

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

Tanya Strydom <sup>1</sup>; Baran Karapunar <sup>2</sup>; Andrew P. Beckerman <sup>1</sup>; Alexander Dunhill <sup>2</sup>

**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 the distribution and strength of interaction (Allesina & Tang, 2012;  
<sup>16</sup> Poisot et al., 2015). Thus, assumptions become meaningful once network structure and complexity are  
<sup>17</sup> interpreted in functional terms or used as templates for simulating community and extinction dynamics. While  
<sup>18</sup> there is a well-developed theoretical framework describing what can be inferred from network properties,  
<sup>19</sup> a central challenge (particularly in paleoecology) lies in how networks are constructed. Unlike modern  
<sup>20</sup> systems, paleoecological interactions are rarely directly observed, with only exceptional cases preserving  
<sup>21</sup> explicit evidence of trophic interactions (*e.g.*, Jenny et al. (2019); Vullo (2011)). As a result, paleo food web  
<sup>22</sup> reconstruction depends on indirect inference, drawing on preserved traits, analogies with modern taxa, and  
<sup>23</sup> ecological theory. Simply put, network reconstruction is not a data recovery process, but rather hypothesis  
<sup>24</sup> generation under constraints.

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

33 and evidence of actual feeding relationships), and purely structural networks (which reproduce ecologically  
34 plausible topologies but lack species-level node identities). In this sense, food-web reconstructions are not  
35 empirical recoveries of a single past ecosystem, but rather represent alternative, model-based, hypotheses  
36 about interaction structure constrained by the fossil record.

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

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

## 61 2 Materials and Methods

### 62 2.1 Study system and fossil data

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

### 69 2.2 Network reconstruction approaches

#### 70 2.2.1 Conceptual classification of network types

71 Most paleo-specific approaches currently operate within the feasibility space (*e.g.*, Shaw et al., 2024; Fricke et  
72 al., 2022; Roopnarine, 2006). Although well suited for reconstructing feasible interactions, these methods  
73 represent only a subset of the broader spectrum of network construction approaches. Here, we present a suite  
74 of models (Table 1) that enable the construction of a wider range of ecological networks and the exploration  
75 of a broader set of ecological questions, provided that their underlying assumptions are compatible with  
76 the constraints of fossil data. For example, some tools require quantitative estimates of body size, which  
77 must often be inferred from size classes or functional morphology in the fossil record. Structural models,  
78 such as the niche model, rely only on species richness and estimates/specification of connectance, but their  
79 species-agnostic nature limits their applicability to trait-based or diet-specific questions, although they do still  
80 accurately recover network structure (Stouffer et al., 2005) . Mechanistic approaches, by contrast, depend on  
81 accurate assignment of feeding traits or robust phylogenetic support. Recognizing how these methodological  
82 requirements intersect with the limits of fossil evidence is essential for selecting an appropriate modelling  
83 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                               |
|---------------------------------------|---|--|---|------------------|--|--|
| Allometric trophic network (ATN)      | 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); Gauzens et al. (2023) |  |
| 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) |

#### <sup>84</sup> 2.2.2 Network generation and replication

<sup>85</sup> We evaluated six models spanning this space Table 1: random and niche models (structural network); allometric  
<sup>86</sup> diet breadth (ADBM), allometric trophic network (ATN), and body-size ratio models (realised network);  
<sup>87</sup> and a paleo food-web inference model (PFIM; feasibility web). More details on parameters can be found  
<sup>88</sup> in the Supplementary Materials. For each of the four communities, we constructed 100 replicate networks  
<sup>89</sup> using each of the six models (2400 networks total). Networks were simplified by removing disconnected  
<sup>90</sup> species. For size-based models, body masses were drawn from uniform distributions bounded by size-class  
<sup>91</sup> limits, allowing for variance between replicates but preserving relative sizes within replicates. Structural  
<sup>92</sup> models were parameterised using connectance values drawn from an empirically realistic range (0.07 – 0.34)  
<sup>93</sup> while holding richness constant. The same parameter draws were used across comparable models within each  
<sup>94</sup> replicate.

### 95 2.3 Network metrics and structural analyses

96 We quantified network structure using a suite of macro-, meso-, and micro-scale metrics Table 2, capturing  
 97 global properties, motif structure, and species-level variability. Differences among models were assessed using  
 98 MANOVA, followed by univariate ANOVAs, post-hoc comparisons, and linear discriminant analysis. Pairwise  
 99 interaction turnover was quantified using link-based beta diversity for models that infer species-specific  
 100 interactions (Poisot et al., 2012)

Table 2: Network properties used for analysis.

| Metric            | Definition  | Scale | Reference (for maths),<br>can make footnotes<br>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),<br>can make footnotes<br>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)                            |

## 101 2.4 Extinction simulations and model evaluation

102 Following Dunhill et al. (2024) and using the pre-extinction and post-extinction networks, we simulated  
 103 species loss under multiple extinction scenarios, including trait-based, network-position-based, and random  
 104 removals, allowing for secondary extinctions. Simulated post-extinction networks were compared to empirical  
 105 post-extinction communities using mean absolute differences (MAD) in network metrics and a modified true  
 106 skill statistic (TSS) at both node and link levels. Scenario rankings were compared across models using  
 107 Kendall's rank correlation coefficient.

## 108 3 Results

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

118 **3.1 Network structure differs among reconstruction approaches**

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

134 [Figure 1 about here.]

135 **3.1.1 Inferred pairwise interactions vary widely among models**

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

140 Pairwise -turnover revealed that some model pairs shared very few links despite comparable macro- or  
141 meso-scale properties Figure 2. ADBM and ATN were highly concordant, reflecting similar underlying  
142 assumptions despite different generative rules, whereas the body-size ratio model consistently exhibited high  
143 differences in pairwise interactions relative to all other approaches. PFIM showed intermediate overlap with  
144 size-based theoretical models. These patterns indicate that agreement in global network metrics does not  
145 guarantee agreement in species-level diets or trophic roles, highlighting the importance of evaluating both  
146 network- and species-level outcomes when comparing reconstruction methods.

147 [Figure 2 about here.]

