

# **Reconstructing food webs in deep time: why model choice matters for ecological inference**

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**Abstract:** Food webs provide a powerful framework for understanding ecosystem structure and function, yet reconstructing them in paleoecological contexts remains challenging because direct evidence of species interactions is rarely preserved. A growing array of models exists for predicting interactions and inferring network structure, but these approaches differ markedly in their assumptions, mechanisms, and data requirements. Here, we evaluate how network reconstruction model choice shapes ecological inference in deep time and which approaches are most appropriate given the constraints of the fossil record. Using the Toarcian Oceanic Anoxic Event (Early Jurassic, ~183 Ma) as a case study, we reconstruct food webs for four successive community states using six contrasting modelling approaches spanning mechanistic, trait-based, and structural network representations. Despite identical taxon pools, models produced strikingly different network structures and species-level interactions, and these differences propagated into divergent inferences about extinction dynamics, interaction loss, and cascading effects. By framing food-web reconstructions as alternative ecological hypotheses (rather than interchangeable representations) this study bridges paleoecology and modern network theory, and demonstrates how model choice fundamentally conditions inference about extinction dynamics in deep time.

**Keywords:** Paleoecological networks, Food-web reconstruction, Ecological networks, Extinction dynamics, Trophic interactions, Toarcian Oceanic Anoxic Event

# <sup>1</sup> 1 Introduction

<sup>2</sup> There is growing interest in using deep-time fossil data and evidence of species interactions in past ecosystems  
<sup>3</sup> (e.g., Dunne et al. (2008); Dunne et al. (2014)) as a foundation for understanding how ecological communities  
<sup>4</sup> respond to multi-stressor environmental change, such as temperature increase, ocean acidification, and hypoxia  
<sup>5</sup> (Dillon et al., 2022; Kiessling et al., 2019). Paleoecological networks therefore represent a particularly valuable  
<sup>6</sup> opportunity to investigate community responses to major environmental transitions as they allow for the  
<sup>7</sup> explicit construction of pre- and post-extinction interaction networks and enable the disentangling of extinction  
<sup>8</sup> drivers as well as broader cascading effects (Dunhill et al., 2024; Roopnarine, 2006; Yeakel et al., 2014).  
<sup>9</sup> Insights gained from these deep-time systems provide a critical context for interpreting present day ecological  
<sup>10</sup> change and anticipating the impacts of ongoing anthropogenic stressors (Barnosky et al., 2012; Roopnarine &  
<sup>11</sup> Dineen, 2018).

<sup>12</sup> Inference from ecological networks regarding structure and complexity is (at its core) a mathematical task  
<sup>13</sup> and is therefore relatively independent of biological assumptions (Delmas et al., 2019). While these structural  
<sup>14</sup> properties can be analysed independently of biological detail, their implications for stability and dynamics  
<sup>15</sup> depend critically on assumptions about interaction strengths, and distributions (Allesina & Tang, 2012; Poisot  
<sup>16</sup> et al., 2015). Thus, assumptions become meaningful once network structure and complexity are interpreted in  
<sup>17</sup> functional terms or used as templates for simulating community and extinction dynamics. While there is a well-  
<sup>18</sup> developed theoretical framework describing what can be inferred from network properties, a central challenge  
<sup>19</sup> (particularly in paleoecology) lies in how networks are constructed. Unlike modern systems, paleoecological  
<sup>20</sup> interactions are rarely directly observed, with only exceptional cases preserving explicit evidence of trophic  
<sup>21</sup> interactions (e.g., Jenny et al. (2019); Vullo (2011)). As a result, paleo food web reconstruction depends on  
<sup>22</sup> indirect inference, drawing on preserved traits, analogies with modern taxa, and ecological theory. Simply put,  
<sup>23</sup> network reconstruction is not a data recovery process, but rather hypothesis generation under constraints.

<sup>24</sup> Although numerous tools exist for inferring species interactions (see Morales-Castilla et al., 2015; Pichler  
<sup>25</sup> & Hartig, 2023; Strydom et al., 2021; Allesina et al., 2008 for reviews), only a subset can be reliably  
<sup>26</sup> applied in paleo contexts, where data on traits, abundances, and community composition are incomplete  
<sup>27</sup> and systematically biased. This makes it essential to clearly articulate which reconstruction approaches are  
<sup>28</sup> appropriate for which inferential purposes. Recent work has shown that reconstruction approaches (e.g.,  
<sup>29</sup> models based on traits, abundances, or co-occurrence) can be categorised by the type of network that they  
<sup>30</sup> predict (Strydom et al., 2026). These include feasible networks (derived from trait matching and phylogenetic  
<sup>31</sup> inference that produce metawebs of plausible interactions), realised networks, (constrained by ecological rules  
<sup>32</sup> and evidence of actual feeding relationships), and purely structural networks (which reproduce ecologically

33 plausible topologies but lack species-level node identities). In this sense, food-web reconstructions are not  
34 empirical recoveries of a single past ecosystem, but rather represent alternative, model-based, hypotheses  
35 about interaction structure constrained by the fossil record.

36 Each of these reconstruction approaches carries distinct assumptions that influence inferred network size,  
37 complexity, structure, and node-level properties, with direct consequences for ecological interpretations of  
38 extinction dynamics, stability, resilience, and ecosystem function (Dunne et al., 2002; Gravel et al., 2019;  
39 Roopnarine, 2006; Solé & Montoya, 2001). Despite this, most paleo food web studies default to constructing  
40 networks using expert knowledge (*e.g.*, Dunne et al. (2008)) or mechanistic feeding rules (*e.g.*, Dunhill et al.  
41 (2024); Roopnarine (2017); Fricke et al. (2022)), approaches that typically result in metawebs. This raises a  
42 critical but underexplored question: to what extent does the choice of network type (and particularly the use  
43 of alternatives to metawebs) control not only inferred food web structure but also conclusions about system  
44 behaviour, especially with respect to extinction cascades and vulnerability.

