

# Model structure conditions ecological inference in food web reconstruction

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## **Abstract:** Aim

Ecological networks are widely used to compare community structure, stability, and responses to disturbance across environmental gradients. However, many networks (particularly those assembled from incomplete interaction data) require model-based reconstruction. We test how alternative reconstruction frameworks condition ecological inference by quantifying their effects on network structure and disturbance dynamics.

## Location

Cleveland Basin, United Kingdom.

## Time period

Toarcian extinction event (Early Jurassic, upper Pliensbachian–upper Toarcian, ~183 Ma).

## Major taxa studied

Marine animal communities.

## Methods

We reconstructed four successive communities from an identical species pool using six contrasting food-web models spanning feasible (trait-based), realised (allometric and energetic), and structural (topological) network representations. For each community and model, 100 replicate networks were generated. We quantified macro-, meso-, and micro-scale network properties and assessed differences among models using multivariate analyses. Pairwise interaction turnover was measured using link-based beta diversity. We then simulated species loss under multiple disturbance scenarios, allowing cascading extinctions, and compared predicted community states using mean absolute differences and rank concordance metrics between models.

## Results

Reconstruction framework strongly influenced inferred network topology (MANOVA,  $p < 0.001$ ), generating distinct structural signatures independent of species composition. Models that were similar in global metrics often diverged in species-level interactions, with high -turnover among inferred link sets. During disturbance simulations, species-level vulnerability rankings were broadly consistent across models, but interaction-level outcomes and cascade dynamics varied substantially. Concordance in extinction-scenario rankings was scale dependent, with higher agreement at the species level than at the interaction level.

## Main conclusions

Network reconstruction functions as a structural prior that conditions ecological inference. While some aggregate patterns are robust across modelling frameworks, detailed interaction-level dynamics are highly model contingent. Comparative network studies across spatial or environmental gradients should therefore align reconstruction framework with inferential goals and explicitly evaluate sensitivity to modelling assumptions.

**Keywords:** Ecological networks, Biotic interactions, Community assembly, Environmental gradients, Interaction turnover, Trophic organisation, Ecosystem resilience, Macroecology

# **1 Introduction**

Understanding how biodiversity is organised across space and time is a central goal of macroecology and biogeography. While early efforts focused primarily on species richness and composition, there is growing recognition that ecological communities are structured not only by which species occur, but by how they interact (Thuiller et al., 2024). Interaction networks are increasingly treated as macroecological state variables where they are used to compare community organisation across environmental gradients, to quantify -diversity in interaction structure, to evaluate stability–complexity relationships, and to infer vulnerability under global change (Carstensen et al., 2014; Gravel et al., 2019; Poisot et al., 2015; Trøjelsgaard & Olesen, 2016; Tylianakis & Morris, 2017). As a result, ecological networks now play a central role in comparative analyses spanning latitudinal gradients, disturbance regimes, and deep-time environmental transitions (Dunhill et al., 2024; Hao et al., 2025; Michalska-Smith & Allesina, 2019; Poisot & Gravel, 2014; Roopnarine, 2006). Implicit in this expansion is the critical assumption that network properties estimated across systems are structurally comparable, and that differences among them reflect ecological signal rather than methodological artefact (Fründ et al., 2016; Jordano, 2016).

Yet most ecological networks are not fully observed (even in contemporary systems) and interaction data are incomplete and sampling is uneven across historical, biogeographic, and deep-time contexts (Catchen et al., 2023; Poisot et al., 2021; Sandra et al., 2025). Interactions must often be inferred indirectly from traits, phylogeny, body size, co-occurrence, or theoretical constraints (Morales-Castilla et al., 2015; Strydom et al., 2021). Network construction therefore constitutes a model-based inference step rather than a purely descriptive exercise. Different reconstruction frameworks encode distinct ecological assumptions about how interactions arise – whether as biologically feasible combinations of traits, energetically optimised realised diets, or topological structures constrained by macroecological regularities. These assumptions act as structural priors over network architecture (Gauzens et al., 2025; Guimarães, 2020; Petchey et al., 2011; Strydom et al., 2026). If alternative reconstruction models systematically generate different trophic configurations, then comparative analyses risk conflating ecological differences among communities with artefacts introduced by modelling choice. The reliability of macroecological inference therefore depends not only on ecological data, but on the structural assumptions embedded in network reconstruction.

Despite rapid methodological development in interaction inference, few studies have directly evaluated how alternative reconstruction frameworks condition macroecological conclusions when applied to the same species pool. This gap is particularly consequential for comparative research, where network metrics are routinely interpreted as indicators of environmental filtering, disturbance intensity, evolutionary history, or community stability (Allesina & Tang, 2012; Delmas et al., 2018; Poisot et al., 2015). If reconstruction models encode

33 distinct structural priors over interaction topology, then differences among communities may reflect modelling  
34 assumptions rather than ecological processes. We therefore test whether macroecological inference derived from  
35 ecological networks is robust to variation in reconstruction framework, asking which aspects of network-based  
36 inference are stable across plausible representations of interaction structure and which are intrinsically model  
37 dependent.

38 Deep-time ecosystems provide an especially stringent test of this issue because interactions are not observed  
39 directly and must be reconstructed explicitly (Dunhill et al., 2024; J. A. Dunne et al., 2008; J. A. Dunne et al.,  
40 2014; Roopnarine, 2006), rendering modelling assumptions transparent. We re-evaluate inferences made by  
41 Dunhill et al. (2024) on community structure and extinction dynamics during the early Toarcian extinction  
42 event (~183 Ma), a volcanic-driven hyperthermal and marine crisis in the Early Jurassic. Using four successive  
43 communities drawn from an identical taxon pool, we reconstruct ecological networks under six contrasting  
44 model classes spanning feasible, realised, and structural representations. For each reconstruction framework,  
45 we quantify emergent topology across scales, measure interaction turnover, and simulate disturbance-driven  
46 collapse. By holding species composition constant while varying structural priors, this design isolates the  
47 influence of model structure on inferred food web organisation and extinction dynamics, allowing us to  
48 distinguish ecological signals that are robust from those that are reconstruction contingent.

## 49 **2 Methods**

### 50 **2.1 Study system and fossil data**

51 We used fossil occurrence data from the Cleveland Basin spanning the upper Pliensbachian to the upper  
52 Toarcian. This interval encompasses a major volcanic-driven hyperthermal and marine extinction event. To  
53 capture network dynamics across this transition, we defined four successive paleo-communities: Pre-extinction  
54 (Pliensbachian), Post-extinction (Lower Toarcian), Early recovery, and Late recovery (Middle/Upper Toarcian).  
55 Each taxon was characterized using the Bambach ecospace framework (Bambach et al., 2007), coding for  
56 tiering, motility, and feeding mode as per Dunhill et al. (2024). Each assemblage was treated as a community  
57 of potentially interacting taxa. The dataset includes 57 taxa across diverse groups (*e.g.*, cephalopods, bivalves,  
58 and gastropods). By restricting our analysis to a single basin with consistent lithofacies, we controlled  
59 for biogeographic noise, ensuring that structural shifts across the four time-bins reflect localised ecological  
60 responses to environmental stress rather than sampling or facies bias.

