

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, late Pliensbachian–late 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 1 Introduction

² Understanding how biodiversity is organised across space and time is a central goal of macroecology and
³ biogeography. While early efforts focused primarily on species richness and composition, there is growing
⁴ recognition that ecological communities are structured not only by which species occur, but by how they
⁵ interact (Thuiller et al., 2024). Interaction networks are increasingly treated as macroecological state variables
⁶ where they are used to compare community organisation across environmental gradients, to quantify -diversity
⁷ in interaction structure, to evaluate stability-complexity relationships, and to infer vulnerability under global
⁸ change (Carstensen et al., 2014; Gravel et al., 2019; Poisot et al., 2015; Trøjelsgaard & Olesen, 2016; Tylianakis
⁹ & Morris, 2017).

¹⁰ As a result, ecological networks now play a central role in comparative analyses spanning latitudinal gradients,
¹¹ disturbance regimes, and deep-time environmental transitions (Dunhill et al., 2024; Hao et al., 2025; Michalska-
¹² Smith & Allesina, 2019; Poisot & Gravel, 2014; Roopnarine, 2006). Implicit in this expansion is the critical
¹³ assumption that network properties estimated across systems are structurally comparable, and that differences
¹⁴ among them reflect ecological signal rather than methodological artefact (Fründ et al., 2016; Jordano, 2016).

¹⁵ Yet most ecological networks are not fully observed as interaction data are incomplete and sampling is
¹⁶ uneven across historical and biogeographic contexts, across both contemporary and deep-time (Catchen et
¹⁷ al., 2023; Poisot et al., 2021; Sandra et al., 2025). Interactions must often be inferred indirectly from traits,
¹⁸ phylogeny, body size, co-occurrence, or theoretical constraints (Morales-Castilla et al., 2015; Strydom et
¹⁹ al., 2021). Network construction therefore constitutes a model-based inference step rather than a purely
²⁰ descriptive exercise. Different reconstruction frameworks encode distinct ecological assumptions about how
²¹ interactions arise - whether as biologically feasible combinations of traits, energetically optimised realised diets,
²² or topological structures constrained by macroecological regularities. These assumptions act as structural
²³ priors over network architecture (Gauzens et al., 2025; Guimarães, 2020; Petchey et al., 2011; Strydom et
²⁴ al., 2026). If alternative reconstruction models systematically generate different trophic configurations, then
²⁵ comparative analyses risk conflating ecological differences among communities with artefacts introduced by
²⁶ modelling choice. The reliability of macroecological inference therefore depends not only on ecological data,
²⁷ but on the structural assumptions embedded in network reconstruction.

²⁸ Despite rapid methodological development in interaction inference, few studies have directly evaluated how
²⁹ alternative reconstruction frameworks condition macroecological conclusions when applied to the same species
³⁰ pool. This gap is particularly consequential for comparative research, where network metrics are routinely
³¹ interpreted as indicators of environmental filtering, disturbance intensity, evolutionary history, or community

32 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; Dunne et al., 2008; Dunne et al., 2014;
40 Karapunar et al., 2026; Roopnarine, 2006), rendering modelling assumptions transparent. Against this
41 stringency, here we re-evaluate inferences made by Dunhill et al. (2024) on community structure and
42 extinction dynamics during the early Toarcian extinction event (~183 Ma), a volcanic-driven hyperthermal and
43 marine crisis in the Early Jurassic (Kemp et al., 2024). Crucially, this re-evaluation allows us to test a pivotal
44 but often overlooked possibility - that the ecological narratives regarding community stability or collapse
45 might be as much a product of the specific reconstruction method chosen as they are of the fossil data itself.
46 By applying alternative models, we can determine if Dunhill et al. (2024) conclusions remain robust or if a
47 different choice of reconstruction method would have led to fundamentally different inferences about extinction
48 dynamics. Using four successive communities drawn from an identical taxon pool, we reconstruct ecological
49 networks under six contrasting model classes spanning feasible, realised, and structural representations. For
50 each reconstruction framework, we quantify emergent topology across scales, measure interaction turnover,
51 and simulate disturbance-driven collapse. By holding species composition constant while varying the food web
52 model used, this design isolates the influence of model constrained structure on inferred food web organisation
53 and extinction dynamics, allowing us to distinguish ecological signals that are robust from those that are
54 reconstruction contingent.