45 In this study, we address this question by explicitly evaluating how network reconstruction model choice  
46 shapes ecological inference in deep time. We link recent advances in food-web reconstruction methods to  
47 a comparative re-evaluation of primary and secondary, trait-based extinction dynamics during the early  
48 Toarcian extinction event, a volcanic-driven hyperthermal and marine crisis in the Early Jurassic (~183 Ma)  
49 (Dunhill et al., 2024). We reconstruct four successive communities (pre-extinction, post-extinction, early  
50 recovery, and late recovery) from the Cleveland Basin of North Yorkshire, UK, using six contrasting network  
51 reconstruction approaches spanning feasible, realised, and structural network representations - as recognised in  
52 recent network inference frameworks (Morales-Castilla et al., 2015; Strydom et al., 2026). For each community,  
53 we compare network-level structure, species-level properties, and inferred interactions across models, allowing  
54 us to assess how reconstruction assumptions propagate into ecological interpretations. Finally, we replicate  
55 the secondary extinction analyses of Dunhill et al. across all six reconstruction methods to explicitly test  
56 how model choice influences inference about extinction drivers, interaction loss, and cascading dynamics. By  
57 explicitly comparing multiple reconstruction approaches within a single paleoecological system, this study  
58 provides a framework for evaluating how methodological assumptions shape interpretations of ancient food-web  
59 structure and dynamics.

## 60 2 Materials and Methods

### 61 2.1 Study system and fossil data

62 We used fossil occurrence data from the Cleveland Basin spanning the upper Pliensbachian to the upper  
63 Toarcian, following Dunhill et al. (2024). Four paleo-communities were defined: pre-extinction, post-extinction,  
64 early recovery, and late recovery. Each assemblage was treated as a community of potentially interacting taxa.  
65 Modes of life were assigned following Dunhill et al. (2024) using the Bambach ecospace framework. Traits  
66 included motility, tiering, feeding mode, and size class, with size defined categorically based on maximum  
67 linear dimensions.

### 68 2.2 Network reconstruction approaches

#### 69 2.2.1 Conceptual classification of network types

70 Most paleo-specific approaches currently operate within the feasibility space (*e.g.*, Shaw et al., 2024; Fricke et  
71 al., 2022; Roopnarine, 2006). Although well suited for reconstructing feasible interactions, these methods  
72 represent only a subset of the broader spectrum of network construction approaches. Here, we present a suite  
73 of models Table 1 that enable the construction of a wider range of ecological networks and the exploration of  
74 a broader set of ecological questions, provided that their underlying assumptions are compatible with the  
75 constraints of fossil data. For example, some tools require quantitative estimates of body size, which must  
76 often be inferred from size classes or functional morphology in the fossil record. Structural models, such  
77 as the niche model, rely only on species richness and connectance, but their species-agnostic nature limits  
78 their applicability to trait-based or diet-specific questions, although they do still accurately recover network  
79 structure (Stouffer et al., 2005). Mechanistic approaches, by contrast, depend on accurate assignment of  
80 feeding traits or robust phylogenetic support. Recognizing how these methodological requirements intersect  
81 with the limits of fossil evidence is essential for selecting an appropriate modelling framework.

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

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

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference	Usage examples
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	realised network	Brose et al. (2006)	
paleo food web inference model (PFIM)	Interactions can be inferred by a mechanistic frame-work/relationships	feeding traits for taxa, mechanistic feeding rules	Assumption made as to the feeding mechanisms, need to elucidate traits from models (although this is a way smaller issue)	feasibility web	Shaw et al. (2024)	Secondary extinctions (Dunhill et al., 2024)

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference	Usage examples
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	realised network	Rohr et al. (2010)	Network collapse (Yeakel et al., 2014)

### 82 2.2.2 Network generation and replication

83 We evaluated six models spanning this space Table 1: random and niche models (structural network); allometric  
 84 diet breadth (ADBM), l-matrix, and body-size ratio models (realised network); and a paleo food-web inference  
 85 model (PFIM; feasibility web). For each community, we constructed 100 replicate networks using each of the  
 86 six models (2 400 networks total). Networks were simplified by removing disconnected species. For size-based  
 87 models, body masses were drawn from uniform distributions bounded by size-class limits, allowing for variance  
 88 between replicates but preserving relative sizes within replicates. Structural models were parameterised using  
 89 connectance values drawn from an empirically realistic ranges (0.07–0.34) while holding richness constant.  
 90 The same parameter draws were used across comparable models within each replicate.

### 91 2.3 Network metrics and structural analyses

92 We quantified network structure using a suite of macro-, meso-, and micro-scale metrics Table 2, capturing  
 93 global properties, motif structure, and species-level variability. Differences among models were assessed using  
 94 MANOVA, followed by univariate ANOVAs, post-hoc comparisons, and linear discriminant analysis. Pairwise  
 95 interaction turnover was quantified using link-based beta diversity for models that infer species-specific  
 96 interactions.

Table 2: Network properties used for analysis.

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

Metric	Definition	Scale	Reference (for maths), can make footnotes probs
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)

## 97 2.4 Extinction simulations and model evaluation

98 Using pre-extinction networks, we simulated species loss under multiple extinction scenarios, including trait-  
 99 based, network-position-based, and random removals, allowing for secondary extinctions. Simulated networks  
 100 were compared to empirical post-extinction communities using mean absolute differences (MAD) in network  
 101 metrics and a modified true skill statistic (TSS) at both node and link levels. Scenario rankings were compared  
 102 across models using Kendall's rank correlation coefficient.

## 103 3 Results

104 Across six reconstruction approaches, both global network structure and species-level interactions differed  
 105 substantially, with implications for interpreting past extinction dynamics. Deterministic models (e.g., PFIM)  
 106 tended to produce more consistent network-level patterns and smoother extinction trajectories, whereas  
 107 stochastic or theory-driven models (e.g., ADBM, niche, L-matrix) showed greater variability in inferred  
 108 interactions and temporal dynamics. Models with similar macro-level metrics sometimes differed in pairwise  
 109 interactions, highlighting that agreement in global structure does not guarantee concordance at the species  
 110 level. Consequently, inferred extinction pathways and secondary extinctions were highly sensitive to model  
 111 choice, emphasizing the importance of evaluating multiple network reconstructions when interpreting ecological  
 112 dynamics in deep time.