61 **2.2 Network reconstruction approaches**

62 **2.2.1 Conceptual classification of network types**

63 Most paleo-specific approaches currently operate within the feasibility space (*e.g.*, Shaw et al., 2024; Fricke et  
64 al., 2022; Roopnarine, 2006). Although well suited for reconstructing feasible interactions, these methods  
65 represent only a subset of the broader spectrum of network construction approaches. Here, we present a suite  
66 of models (Table 1) that enable the construction of a wider range of ecological networks and the exploration  
67 of a broader set of ecological questions, provided that their underlying assumptions are compatible with  
68 the constraints of fossil data. For example, some tools require quantitative estimates of body size, which  
69 must often be inferred from size classes or functional morphology in the fossil record. Structural models,  
70 such as the niche model, rely only on species richness and estimates/specification of connectance, but their  
71 species-agnostic nature limits their applicability to trait-based or diet-specific questions, although they do still  
72 accurately recover network structure (Stouffer et al., 2005) . Mechanistic approaches, by contrast, depend on  
73 accurate assignment of feeding traits or robust phylogenetic support. Recognizing how these methodological  
74 requirements intersect with the limits of fossil evidence is essential for selecting an appropriate modelling  
75 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 (feasibility, 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 assigned randomly	Species richness, number of links	Parameter assumptions, species agnostic	Structural	Erdős & Rényi (1959)	Null-model comparisons; testing whether observed network structure (connectance, motifs) deviates from random expectations
Niche	Species ordered along a ‘niche axis’; interactions interval-constrained	Species richness, connectance	Parameter assumptions, species agnostic	Structural	Williams & Martinez (2008)	Evaluating trophic hierarchy and motif structure; baseline structural predictions
Allometric diet breadth model (ADBM)	Energy-maximizing predator diets	Body mass, abundance/dance/biomass	Assumes optimal foraging; does not account for forbidden links	Realised	Petchey et al. (2008)	Predicting realized predator diets; exploring secondary extinctions

Model family	Assumptions	Data needs	Limitation	Network type	Key reference	Usage examples
Allometric trophic network (ATN)	Links constrained by body-size ratios and functional response	Body mass, number of basal species	Assumes only mechanico/energetic constraints	Realised	Brose et al. (2006); Gauzens et al. (2023)	Simulating species loss; evaluating network collapse dynamics
Paleo food web inference model (PFIM)	Interactions inferred using trait-based mechanistic rules	Feeding traits	Assumes feeding mechanisms; trait resolution required	Feasibility	Shaw et al. (2024)	Mapping feasible trophic interactions; assessing secondary extinctions
Body-size ratio model	Probabilistic assignment of links based on predator-prey size ratios	Body mass	Does not account for forbidden links	Realised	Rohr et al. (2010)	Estimating likely interactions; simulating cascading effects.

76 The three body mass-based models (ADBM, ATN, Body-size ratio) differ primarily in their underlying  
 77 ecological assumptions. Although all three models use body mass to infer food web structure, they differ in  
 78 their ecological assumptions. The ADBM is based on energy maximization under optimal foraging theory,  
 79 the ATN constrains interactions via mechanically optimal consumer-resource size ratios, and the Body-size  
 80 ratio model defines links probabilistically within a fixed allometric niche. Together, these approaches span  
 81 bioenergetic, mechanical, and statistical interpretations of size-structured interactions.

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), allometric trophic network (ATN), and Body-size ratio models (realised network);  
85 and a paleo food web inference model (PFIM; feasibility web). Expanded descriptions of model assumptions,  
86 parameterisation, and link-generation rules are provided in Supplementary Material S1. For each community,  
87 100 networks were generated per model ( $n = 2400$ ) to capture stochastic variation in link assignment. Where  
88 models required species body mass or trait values, these were sampled within biologically reasonable ranges  
89 to preserve relative differences among species. We adopted uniform sampling by default, as alternative  
90 distributions (lognormal, truncated lognormal) have negligible impact on topology (Supplementary Material  
91 S2; Figure S1). Structural models were parameterized using connectance values drawn from an empirically  
92 realistic range (0.07 – 0.34), with species richness held constant. Identical parameter draws were applied  
93 across comparable models within each replicate to ensure comparability. For the Body-size ratio model, we  
94 followed the approach of Yeakel et al. (2014) and excluded latent trait terms as opposed fitting the full model,  
95 which introduces additional inference and assumptions.

96 **2.3 Network metrics and structural analyses**

97 We quantified network structure using a suite of macro-, meso-, and micro-scale metrics Table 2, capturing  
98 global properties, motif structure, and species-level variability. Differences among reconstruction approaches  
99 were assessed using a multivariate analysis of variance (MANOVA), with model identity as a fixed factor  
100 and the full set of network metrics as response variables. Pairwise interaction turnover was quantified using  
101 link-based beta diversity, which measures dissimilarity in the identity of trophic links between networks,  
102 capturing differences due to species turnover or changes in interactions among shared species (Poisot et al.,  
103 2012).

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	

Metric	Definition	Scale	Reference (for maths), can make footnotes probs
Links	Normalized standard deviation of links (number of consumers plus resources per taxon)	Micro	
Connectance	$L/S^2$ , where $S$ is the number of species and $L$ the number of links	Macro	
Max trophic level	Prey-weighted trophic level averaged across taxa	Macro	Williams & Martinez (2004)
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)
Generality	Normalized standard deviation of generality of a species, standardised by $L/S$	Micro	Williams & Martinez (2000)
Vulnerability	Normalized standard deviation of vulnerability of a species, standardised by $L/S$	Micro	Williams & Martinez (2000)

104 **2.4 Extinction simulations and model evaluation**

105 Following Dunhill et al. (2024) and using the pre-extinction and post-extinction networks, we simulated  
106 species loss under multiple extinction scenarios. We simulated species loss under multiple scenarios, including  
107 trait-based, network-position-based, and random removals, allowing cascading extinctions to propagate.  
108 Simulated outcomes were compared to observed or expected community states using mean absolute differences  
109 (MAD) and modified true skill statistics (TSS) at node and link levels. Kendall's rank correlation coefficient  
110 was used to evaluate concordance in scenario rankings across reconstruction models, providing a measure of  
111 robustness in inferred community responses.

112 **3 Results**

113 Across six network reconstruction approaches, inferred food web structure, species interactions, and extinction  
114 dynamics differed consistently. Multivariate analyses showed pronounced separation among models in  
115 network metric space. Reconstruction approach explained most of the variance in structural properties,  
116 leaving a distinct signature independent of community composition. Notably, agreement among models  
117 depended on scale - approaches that were statistically similar in multivariate structural space often diverged in  
118 inferred interactions or extinction dynamics. This demonstrates that structural similarity does not guarantee  
119 concordance in species-level diets or trophic roles. Model choice also substantially influenced inferred extinction  
120 dynamics. Temporal trajectories of network collapse, interaction loss, and motif reorganization differed among  
121 approaches. Although species-level extinction rankings were often broadly consistent, link-level outcomes  
122 and extinction inferences were highly sensitive to reconstruction assumptions. Together, these results show  
123 that ecological inferences drawn from paleo networks depend critically on the reconstruction framework  
124 employed. Importantly, agreement among models was not consistent across analytical scales - models that  
125 were statistically indistinguishable in multivariate structural space often diverged in inferred interactions  
126 or extinction dynamics. Together these results show that reconstruction approaches that appear similar  
127 when evaluated using global network metrics can yield fundamentally different ecological narratives when  
128 interrogated at the level of interactions and extinction dynamics.