55 **2 Methods**

56 **2.1 Study system and fossil data**

57 We used fossil occurrence data from the Cleveland Basin spanning the upper Pliensbachian to the upper
58 Toarcian. This interval encompasses a major volcanic-driven hyperthermal and marine extinction event. To
59 capture network dynamics across this transition, we defined four successive paleo-communities: Pre-extinction
60 (Pliensbachian), Post-extinction (Lower Toarcian), Early recovery, and Late recovery (Middle/Upper Toarcian).
61 Each taxon was characterized using their size and Bambach's ecospace framework (Bambach et al., 2007),

62 coding for tiering, motility, and feeding mode as per Dunhill et al. (2024). Each assemblage was treated
63 as a community of potentially interacting taxa. The dataset includes 57 taxa across diverse groups (*e.g.*,
64 cephalopods, bivalves, and gastropods). By restricting our analysis to a single basin with consistent lithofacies,
65 we controlled for biogeographic noise, ensuring that structural shifts across the four time-bins reflect localised
66 ecological responses to environmental stress rather than sampling or facies bias.

67 **2.2 Network reconstruction approaches**

68 **2.2.1 Conceptual classification of network types**

69 Most paleo-specific research (*e.g.*, Fricke et al. (2022); Roopnarine (2006); Shaw et al. (2024)) currently uses
70 models from within the feasibility space. That is, the model reconstructions identify and encode the entire
71 feasible diet of a species to build the network. These methods, however, represent only a subset of the broader
72 spectrum of network construction approaches. Here, we present a suite of methods (Table 1) that enable
73 the construction of a wider range of ecological networks and the exploration of a broader set of ecological
74 questions, provided that their underlying assumptions are compatible with the constraints of fossil data. The
75 methods include a) structural models that create species agnostic networks that are structurally ‘correct’ by
76 assigning links between nodes based on assumptions of link distributions; and b) realised models that create
77 networks where links between species are constrained based on some form of ‘species choice’ *e.g.*, maximising
78 energy gain.

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 | 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 | 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. |

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

85 **2.2.2 Network generation and replication**

86 We evaluated six models spanning this space Table 1: random and niche models (structural networks);
87 allometric diet breadth (ADBM), allometric trophic network (ATN), and Body-size ratio models (realised
88 networks); and a paleo food web inference model (PFIM; feasibility network). Expanded descriptions of
89 model assumptions, parameterisation, and link-generation rules are provided in Supplementary Material
90 S1. For each community, 100 networks were generated per model per successive community ($n = 2400$) to
91 capture stochastic variation in link assignment. Where models required species body mass or trait values,
92 these were sampled within biologically reasonable ranges to preserve relative differences among species. We
93 adopted uniform sampling by default, as alternative distributions (lognormal, truncated lognormal) have
94 negligible impact on topology (Supplementary Material S2; Figure S1). Structural models were parameterized
95 using connectance values drawn from an empirically realistic range (0.07 – 0.34), with species richness held
96 constant. Identical parameter draws were applied across comparable models within each replicate to ensure
97 comparability. For the Body-size ratio model, we followed the approach of Yeakel et al. (2014) and excluded
98 latent trait terms as opposed fitting the full model, which introduces additional inference and assumptions.

99 **2.3 Network metrics and structural analyses**

100 We quantified network structure using a suite of macro-, meso-, and micro-scale metrics Table 2, capturing
101 global properties, motif structure, and species-level variability. Differences among reconstruction approaches
102 were assessed using a multivariate analysis of variance (MANOVA), with model identity as a fixed factor
103 and the full set of network metrics as response variables. Pairwise interaction turnover was quantified using
104 link-based -diversity following the framework of Poisot et al. (2012). For each pair of reconstructed networks,
105 we represented trophic interactions as binary adjacency matrices and calculated their dissimilarity. Specifically
106 we looked at interaction rewiring among shared species (β_{OS}), which allows separation of differences arising
107 from altered interaction identities among species common to both networks. All calculations were performed
108 for all model combinations within the same community (time bin).

