

# **Reconstructing food webs in deep time: Network models as explicit hypotheses for paleoecological inference**

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**Abstract:** Food webs provide a powerful framework for understanding ecosystem structure and function, yet reconstructing them in paleoecological contexts remains challenging because direct evidence of species interactions is rarely preserved. A growing array of models exists for predicting interactions and inferring network structure, but these approaches differ markedly in their assumptions, mechanisms, and data requirements. Here, we evaluate how network reconstruction model choice shapes ecological inference in deep time, and which aspects of inference are robust to alternative assumptions. 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 interaction loss, cascade dynamics, and temporal pathways of collapse. At the same time, models converged on similar species-level extinction patterns and dominant drivers, indicating that some ecological signals are robust across reconstruction assumptions. By framing food-web reconstructions as alternative ecological hypotheses rather than interchangeable representations, this study demonstrates how model choice conditions both the accuracy and precision of paleoecological inference, and provides a framework for identifying which conclusions about extinction dynamics in deep time are robust and which remain model dependent.

**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)	Null-model comparisons; testing whether observed network structure (connectance, motifs) deviates from random expectations
Niche	Networks are interval, species can be ordered on a 'niche axis'	richness, connectance	parameter assumptions, species	structural network	Williams & Martinez (2008)	Evaluating the influence of trophic hierarchy or intervality on network topology; generating baseline predictions for motifs and connectance

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference	Usage examples
Allometric diet breadth model (ADBM)	Interactions are determined by energetic costs (foraging ecology)	body mass, biomass (abundance)	does not account for forbidden links in terms of trait compatibility, assumptions on body size and biomass (abundance) from fossil data	realised network	Petchey et al. (2008)	Predicting realised predator diets under energy-maximization rules; exploring secondary extinctions and trophic bottlenecks
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 and biomass (abundance) from fossil data, assumptions as to the number of producer species	realised network	Brose et al. (2006); Gauzens et al. (2023)	Simulating effects of species loss on network structure; examining consequences of mechanical constraints on predator-prey interactions

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference	Usage examples
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)	Mapping feasible trophic interactions based on trait compatibility; assessing vulnerability and secondary extinctions in paleo-communities (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)	Estimating likely interaction networks from body-size constraints; evaluating cascading effects and network collapse under extinction scenarios (Yeakel et al., 2014).

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

90 **2.2.2 Network generation and replication**

91 We evaluated six models spanning this space Table 1: random and niche models (structural network); allometric  
 92 diet breadth (ADBM), allometric trophic network (ATN), and body-size ratio models (realised network);  
 93 and a paleo food-web inference model (PFIM; feasibility web). Expanded descriptions of model assumptions,

94 parameterisation, and link-generation rules are provided in Supplementary Material S1. For each of the  
 95 four communities, we constructed 100 replicate networks using each of the six models (2400 networks total).  
 96 Networks were simplified by removing disconnected species. For size-based models, body masses were drawn  
 97 from uniform distributions bounded by size-class limits, allowing for variance between replicates but preserves  
 98 relative sizes within replicates. We adopt uniform sampling by default, as alternative distributions (lognormal,  
 99 truncated lognormal) have negligible impact on topology (Supplementary Material S2; Figure S1). Structural  
 100 models were parameterised using connectance values drawn from an empirically realistic range (0.07 – 0.34)  
 101 while holding richness constant. The same parameter draws were used across comparable models within each  
 102 replicate. For the Body-size ratio model, we followed (Yeakel et al., 2014) and excluded latent trait terms,  
 103 rather than fitting the full model with additional inferred preferences.

### 104 **2.3 Network metrics and structural analyses**

105 We quantified network structure using a suite of macro-, meso-, and micro-scale metrics Table 2, capturing  
 106 global properties, motif structure, and species-level variability. Differences among models were assessed using  
 107 MANOVA, followed by univariate ANOVAs, post-hoc comparisons, and linear discriminant analysis. Pairwise  
 108 interaction turnover was quantified using link-based beta diversity, which measures dissimilarity in the identity  
 109 of trophic links between networks, capturing differences due to species turnover or changes in interactions  
 110 among shared species (Poisot et al., 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	
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	

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

## <sup>111</sup> 2.4 Extinction simulations and model evaluation

<sup>112</sup> Following Dunhill et al. (2024) and using the pre-extinction and post-extinction networks, we simulated  
<sup>113</sup> species loss under multiple extinction scenarios, including trait-based, network-position-based, and random  
<sup>114</sup> removals, allowing for secondary extinctions. Simulated post-extinction networks were compared to empirical  
<sup>115</sup> post-extinction communities using mean absolute differences (MAD) in network metrics and a modified true  
<sup>116</sup> skill statistic (TSS) at both node and link levels. Scenario rankings were compared across models using  
<sup>117</sup> Kendall's rank correlation coefficient.