<sup>148</sup> **3.2 Model choice influences inferred extinction dynamics**

<sup>149</sup> To quantify how network structure changed over time during extinction simulations and whether these  
<sup>150</sup> dynamics differed among reconstruction models, we fit generalized additive models (GAMs) to time series of  
<sup>151</sup> network-level metrics. GAMs capture nonlinear temporal trajectories, allowing formal tests of whether the  
<sup>152</sup> shape of these trajectories differs among models. These model-specific temporal trajectories are shown in  
<sup>153</sup> Figure 3. For connectance, the model-specific smooth terms were all significant (*e.g.*, PFIM: EDF = 2.99, F  
<sup>154</sup> = 113.8,  $p < 0.001$ ; ADBM: EDF = 2.92, F = 22.6,  $p < 0.001$ ), indicating distinct temporal patterns across  
<sup>155</sup> reconstruction approaches. Trophic level trajectories also differed among models (PFIM: EDF = 2.96, F =  
<sup>156</sup> 36.7,  $p < 0.001$ ; Niche: EDF = 2.96, F = 94.9,  $p < 0.001$ ). Deterministic approaches, such as PFIM, produced  
<sup>157</sup> more consistent and smooth trajectories, whereas stochastic, theory-driven models (niche, ADBM, ATN)  
<sup>158</sup> displayed greater variability in timing and magnitude of structural change. These results demonstrate that  
<sup>159</sup> inferred pathways of collapse, trophic bottlenecks, and secondary extinctions are highly sensitive to model  
<sup>160</sup> choice. Corresponding raw temporal trajectories are shown in Fig. S3.

<sup>161</sup> [Figure 3 about here.]

<sup>162</sup> To evaluate how model choice affects inferred extinction dynamics, we compared simulated post-extinction  
<sup>163</sup> networks to observed networks using mean absolute differences (MAD) for network-level metrics and total  
<sup>164</sup> sum-of-squares (TSS) for node- and link-level outcomes Figure 4. Overall, models were more consistent in  
<sup>165</sup> ranking extinction scenarios at the network level: Kendall's  $\tau$  values for MAD-based rankings were generally  
<sup>166</sup> positive, with strong agreement between ADBM and ATN models ( $\tau = 0.82$ ) and weaker or inconsistent  
<sup>167</sup> correlations involving stochastic models such as log ratio or random ( $\tau$  ranging from -0.26 to 0.44). Node-level  
<sup>168</sup> TSS scores similarly showed broad consistency across models, reflecting comparable species removal sequences  
<sup>169</sup> ( $\tau = 0.38\text{--}0.46$  between ADBM and niche or PFIM). In contrast, link-level outcomes were more variable:  
<sup>170</sup> deterministic models like PFIM maintained moderate agreement with observed post-extinction links ( $\tau = 0.44$ ),  
<sup>171</sup> whereas stochastic, theory-driven models exhibited low or inconsistent correlations ( $\tau$  as low as -0.44). These  
<sup>172</sup> results indicate that while different models often recover similar species-level extinction patterns, inferred  
<sup>173</sup> interaction loss and cascade dynamics are highly sensitive to model choice.

<sup>174</sup> [Figure 4 about here.]

<sub>175</sub> **4 Discussion**

<sub>176</sub> **5 Model choice as a component of ecological inference**

<sub>177</sub> Reconstructing food webs from fossil data is inherently an exercise in inference under uncertainty. It involves  
<sub>178</sub> not only assembling data but also making explicit assumptions about how species interact and how those  
<sub>179</sub> interactions are represented mathematically (Dunne et al., 2008; Morales-Castilla et al., 2015; Strydom et  
<sub>180</sub> al., 2026). This process has parallels in modern ecological network studies, where the tension between data  
<sub>181</sub> limitations and the goal of meaningful ecological inference is well recognised (Delmas et al., 2019; Poisot et  
<sub>182</sub> al., 2021). Results demonstrate that the choice of network reconstruction model is itself a major ecological  
<sub>183</sub> decision, shaping not only the structural properties of inferred networks but also downstream interpretations  
<sub>184</sub> of extinction dynamics (Allesina & Tang, 2012; Solé & Montoya, 2001).

<sub>185</sub> These differences arise not from the fossil evidence per se, but from the assumptions embedded in each model  
<sub>186</sub> family (Pichler & Hartig, 2023; Strydom et al., 2021), such as how trophic links are defined (trait compatibility  
<sub>187</sub> versus energetic constraints), how interaction probability is parameterised, and whether network topology is  
<sub>188</sub> informed by macroecological theory (*e.g.*, niche structure) or by mechanistic rules (*e.g.*, body-size ratios).  
<sub>189</sub> Consequently, network reconstruction is not a neutral methodological step; model choice shapes the ecological  
<sub>190</sub> narratives we extract from ancient ecosystems. This sensitivity mirrors challenges faced in modern network  
<sub>191</sub> ecology, where the choice of model and metric influences the interpretation of patterns such as connectance,  
<sub>192</sub> modularity, or motif distributions (Michalska-Smith & Allesina, 2019; Poisot & Gravel, 2014) .

<sub>193</sub> While previous studies have emphasized the role of model assumptions in metaweb reconstruction (Dunhill  
<sub>194</sub> et al., 2024; Roopnarine, 2006), our results demonstrate that these assumptions create distinct, predictable  
<sub>195</sub> clusters of network properties. These clusters map directly onto the conceptual divide between feasible,  
<sub>196</sub> realised, and structural network types (Strydom et al., 2026). Specifically, mechanistic models (PFIM) identify  
<sub>197</sub> a broad landscape of trait-compatible interactions, theoretical models (ADBM, ATN) impose energetic filters  
<sub>198</sub> to approximate realised energy flow, and structural models (niche, random) prioritise topological patterns  
<sub>199</sub> over species identity.

<sub>200</sub> Pairwise -turnover analysis underscores that disagreements among reconstruction approaches are not merely  
<sub>201</sub> quantitative differences in metrics, but qualitative differences in the identity of inferred interactions. Models  
<sub>202</sub> that may produce similar aggregate properties (*e.g.*, connectance) can still disagree strongly on species-level  
<sub>203</sub> diets and trophic roles. This reinforces concerns raised in both paleoecological and modern studies that  
<sub>204</sub> metrics alone can mask substantive differences in network structure and function (Fricke et al., 2022; Shaw et

205 al., 2024).