129 **3.1 Network structure differs among reconstruction approaches**

130 Across six reconstruction approaches, network structure differed significantly (MANOVA, Pillai's trace =  
131 3.84, approximate  $F_{40,11955} = 987.35$ ,  $p < 0.001$ ), indicating that model choice systematically alters inferred  
132 food web topology. Canonical discriminant analysis identified two dominant axes of variation, explaining 86%

<sup>133</sup> of between-model variance. LD1 correlated with vulnerability, direct competition motifs, and connectance.  
<sup>134</sup> LD2 correlated with maximum trophic level and apparent competition motifs, reflecting vertical trophic  
<sup>135</sup> structure (Figure 1; Table S1, Figure S1). All higher-order canonical variates each explained less than 9% of  
<sup>136</sup> the remaining variance.

<sup>137</sup> [Figure 1 about here.]

<sup>138</sup> **3.1.1 Variance partitioning of network structure**

<sup>139</sup> Permutational multivariate analysis of variance revealed that reconstruction framework accounted for the  
<sup>140</sup> majority of variation in multivariate network structure ( $R^2 = 0.795$ ,  $p < 0.001$ ), whereas temporal turnover  
<sup>141</sup> across extinction phases explained a comparatively small proportion of variance ( $R^2 = 0.064$ ,  $p < 0.001$ ).  
<sup>142</sup> The model  $\times$  time interaction contributed a further 7.1% of variance ( $R^2 = 0.071$ ,  $p < 0.001$ ), indicating  
<sup>143</sup> limited but significant time-dependent divergence among reconstruction frameworks. Thus, differences among  
<sup>144</sup> modelling approaches were more than an order of magnitude greater than structural differences associated  
<sup>145</sup> with ecological turnover through the extinction sequence.

<sup>146</sup> To determine whether the dominance of reconstruction framework reflected absolute mean shifts among time  
<sup>147</sup> bins, we repeated the analysis after centring network metrics within each extinction phase. This procedure  
<sup>148</sup> removes between-phase differences while retaining within-phase structural variation. Even after temporal  
<sup>149</sup> centring, reconstruction framework explained 84.8% of multivariate variance ( $R^2 = 0.848$ ,  $p < 0.001$ ). These  
<sup>150</sup> results demonstrate that the influence of structural priors is not driven by temporal mean differences, but  
<sup>151</sup> reflects intrinsic divergence among reconstruction frameworks in how ecological interactions are organised.

<sup>152</sup> **3.1.2 Inferred pairwise interactions vary widely among models**

<sup>153</sup> Despite some models showing similar global metrics, specific pairwise interactions often differed. Pairwise  
<sup>154</sup> turnover revealed that certain model pairs shared very few links Figure 2. Size-based models (ADBM, ATN)  
<sup>155</sup> were broadly similar due to shared reliance on body-size constraints, whereas the Body-size ratio model  
<sup>156</sup> exhibited consistently higher differences to other models. PFIM showed intermediate overlap with theoretical  
<sup>157</sup> models. These results demonstrate that agreement in global network structure does not guarantee concordance  
<sup>158</sup> in species-level interactions.

<sup>159</sup> [Figure 2 about here.]

160 **3.2 Model choice influences inferred extinction dynamics**

161 To quantify how network structure changed over time during extinction simulations and whether these  
162 dynamics differed among reconstruction models, we fit generalized additive models (GAMs) to time series  
163 of network-level metrics. GAMs capture non-linear temporal trajectories, allowing formal tests of whether  
164 the shape of these trajectories differs among models. These model-specific temporal trajectories are shown  
165 in Figure 3. For all metrics examined, the inclusion of model-specific smooth terms significantly improved  
166 model fit (ANOVA model comparison:  $p < 0.001$  for all metrics). Model-specific smooths differed not only  
167 in magnitude but also in the timing and abruptness of change, indicating distinct modes of collapse across  
168 reconstruction approaches (Tables S3–S4). Deterministic, data-driven approaches (PFIM) and allometric  
169 models (ADBM, ATN) exhibited highly non-linear trajectories, showing structural shifts in connectivity  
170 and motif frequency. In contrast, the Niche model produced the most consistent and gradual trajectories,  
171 effectively smoothing the perceived magnitude of structural change during community collapse. These results  
172 demonstrate that inferred pathways of collapse, trophic bottlenecks, and secondary extinctions are highly  
173 sensitive to model choice. Corresponding raw temporal trajectories are shown in Figure S2.

174 [Figure 3 about here.]

175 To evaluate how model choice affects inferred extinction dynamics, we compared simulated post-extinction  
176 networks to observed networks using mean absolute differences (MAD) for network-level metrics and total  
177 sum-of-squares (TSS) for node- and link-level outcomes Figure 4. Across models, MAD-based rankings were  
178 generally positively correlated (Kendall's  $\tau = 0.13$  across structural metrics), indicating broad agreement on  
179 the relative importance of extinction drivers despite substantial differences in reconstructed network structure.  
180 However, agreement within the allometric models differed from patterns observed for reconstructed network  
181 structure. Whereas earlier multivariate analyses showed strongest structural similarity between the ADBM  
182 and Body-size ratio models, extinction-driven network responses aligned most closely between the ADBM  
183 and ATN models (mean  $\tau = 0.67$  across structural metrics), with little correspondence between ADBM and  
184 Body-size ratio model outcomes (mean  $\tau = 0.05$ ). This reversal relative to structural similarity analyses  
185 demonstrates that model concordance is context dependent, with emergent topology and extinction dynamics  
186 emphasizing different aspects of model assumptions. Node-level TSS rankings were similarly consistent across  
187 models ( $\tau = 0.26\text{--}0.90$ ), reflecting broadly comparable species removal sequences. In contrast, link-level  
188 outcomes were far more variable ( $\tau = -0.48\text{--}0.29$ ), highlighting that inferences about which interactions are  
189 lost, retained, or re-established during collapse and recovery are highly model contingent. Together, these  
190 results suggest that while alternative models converge on similar species-level extinction patterns, the inferred  
191 pathways of interaction loss and cascading dynamics depend strongly on both reconstruction approach.

193 **4 Discussion**

194 **4.1 Network reconstruction is not neutral: structural priors shape ecological  
195 theory**

196 Food web ecology has long treated network reconstruction as a technical step preceding ecological analysis.  
 197 Once a network is assembled (whether from observation, inference, or simulation) its properties are typically  
 198 analysed as reflections of underlying ecological organisation. Implicit in this workflow is a powerful assumption  
 199 - that reconstructed networks provide structurally comparable representations of ecological communities,  
 200 such that differences in connectance, trophic structure, motif composition, or robustness primarily reflect  
 201 biological variation. Our results challenge this assumption. Across an identical species pool, reconstruction  
 202 framework explained the majority of variance in network topology, generating distinct structural signatures  
 203 independent of community composition. Although some model classes converged on similar global metrics,  
 204 pairwise interaction turnover revealed substantial divergence in inferred trophic links. Structural similarity  
 205 at the level of connectance or trophic height therefore does not guarantee concordance in species roles or  
 206 interaction architecture.

