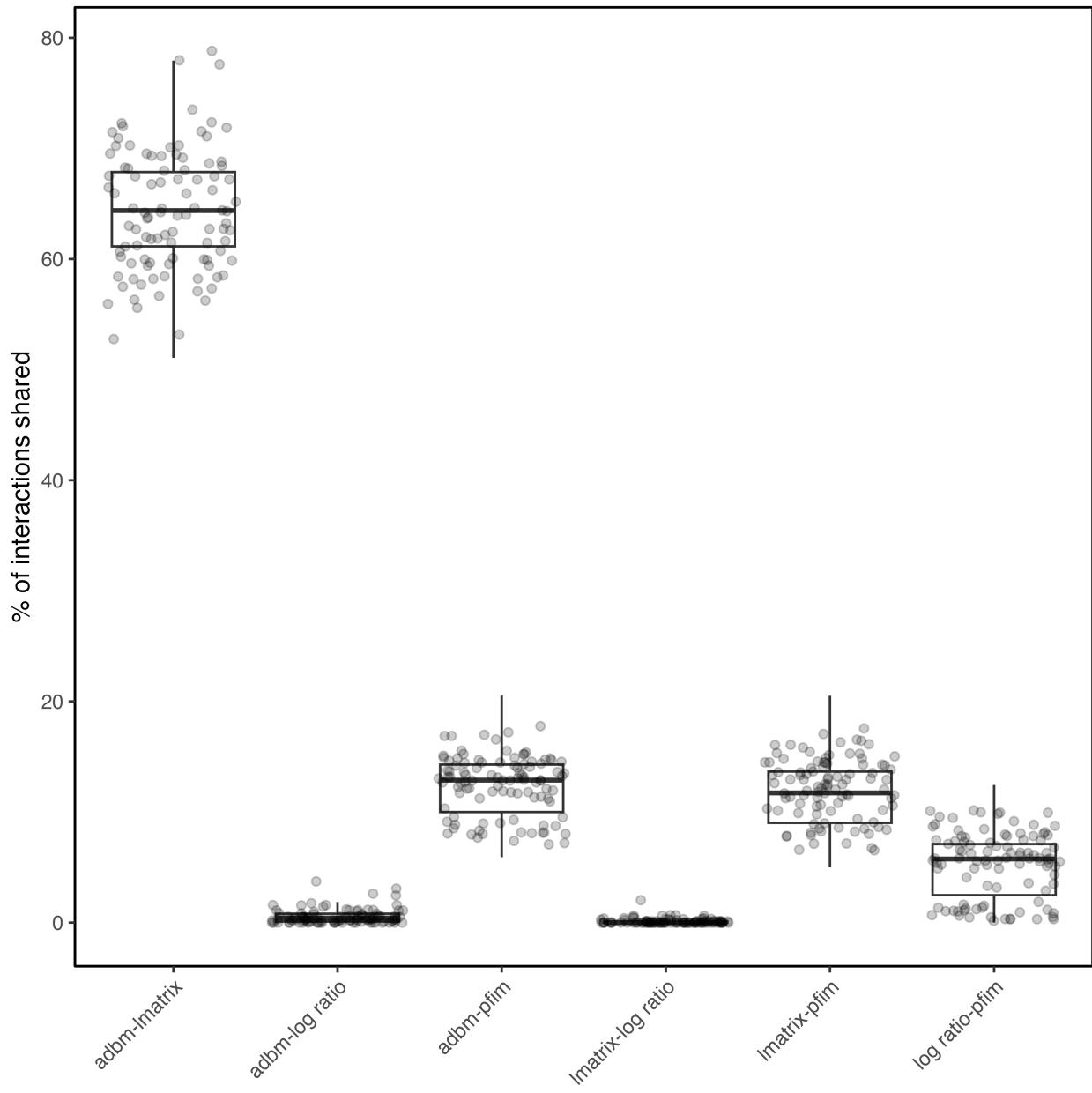


Figure 3: % interaction shared is calculated as number shared interactions / ((number interactions left - shared interactions) + (number interactions right - shared interactions) + shared interactions). Additionally niche and random models are excluded as it is illogical since both of these models are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