113 **3.1 Network structure differs among reconstruction approaches**

114 To test whether network reconstruction approach influences inferred food-web structure, we compared  
115 multivariate patterns of network metrics across all six models using a MANOVA. Network structure differed  
116 strongly among reconstruction approaches (MANOVA, Pillai's trace = 3.81, approximate  $F_{40,11955} = 962.12$ ,  
117  $p < 0.001$ ). Univariate analyses showed that model choice explained a large proportion of variance in most  
118 network metrics, with high partial  $\eta^2$  values for connectance, generality, vulnerability, and motif frequencies  
119 ( $\eta^2 = 0.66\text{--}0.92$ ). In contrast, maximum trophic level exhibited a much smaller effect of model choice ( $\eta^2 =$   
120 0.04). Estimated marginal means and Tukey-adjusted comparisons indicated consistent differences among  
121 reconstruction approaches, with PFIM differing significantly from all other models ( $p = 0.026$ ), while ADBM  
122 and L-matrix did not differ from one another ( $p = 1.00$ ). Linear discriminant analysis (LDA) further  
123 distinguished reconstruction approaches in multivariate network space Figure 1, with the first two axes  
124 explaining 86.5% of between-model variance (LD1 = 53.9%, LD2 = 32.6%). LD1 was most strongly correlated  
125 with vulnerability, connectance, and S4 motifs, whereas LD2 was associated primarily with generality, S2, and  
126 S5 motifs. Higher-order axes each explained less than 9% of the remaining variance. This demonstrates that  
127 reconstruction approach leaves a strong multivariate signature independent of community composition.

128 [Figure 1 about here.]

129 **3.1.1 Inferred pairwise interactions vary widely among models**

130 Building on differences in global network structure, we next examined how reconstruction approach influences  
131 species-level ecological inference by quantifying turnover in inferred pairwise interactions among networks  
132 constructed from the same taxon pool. While models that produced similar global metrics sometimes agreed  
133 broadly on network structure, they often differed sharply in the specific interactions they inferred.

134 Pairwise -turnover revealed that some model pairs shared very few links despite comparable macro- or  
135 meso-scale properties Figure 2. ADBM and L-matrix were highly concordant, reflecting similar underlying  
136 assumptions, whereas the body-size ratio model consistently exhibited high turnover relative to all other  
137 approaches. PFIM showed intermediate overlap with size-based theoretical models. These patterns indicate  
138 that agreement in global network metrics does not guarantee agreement in species-level diets or trophic  
139 roles, highlighting the importance of evaluating both network- and species-level outcomes when comparing  
140 reconstruction methods.

141 [Figure 2 about here.]

142 **3.2 Model choice influences inferred extinction dynamics**

143 To quantify how network structure changed over time during extinction simulations and whether these  
144 dynamics differed among reconstruction models, we fit generalized additive models (GAMs) to network-level  
145 metrics. GAMs capture nonlinear temporal trajectories, allowing formal tests of whether the shape of these  
146 trajectories differs among models. For connectance, the model-specific smooth terms were all significant (e.g.,  
147 PFIM: EDF = 2.99, F = 113.8, p < 0.001; ADBM: EDF = 2.92, F = 22.6, p < 0.001), indicating distinct  
148 temporal patterns across reconstruction approaches. Trophic level trajectories also differed among models  
149 (PFIM: EDF = 2.96, F = 36.7, p < 0.001; Niche: EDF = 2.96, F = 94.9, p < 0.001). Deterministic approaches,  
150 such as PFIM, produced more consistent and smooth trajectories, whereas stochastic, theory-driven models  
151 (niche, ADBM, L-matrix) displayed greater variability in timing and magnitude of structural change. These  
152 results demonstrate that inferred pathways of collapse, trophic bottlenecks, and secondary extinctions are  
153 highly sensitive to model choice.

154 To evaluate how model choice affects inferred extinction dynamics, we compared simulated post-extinction  
155 networks to observed networks using mean absolute differences (MAD) for network-level metrics and total  
156 sum-of-squares (TSS) for node- and link-level outcomes Figure 3. Overall, models were more consistent in  
157 ranking extinction scenarios at the network level: Kendall's  $\tau$  values for MAD-based rankings were generally  
158 positive, with strong agreement between ADBM and L-matrix models ( $\tau$  0.82) and weaker or inconsistent  
159 correlations involving stochastic models such as log ratio or random ( $\tau$  ranging from -0.26 to 0.44). Node-level  
160 TSS scores similarly showed broad consistency across models, reflecting comparable species removal sequences  
161 ( $\tau$  0.38–0.46 between ADBM and niche or PFIM). In contrast, link-level outcomes were more variable:  
162 deterministic models like PFIM maintained moderate agreement with observed post-extinction links ( $\tau$  0.44),  
163 whereas stochastic, theory-driven models exhibited low or inconsistent correlations ( $\tau$  as low as -0.44). These  
164 results indicate that while different models often recover similar species-level extinction patterns, inferred  
165 interaction loss and cascade dynamics are highly sensitive to model choice.

166 [Figure 3 about here.]

167 **4 Discussion**

168 **5 Model choice as a component of ecological inference**

169 Reconstructing food webs from fossil data is inherently an exercise in inference under uncertainty, where  
170 ecological conclusions depend as much on modelling assumptions as on preserved evidence (Dunne et al., 2008;

<sup>171</sup> Morales-Castilla et al., 2015). Our results demonstrate that the choice of network reconstruction model is  
<sup>172</sup> itself a major ecological decision, shaping not only the structural properties of inferred networks but also  
<sup>173</sup> downstream interpretations of extinction dynamics (Allesina & Tang, 2012; Solé & Montoya, 2001). Even with  
<sup>174</sup> identical taxon pools, different models yield networks that diverge in global metrics, species-level interactions,  
<sup>175</sup> and temporal patterns of collapse. These divergences do not stem from differences in fossil evidence or taxon  
<sup>176</sup> composition, but from the assumptions embedded within each reconstruction approach (Pichler & Hartig,  
<sup>177</sup> 2023; Strydom et al., 2021). Consequently, network reconstruction is not a neutral methodological step; model  
<sup>178</sup> choice shapes the ecological narratives we extract from ancient ecosystems.