<sup>118</sup> **3 Results**

<sup>119</sup> Across six network reconstruction approaches, inferred food-web structure, species interactions, and extinction  
<sup>120</sup> dynamics differed consistently. Multivariate analyses showed pronounced separation among models in  
<sup>121</sup> network metric space. Reconstruction approach explained most of the variance in structural properties,  
<sup>122</sup> leaving a distinct signature independent of community composition. Notably, agreement among models  
<sup>123</sup> depended on scale - approaches that were statistically similar in multivariate structural space often diverged in  
<sup>124</sup> inferred interactions or extinction dynamics. This demonstrates that structural similarity does not guarantee  
<sup>125</sup> concordance in species-level diets or trophic roles. Model choice also substantially influenced inferred extinction  
<sup>126</sup> dynamics. Temporal trajectories of network collapse, interaction loss, and motif reorganization differed among  
<sup>127</sup> approaches. Although species-level extinction rankings were often broadly consistent, link-level outcomes  
<sup>128</sup> and extinction inferences were highly sensitive to reconstruction assumptions. Together, these results show  
<sup>129</sup> that ecological inferences drawn from paleo networks depend critically on the reconstruction framework  
<sup>130</sup> employed. Importantly, agreement among models was not consistent across analytical scales - models that  
<sup>131</sup> were statistically indistinguishable in multivariate structural space often diverged in inferred interactions  
<sup>132</sup> or extinction dynamics. Together these results show that reconstruction approaches that appear similar  
<sup>133</sup> when evaluated using global network metrics can yield fundamentally different ecological narratives when  
<sup>134</sup> interrogated at the level of interactions and extinction dynamics.

<sup>135</sup> **3.1 Network structure differs among reconstruction approaches**

<sup>136</sup> To test whether network reconstruction approach influences inferred food-web structure, we compared  
<sup>137</sup> multivariate patterns of network metrics across all six models using a MANOVA. Network structure differed  
<sup>138</sup> strongly among reconstruction approaches (MANOVA, Pillai's trace = 3.84, approximate  $F_{40,11955} = 987.35$ ,  
<sup>139</sup>  $p < 0.001$ ). Univariate analyses showed that model choice explained a large proportion of variance in most  
<sup>140</sup> network metrics, with high partial  $\eta^2$  values for all network structural metrics. In several cases, reconstruction  
<sup>141</sup> approach accounted for the majority of observed variance ( $\text{partial } \eta^2 > 0.8$ ), indicating that model identity  
<sup>142</sup> dominated over stochastic variation among network replicates (Table S2. S3). Estimated marginal means and  
<sup>143</sup> Tukey-adjusted comparisons indicated consistent differences among reconstruction approaches, with PFIM  
<sup>144</sup> differing significantly from all other models ( $p < 0.0001$ ). Within the allometric frameworks we observed a  
<sup>145</sup> notable divergence between the ADBM and ATN models ( $p < 0.0001$ ), demonstrating that bioenergetic ranking  
<sup>146</sup> and mechanical-efficiency rules do not converge on a single structural solution. Interestingly, the only pair to  
<sup>147</sup> exhibit statistical consensus in multivariate space was the ADBM and the log-ratio model ( $p = 0.99$ ).

<sup>148</sup> Linear discriminant analysis (LDA) visualized distinctions among reconstruction approaches in multivariate

149 network space Figure 1. The first two axes explained 86% of between-model variance (LD1 = 53%, LD2 =  
150 33%). LD1 correlated most strongly with vulnerability ( $r = 0.86$ ), direct competition motifs ( $r = 0.81$ ), and  
151 connectance ( $r = 0.75$ ). LD2 correlated primarily with maximum trophic level ( $r = -0.76$ ) and, positively,  
152 with apparent competition motifs ( $r = 0.73$ ). These loadings suggest that the primary axis separates models  
153 by predation pressure and competitive overlap, while the secondary axis distinguishes models by vertical  
154 trophic structure. All higher-order axes explained less than 9% of the remaining variance (Tables S4–S5).

155 [Figure 1 about here.]

### 156 3.1.1 Inferred pairwise interactions vary widely among models

157 Building on differences in global network structure, we next examined how reconstruction approach influences  
158 species-level ecological inference by quantifying turnover in inferred pairwise interactions among networks  
159 constructed from the same taxon pool. While models that produced similar global metrics sometimes agreed  
160 broadly on network structure, they often differed in the specific interactions they inferred. In some cases,  
161 networks with comparable connectance and motif frequencies assigned fundamentally different consumer diets  
162 to the same taxa.