Table 2: Network properties used for analysis.

| Metric | Definition | Scale | Reference |
|-------------|--|-------|-----------|
| Connectance | L/S^2 , where S is the number of species and L the number of links | Macro | |

| Metric | Definition | Scale | Reference |
|-------------------|--|-------|--|
| 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) |

109 2.4 Extinction simulations and model evaluation

110 Following Dunhill et al. (2024), we simulated species loss from Pre-extinction networks under trait-based,
 111 network-position-based, and random removal scenarios. Species were deleted sequentially, with cascading
 112 secondary extinctions allowed to propagate. Simulated post-extinction states were compared to ‘observed’
 113 networks using mean absolute differences (MAD) of food-web metrics Table 2 and modified true skill statistics
 114 (TSS) calculated separately at the node level (species presence/absence) and link level (presence/absence of
 115 interactions between species pairs). Scenarios were ranked within each reconstruction framework based on
 116 MAD and TSS performance, and Kendall’s rank correlation coefficient () was used to quantify concordance
 117 in scenario ordering across models. Full methodological details are provided in the Supplementary Materials.

118 **2.5 Software and Reproducibility**

119 Ecological network reconstruction and extraction of structural metrics were conducted in Julia v1.11.4
120 (Bezanson et al., 2017). All statistical analyses, model fitting (MANOVA, PERMANOVA, GAMs), and figure
121 production were performed in R v4.5.2 (R Core Team, 2024). The empirical data, derived network datasets
122 and code implementing network reconstruction, extinction simulations, and all analytical workflows is archived
123 at [Zenodo DOI].

124 **3 Results**

125 Results show that reconstruction approaches that appear similar when evaluated using global network metrics
126 can yield fundamentally different ecological narratives when interrogated at the level of interactions and
127 extinction dynamics. Across six network reconstruction approaches, inferred food web structure, species
128 interactions, and extinction dynamics differed consistently. Multivariate analyses showed pronounced separation
129 among models in network metric space. Reconstruction approach explained most of the variance in structural
130 properties, leaving a distinct signature independent of community composition. Notably, agreement among
131 models depended on the scale at which the comparison was made- approaches that were statistically similar in
132 multivariate structural space (scale 1) often diverged in inferred interactions (scale 2) or extinction dynamics
133 (scale 3). This demonstrates that structural similarity does not guarantee concordance in species-level diets or
134 trophic roles.

135 Model choice substantially influenced inferred extinction dynamics. Temporal trajectories of network collapse,
136 interaction loss, and motif reorganization differed among approaches. Although species-level extinction
137 rankings were often broadly consistent, link-level outcomes and extinction inferences were highly sensitive
138 to reconstruction assumptions. Together, these results show that ecological inferences drawn from networks
139 depend critically on the reconstruction framework employed.

140 **3.1 Network structure differs among reconstruction approaches**

141 Across six reconstruction approaches, network structure (network properties listed in Table 2) differed
142 significantly (MANOVA, Pillai's trace = 3.84, approximate $F_{40,11955} = 987.35$, $p < 0.001$), indicating that
143 model choice systematically alters inferred food web topology. Canonical discriminant analysis identified two
144 dominant axes of variation, explaining 86% of between-model variance. LD1 correlated with vulnerability,
145 direct competition motifs, and connectance. LD2 correlated with maximum trophic level and apparent
146 competition motifs, reflecting vertical trophic structure (Figure 1; Table S1, Figure S1). All higher-order

¹⁴⁷ canonical variates each explained less than 9% of the remaining variance.

¹⁴⁸ [Figure 1 about here.]