207 Reconstruction framework explained the majority of variance in inferred food web topology, far outweighing  
 208 the influence of temporal turnover across extinction phases. These patterns demonstrate that the divergence  
 209 among reconstruction approaches reflects intrinsic differences in how models organise interactions, not temporal  
 210 shifts in network structure. In other words, different reconstruction approaches impose distinct structural  
 211 priors on ecological organisation. These priors are not subtle - they propagate into emergent topology,  
 212 species roles, and dynamical predictions. Network structure is therefore not solely a property of ecological  
 213 communities; it is jointly determined by ecological data, modelling assumptions, and level of organisation  
 214 (Gauzens et al., 2025; Guimarães, 2020; Pichler & Hartig, 2023; Strydom et al., 2021; Strydom et al., 2026).

215 This has direct implications for the interpretation of comparative network studies. Feasible, realised, and  
 216 structural models encode different assumptions about constraint, optimisation, and topology, and these  
 217 assumptions propagate into emergent metrics and dynamical predictions (Allesina & Tang, 2012; J. Dunne et  
 218 al., 2002; Michalska-Smith & Allesina, 2019; Poisot & Gravel, 2014; Solé & Montoya, 2001). When networks  
 219 reconstructed under different model classes are compared across spatial gradients, disturbance regimes, or  
 220 evolutionary transitions, part of the observed variation may derive from structural priors rather than ecological  
 221 process. Without explicit standardisation or sensitivity analysis, methodological heterogeneity can be mistaken

222 for biological signal. Food web ecology has devoted substantial effort to understanding how topology shapes  
223 dynamics; comparatively less attention has been paid to how reconstruction shapes topology. Our findings  
224 indicate that these two questions cannot be separated.

## 225 4.2 Scale-dependent robustness in network-based inference

226 Importantly, reconstruction sensitivity was not uniform across analytical scales. Species-level extinction  
227 rankings were broadly consistent among model classes, whereas interaction-level outcomes and cascade  
228 trajectories were highly contingent on structural prior. The predominance of reconstruction framework over  
229 temporal turnover (~80% vs. 6% variance explained) illustrates why coarse-grained patterns like species-level  
230 extinction rankings are more robust. Model-imposed structure dominates the overall topology, leaving finer-  
231 scale interaction dynamics highly contingent on framework choice. This asymmetry reveals a scale-dependent  
232 pattern of robustness. Coarse-grained macroecological patterns (such as relative species vulnerability or overall  
233 collapse magnitude) can emerge from multiple plausible interaction architectures. By contrast, fine-grained  
234 inferences about which links are lost, retained, or reorganised depend strongly on how interactions are inferred.

235 This distinction challenges a central ambition of food web ecology - the use of detailed interaction structure to  
236 diagnose mechanisms of stability and collapse (*e.g.*, Dunhill et al., 2024). If interaction-level cascade pathways  
237 vary substantially across equally plausible reconstructions, then mechanistic narratives derived from a single  
238 inferred topology may overstate their precision (Allesina & Tang, 2012; Curtsdotter et al., 2011; J. Dunne  
239 et al., 2002). The apparent determinism of extinction cascades or trophic bottlenecks may partly reflect  
240 model-imposed structure rather than ecological inevitability.

241 For macroecology, this scale dependence clarifies where network-based inference is accurate. Aggregate  
242 properties may be comparatively robust to reconstruction assumptions, whereas conclusions about interaction  
243 turnover, motif reorganisation, or fine-scale trophic dynamics are intrinsically uncertain unless reconstruction  
244 uncertainty is explicitly incorporated. Recognising this asymmetry is essential if network analyses are to  
245 inform comparative synthesis across space and time.

246 Taken together, these results underscore that network reconstruction is not a neutral preprocessing step but  
247 a hypothesis-generating process in which each model encodes a distinct set of ecological assumptions. The  
248 inferred topology and dynamics of a food web therefore reflect not only ecological data, but the theoretical  
249 assumptions embedded in the reconstruction framework. Disagreement among models does not imply that  
250 any single approach is ‘wrong’, but rather that different models capture different facets of ecological reality  
251 (Petchey et al., 2011; Stouffer, 2019). Disagreement among models does not imply that any single approach  
252 is ‘incorrect’. Rather, different models capture different facets of ecological constraint—trait compatibility,

253 energetic optimisation, or topological regularity. The critical point is that these facets are not interchangeable.  
254 This perspective reframes reconstruction choice as part of hypothesis specification. Researchers must align  
255 reconstruction approaches with the ecological signals of interest (whether potential interactions, realised  
256 diets, or macro-scale structural properties) rather than treating model selection as a technical convenience.  
257 Viewed through the lens of accuracy and precision, our results indicate that some network-based inferences are  
258 relatively robust across structural priors, whereas others remain intrinsically uncertain. High-level extinction  
259 rankings were broadly convergent, suggesting relative accuracy at coarse resolution, but interaction-level  
260 details and temporal cascade dynamics diverged substantially, indicating limited precision in reconstructing  
261 the fine structure of collapse. Recognising and explicitly accounting for this distinction is essential if food web  
262 ecology is to move beyond descriptive reconstruction toward rigorous comparative inference.

### 263 **4.3 Implications for comparative biogeography and global change research**

264 Network approaches are increasingly applied to examine how ecological organisation varies across latitudinal  
265 gradients, environmental filters, disturbance regimes, and climate-driven transitions. These studies frequently  
266 interpret variation in connectance, trophic height, interaction -diversity, or robustness as indicators of  
267 ecological differentiation among regions or time intervals. Yet reconstruction frameworks often differ among  
268 systems due to variation in sampling intensity, trait resolution, or modelling preference. Our results show  
269 that such differences can systematically alter inferred topology and disturbance dynamics even when species  
270 composition is held constant.

271 This finding has consequences for interaction biogeography. Apparent differences in network turnover across  
272 spatial gradients may reflect divergence in structural priors rather than genuine ecological reorganisation.

273 Similarly, projected differences in vulnerability under climate change may depend on how realised interactions  
274 are modelled, not solely on community composition. Without explicit treatment of reconstruction assumptions,  
275 comparative network analyses risk conflating modelling artefact with macroecological process.

276 If ecological networks are to function as reliable macroecological state variables, reconstruction framework must  
277 be treated as a formal component of hypothesis specification. Cross-system comparisons should standardise  
278 modelling approaches wherever possible, or explicitly evaluate sensitivity to alternative structural priors.  
279 Ensemble reconstruction—treating networks as distributions rather than single topologies—offers a principled  
280 pathway toward incorporating structural uncertainty into comparative synthesis.

281 **4.4 Toward a more explicit modelling paradigm in food web ecology**

282 The broader implication is not that any single reconstruction framework is ‘correct’ or ‘incorrect’. Rather, each  
283 model class represents a distinct hypothesis about how interactions are constrained—by trait compatibility,  
284 energetic optimisation, or topological regularity (Petchey et al., 2011). Food web reconstruction is therefore  
285 theory-laden. Making this explicit shifts reconstruction from a preparatory step to a central component of  
286 ecological modelling.