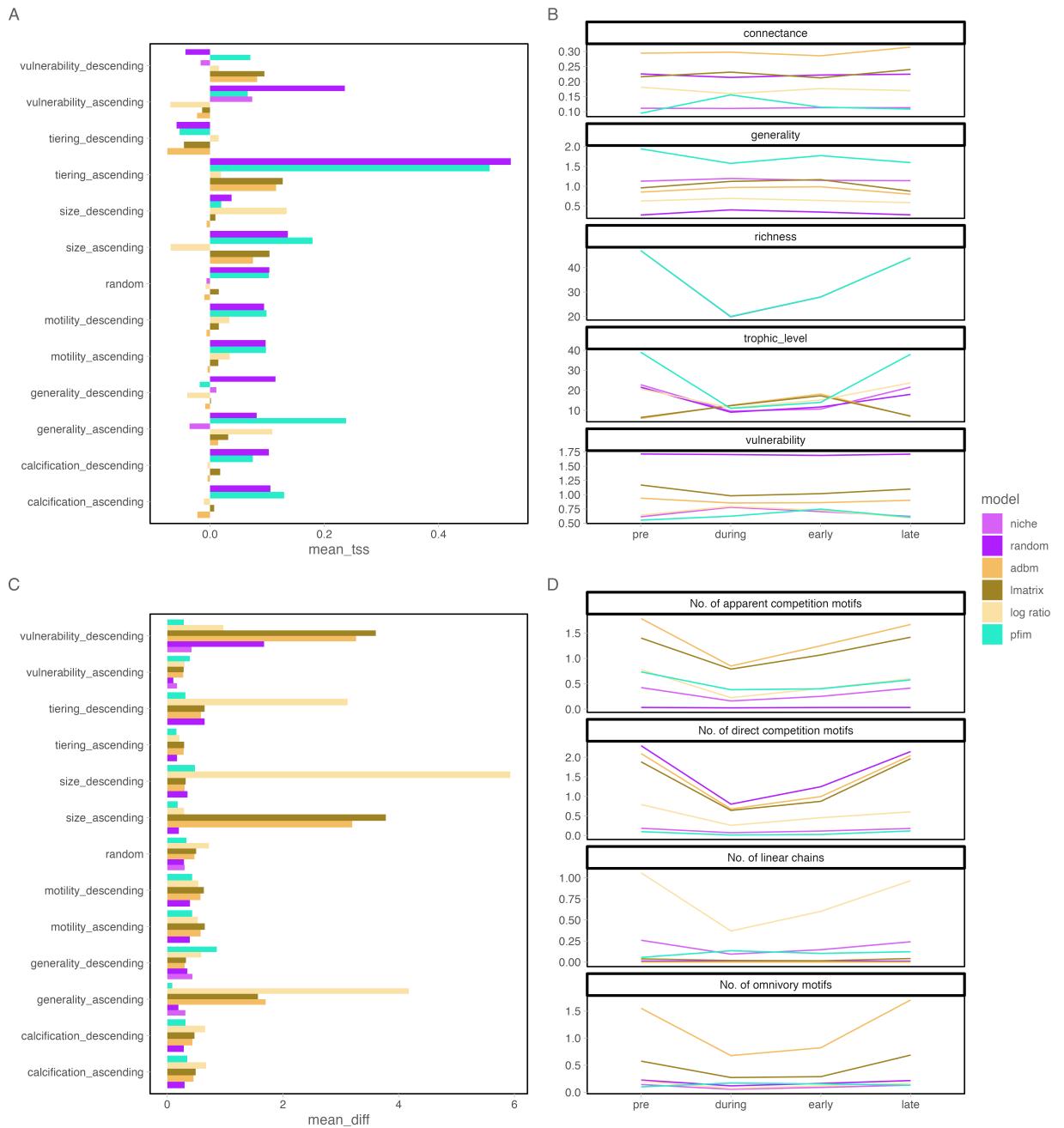


Figure 4: stuff... Recreation of the figure from Dunhill 2024. I think it makes sense to split and divide into the below sections (depending on potential figure limitations of target journal)