163 Pairwise -turnover revealed that some model pairs shared very few links despite comparable macro- or  
164 meso-scale properties Figure 2. ADBM and ATN were similar and likely reflects their shared reliance on  
165 ranked size-based constraints, which strongly shape realised diets even when emergent network structure  
166 differs. The body-size ratio model consistently exhibited high differences in pairwise interactions relative to  
167 all other approaches. PFIM showed intermediate overlap with size-based theoretical models. These patterns  
168 indicate that agreement in global network metrics does not guarantee agreement in species-level diets or  
169 trophic roles, highlighting the importance of evaluating both network- and species-level outcomes when  
170 comparing reconstruction methods. Consequently, agreement in global network properties does not guarantee  
171 concordance in inferred trophic roles, vulnerability, or competitive relationships among taxa.

172 [Figure 2 about here.]

### 173 3.2 Model choice influences inferred extinction dynamics

174 To quantify how network structure changed over time during extinction simulations and whether these  
175 dynamics differed among reconstruction models, we fit generalized additive models (GAMs) to time series  
176 of network-level metrics. GAMs capture nonlinear temporal trajectories, allowing formal tests of whether  
177 the shape of these trajectories differs among models. These model-specific temporal trajectories are shown  
178 in Figure 3. For all metrics examined, the inclusion of model-specific smooth terms significantly improved

model fit (ANOVA model comparison:  $p < 0.001$  for all metrics). Model-specific smooths differed not only in magnitude but also in the timing and abruptness of change, indicating distinct modes of collapse across reconstruction approaches (Tables S6–S7). Deterministic, data-driven approaches (PFIM) and allometric models (ADBM, ATN) exhibited highly non-linear trajectories, showing structural shifts in connectivity and motif frequency. In contrast, the Niche model produced the most consistent and gradual trajectories, effectively smoothing the perceived magnitude of structural change during community collapse. These results demonstrate that inferred pathways of collapse, trophic bottlenecks, and secondary extinctions are highly sensitive to model choice. Corresponding raw temporal trajectories are shown in Fig. S3.

[Figure 3 about here.]

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

[Figure 4 about here.]

206 **4 Discussion**

207 **4.1 Model choice as a component of ecological inference**

208 Reconstructing food webs from fossil data is inherently an exercise in inference under uncertainty. It requires  
209 not only assembling paleontological data but also making explicit assumptions about how species interact  
210 and how those interactions are represented mathematically (Dunne et al., 2008; Morales-Castilla et al., 2015;  
211 Strydom et al., 2026). This process parallels modern ecological network studies, where the tension between  
212 data limitations and meaningful ecological inference is well recognised (Delmas et al., 2019; Poisot et al., 2021).  
213 Here we demonstrate that the choice of network reconstruction model is itself a major ecological decision,  
214 shaping both the structural properties of inferred networks and downstream interpretations of extinction  
215 dynamics (Allesina & Tang, 2012; Solé & Montoya, 2001). Crucially, results show that the consequences of  
216 this decision depend on analytical scale and models that appear similar when evaluated using global network  
217 metrics can diverge substantially in inferred interactions and extinction dynamics.

218 Differences among models do not arise from the fossil evidence itself, but from assumptions embedded in each  
219 model family (Pichler & Hartig, 2023; Strydom et al., 2021). These assumptions include how trophic links  
220 are defined (trait compatibility versus energetic constraints), how interaction probabilities are parameterised,  
221 and whether network topology is guided by macroecological theory (*e.g.*, niche structure) or mechanistic  
222 rules (*e.g.*, body-size ratios). Consequently, network reconstruction is not neutral and it explicitly encodes  
223 ecological assumptions that shape inferred structure and downstream dynamical narratives. This sensitivity  
224 parallels challenges in modern network ecology, where model and metric selection influence interpretations of  
225 connectance, modularity, and motif distributions (Michalska-Smith & Allesina, 2019; Poisot & Gravel, 2014).

226 Multivariate analyses of network metrics reveal that reconstruction approach explains a large portion of  
227 variance in structural properties. These patterns demonstrate a strong, model-specific signature independent  
228 of community composition. While some models occasionally converged on some global metrics (*e.g.*, ADBM  
229 and log-ratio models), pairwise turnover revealed disagreements in inferred species-level interactions. Thus,  
230 structural similarity does not guarantee concordance in trophic roles, highlighting that uncertainty in  
231 reconstructed networks follows structured, predictable patterns rather than random noise. For example,  
232 allometric models tended to converge on similar species removal sequences while diverging in inferred interaction  
233 loss, whereas structural models dampened the apparent magnitude and variability of collapse. Comparing  
234 multiple reconstruction approaches provides a means to identify robust ecological signals while delineating  
235 areas where inference remains model-dependent.