287 A mature modelling paradigm in food web ecology would treat structural priors as testable assumptions,  
288 incorporate probabilistic link inference where possible, and quantify the sensitivity of macroecological  
289 conclusions to alternative representations of interaction structure. Such an approach aligns with recent  
290 advances in probabilistic and ensemble network modelling and would strengthen the interpretability of  
291 network-based inference under global change (Banville et al., 2025; Baskerville et al., 2011; Elmasri et al.,  
292 2020; Perez-Lamarque et al., 2026; Poisot et al., 2016).

293 **5 Conclusions**

294 Ecological network reconstruction is not a neutral technical procedure but a theoretical act that shapes  
295 ecological inference. By applying six contrasting reconstruction frameworks to an identical species pool, we  
296 show that structural priors systematically influence inferred food-web topology, interaction identity, and  
297 disturbance dynamics. Some coarse-grained patterns, such as relative species vulnerability, are comparatively  
298 robust across representations. In contrast, fine-scale interaction structure and cascade pathways are highly  
299 contingent on modelling assumptions. The reliability of network-based inference is therefore scale dependent.

300 These results challenge the implicit assumption that reconstructed networks are structurally commensurable  
301 across systems. When reconstruction frameworks differ, variation in connectance, trophic organisation,  
302 robustness, or interaction turnover may reflect embedded modelling assumptions as much as ecological  
303 process. Network reconstruction should thus be treated as an explicit component of hypothesis specification  
304 in comparative macroecology and biogeography.

305 No single model captures the full complexity of ecological organisation, but neither are alternative models  
306 interchangeable. Aligning reconstruction framework with inferential goals, standardising approaches across  
307 comparative studies, and incorporating ensemble or probabilistic representations will be essential for strength-  
308 ening the interpretability of network analyses across spatial and temporal gradients. As ecological networks  
309 increasingly inform global change research, recognising structural priors as fundamental determinants of  
310 inference is critical for advancing food web ecology from descriptive reconstruction toward rigorous comparative

<sup>311</sup> synthesis.

## <sup>312</sup> References

- <sup>313</sup> Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483(7388), 205–208.  
<sup>314</sup> <https://doi.org/10.1038/nature10832>
- <sup>315</sup> Bambach, R. K., Bush, A. M., & Erwin, D. H. (2007). Autecology and the filling of ecospace: Key metazoan  
<sup>316</sup> radiations. *Palaeontology*, 50(1), 1–22. <https://doi.org/10.1111/j.1475-4983.2006.00611.x>
- <sup>317</sup> Banville, F., Strydom, T., Blyth, P. S. A., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G.,  
<sup>318</sup> Malpas, T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2025). Deciphering probabilistic species  
<sup>319</sup> interaction networks. *Ecology Letters*, 28(6), e70161. <https://doi.org/10.1111/ele.70161>
- <sup>320</sup> Baskerville, E. B., Dobson, A. P., Bedford, T., Allesina, S., Anderson, T. M., & Pascual, M. (2011). Spatial  
<sup>321</sup> guilds in the serengeti food web revealed by a bayesian group model. *PLOS Computational Biology*, 7(12),  
<sup>322</sup> e1002321. <https://doi.org/10.1371/journal.pcbi.1002321>
- <sup>323</sup> Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey,  
<sup>324</sup> T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith,  
<sup>325</sup> S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., ... Cohen, J. E. (2006). Consumer–resource  
<sup>326</sup> 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)
- <sup>327</sup> Carstensen, D. W., Sabatino, M., Trøjelsgaard, K., & Morellato, L. P. C. (2014). Beta diversity of plant-  
<sup>328</sup> pollinator networks and the spatial turnover of pairwise interactions. *PLOS ONE*, 9(11), e112903.  
<sup>329</sup> <https://doi.org/10.1371/journal.pone.0112903>
- <sup>330</sup> Catchen, M. D., Lin, M., Poisot, T., Rolnick, D., & Gonzalez, A. (2023). *Improving ecological connectivity  
assessments with transfer learning and function approximation*. <https://ecoenvxiv.org/repository/view/5348/>
- <sup>331</sup> Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A., & Rall,  
<sup>332</sup> B. C. (2011). Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and  
<sup>333</sup> dynamic food webs. *Basic and Applied Ecology*, 12(7), 571–580. <https://doi.org/10.1016/j.baae.2011.09.008>
- <sup>334</sup> Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Dalla Riva, G. V., Fortin, M.-J., Gravel, D., Guimarães, P.  
<sup>335</sup> R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2018). Analysing  
<sup>336</sup> ecological networks of species interactions. *Biological Reviews*, 112540. <https://doi.org/10.1111/brv.12433>
- <sup>337</sup> Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).  
<sup>338</sup> Extinction cascades, community collapse, and recovery across a mesozoic hyperthermal event. *Nature*  
<sup>339</sup>

- 342      *Communications*, 15(1), 8599. <https://doi.org/10.1038/s41467-024-53000-2>
- 343      Dunne, J. A., Labandeira, C. C., & Williams, R. J. (2014). Highly resolved early eocene food webs show  
344      development of modern trophic structure after the end-cretaceous extinction. *Proceedings of the Royal  
345      Society B: Biological Sciences*, 281(1782), 20133280. <https://doi.org/10.1098/rspb.2013.3280>
- 346      Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and network  
347      analyses of cambrian food webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 348      Dunne, J., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs:  
349      Robustness increases with connectance. *Ecol. Lett.*, 5(4), 558–567.
- 350      Elmasri, M., Farrell, M. J., Davies, T. J., & Stephens, D. A. (2020). A hierarchical bayesian model for  
351      predicting ecological interactions using scaled evolutionary relationships. *The Annals of Applied Statistics*,  
352      14(1), 221–240. <https://doi.org/10.1214/19-AOAS1296>
- 353      Erdős, P., & Rényi, A. (1959). On random graphs. i. *Publicationes Mathematicae Debrecen*, 6(3-4), 290–297.  
354      <https://doi.org/10.5486/pmd.1959.6.3-4.12>
- 355      Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,  
356      J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the late pleistocene. *Science*,  
357      377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 358      Fründ, J., McCann, K. S., & Williams, N. M. (2016). Sampling bias is a challenge for quantifying specialization  
359      and network structure: Lessons from a quantitative niche model. *Oikos*, 125(4), 502–513. <https://doi.org/10.1111/oik.02256>
- 360      Gauzens, B., Brose, U., Delmas, E., & Berti, E. (2023). ATNr: Allometric trophic network models in r.  
361      *Methods in Ecology and Evolution*, 14(11), 2766–2773. <https://doi.org/10.1111/2041-210X.14212>
- 362      Gauzens, B., Thouvenot, L., Srivastava, D. S., Kratina, P., Romero, G. Q., Berti, E., O’Gorman, E. J.,  
363      González, A. L., Dézerald, O., Eisenhauer, N., Pires, M., Ryser, R., Farjalla, V. F., Rogy, P., Brose, U.,  
364      Petermann, J. S., Geslin, B., & Hines, J. (2025). Tailoring interaction network types to answer different  
365      ecological questions. *Nature Reviews Biodiversity*, 1–10. <https://doi.org/10.1038/s44358-025-00056-7>
- 366      Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B.,  
367      Tylianakis, J. M., Wood, S. A., & Roslin, T. (2019). Bringing elton and grinnell together: A quantitative  
368      framework to represent the biogeography of ecological interaction networks. *Ecography*, 42(3), 401–415.  
369      <https://doi.org/https://doi.org/10.1111/ecog.04006>
- 370      Guimarães, P. R. (2020). The structure of ecological networks across levels of organization. *Annual Review of  
371      Ecology, Evolution, and Systematics*, 51(1). <https://doi.org/10.1146/annurev-ecolsys-012220-120819>
- 372      Hao, X., Holyoak, M., Zhang, Z., & Yan, C. (2025). Global projection of terrestrial vertebrate food webs  
373      under future climate and land-use changes. *Global Change Biology*, 31(2), e70061. <https://doi.org/10.1111/gcb.15931>