¹⁴⁹ **3.1.1 Variance partitioning of network structure**

¹⁵⁰ Permutational multivariate analysis of variance revealed that reconstruction framework accounted for the
¹⁵¹ majority of variation in multivariate network structure ($R^2 = 0.795$, $p < 0.001$), whereas temporal turnover
¹⁵² across extinction phases explained a comparatively small proportion of variance ($R^2 = 0.064$, $p < 0.001$).
¹⁵³ The model \times time interaction contributed a further 7.1% of variance ($R^2 = 0.071$, $p < 0.001$), indicating
¹⁵⁴ limited but significant time-dependent divergence among reconstruction frameworks. Thus, differences among
¹⁵⁵ modelling approaches were more than an order of magnitude greater than structural differences associated
¹⁵⁶ with ecological turnover through the extinction sequence, even if the Toarcian dataset was characterized with
¹⁵⁷ a significant community turnover.

¹⁵⁸ To determine whether the dominance of the reconstruction framework reflected absolute mean shifts among
¹⁵⁹ time bins, we repeated the analysis after centring network metrics within each extinction phase. This procedure
¹⁶⁰ removes between-phase differences while retaining within-phase structural variation. Even after temporal
¹⁶¹ bin-standardised centring, the reconstruction framework explained 84.8% of multivariate variance ($R^2 = 0.848$,
¹⁶² $p < 0.001$). These results demonstrate that the influence of model choice is not driven by temporal mean
¹⁶³ differences, but reflects intrinsic divergence among reconstruction frameworks in how ecological interactions
¹⁶⁴ are organised.

¹⁶⁵ **3.1.2 Statistical Drivers of Network Variation**

¹⁶⁶ The structural organization of the reconstructed food webs was dictated by the choice of modeling framework,
¹⁶⁷ which exerted a significantly stronger influence on network topology than the ecological signal of species loss.
¹⁶⁸ A two-way factorial ANOVA across all eight network metrics confirmed that the reconstruction approach
¹⁶⁹ was the dominant driver of variance, with partial eta-squared values (η_p^2) consistently exceeding 0.82 and
¹⁷⁰ reaching 0.97 for meso-scale motifs (Figure 2; Table S3). While the extinction event (time bin) significantly
¹⁷¹ altered network structure ($p < 0.001$), its relative importance remained secondary, typically explaining a
¹⁷² smaller fraction of the total topological variation. This is clear in Figure 2 where all metrics are within the
¹⁷³ bottom-right (model-dominated) quadrant of this space, emphasising that framework assumptions outweigh
¹⁷⁴ the ecological signal of species loss. Furthermore, the high inter-model Coefficient of Variation (CV) observed
¹⁷⁵ for some metrics (Table S4, Figure S4) highlights a sensitivity. The properties that are influenced by time
¹⁷⁶ are also those upon which the models disagree most profoundly. Demonstrating that our understanding of

177 structural food web collapse in the fossil record is highly contingent on the chosen reconstruction framework,
178 particularly when examining complex trophic pathways beyond simple macro-scale properties like connectance.

179 [Figure 2 about here.]

180 **3.1.3 Inferred pairwise interactions vary widely among models**

181 Despite some models showing similar global metrics, specific pairwise interactions often differed. Pairwise
182 -turnover revealed that certain model pairs shared very few links Figure 3. Size-based models (ADBM,
183 ATN) were broadly similar due to shared sole reliance on body-size constraints, whereas the Body-size ratio
184 model exhibited consistently higher differences to other models. PFIM showed intermediate overlap with
185 theoretical models. These results demonstrate that agreement in global network structure does not guarantee
186 concordance in species-level interactions.

187 [Figure 3 about here.]

188 **3.2 Model choice influences inferred extinction dynamics**

189 To evaluate how model choice affects inferred extinction dynamics, we compared simulated post-extinction
190 networks to observed networks using mean absolute differences (MAD) for network-level metrics and true
191 skills statistics (TSS) for node- and link-level outcomes Figure 4. Across models, MAD-based rankings were
192 generally positively correlated (Kendall's $\tau = 0.13$ across structural metrics), indicating broad agreement on
193 the relative importance of extinction drivers despite substantial differences in reconstructed network structure.
194 However, agreement within the allometric models differed from patterns observed for reconstructed network
195 structure.