236 Mechanistic models (PFIM) typically identify a broad landscape of trait-compatible interactions, theoretical

size-based models (ADBM, ATN, Body-size ratio) impose energetic filters to approximate realised diets, and structural models (niche, random) prioritise topological patterns over species identity. Notably, similarity relationships among models shifted across analyses, while the ADBM clustered most closely with the body-size ratio in multivariate structural space, its extinction dynamics aligned more closely with the ATN, underscoring that model agreement is context dependent. Temporal trajectories of network collapse, interaction loss, and motif reorganization varied markedly among approaches. Species-level extinction rankings were often broadly consistent across models. In contrast, link-level outcomes and secondary extinctions were highly sensitive to reconstruction assumptions. This reflects how extinction pathways depend on the specification of interactions, demonstrating that interaction-level inferences about cascade dynamics are inherently model dependent (Allesina & Tang, 2012; Curtsdotter et al., 2011; Dunne et al., 2002).

Taken together, these results underscore that network reconstruction is a hypothesis-generating process where each model encodes a distinct set of ecological assumptions, and the inferred structure and dynamics reflect these assumptions. Accordingly, paleoecologists should carefully align reconstruction approaches with the specific ecological signals of interest, whether potential interactions, realised diets, or macro scale structural properties. Disagreement among models does not imply that any single approach is ‘wrong’, but rather that different models capture different facets of ecological reality (Stouffer, 2019). Viewed through the lens of accuracy and precision, our results suggest that some paleoecological inferences are robust across reconstruction assumptions, while others remain intrinsically uncertain. Models consistently recover similar high-level extinction patterns, implying relative accuracy, but disagree on interaction-level details and temporal dynamics, indicating limited precision in reconstructing the fine structure of collapse. Recognizing and explicitly accounting for these differences is essential for advancing paleoecology beyond descriptive reconstruction toward rigorous comparative inference.

## 4.2 Aligning ecological questions with model choice

A central insight from this study is that different ecological questions require different network representations, echoing broader efforts in network ecology to clarify what models and metrics can validly infer about ecological systems (Gauzens et al., 2025; Strydom et al., 2026). Here we identify a conceptual divide among feasible, realised, and structural networks, providing a practical framework to match research goals with appropriate reconstruction approaches.

**Feasibility networks:** (*e.g.*, trait- and phylogeny-based metaweb approaches) are most suitable for exploring potential trophic links and dietary breadth. These models capture the set of interactions that are biologically plausible given species traits, even if not all are realised in a particular community, aligning with metaweb

268 concepts in modern ecology (Tylianakis & Morris, 2017). As reflected in our PFIM results, such approaches  
269 maximise interaction diversity but are less suited to inferring realised extinction cascades.

270 **Realised networks:** (*e.g.*, allometric or energetic models such as ADBM, ATN, and body-size ratio  
271 approaches) are appropriate when the goal is to infer the most likely interactions. By embedding energetic or  
272 foraging rules, these models approximate realised diets and energy transfer, improving ecological plausibility  
273 compared to purely combinatorial approaches (Brose et al., 2006; Petchey et al., 2008). In our analyses, these  
274 models consistently produced more abrupt and nonlinear collapse trajectories, reflecting the propagation of  
275 energetic constraints during extinction.

276 **Structural networks:** (*e.g.*, niche, cascade) focus on topological patterns rather than species identity,  
277 making them useful when broad questions about connectance, trophic depth, or motif frequency are the focus.  
278 Such models have a long history as null frameworks in network ecology (Allesina et al., 2008; Williams &  
279 Martinez, 2008).

280 Recognising this alignment helps avoid misinterpretation; for instance, treating predicted metaweb links as  
281 realised interactions conflates potential and actual diets, potentially exaggerating inferred interaction diversity.

### 282 4.3 Implications for paleoecological network studies

283 Findings carry three key implications for paleoecology:

284 1. **Explicitly acknowledge model assumptions:** Interpretations of ancient food webs must clearly  
285 articulate the assumptions underlying reconstruction models. Without this, differences between networks  
286 from different datasets or research groups could be misattributed to ecological variation rather than  
287 methodological choice.

288 2. **Standardise comparative frameworks:** When comparing food webs across studies, networks  
289 should be constructed and analysed using comparable model families. Failing to do so risks conflating  
290 methodological differences with ecological or temporal variation.

291 3. **Leverage modern theory to expand inference:** Integrating modern network ecology frameworks  
292 and methods enriches the paleoecological toolkit(Dunne et al., 2014; Solé & Montoya, 2001). Models  
293 developed for modern systems can be adapted to the constraints of fossil data (*e.g.*, Perez-Lamarque et  
294 al., 2026), enabling more nuanced insights into deep-time dynamics.