- 375      [1111/gcb.70061](https://doi.org/10.1111/gcb.70061)
- 376      Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12763>
- 377      1111/1365-2435.12763
- 378      Michalska-Smith, M. J., & Allesina, S. (2019). Telling ecological networks apart by their structure: A  
379      computational challenge. *PLOS Computational Biology*, 15(6), e1007076. <https://doi.org/10.1371/journal.pcbi.1007076>
- 380      pcbi.1007076
- 381      Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple  
382      building blocks of complex networks. *Science*, 298(5594), 824–827. <https://doi.org/10.1126/science.298.5594.824>
- 384      Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from  
385      proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 386      Perez-Lamarque, B., Andréoletti, J., Morillon, B., Pion-Piola, O., Lambert, A., & Morlon, H. (2026). Darwin's  
387      entangled bank through deep time: Structural stability of mutualistic networks over large geographic and  
388      temporal scales. *EcoEvoRxiv*. <https://doi.org/10.1101/2025.10.08.681159>
- 389      Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure.  
390      *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 392      Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology:  
393      Some thoughts on judging food web models. *Journal of Theoretical Biology*, 279(1), 169–171. <https://doi.org/10.1016/j.jtbi.2011.03.019>
- 395      Pichler, M., & Hartig, F. (2023). Machine learning and deep learning—a review for ecologists. *Methods in  
396      Ecology and Evolution*, 14(4), 994–1016. <https://doi.org/10.1111/2041-210X.14061>
- 397      Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &  
398      Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,  
399      jbi.14127. <https://doi.org/10.1111/jbi.14127>
- 400      Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of species interaction  
401      networks. *Ecology Letters*, 15(12), 1353–1361. <https://doi.org/10.1111/ele.12002>
- 402      Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of  
403      probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303312. <https://doi.org/10.1111/2041-210X.12802>
- 404      Poisot, T., & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree  
405      distribution and emerging network properties. *PeerJ*, 2, e251. <https://doi.org/10.7717/peerj.251>
- 406      Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
407      through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>

- 408 Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring  
409 unexplained structure using latent traits. *The American Naturalist*, 176(2), 170–177. <https://doi.org/10.1086/653667>
- 410
- 411 Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32(1),  
412 1–19. <https://www.jstor.org/stable/4096814>
- 413 Sandra, H.-P., Traveset, A., Nogales, M., Heleno, R., Llewelyn, J., & Strona, G. (2025). Sampling biases  
414 across interaction types affect the robustness of ecological multilayer networks. *Ecological Informatics*,  
415 103183. <https://doi.org/10.1016/j.ecoinf.2025.103183>
- 416 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for  
417 reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 418
- 419 Solé, R. V., & Montoya, M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal  
420 Society of London. Series B: Biological Sciences*, 268(1480), 2039–2045. <https://doi.org/10.1098/rspb.2001.1767>
- 421
- 422 Stouffer, D. B., Camacho, J., Guimerà, R., Ng, C. A., & Nunes Amaral, L. A. (2005). Quantitative patterns  
423 in the structure of model and empirical food webs. *Ecology*, 86(5), 1301–1311. <https://doi.org/10.1890/04-0957>
- 424
- 425 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*,  
426 88(2), 192–195. <https://doi.org/10.1111/1365-2656.12949>
- 427
- 428 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust  
429 pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621),  
1931–1940. <https://doi.org/10.1098/rspb.2007.0571>
- 430
- 431 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,  
N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap  
432 towards predicting species interaction networks (across space and time). *Philosophical Transactions of the  
433 Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 434
- 435 Strydom, T., Dunhill, A. M., Dunne, J. A., Poisot, T., & Beckerman, A. P. (2026). Scaling from metawebs  
to realised webs: A hierarchical approach to network ecology. *EcoEvoRxiv*. <https://doi.org/10.32942/X2JW8K>
- 436
- 437 Thuiller, W., Calderón-Sanou, I., Chalmandrier, L., Gaüzère, P., O'Connor, L. M. J., Ohlmann, M., Poggianto,  
G., & Münkemüller, T. (2024). Navigating the integration of biotic interactions in biogeography. *Journal  
438 of Biogeography*, 51(4), 550–559. <https://doi.org/10.1111/jbi.14734>
- 439
- 440 Trøjelsgaard, K., & Olesen, J. M. (2016). Ecological networks in motion: Micro- and macroscopic variability

- 441 across scales. *Functional Ecology*, 30(12), 1926–1935. <https://doi.org/https://doi.org/10.1111/1365->
- 442 [2435.12710](#)
- 443 Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of*  
444 *Ecology, Evolution, and Systematics*, 48(1), 25–48. <https://doi.org/10.1146/annurev-ecolsys-110316-022821>
- 445 Williams, R. J., & Martinez, N. D. (2004). Stabilization of chaotic and non-permanent food-web dynamics.  
446 *The European Physical Journal B - Condensed Matter*, 38(2), 297–303. <https://doi.org/10.1140/epjb/e2004->
- 447 [00122-1](#)
- 448 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.  
449 <https://doi.org/10.1038/35004572>
- 450 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food  
451 webs. *The Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 452 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T.  
453 (2014). Collapse of an ecological network in ancient egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>
- 454