<sup>179</sup> While previous studies have emphasized the role of model assumptions in metaweb reconstruction (Dunhill  
<sup>180</sup> et al., 2024; Roopnarine, 2006), our results demonstrate that these assumptions create distinct, predictable  
<sup>181</sup> clusters of network properties. These clusters map directly onto the conceptual divide between feasible,  
<sup>182</sup> realised, and structural network types (Strydom et al., 2026). Specifically, mechanistic models (PFIM) identify  
<sup>183</sup> a broad landscape of trait-compatible interactions, theoretical models (ADBM, L-matrix) impose energetic  
<sup>184</sup> filters to approximate realised energy flow, and structural models (niche, random) prioritise topological  
<sup>185</sup> patterns over species identity. Our pairwise turnover analysis confirms that these differences are not merely  
<sup>186</sup> quantitative; models fundamentally disagree on link identity, reinforcing concerns that traditional metawebs  
<sup>187</sup> may significantly overestimate realised interaction diversity (Fricke et al., 2022; Shaw et al., 2024). This  
<sup>188</sup> distinction is central to paleoecological inference, where feasible interactions are often mistaken for realised  
<sup>189</sup> trophic relationships.

<sup>190</sup> The downstream consequences of model choice are most pronounced when evaluating extinction dynamics  
<sup>191</sup> (Dunne et al., 2002; Sahasrabudhe & Motter, 2011). While broad, trait-driven patterns of species loss are  
<sup>192</sup> relatively robust across models, the identity of lost interactions, secondary extinctions, and cascade dynamics  
<sup>193</sup> are sensitive to the type of network reconstructed. Node-level patterns tend to be more consistent across models  
<sup>194</sup> because they primarily reflect intrinsic species traits, whereas link-level outcomes are emergent properties of  
<sup>195</sup> model assumptions. This distinction mirrors findings in modern food-web studies, where deterministic and  
<sup>196</sup> stochastic model assumptions influence the magnitude and timing of secondary extinctions (Allesina & Tang,  
<sup>197</sup> 2012; Curtsdotter et al., 2011; Dunne et al., 2002; Yeakel et al., 2014). Our results suggest that interpretations  
<sup>198</sup> of trophic collapse, bottlenecks, and recovery trajectories are shaped not only by the fossil record but also by  
<sup>199</sup> the choice of network model. Consequently, paleoecologists must carefully consider which ecological signals  
<sup>200</sup> they aim to recover (potential interactions, realized diets, or macro-scale structural properties) before selecting  
<sup>201</sup> a reconstruction approach. Importantly, disagreement among models does not imply that any single approach  
<sup>202</sup> is ‘wrong’, but rather reflects the fact that different models capture different ecological signals (Stouffer, 2019).

<sup>203</sup> The challenge therefore lies not in identifying a universally correct model, but rather in aligning model choice  
<sup>204</sup> with the ecological question being asked.

## <sup>205</sup> 5.1 Aligning ecological questions with model choice

<sup>206</sup> A central insight from our study is that different ecological questions require different network representations.  
<sup>207</sup> Feasibility networks are most appropriate for evaluating potential trophic links or dietary breadth; realised  
<sup>208</sup> networks capture energetically constrained, ecologically plausible interactions; and structural networks are  
<sup>209</sup> suited for exploring generic topological patterns such as connectance or trophic depth. Link-level dynamics  
<sup>210</sup> and cascade sensitivity are particularly sensitive to network choice, whereas higher-level patterns of species  
<sup>211</sup> loss are less so.

<sup>212</sup> This alignment between question and model type reflects a broader trend in network ecology emphasizing  
<sup>213</sup> the role of assumptions in determining which inferences are valid (Delmas et al., 2019; Petchey et al., 2008;  
<sup>214</sup> Schneider et al., 2016). By explicitly matching network representation to research question, paleoecologists  
<sup>215</sup> can avoid overinterpreting model-dependent artifacts as biological signals.

<sup>216</sup> Below is a conceptual summary:

Ecological question	Recommended network type	Rationale
What <i>could</i> have eaten what? (feasible interactions; trophic potential)	Feasibility web (PFIM, trait-based, evolutionary-signal models)	Captures all trait-feasible links; appropriate for reconstructing dietary breadth or assessing potential niches.
What interactions were <i>likely realised</i> ?	Realised network (ADBM, l-matrix)	Encodes foraging ecology and energetic constraints; provides ecologically plausible ‘realised’ networks.
How do global macro structural properties vary?	Structural network (niche, random as baseline)	Useful for understanding generic patterns (connectance, trophic depth) without trait reliance.
How do traits influence dynamics (e.g., cascade sensitivity)?	Realised network	Capture body-size scaling, energetic constraints, and trophic dependencies.

<b>Ecological question</b>	<b>Recommended network type</b>	<b>Rationale</b>
How robust are inferences to uncertainty?	Ensembles across multiple network types	Allows quantifying how conclusions depend on assumptions.

## 217 **5.2 Implications for paleoecological network studies**

218 Our analysis underscores three important implications for the broader field:

- 219 1. **Interpretations of ancient food webs must explicitly acknowledge model assumptions:** Without this, differences in reconstructed networks may be mistakenly attributed to biological change rather than methodological artifacts.
- 220 2. **Comparisons across studies must be standardised by model family:** Comparing a metaweb from one study to a realised network from another risks generating misleading conclusions about ecological differences across space or time.
- 221 3. **Integrating theory-driven models expands inference:** Mechanistic paleo-specific models alone capture only a subset of feasible networks. Incorporating modern theory-based approaches allows researchers to explore alternative network archetypes, extending the range of questions that can be addressed (Dunne et al., 2014; Solé & Montoya, 2001).