295 **4.4 Recommendations for network reconstruction in paleoecology**

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

- 298 **1. Define the Inferential Goal First:** Before reconstructing networks, researchers should articulate  
299 whether they aim to infer potential interactions, likely realised diets, or general structural properties.  
300 This will inform the selection of an appropriate model family consistent with the ecological question at  
301 hand (*e.g.*, metaweb for complete diets, energetic models for trophic energy flows, or structural models  
302 for generic topologies)
- 303 **2. Use ensemble and sensitivity frameworks:** Rather than relying on a single model output, researchers  
304 should adopt ensemble approaches that generate and compare multiple network reconstructions. This  
305 not only quantifies model uncertainty but also reveals which ecological conclusions are robust biological  
306 signals and which are methodological artifacts.
- 307 **3. Standardise cross-study comparisons:** Comparisons of networks from different palaeoecological  
308 studies should be standardised by model family. When models differ, interpretations about ecological or  
309 environmental change should explicitly address how model choice may contribute to observed differences.
- 310 **4. Interpret scale-specific results with caution:** Because robustness to model choice varies by  
311 scale (with node-level patterns more consistent than interaction-level outcomes) researchers should  
312 prioritise interpretations at the appropriate scale. Structural conclusions about cascade pathways or  
313 secondary extinctions should be framed as model-dependent hypotheses rather than definitive historical  
314 reconstructions.

315 **4.5 Future directions**

316 Advances in modern network ecology offer several promising directions for paleoecology. These include  
317 probabilistic and Bayesian approaches to quantify uncertainty in link prediction (Baskerville et al., 2011;  
318 Elmasri et al., 2020), maximum entropy methods to infer network structure under limited data (Banville et  
319 al., 2023), and multi-layer network representations that integrate trophic and non-trophic interactions (Pilosof  
320 et al., 2017). Combined with increasingly available trait and phylogenetic information, such developments  
321 can bridge fossil constraints and ecological inference, enabling more nuanced, probabilistically grounded  
322 reconstructions of deep-time ecosystems (Banville et al., 2025; Perez-Lamarque et al., 2026; Poisot et al.,  
323 2016).

324 **5 Conclusions**

325 Ecological network reconstruction in deep time is not merely a technical step but a fundamental component  
326 of ecological inference. By explicitly comparing six contrasting reconstruction approaches for a single  
327 extinction event and location, we show that model choice strongly shapes inferred food-web structure, species  
328 interactions, and extinction dynamics (even when the underlying fossil data are identical). While broad,  
329 trait-based patterns of species loss are relatively robust, conclusions about pairwise interactions, secondary  
330 extinctions, and cascading dynamics depend critically on the assumptions embedded in the chosen network  
331 reconstruction approach. By contrast, interaction and extinction based interpretations are far more sensitive  
332 to reconstruction assumptions, and should be treated as model-dependent hypotheses rather than definitive  
333 historical outcomes. Network reconstruction is inherently hypothesis-driven: each model encodes distinct  
334 ecological assumptions that influence both network structure and inferred dynamics. No single approach  
335 captures all aspects of past ecosystems, but careful alignment of model choice with research goals, combined  
336 with ensemble or comparative frameworks, allows robust inference while quantifying uncertainty. These results  
337 underscore the need for paleoecological studies to evaluate the sensitivity of key conclusions to alternative  
338 network representations and highlight that understanding past ecosystem collapse requires not only better  
339 fossil data, but also transparent, question-driven modelling frameworks that explicitly encode and interrogate  
340 the assumptions underlying ecological inference.