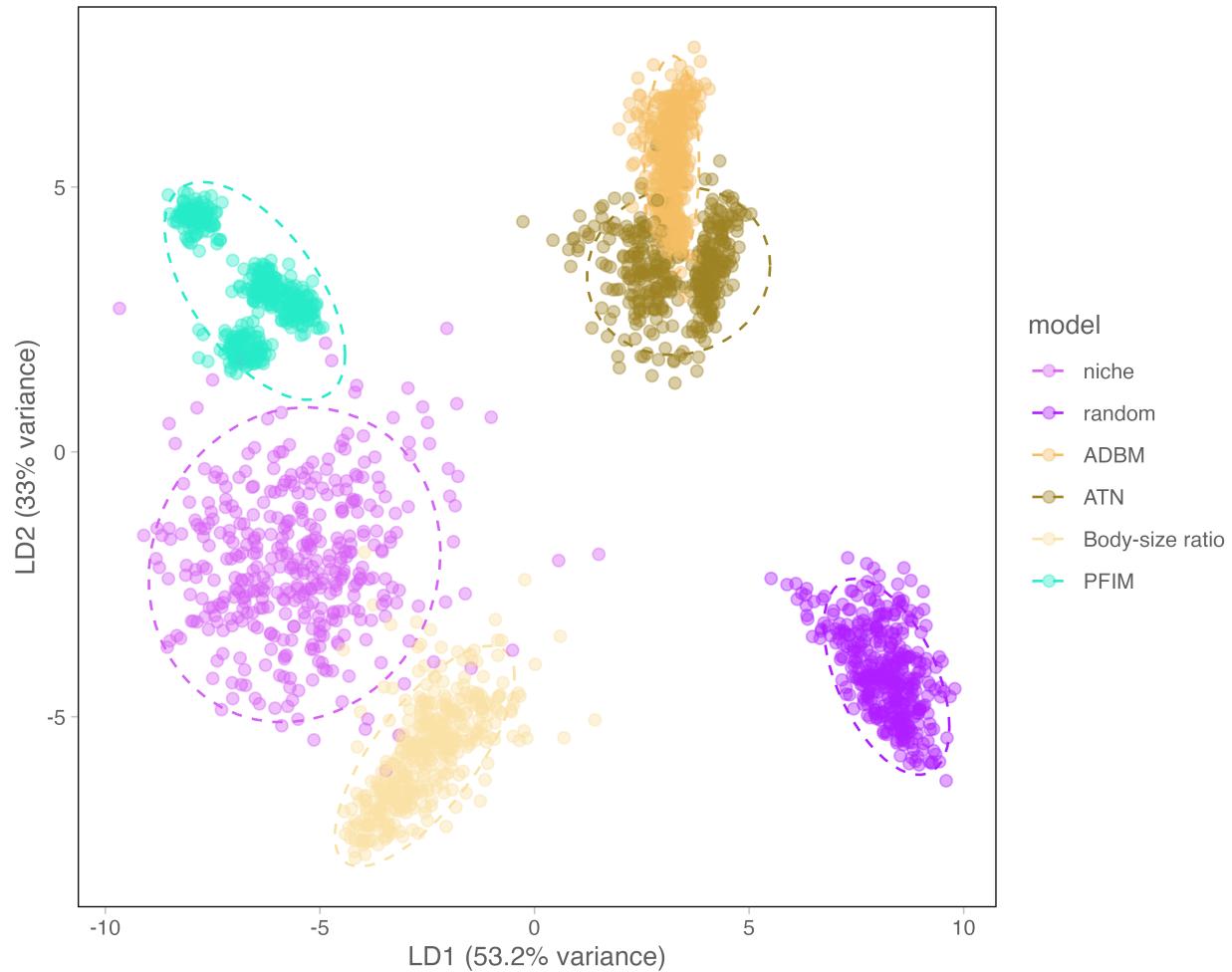


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

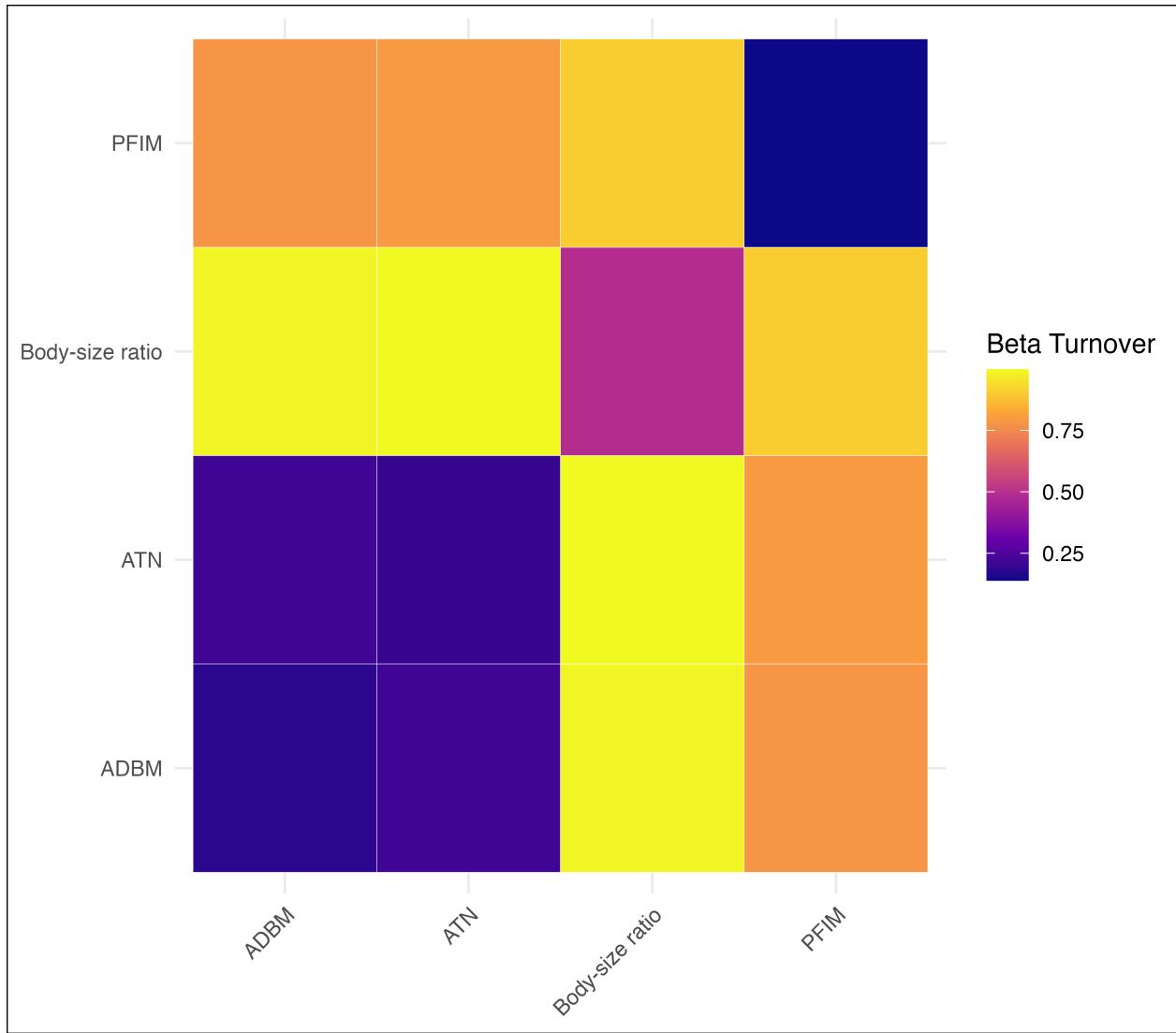


Figure 2: Pairwise  $\beta$ -turnover in species interactions among four ecological network models (ADBM, ATN, Body-size ratio, and PFIM). Each cell represents the mean turnover value between a pair of models, with warmer colours indicating greater dissimilarity in inferred interactions. The diagonal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