## 229 **5.3 Recommendations for network reconstruction in paleoecology**

230 To support consistent, transparent use of network reconstruction methods in paleoecology, we propose the  
231 following guidelines :

- 232 1. **Establish the Inferential Goal First:** Explicitly define whether the study aims to capture potential interactions (feasibility), energetic flows (realised), or global patterns (structural). This choice dictates the appropriate model family and prevents the common error of treating metawebs as local diet realisations.
- 233 2. **Implement an Ensemble Modelling Framework:** Rather than just using multiple models, advocate for an ensemble approach. Evaluating a suite of models allows researchers to quantify model uncertainty identifying which ecological conclusions are robust biological signals and which are methodological artifacts.

240     **3. Standardise Comparative Analyses:** To avoid misleading comparisons across studies, researchers  
241       should only compare networks constructed within the same model family. If comparing a new metaweb  
242       to a published realised web, the differences must be explicitly attributed to the representation gap rather  
243       than environmental change.

244     **4. Prioritize Scale-Specific Interpretation:** Distinguish clearly between node- and link-level results.  
245       Since node-level patterns (who goes extinct) are generally more robust to model choice, they can be  
246       interpreted with higher confidence than specific link-level pathways (the exact cascade route), which are  
247       highly sensitive to model assumptions.

## 248     6 Conclusions

249     Ecological network reconstruction in deep time is not merely a technical step but a fundamental component  
250       of ecological inference. By explicitly comparing six contrasting reconstruction approaches within a single  
251       extinction event and location we show that model choice strongly shapes inferred food-web structure, species  
252       interactions, and extinction dynamics, even when underlying fossil data are identical. While broad, trait-based  
253       patterns of species loss appear relatively robust, conclusions about pairwise interactions, secondary extinctions,  
254       and cascading dynamics depend critically on the assumptions embedded in the chosen network reconstruction  
255       approach. These results underscore the need for paleoecological studies to align reconstruction methods  
256       with specific ecological questions and to evaluate the sensitivity of key conclusions to alternative network  
257       representations. More broadly, our findings highlight that understanding past ecosystem collapse requires not  
258       only better fossil data, but also transparent, question-driven modelling frameworks that make explicit the  
259       assumptions underlying ecological inference.

## 260     References

- 261     Allesina, S., Alonso, D., & Pascual, M. (2008). A general model for food web structure. *Science*, 320(5876),  
262       658–661. <https://doi.org/10.1126/science.1156269>
- 263     Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483(7388), 205–208.  
264       <https://doi.org/10.1038/nature10832>
- 265     Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte,  
266       J., Hastings, A., Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J.  
267       W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., ... Smith, A. B. (2012). Approaching a state shift in  
268       earth's biosphere. *Nature*, 486(7401), 52–58. <https://doi.org/10.1038/nature11018>

- 269 Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey,  
270 T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith,  
271 S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., ... Cohen, J. E. (2006). Consumer–resource  
272 body-size relationships in natural food webs. *Ecology*, 87(10), 2411–2417. [https://doi.org/https://doi.org/10.1890/0012-9658\(2006\)87%5B2411:CBRINF%5D2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2006)87%5B2411:CBRINF%5D2.0.CO;2)
- 273
- 274 Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A., & Rall,  
275 B. C. (2011). Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and  
276 dynamic food webs. *Basic and Applied Ecology*, 12(7), 571–580. <https://doi.org/10.1016/j.baae.2011.09.008>
- 277 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,  
278 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).  
279 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111;brv.12433>
- 280
- 281 Dillon, E. M., Pier, J. Q., Smith, J. A., Raja, N. B., Dimitrijević, D., Austin, E. L., Cybulski, J. D., De  
282 Entrambasaguas, J., Durham, S. R., Grether, C. M., Haldar, H. S., Kocáková, K., Lin, C.-H., Mazzini, I.,  
283 Mychajliw, A. M., Ollendorf, A. L., Pimiento, C., Regalado Fernández, O. R., Smith, I. E., & Dietl, G. P.  
284 (2022). What is conservation paleobiology? Tracking 20 years of research and development. *Frontiers in  
285 Ecology and Evolution*, 10. <https://doi.org/10.3389/fevo.2022.1031483>
- 286 Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).  
287 Extinction cascades, community collapse, and recovery across a mesozoic hyperthermal event. *Nature  
288 Communications*, 15(1), 8599. <https://doi.org/10.1038/s41467-024-53000-2>
- 289 Dunne, J. A., Labandeira, C. C., & Williams, R. J. (2014). Highly resolved early eocene food webs show  
290 development of modern trophic structure after the end-cretaceous extinction. *Proceedings of the Royal  
291 Society B: Biological Sciences*, 281(1782), 20133280. <https://doi.org/10.1098/rspb.2013.3280>
- 292 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and network  
293 analyses of cambrian food webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 294 Dunne, J., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs:  
295 Robustness increases with connectance. *Ecol. Lett.*, 5(4), 558–567.
- 296 Erdős, P., & Rényi, A. (1959). On random graphs. i. *Publicationes Mathematicae Debrecen*, 6(3-4), 290–297.  
297 <https://doi.org/10.5486/pmd.1959.6.3-4.12>
- 298 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,  
299 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the late pleistocene. *Science*,  
300 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 301 Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B.,