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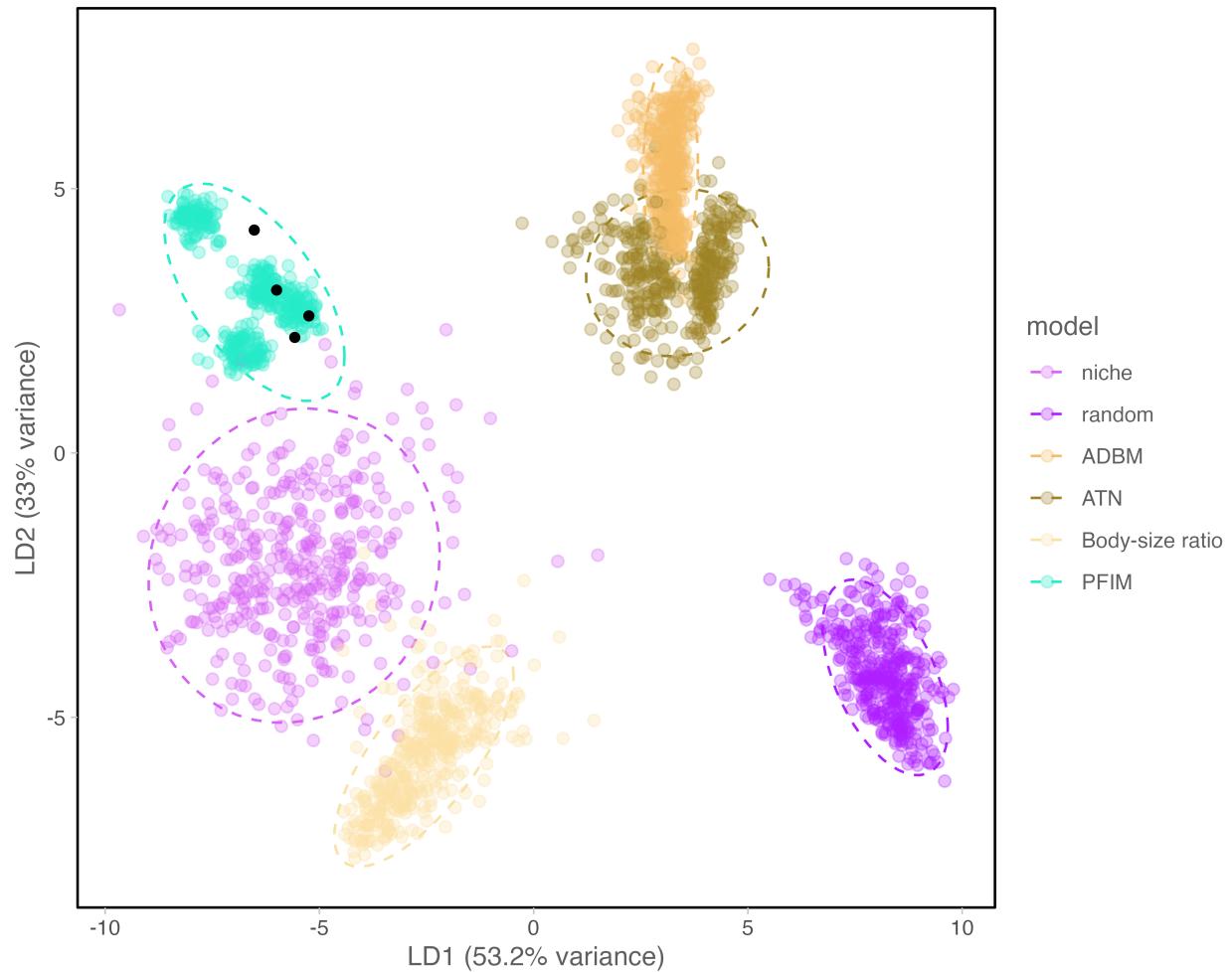