206 The implications of these differences are most pronounced when interpreting extinction dynamics (Dunne  
207 et al., 2002; Sahasrabudhe & Motter, 2011). While broad, trait-driven patterns of species loss are relatively  
208 robust across models, the identity of lost interactions, secondary extinctions, and cascade dynamics are  
209 sensitive to the type of network reconstructed. Node-level patterns of species loss (such as which taxa are  
210 more likely to go extinct under certain scenarios) tend to be relatively robust across models, likely because  
211 they reflect consistent trait-based vulnerabilities. However, inferred link-level outcomes vary markedly with  
212 reconstruction assumptions as extinctions are determined by network structure, *i.e.*, are emergent properties  
213 of model assumptions. This distinction mirrors findings in modern food-web studies, where deterministic and  
214 stochastic model assumptions influence the magnitude and timing of secondary extinctions (Allesina & Tang,  
215 2012; Curtsdotter et al., 2011; Dunne et al., 2002; Yeakel et al., 2014).

216 Taken together, these results highlight that network reconstruction is not neutral. Rather, it is a hypothesis  
217 generation process where the chosen model encodes a set of ecological assumptions. Consequently, paleoecolo-  
218 gists must carefully consider which ecological signals they aim to recover (potential interactions, realised diets,  
219 or macro-scale structural properties) before selecting a reconstruction approach. Importantly, disagreement  
220 among models does not imply that any single approach is ‘wrong’, but rather reflects the fact that different  
221 models capture different ecological signals (Stouffer, 2019). The challenge therefore lies not in identifying  
222 a universally correct model, but rather in aligning model choice with the ecological question being asked.  
223 Recognising this is critical for advancing paleoecology beyond descriptive reconstruction toward rigorous  
224 comparative inference.

## 225 5.1 Aligning ecological questions with model choice

226 A central insight from our study is that different ecological questions require different network representations.  
227 This conclusion parallels broader efforts in network ecology to clarify what various models and metrics  
228 can validly infer about ecological systems (Gauzens et al., 2025; Strydom et al., 2026). Here we provide a  
229 conceptual divide between feasible, realised, and structural network types and provides a practical framework  
230 for matching research goals with appropriate reconstruction approaches.

231 **Feasibility networks:** (*e.g.*, trait- and phylogeny-based metaweb approaches) are best suited for questions  
232 about potential trophic links and dietary breadth. These models aim to capture the range of interactions  
233 that are biologically plausible given species traits, even if not all are realised in any given context. Such an  
234 approach aligns with metaweb concepts in modern ecology, where large pools of potential interactions are  
235 used to understand regional species interaction potentials and local assembly processes (Tylianakis & Morris,

<sup>236</sup> 2017).

<sup>237</sup> **Realised networks:** (*e.g.*, models incorporating energetic and foraging constraints such as body-size  
<sup>238</sup> allometry) are more appropriate when the goal is to infer the most likely realised interactions. These models  
<sup>239</sup> embed ecological rules that approximate energy transfer and foraging ecology, improving ecological plausibility  
<sup>240</sup> of predicted links as compared with purely combinatorial approaches (Brose et al., 2006; Petchey et al., 2008).

<sup>241</sup> **Structural networks:** (*e.g.*, niche, cascade, and random models) strip away species identities in favour of  
<sup>242</sup> topological patterns, and are useful when broad questions about connectance or trophic depth are the focus.  
<sup>243</sup> Structural models have a long history in network ecology for generating null expectations about network  
<sup>244</sup> topology (Allesina et al., 2008; Williams & Martinez, 2008).

<sup>245</sup> Recognising this alignment helps avoid misinterpretation. For example, reconstructing a metaweb and treating  
<sup>246</sup> predicted links as realised trophic interactions conflates potential with actual diet, potentially exaggerating  
<sup>247</sup> inferred interaction diversity.

## <sup>248</sup> 5.2 Implications for paleoecological network studies

<sup>249</sup> Our findings have three major implications for the field of paleoecological networks:

- <sup>250</sup> 1. **Explicitly acknowledge model assumptions:** Interpretations of ancient food webs must clearly  
<sup>251</sup> articulate the assumptions underlying reconstruction models. Without this, differences in networks  
<sup>252</sup> reconstructed from different datasets or by different research groups may be misattributed to ecological  
<sup>253</sup> differences rather than methodological choices.
- <sup>254</sup> 2. **Standardise comparative frameworks:** When comparing food webs across studies, researchers  
<sup>255</sup> should ensure that networks are constructed and analysed using comparable model families. Without  
<sup>256</sup> such standardisation, meta-analyses risk conflating methodological differences with ecological or temporal  
<sup>257</sup> variation.
- <sup>258</sup> 3. **Leverage modern theory to expand inference:** Integrating modern network ecology frameworks  
<sup>259</sup> and methods with paleo-specific approaches enriches the inferential toolkit available to paleoecologists  
<sup>260</sup> (Dunne et al., 2014; Solé & Montoya, 2001). Models developed for modern systems (*e.g.*, allometric or  
<sup>261</sup> trait-based energy models) can be adapted to the constraints of fossil data (*e.g.*, Perez-Lamarque et al.,  
<sup>262</sup> 2026), enabling novel insights into deep-time dynamics.

263 **5.3 Recommendations for network reconstruction in paleoecology**

264 Given the sensitivity of ecological inference to reconstruction model choice, we propose the following guidelines  
265 to improve consistency, transparency, and ecological relevance:

- 266 **1. Define the Inferential Goal First:** Before reconstructing networks, researchers should articulate  
267 whether they aim to infer potential interactions, likely realised diets, or general structural properties.  
268 This will inform the selection of an appropriate model family consistent with the ecological question at  
269 hand (*e.g.*, metaweb for complete diets, energetic models for trophic energy flows, or structural models  
270 for generic topologies)
- 271 **2. Use ensemble and sensitivity frameworks:** Rather than relying on a single model output, researchers  
272 should adopt ensemble approaches that generate and compare multiple network reconstructions. This  
273 not only quantifies model uncertainty but also reveals which ecological conclusions are robust biological  
274 signals and which are methodological artifacts.
- 275 **3. Standardise cross-study comparisons:** Comparisons of networks from different palaeoecological  
276 studies should be standardised by model family. When models differ, interpretations about ecological or  
277 environmental change should explicitly address how model choice may contribute to observed differences.
- 278 **4. Interpret scale-specific results with caution:** Because node-level patterns tend to be more robust  
279 to model choice than link-level patterns, researchers should prioritise interpretations at the appropriate  
280 scale. Structural conclusions about cascade pathways or secondary extinctions should be framed as  
281 model-dependent hypotheses rather than definitive historical reconstructions.