- 302 Tylianakis, J. M., Wood, S. A., & Roslin, T. (2019). Bringing elton and grinnell together: A quantitative  
303 framework to represent the biogeography of ecological interaction networks. *Ecography*, 42(3), 401–415.  
304 [https://doi.org/https://doi.org/10.1111/ecog.04006](https://doi.org/10.1111/ecog.04006)
- 305 Jenny, D., Fuchs, D., Arkhipkin, A. I., Hauff, R. B., Fritschi, B., & Klug, C. (2019). Predatory behaviour  
306 and taphonomy of a jurassic belemnoid coleoid (diplobelida, cephalopoda). *Scientific Reports*, 9(1), 7944.  
307 <https://doi.org/10.1038/s41598-019-44260-w>
- 308 Kiessling, W., Raja, N. B., Roden, V. J., Turvey, S. T., & Saupe, E. E. (2019). Addressing priority questions  
309 of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B:  
310 Biological Sciences*, 374(1788), 20190222. <https://doi.org/10.1098/rstb.2019.0222>
- 311 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple  
312 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.<br/>313 5594.824)
- 314 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from  
315 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 316 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure.  
317 *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. [https://doi.org/10.1073/pnas.0710672105](https://doi.org/10.1073/pnas.<br/>318 0710672105)
- 319 Pichler, M., & Hartig, F. (2023). Machine learning and deep learning—a review for ecologists. *Methods in  
320 Ecology and Evolution*, 14(4), 994–1016. <https://doi.org/10.1111/2041-210X.14061>
- 321 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
322 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 323 Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring  
324 unexplained structure using latent traits. *The American Naturalist*, 176(2), 170–177. [https://doi.org/10.1086/653667](https://doi.org/10.<br/>325 1086/653667)
- 326 Roopnarine, P. D. (2017). *Ecological modelling of paleocommunity food webs* (pp. 201–226). University of  
327 Chicago Press.
- 328 Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32(1),  
329 1–19. <https://www.jstor.org/stable/4096814>
- 330 Roopnarine, P. D., & Dineen, A. A. (2018). *Coral reefs in crisis: The reliability of deep-time food web  
331 reconstructions as analogs for the present* (C. L. Tyler & C. L. Schneider, Eds.; pp. 105–141). Springer  
332 International Publishing. [https://doi.org/10.1007/978-3-319-73795-9\\_6](https://doi.org/10.1007/978-3-319-73795-9_6)
- 333 Sahasrabudhe, S., & Motter, A. E. (2011). Rescuing ecosystems from extinction cascades through compensatory  
334 perturbations. *Nature Communications*, 2(1), 170. <https://doi.org/10.1038/ncomms1163>

- 335 Schneider, F. D., Brose, U., Rall, B. C., & Guill, C. (2016). Animal diversity and ecosystem functioning in  
336 dynamic food webs. *Nature Communications*, 7(1), 12718. <https://doi.org/10.1038/ncomms12718>
- 337 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*  
338 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 340 Solé, R. V., & Montoya, M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal*  
341 *Society of London. Series B: Biological Sciences*, 268(1480), 2039–2045. <https://doi.org/10.1098/rspb.2001.1767>
- 343 Stouffer, D. B., Camacho, J., Guimerà, R., Ng, C. A., & Nunes Amaral, L. A. (2005). Quantitative patterns  
344 in the structure of model and empirical food webs. *Ecology*, 86(5), 1301–1311. <https://doi.org/10.1890/04-0957>
- 346 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*,  
347 88(2), 192–195. [https://doi.org/https://doi.org/10.1111/1365-2656.12949](https://doi.org/10.1111/1365-2656.12949)
- 348 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust  
349 pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621),  
350 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>
- 351 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
352 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
353 towards predicting species interaction networks (across space and time). *Philosophical Transactions of the*  
354 *Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 355 Strydom, T., Dunhill, A. M., Dunne, J. A., Poisot, T., & Beckerman, A. P. (2026). Scaling from metawebs  
356 to realised webs: A hierarchical approach to network ecology. *EcoEvoRxiv*. <https://doi.org/10.32942/X2JW8K>
- 358 Vullo, R. (2011). Direct evidence of hybodont shark predation on late jurassic ammonites. *Naturwissenschaften*,  
359 98(6), 545–549. <https://doi.org/10.1007/s00114-011-0789-9>
- 360 Williams, R. J., & Martinez, N. D. (2004). Stabilization of chaotic and non-permanent food-web dynamics.  
361 *The European Physical Journal B - Condensed Matter*, 38(2), 297–303. <https://doi.org/10.1140/epjb/e2004-00122-1>
- 363 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.  
364 <https://doi.org/10.1038/35004572>
- 365 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food  
366 webs. *The Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 367 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T.

<sup>368</sup> (2014). Collapse of an ecological network in ancient egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>