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

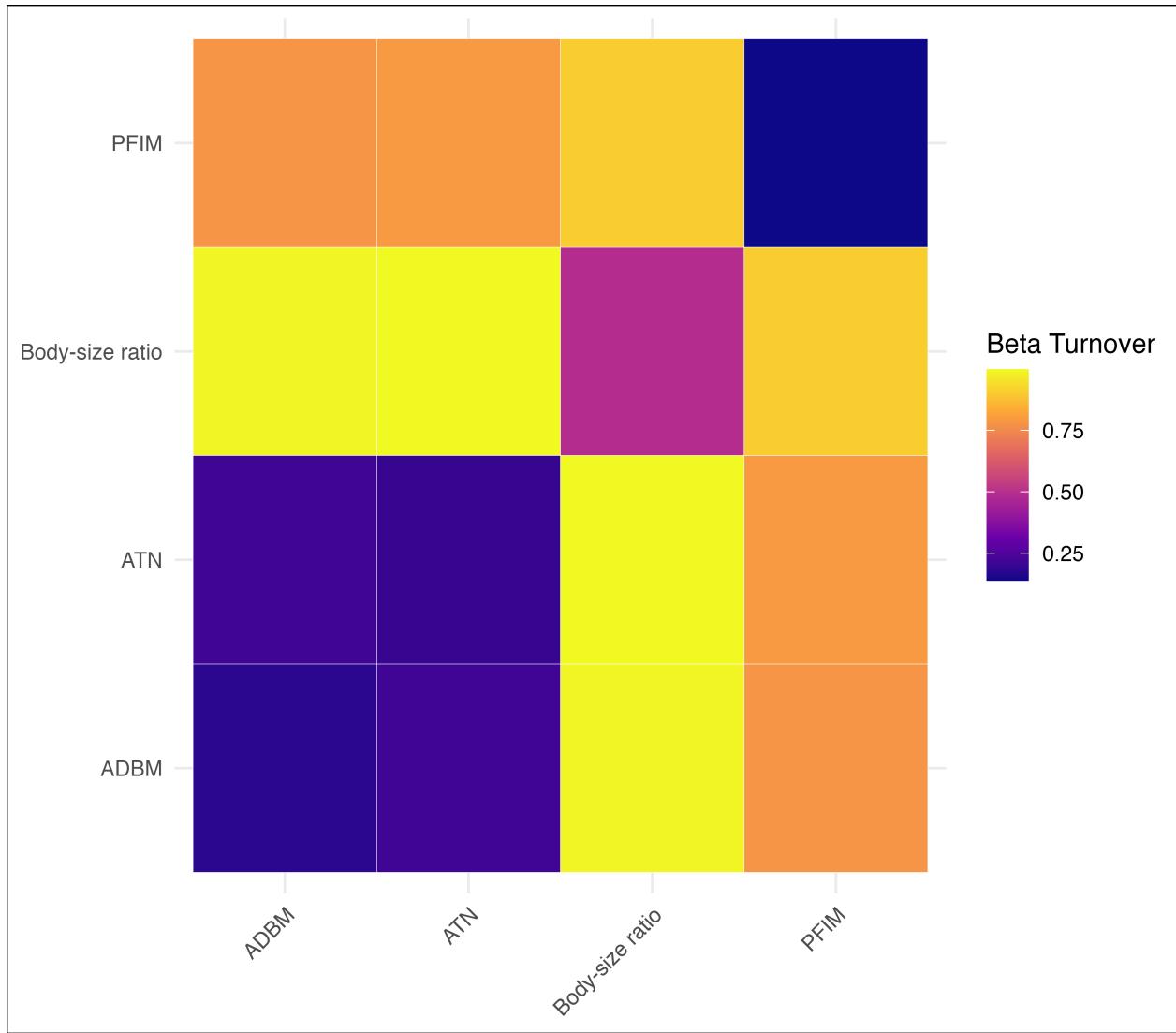


Figure 2: Pairwise  $\beta$ -turnover in species interactions among four ecological network models (ADBM, lmatrix, body-size ratio, and pfim). Each cell represents the mean turnover value between a pair of models, with warmer colors indicating greater dissimilarity in inferred interactions. The diagonal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