282 **5.4 Future directions**

283 Looking ahead, paleoecological network reconstruction would benefit from deeper integration with advances  
284 in modern network ecology. This includes incorporating probabilistic and Bayesian approaches to quantify  
285 uncertainty in link prediction, such as Bayesian group models (Baskerville et al., 2011; Elmasri et al., 2020),  
286 developing maximum entropy methods to predict network structure under constrained information (Banville  
287 et al., 2023), and exploring multi-layer network representations that integrate trophic interactions with  
288 other types of ecological relationships (Pilosof et al., 2017). Such developments, combined with increasing  
289 availability of trait and phylogenetic information, can help bridge the gap between fossil constraints and  
290 ecological inference, enabling more nuanced and probabilistically grounded reconstructions of deep-time  
291 ecosystems (Banville et al., 2025; Perez-Lamarque et al., 2026; Poisot et al., 2016).

<sup>292</sup> **6 Conclusions**

<sup>293</sup> Ecological network reconstruction in deep time is not merely a technical step but a fundamental component  
<sup>294</sup> of ecological inference. By explicitly comparing six contrasting reconstruction approaches within a single  
<sup>295</sup> extinction event and location we show that model choice strongly shapes inferred food-web structure, species  
<sup>296</sup> interactions, and extinction dynamics, even when underlying fossil data are identical. While broad, trait-based  
<sup>297</sup> patterns of species loss appear relatively robust, conclusions about pairwise interactions, secondary extinctions,  
<sup>298</sup> and cascading dynamics depend critically on the assumptions embedded in the chosen network reconstruction  
<sup>299</sup> approach. These results underscore the need for paleoecological studies to align reconstruction methods  
<sup>300</sup> with specific ecological questions and to evaluate the sensitivity of key conclusions to alternative network  
<sup>301</sup> representations. More broadly, our findings highlight that understanding past ecosystem collapse requires not  
<sup>302</sup> only better fossil data, but also transparent, question-driven modelling frameworks that make explicit the  
<sup>303</sup> assumptions underlying ecological inference.

<sup>304</sup> **References**

- <sup>305</sup> Allesina, S., Alonso, D., & Pascual, M. (2008). A general model for food web structure. *Science*, *320*(5876),  
<sup>306</sup> 658–661. <https://doi.org/10.1126/science.1156269>
- <sup>307</sup> Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, *483*(7388), 205–208.  
<sup>308</sup> <https://doi.org/10.1038/nature10832>
- <sup>309</sup> Banville, F., Gravel, D., & Poisot, T. (2023). What constrains food webs? A maximum entropy framework  
<sup>310</sup> for predicting their structure with minimal biases. *PLOS Computational Biology*, *19*(9), e1011458.  
<sup>311</sup> <https://doi.org/10.1371/journal.pcbi.1011458>
- <sup>312</sup> Banville, F., Strydom, T., Blyth, P. S. A., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G.,  
<sup>313</sup> Malpas, T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2025). Deciphering probabilistic species  
<sup>314</sup> interaction networks. *Ecology Letters*, *28*(6), e70161. <https://doi.org/10.1111/ele.70161>
- <sup>315</sup> Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte,  
<sup>316</sup> J., Hastings, A., Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J.  
<sup>317</sup> W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., ... Smith, A. B. (2012). Approaching a state shift in  
<sup>318</sup> earth's biosphere. *Nature*, *486*(7401), 52–58. <https://doi.org/10.1038/nature11018>
- <sup>319</sup> Baskerville, E. B., Dobson, A. P., Bedford, T., Allesina, S., Anderson, T. M., & Pascual, M. (2011). Spatial  
<sup>320</sup> guilds in the serengeti food web revealed by a bayesian group model. *PLOS Computational Biology*, *7*(12),  
<sup>321</sup> e1002321. <https://doi.org/10.1371/journal.pcbi.1002321>

- 322 Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey,  
323 T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith,  
324 S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., ... Cohen, J. E. (2006). Consumer–resource  
325 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)
- 326
- 327 Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A., & Rall,  
328 B. C. (2011). Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and  
329 dynamic food webs. *Basic and Applied Ecology*, 12(7), 571–580. <https://doi.org/10.1016/j.baae.2011.09.008>
- 330 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,  
331 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).  
332 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111;brv.12433>
- 333
- 334 Dillon, E. M., Pier, J. Q., Smith, J. A., Raja, N. B., Dimitrijević, D., Austin, E. L., Cybulski, J. D., De  
335 Entrambasaguas, J., Durham, S. R., Grether, C. M., Haldar, H. S., Kocáková, K., Lin, C.-H., Mazzini, I.,  
336 Mychajliw, A. M., Ollendorf, A. L., Pimiento, C., Regalado Fernández, O. R., Smith, I. E., & Dietl, G. P.  
337 (2022). What is conservation paleobiology? Tracking 20 years of research and development. *Frontiers in  
338 Ecology and Evolution*, 10. <https://doi.org/10.3389/fevo.2022.1031483>
- 339 Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).  
340 Extinction cascades, community collapse, and recovery across a mesozoic hyperthermal event. *Nature  
341 Communications*, 15(1), 8599. <https://doi.org/10.1038/s41467-024-53000-2>
- 342 Dunne, J. A., Labandeira, C. C., & Williams, R. J. (2014). Highly resolved early eocene food webs show  
343 development of modern trophic structure after the end-cretaceous extinction. *Proceedings of the Royal  
344 Society B: Biological Sciences*, 281(1782), 20133280. <https://doi.org/10.1098/rspb.2013.3280>
- 345 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and network  
346 analyses of cambrian food webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 347 Dunne, J., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs:  
348 Robustness increases with connectance. *Ecol. Lett.*, 5(4), 558–567.
- 349 Elmasri, M., Farrell, M. J., Davies, T. J., & Stephens, D. A. (2020). A hierarchical bayesian model for  
350 predicting ecological interactions using scaled evolutionary relationships. *The Annals of Applied Statistics*,  
351 14(1), 221–240. <https://doi.org/10.1214/19-AOAS1296>
- 352 Erdős, P., & Rényi, A. (1959). On random graphs. i. *Publicationes Mathematicae Debrecen*, 6(3-4), 290–297.  
353 <https://doi.org/10.5486/pmd.1959.6.3-4.12>
- 354 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,