196 Node-level TSS rankings were similarly consistent across models ($\tau = 0.26\text{--}0.90$), reflecting broadly comparable
197 species removal sequences. In contrast, link-level outcomes were far more variable ($\tau = -0.48\text{--}0.29$), highlighting
198 that inferences about which interactions are lost, retained, or re-established during collapse and recovery are
199 highly model contingent. Together, these results suggest that while alternative models converge on similar
200 species-level extinction patterns, the inferred pathways of interaction loss and cascading dynamics depend
201 strongly on both reconstruction approaches.

202 [Figure 4 about here.]

203 **4 Discussion**

204 **4.1 Network reconstruction is not neutral: structural priors shape ecological
205 theory**

206 Food web ecology has long treated network reconstruction as a technical step preceding ecological analysis.
207 Once a network is assembled (whether from observation, inference, or simulation) its properties are typically
208 analysed as reflections of underlying ecological organisation. Implicit in this workflow is a powerful assumption
209 - that reconstructed networks provide structurally comparable representations of ecological communities, such
210 that differences in connectance, trophic structure, motif composition, or robustness primarily reflect biological
211 variation.

212 This assumption is particularly critical to evaluate within the context of deep-time paleoecological data. Because
213 interactions in fossil ecosystems are never observed directly, they must explicitly be reconstructed through some
214 form of reconstruction approach. This necessity renders the underlying assumptions transparent but also makes
215 the resulting ecological narratives highly susceptible to the constraints inherent in the chosen reconstruction
216 framework. In these settings the risk is not just incomplete data, but the potential for methodological artefacts
217 to be misinterpreted as genuine macroevolutionary or paleoecological signals. Consequently, deep-time studies
218 offer a unique and stringent testing ground for determining whether community-level responses (such as
219 stability or collapse during mass extinctions) are robust features of the ecosystem or merely byproducts of
220 how we choose to construct the links between species.

221 Our results challenge this assumption and reveal strong sensitivity of inference about secondary extinction
222 dynamics in paleo-foodwebs. Across an identical species pool, reconstruction frameworks explained the majority
223 of variance among reconstructed network topologies, generating distinct structural signatures independent of
224 community composition. Demonstrating that the divergence among reconstruction approaches reflects intrinsic
225 differences in how models organise interactions, not temporal shifts in network structure. The dominance
226 of these structural signatures is systemic. Reconstruction frameworks occupy distinct and non-overlapping
227 regions of multivariate space Figure 1, with the model identity explaining nearly all of the observed variance.
228 Even when focusing on individual metrics, it is the choice of reconstruction approach that drives the observed
229 differences through the extinction interval Figure 2. This suggests that in paleo-food webs, the structure of
230 the network is pre-defined by the chosen reconstruction approach, leaving the extinction process to merely
231 reorganize the remaining links within a strictly pre-constrained architectural space. Network structure is
232 therefore not solely a property of ecological communities; it is jointly determined by ecological data, modelling
233 assumptions, and level of organisation (Gauzens et al., 2025; Guimarães, 2020; Pichler & Hartig, 2023;

²³⁴ Strydom et al., 2021; Strydom et al., 2026).

²³⁵ Reconstruction framework explained the majority of variance in inferred food web topology, far outweighing
²³⁶ the influence of temporal turnover across extinction phases. These patterns demonstrate that the divergence
²³⁷ among reconstruction approaches reflects intrinsic differences in how models organise interactions, not temporal
²³⁸ shifts in network structure. In other words, different reconstruction approaches impose distinct structural
²³⁹ priors on inference of ecological organisation. These priors are not subtle - they propagate into emergent
²⁴⁰ topology, species roles, and dynamical predictions. Network structure is therefore not solely a property
²⁴¹ of ecological communities; it is jointly determined by ecological data, modelling assumptions, and level of
²⁴² organisation (Gauzens et al., 2025; Guimarães, 2020; Pichler & Hartig, 2023; Strydom et al., 2021; Strydom
²⁴³ et al., 2026).