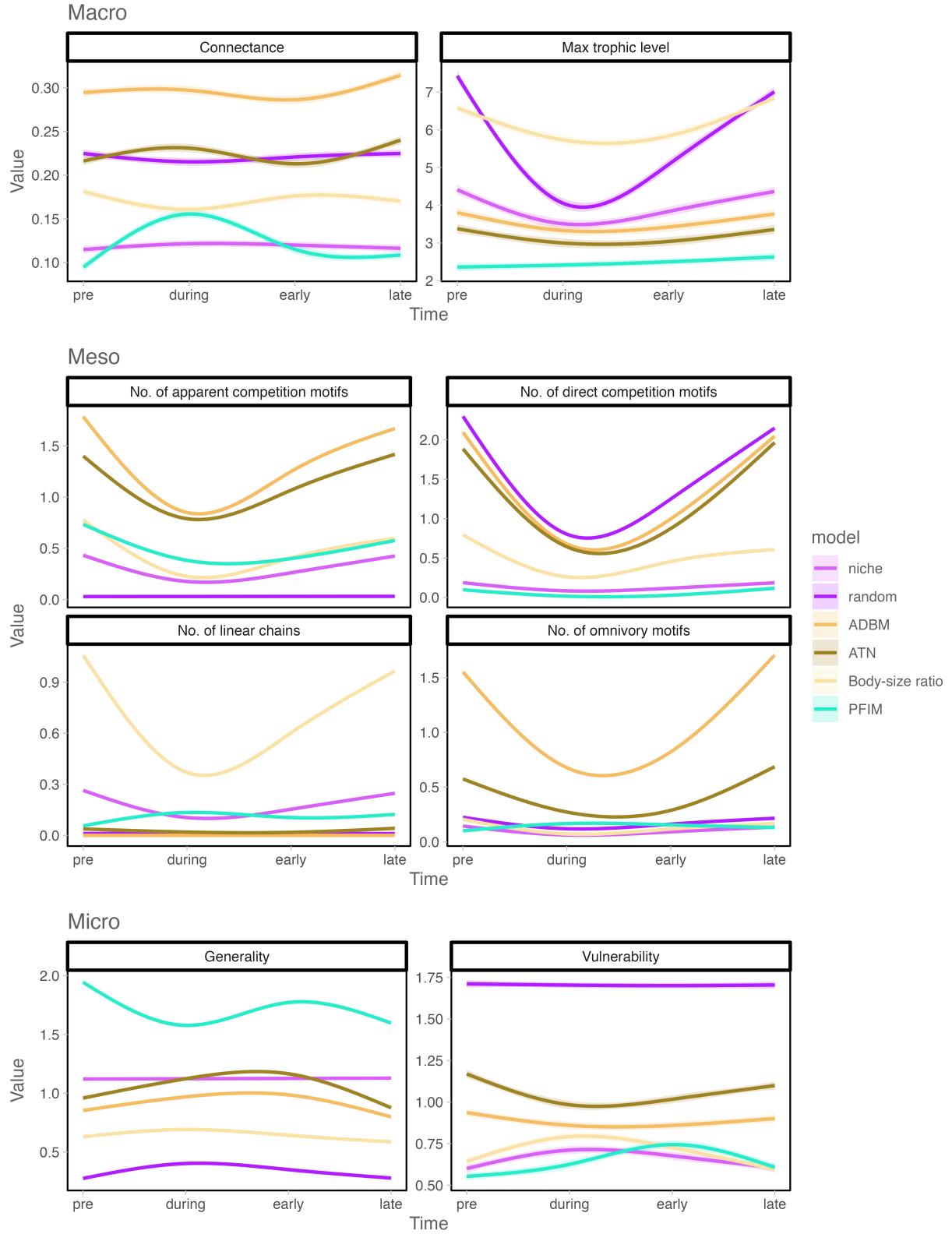


Figure 3: GAM-predicted trajectories of network structure during extinction simulations reveal pronounced differences in the timing and magnitude of change across reconstruction models. Lines show model-specific smooths and shaded areas indicate 95% confidence intervals. Deterministic approaches produce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

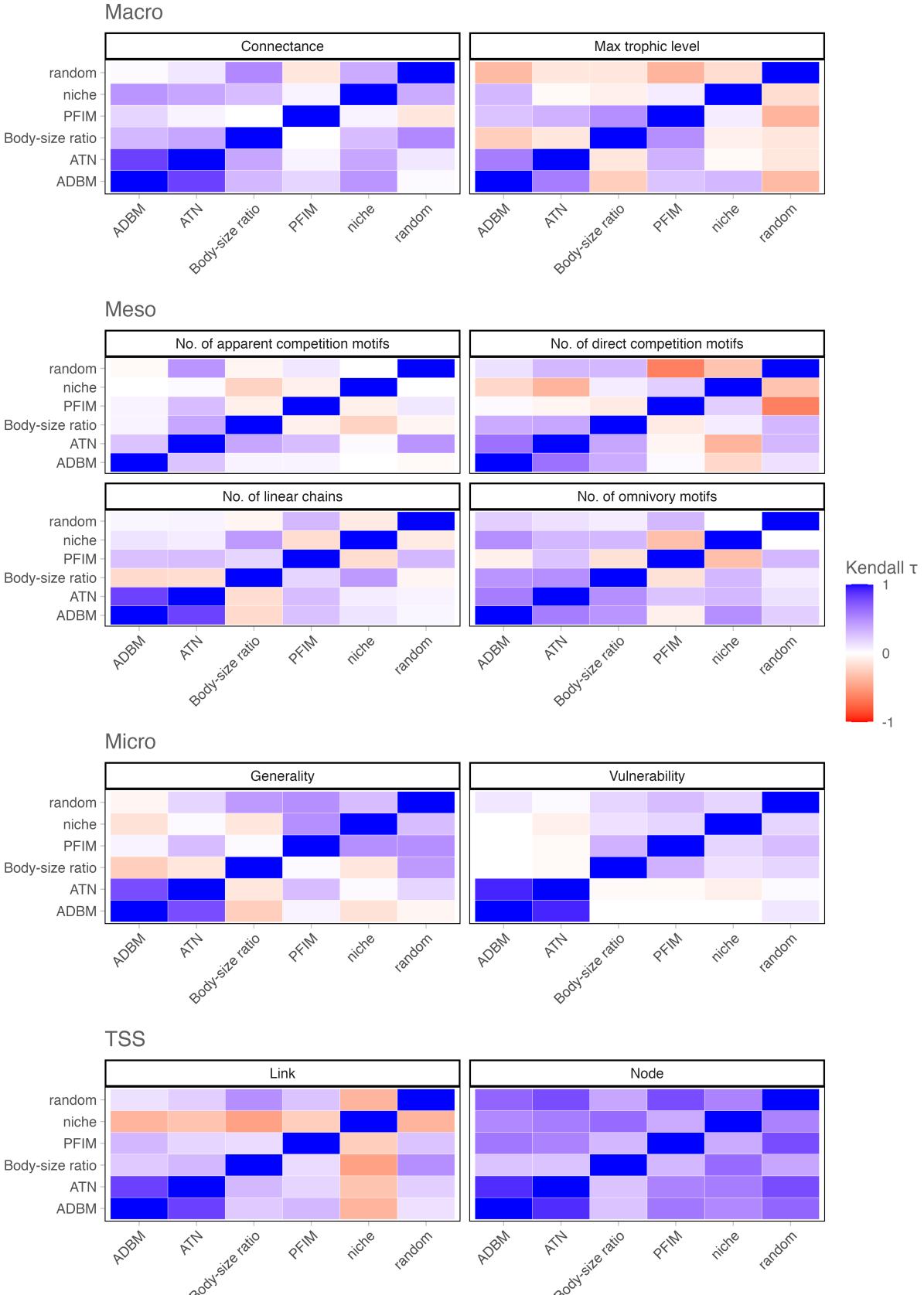


Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients ( $\tau$ ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between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