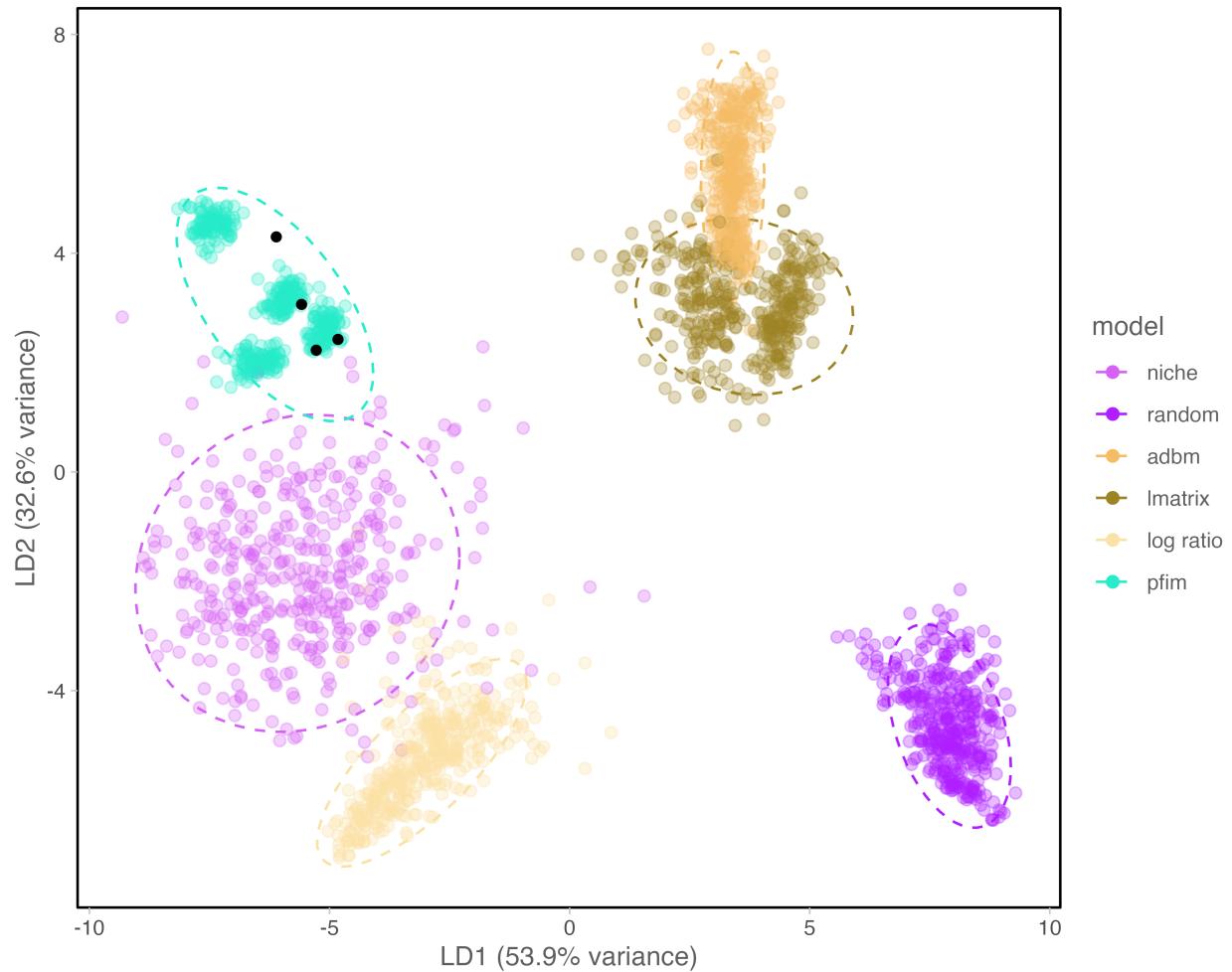


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

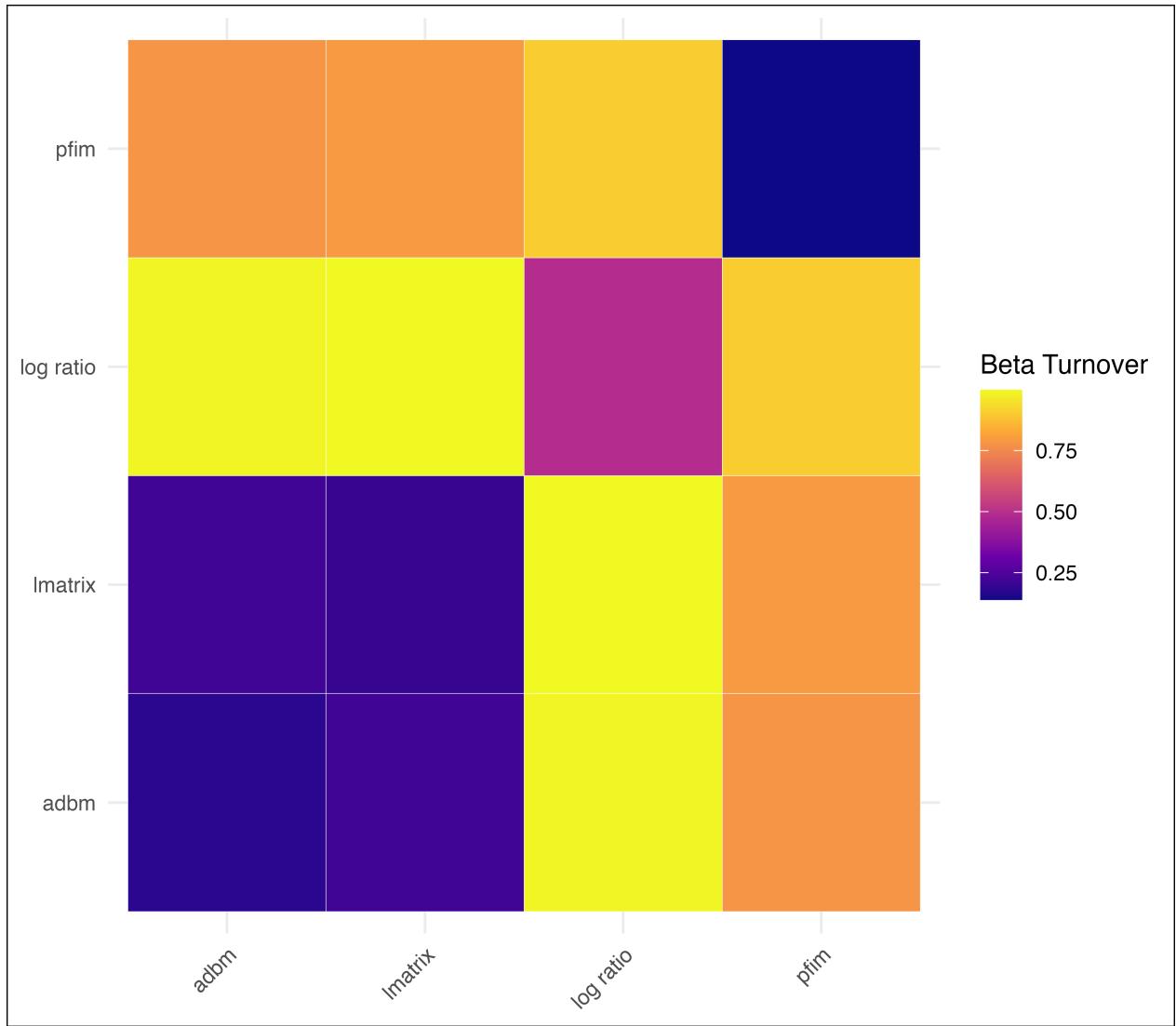
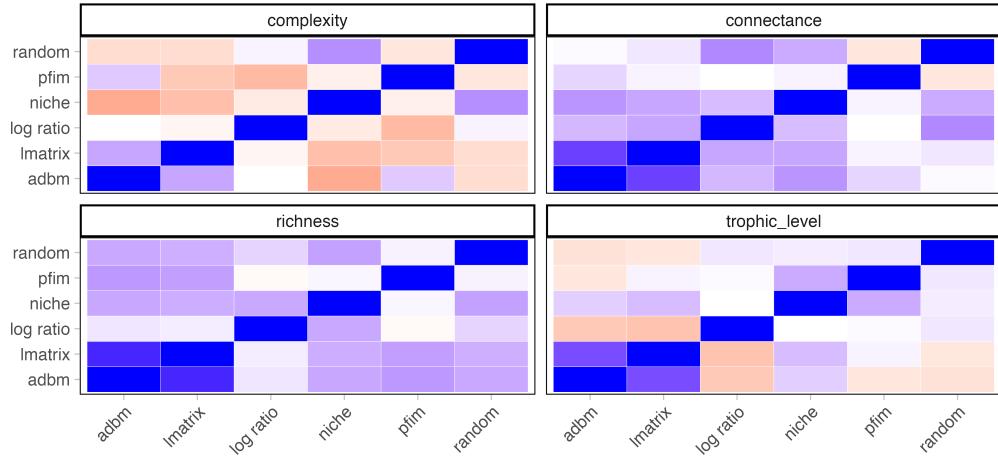
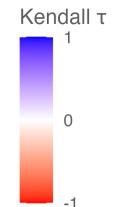
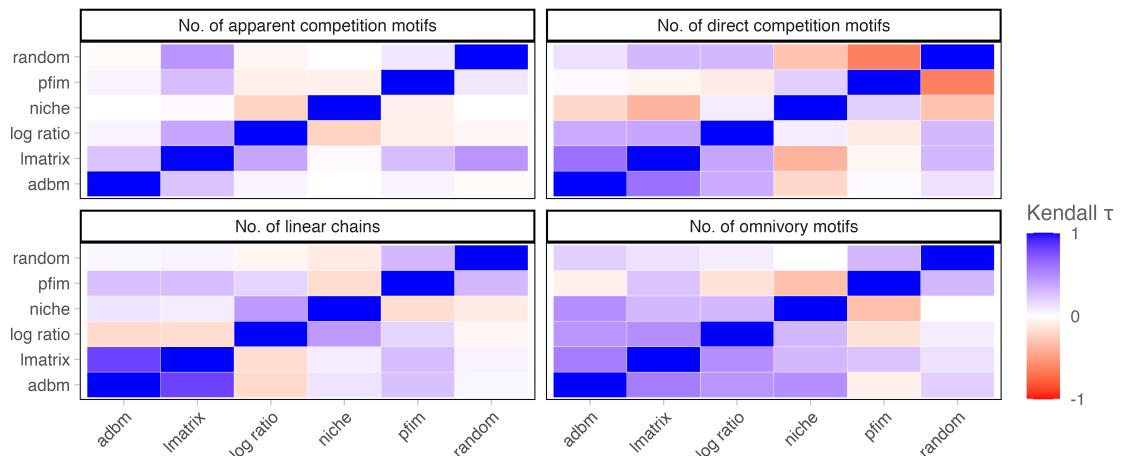