²⁴⁴ This has direct implications for the interpretation of comparative network studies. Feasible, realised, and
²⁴⁵ structural models encode different assumptions about constraint, optimisation, and topology, with these
²⁴⁶ assumptions propagating into emergent metrics and dynamical predictions (Allesina & Tang, 2012; Dunne et
²⁴⁷ al., 2002; Michalska-Smith & Allesina, 2019; Poisot & Gravel, 2014; Solé & Montoya, 2001). When networks
²⁴⁸ reconstructed under different model classes are compared across spatial gradients, disturbance regimes, or
²⁴⁹ evolutionary transitions, part of the observed variation may derive from reconstruction choice rather than
²⁵⁰ ecological process. Without explicit standardisation or sensitivity analysis, methodological heterogeneity can
²⁵¹ be mistaken for biological signal. Food web ecology has devoted substantial effort to understanding how
²⁵² topology shapes dynamics; comparatively less attention has been paid to how reconstruction method shapes
²⁵³ topology. Our findings indicate that these two questions cannot be separated.

²⁵⁴ 4.2 Scale-dependent robustness in network-based inference

²⁵⁵ Importantly, reconstruction sensitivity was not uniform across network scales (macro-, meso-, micro- level
²⁵⁶ properties). Species-level extinction rankings were broadly consistent among model classes, whereas interaction-
²⁵⁷ level outcomes and cascade trajectories were highly contingent on reconstruction approach. The predominance
²⁵⁸ of reconstruction framework over temporal turnover (~80% vs. 6% variance explained) illustrates why coarse-
²⁵⁹ grained patterns like species-level extinction rankings are more robust. Model-imposed structure dominates
²⁶⁰ the overall topology, leaving interaction dynamics highly contingent on framework choice. This asymmetry
²⁶¹ reveals a context-dependent pattern of robustness. Coarse-grained macroecological patterns (such as the
²⁶² vulnerability of a community to collapse) can emerge from multiple plausible interaction architectures. By
²⁶³ contrast, fine-grained inferences about which links are lost, retained, or reorganised depend strongly on how
²⁶⁴ interactions are inferred.

265 This distinction challenges a central ambition of food web ecology: the use of detailed interaction structure to
266 diagnose mechanisms of stability and collapse. Our findings suggest that while coarse-grained patterns might
267 be shared across methods, fine-grained mechanistic narratives (such as the specific pathways of interaction
268 loss) are much more precarious. This implies that had Dunhill et al. (2024) selected a different reconstruction
269 method, the resulting inferences regarding the drivers of extinctions could have pointed to entirely different
270 ecological mechanisms. If interaction-level cascade pathways vary substantially across equally plausible
271 reconstructions, then mechanistic narratives derived from a single inferred topology may overstate their
272 precision (Allesina & Tang, 2012; Curtsdotter et al., 2011; Dunne et al., 2002). The apparent determinism
273 of extinction cascades may therefore partly reflect reconstruction-imposed structure rather than ecological
274 inevitability.

275 For macroecology, this metric dependence clarifies where network-based inference is accurate. Aggregate
276 properties may be comparatively robust to reconstruction assumptions, whereas conclusions about interaction
277 turnover, motif reorganisation, or fine-scale trophic dynamics are intrinsically uncertain. Recognising this
278 asymmetry is essential if network analyses are to inform comparative synthesis across space and time.

279 Taken together, these results underscore that network reconstruction is not a neutral preprocessing step but
280 an additional part of the hypothesis-generating process in which each model encodes a distinct set of ecological
281 assumptions. The inferred topology and dynamics of a food web therefore reflect not only ecological data, but
282 the theoretical assumptions embedded in the reconstruction framework. Disagreement among models does
283 not imply that any single approach is ‘wrong’, but rather that different models capture different facets of
284 ecological reality (Petchey et al., 2011; Stouffer, 2019). Disagreement among models does not imply that any
285 single approach is ‘incorrect’. Rather, different models capture different facets of ecological constraint—trait
286 compatibility, energetic optimisation, or topological regularity. The critical point is that these facets are not
287 interchangeable.