- 355 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the late pleistocene. *Science*,  
356 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 357 Gauzens, B., Brose, U., Delmas, E., & Berti, E. (2023). ATNr: Allometric trophic network models in r.  
358 *Methods in Ecology and Evolution*, 14(11), 2766–2773. <https://doi.org/10.1111/2041-210X.14212>
- 359 Gauzens, B., Thouvenot, L., Srivastava, D. S., Kratina, P., Romero, G. Q., Berti, E., O’Gorman, E. J.,  
360 González, A. L., Dézerald, O., Eisenhauer, N., Pires, M., Ryser, R., Farjalla, V. F., Rogy, P., Brose, U.,  
361 Petermann, J. S., Geslin, B., & Hines, J. (2025). Tailoring interaction network types to answer different  
362 ecological questions. *Nature Reviews Biodiversity*, 1–10. <https://doi.org/10.1038/s44358-025-00056-7>
- 363 Gravel, D., Baiser, B., Dunne, J. A., Kopalke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B.,  
364 Tylianakis, J. M., Wood, S. A., & Roslin, T. (2019). Bringing elton and grinnell together: A quantitative  
365 framework to represent the biogeography of ecological interaction networks. *Ecography*, 42(3), 401–415.  
366 <https://doi.org/https://doi.org/10.1111/ecog.04006>
- 367 Jenny, D., Fuchs, D., Arkhipkin, A. I., Hauff, R. B., Fritschi, B., & Klug, C. (2019). Predatory behaviour  
368 and taphonomy of a jurassic belemnoid coleoid (diplobelida, cephalopoda). *Scientific Reports*, 9(1), 7944.  
369 <https://doi.org/10.1038/s41598-019-44260-w>
- 370 Kiessling, W., Raja, N. B., Roden, V. J., Turvey, S. T., & Saupe, E. E. (2019). Addressing priority questions  
371 of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B:  
372 Biological Sciences*, 374(1788), 20190222. <https://doi.org/10.1098/rstb.2019.0222>
- 373 Michalska-Smith, M. J., & Allesina, S. (2019). Telling ecological networks apart by their structure: A  
374 computational challenge. *PLOS Computational Biology*, 15(6), e1007076. [https://doi.org/10.1371/journal.pcbi.1007076](https://doi.org/10.1371/journal.<br/>375 pcbi.1007076)
- 376 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple  
377 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/>378 5594.824)
- 379 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from  
380 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 381 Perez-Lamarque, B., Andréoletti, J., Morillon, B., Pion-Piola, O., Lambert, A., & Morlon, H. (2026). Darwin’s  
382 entangled bank through deep time: Structural stability of mutualistic networks over large geographic and  
383 temporal scales. *EcoEvoRxiv*. <https://doi.org/10.1101/2025.10.08.681159>
- 384 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure.  
385 *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/>386 0710672105)
- 387 Pichler, M., & Hartig, F. (2023). Machine learning and deep learning—a review for ecologists. *Methods in*

- 388      *Ecology and Evolution*, 14(4), 994–1016. <https://doi.org/10.1111/2041-210X.14061>
- 389      Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 390      Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
- 391      Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,
- 392      jbi.14127. <https://doi.org/10.1111/jbi.14127>
- 393      Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of species interaction
- 394      networks. *Ecology Letters*, 15(12), 1353–1361. <https://doi.org/10.1111/ele.12002>
- 395      Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of
- 396      probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303312. <https://doi.org/10.1111/mee.12470>
- 397      Poisot, T., & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree
- 398      distribution and emerging network properties. *PeerJ*, 2, e251. <https://doi.org/10.7717/peerj.251>
- 399      Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
- 400      through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 401      Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring
- 402      unexplained structure using latent traits. *The American Naturalist*, 176(2), 170–177. <https://doi.org/10.1086/653667>
- 403      Roopnarine, P. D. (2017). *Ecological modelling of paleocommunity food webs* (pp. 201–226). University of
- 404      Chicago Press.
- 405      Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32(1),
- 406      1–19. <https://www.jstor.org/stable/4096814>
- 407      Roopnarine, P. D., & Dineen, A. A. (2018). *Coral reefs in crisis: The reliability of deep-time food web*
- 408      *reconstructions as analogs for the present* (C. L. Tyler & C. L. Schneider, Eds.; pp. 105–141). Springer
- 409      International Publishing. [https://doi.org/10.1007/978-3-319-73795-9\\_6](https://doi.org/10.1007/978-3-319-73795-9_6)
- 410      Sahasrabudhe, S., & Motter, A. E. (2011). Rescuing ecosystems from extinction cascades through compensatory
- 411      perturbations. *Nature Communications*, 2(1), 170. <https://doi.org/10.1038/ncomms1163>
- 412      Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*
- 413      *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 414      Solé, R. V., & Montoya, M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal*
- 415      *Society of London. Series B: Biological Sciences*, 268(1480), 2039–2045. <https://doi.org/10.1098/rspb.2001.1767>
- 416      Stouffer, D. B., Camacho, J., Guimerà, R., Ng, C. A., & Nunes Amaral, L. A. (2005). Quantitative patterns
- 417      of fragmentation in ecological networks. *Ecology Letters*, 8(10), 1029–1037. <https://doi.org/10.1111/j.1462-2920.2005.00783.x>
- 418      Vissault, S., Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
- 419      Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,
- 420      jbi.14127. <https://doi.org/10.1111/jbi.14127>