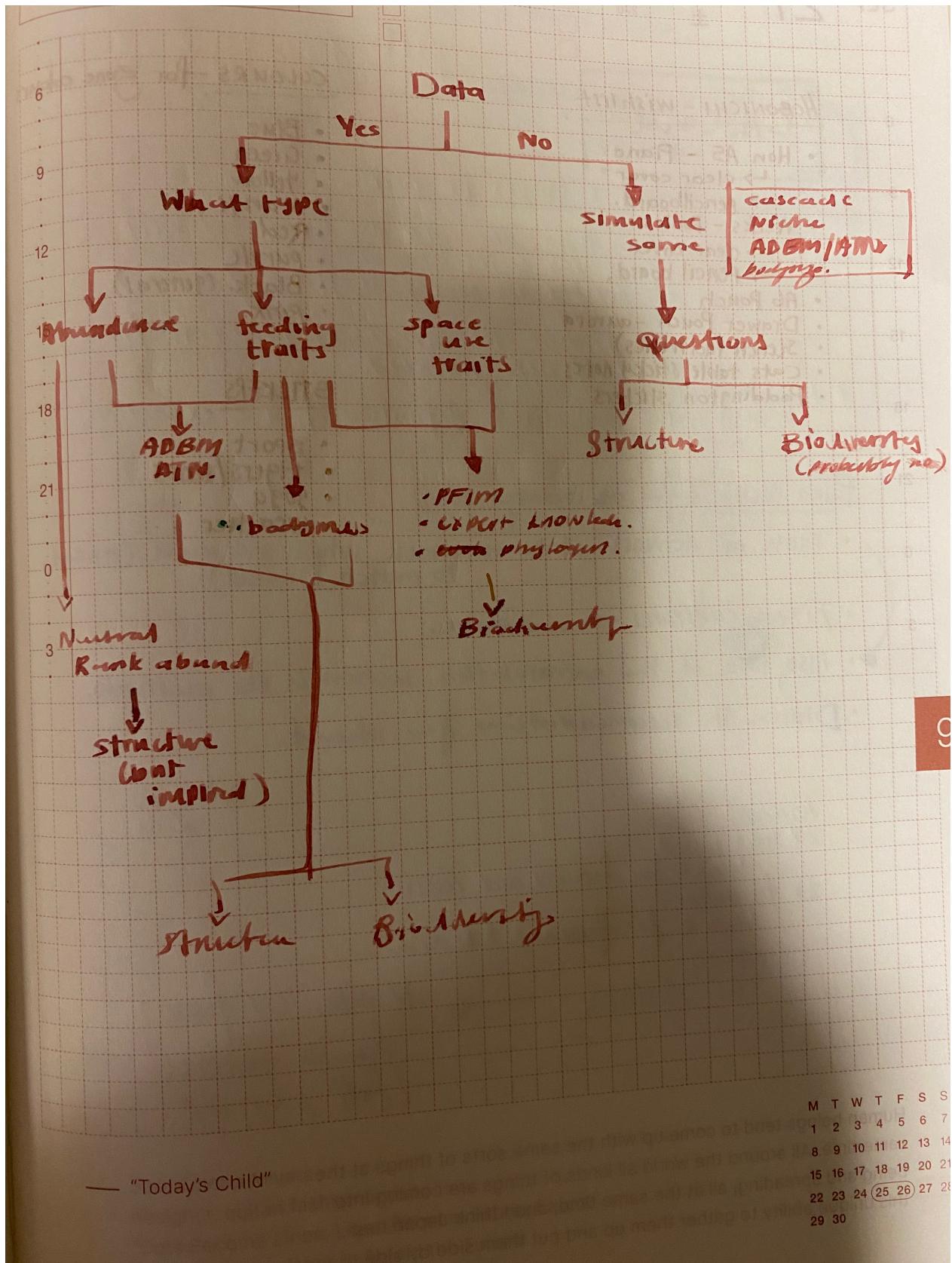


Figure 5: TODO.