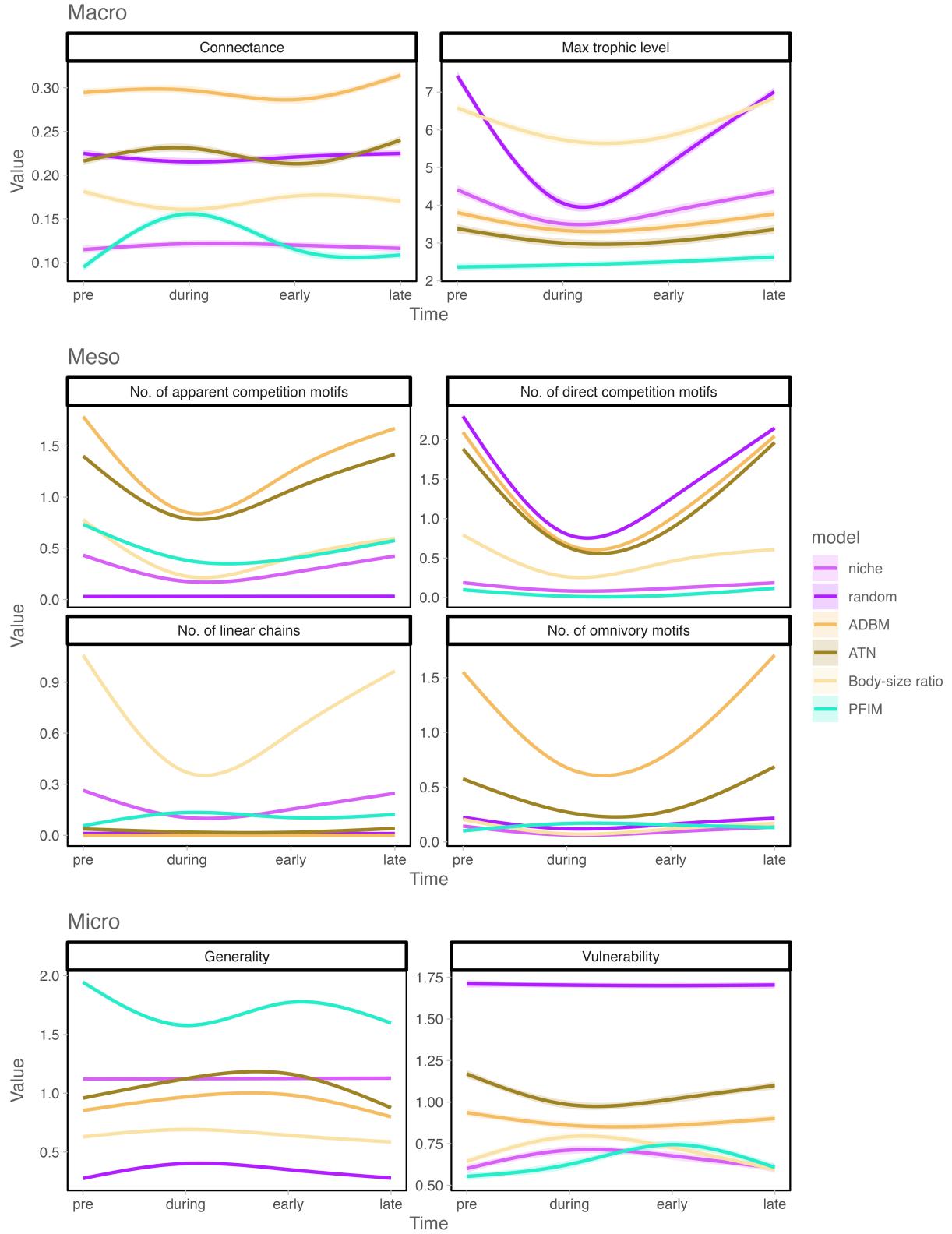


Figure 3: GAM-predicted trajectories of network structure during extinction simulations reveal pronounced differences in the timing and magnitude of change across reconstruction models. Lines show model-specific smooths and shaded areas indicate 95% confidence intervals. Deterministic approaches produce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

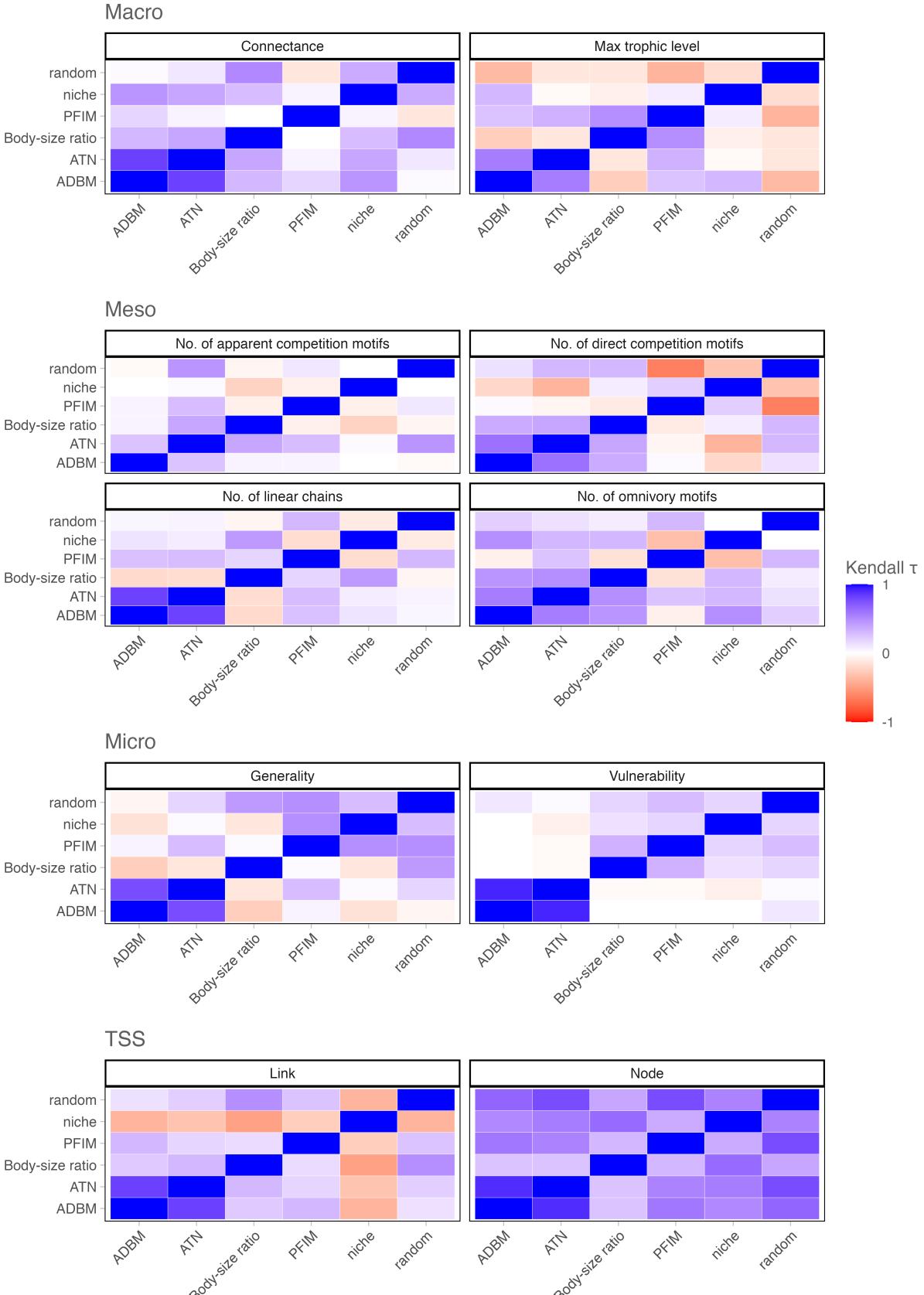


Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients ( $\tau$ ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between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