- 421 in the structure of model and empirical food webs. *Ecology*, 86(5), 1301–1311. <https://doi.org/10.1890/04-0957>
- 422
- 423 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*,  
424 88(2), 192–195. [https://doi.org/https://doi.org/10.1111/1365-2656.12949](https://doi.org/10.1111/1365-2656.12949)
- 425 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust  
426 pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621),  
427 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>
- 428 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
429 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
430 towards predicting species interaction networks (across space and time). *Philosophical Transactions of the  
431 Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 432 Strydom, T., Dunhill, A. M., Dunne, J. A., Poisot, T., & Beckerman, A. P. (2026). Scaling from metawebs  
433 to realised webs: A hierarchical approach to network ecology. *EcoEvoRxiv*. <https://doi.org/10.32942/X2JW8K>
- 434
- 435 Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of  
436 Ecology, Evolution, and Systematics*, 48(1), 25–48. <https://doi.org/10.1146/annurev-ecolsys-110316-022821>
- 436
- 437 Vullo, R. (2011). Direct evidence of hybodont shark predation on late jurassic ammonites. *Naturwissenschaften*,  
438 98(6), 545–549. <https://doi.org/10.1007/s00114-011-0789-9>
- 439 Williams, R. J., & Martinez, N. D. (2004). Stabilization of chaotic and non-permanent food-web dynamics.  
440 *The European Physical Journal B - Condensed Matter*, 38(2), 297–303. <https://doi.org/10.1140/epjb/e2004-00122-1>
- 441
- 442 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.  
443 <https://doi.org/10.1038/35004572>
- 444 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food  
445 webs. *The Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 446 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T.  
447 (2014). Collapse of an ecological network in ancient egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>
- 448