Figure 2: Pairwise beta turnover in species interactions among four ecological network models (ADBm, lmatrix, body-size ratio, and pfim). Each cell represents the mean turnover value between a pair of models, with warmer colors indicating greater dissimilarity in inferred interactions. The diagonal is omitted. High turnover values (yellow) indicate strong disagreement in network structure between models, whereas lower values (blue–purple) indicate greater similarity.

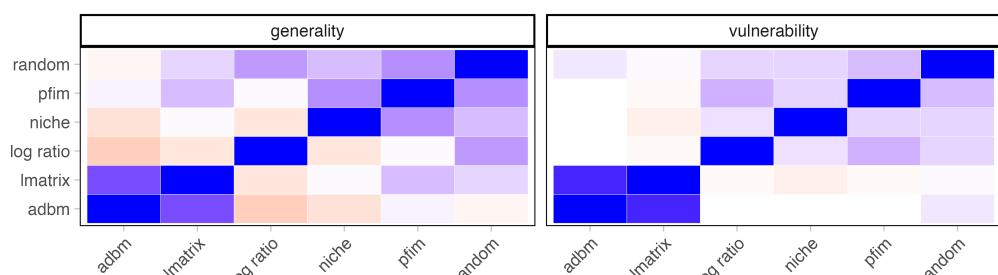
### Macro



### Meso



### Micro



### TSS

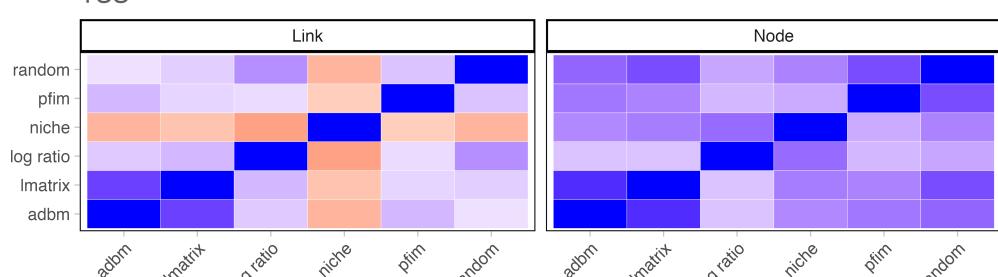


Figure 3: Heatmaps showing pairwise Kendall rank correlation coefficients ( $\tau$ ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between observed and predicted network values. Positive  $\tau$  values (blue) indicate concordant rankings between models, whereas negative  $\tau$  values (red) indicate opposing rankings. Warmer colours approaching zero represent little or no agreement. Panels