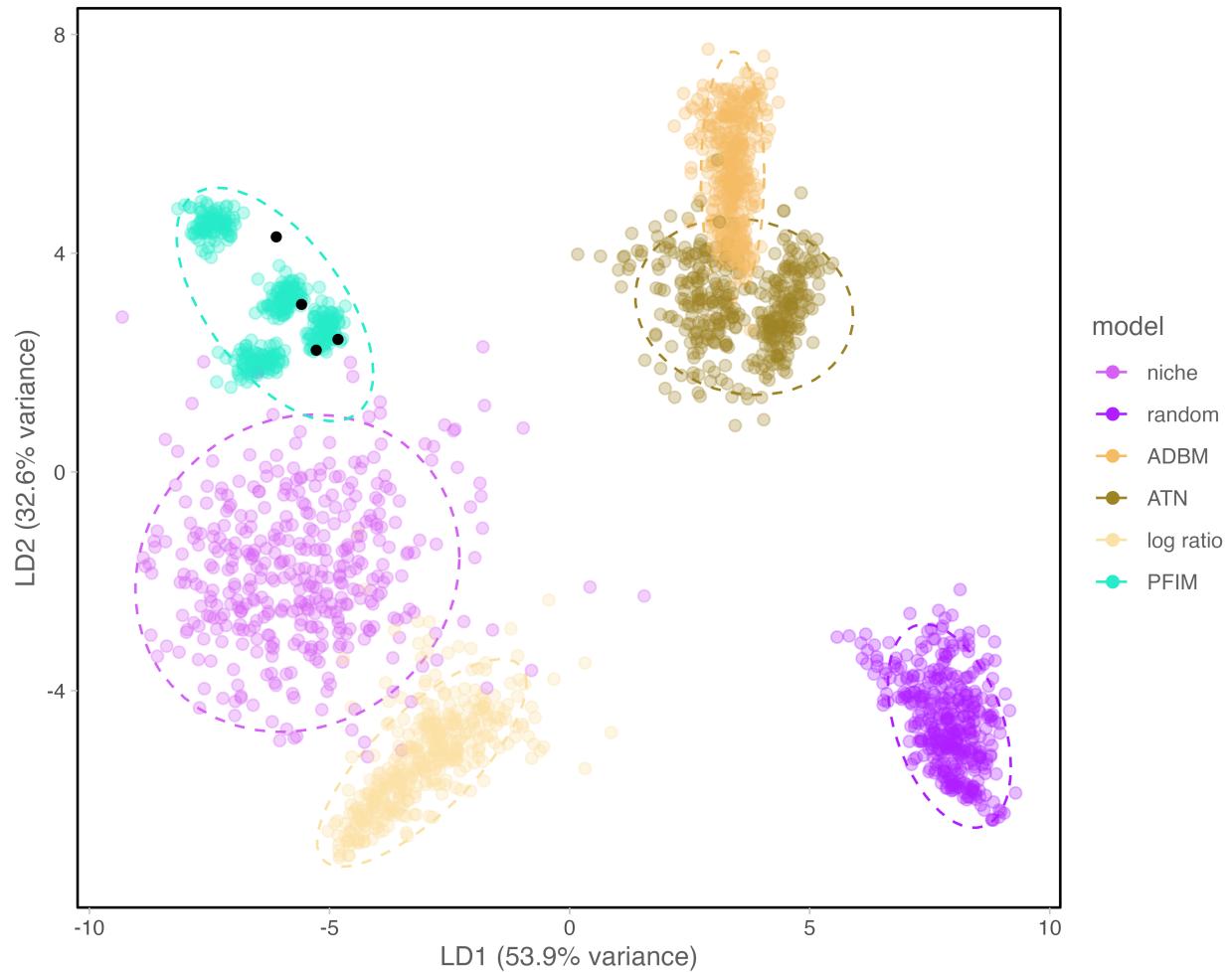


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

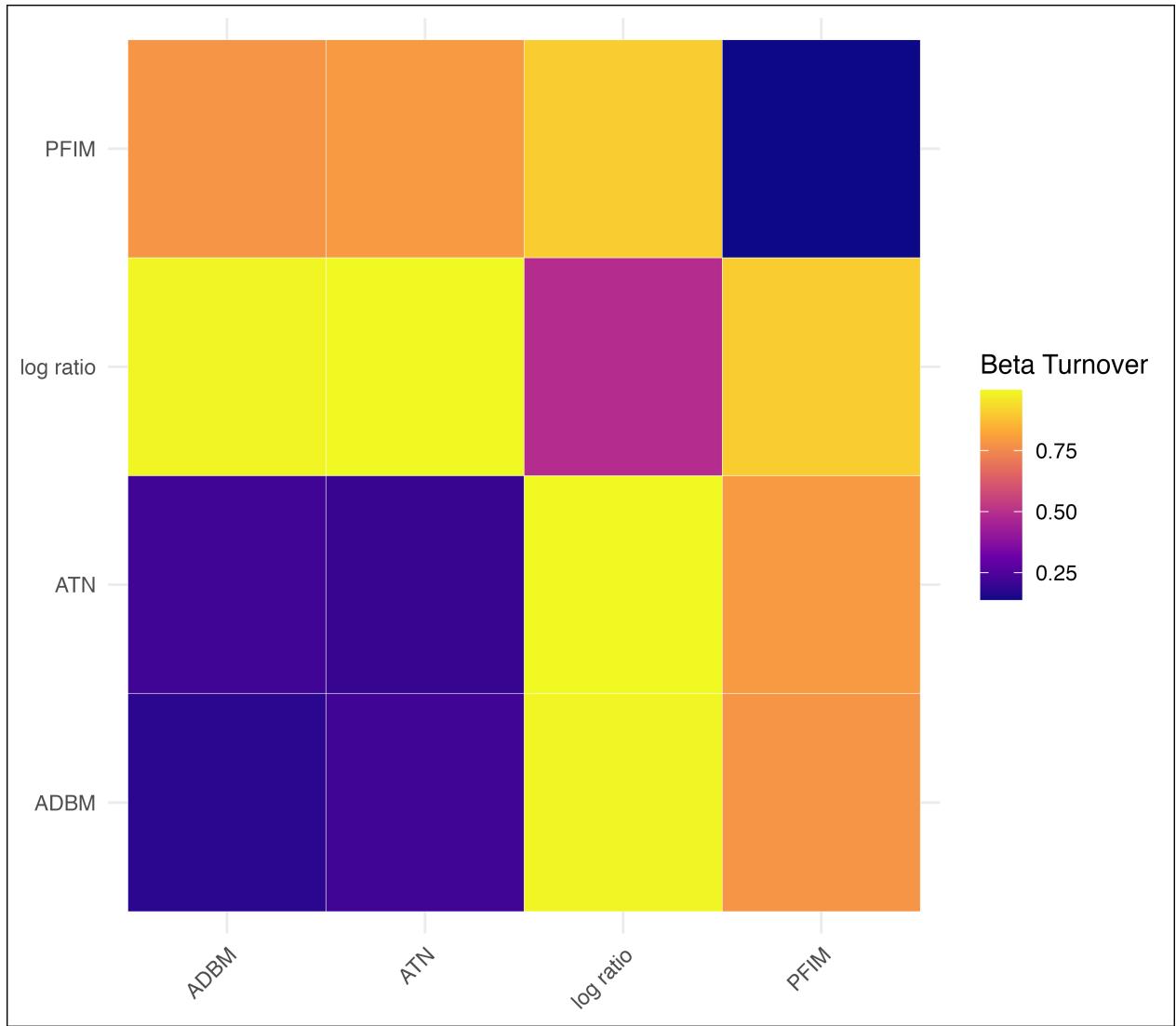


Figure 2: Pairwise beta turnover in species interactions among four ecological network models (ADBM, lmatrix, body-size ratio, and pfim). Each cell represents the mean turnover value between a pair of models, with warmer colors indicating greater dissimilarity in inferred interactions. The diagonal is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

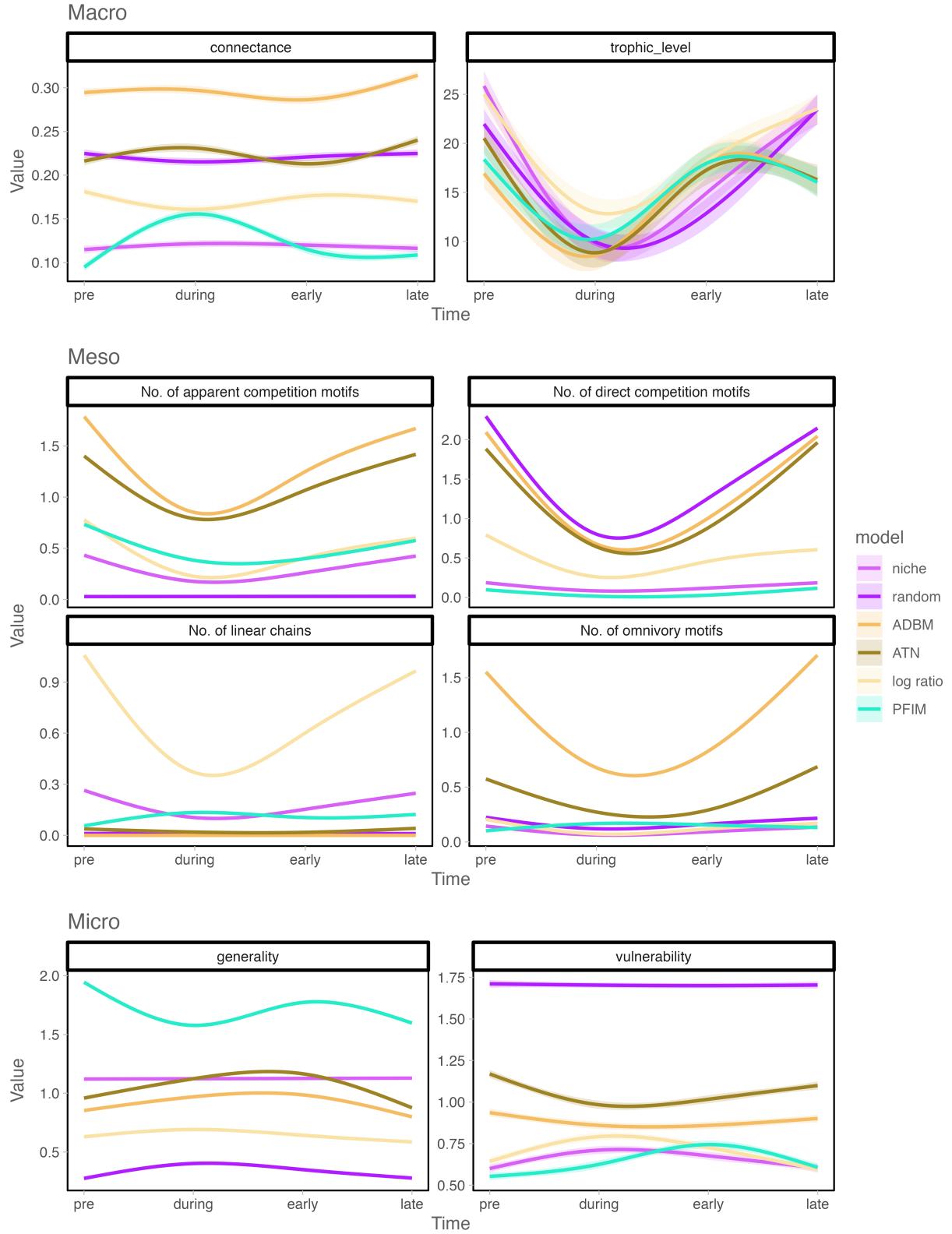
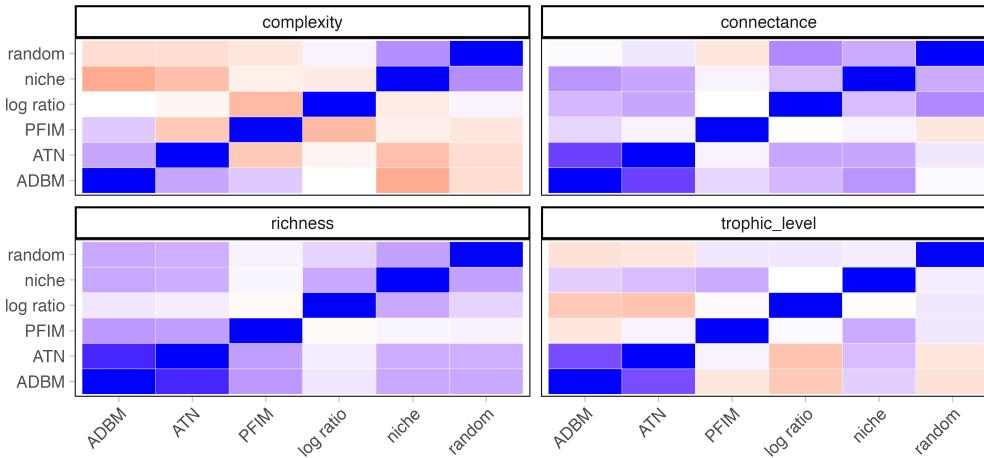
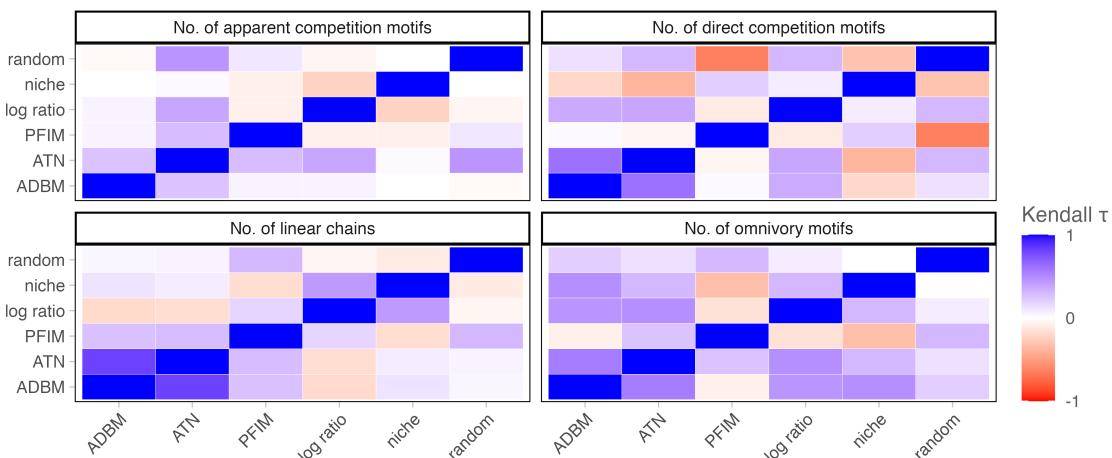


Figure 3: GAM-predicted trajectories of network structure during extinction simulations reveal pronounced differences in the timing and magnitude of change across reconstruction models. Lines show model-specific smooths and shaded areas indicate 95% confidence intervals. Deterministic approaches produce smoother, more consistent dynamics, whereas stochastic models exhibit greater variability, underscoring the sensitivity of inferred collapse pathways to reconstruction assumptions.

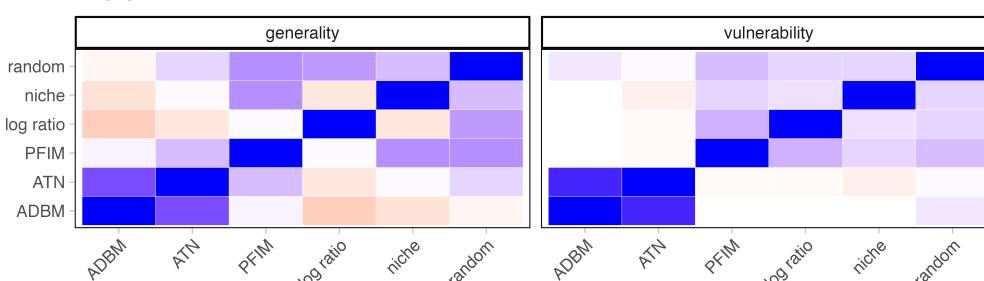
### Macro



### Meso



### Micro



### TSS

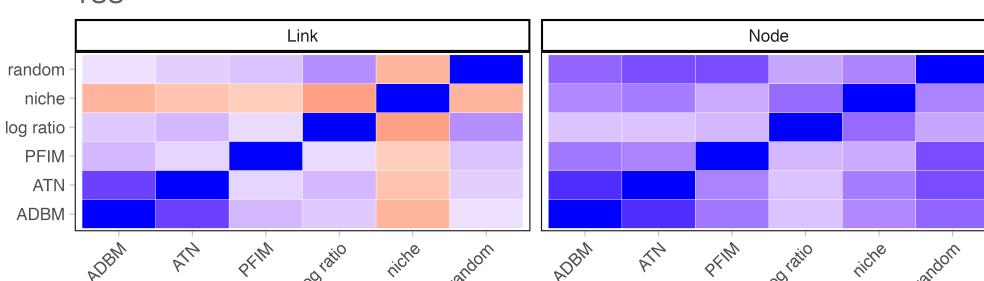


Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients ( $\tau$ ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between 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