288 This perspective reframes reconstruction choice as part of hypothesis specification. Researchers must align
289 reconstruction approaches with the ecological signals of interest (whether potential interactions, realised
290 diets, or macro-scale structural properties) rather than treating model selection as a technical convenience.
291 Viewed through the lens of accuracy and precision, our results indicate that some network-based inferences
292 are relatively robust across reconstruction approaches, whereas others remain intrinsically uncertain. High-
293 level extinction rankings were broadly convergent, suggesting relative accuracy at coarse resolution, but
294 interaction-level details and temporal cascade dynamics diverged substantially, indicating limited precision
295 in reconstructing the fine structure of collapse. Recognising and explicitly accounting for this distinction
296 is essential if food web ecology is to move beyond descriptive reconstruction toward rigorous comparative

297 inference.

298 4.3 Implications for comparative biogeography and global change research

299 Network approaches are increasingly applied to examine how ecological organisation varies across latitudinal
300 gradients, environmental filters, disturbance regimes, and climate-driven transitions (Gilman et al., 2010;
301 Tylianakis et al., 2008). In global change ecology, networks are used to project vulnerability under warming,
302 quantify rewiring of interactions, and assess stability under species loss (*e.g.*, Hao et al., 2025; Marjakangas et
303 al., 2025). These studies frequently interpret variation in connectance, trophic height, interaction -diversity,
304 or robustness as indicators of ecological differentiation among regions or time intervals (*e.g.*, Pellissier et al.,
305 2018; Trøjelsgaard & Olesen, 2016). Our results show that such differences can systematically alter inferred
306 topology and disturbance dynamics even when species composition is held constant. This suggests that
307 apparent differences in network structure across spatial or climate gradients may reflect variation in structural
308 priors as much as ecological process.

309 Deep-time paleo-food webs provide a complementary perspective because they capture ecosystem responses to
310 large-scale environmental perturbations and extinction events under past climate change (*e.g.*, Dunhill et al.
311 (2024); Smith et al. (2025)). Fossil networks therefore represent natural experiments for evaluating resilience,
312 trophic reorganisation, and recovery following extreme environmental change. Studies of fossil food webs have
313 demonstrated how network structure mediates extinction cascades and post-disturbance reassembly (Dunne
314 et al., 2008; Roopnarine, 2006), providing empirical constraints on long-term ecological stability.

315 However, our results emphasise that even in deep-time systems structural conclusions remain sensitive
316 to modelling assumptions. Treating reconstructed networks as ensembles rather than single deterministic
317 representations provides a more transparent framework for incorporating uncertainty into comparative
318 macroecology and for using paleo data to inform expectations about modern climate-driven reorganisation.

319 4.4 Toward a more explicit modelling paradigm in food web ecology

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

325 A mature modelling paradigm in food web ecology would treat structural priors as testable assumptions,

326 incorporate probabilistic link inference where possible, and quantify the sensitivity of macroecological
327 conclusions to alternative representations of interaction structure. Such an approach aligns with recent
328 advances in probabilistic and ensemble network modelling and would strengthen the interpretability of
329 network-based inference under global change (Banville et al., 2025; Baskerville et al., 2011; Elmasri et al.,
330 2020; Perez-Lamarque et al., 2026; Poisot et al., 2016).

331 5 Conclusions

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

338 These results challenge the implicit assumption that reconstructed networks are comparable across systems —
339 whether comparing modern communities across environmental gradients or fossil assemblages across extinction
340 intervals. When reconstruction frameworks differ, variation in connectance, trophic organisation, robustness,
341 or interaction turnover may reflect embedded modelling assumptions as much as ecological processes. Network
342 reconstruction should thus be treated as an explicit component of hypothesis specification in comparative
343 macroecology and biogeography.

344 No single model captures the full complexity of ecological organisation, but neither are alternative models
345 interchangeable. Aligning reconstruction framework with inferential goals, standardising approaches across
346 comparative studies, and incorporating ensemble or probabilistic representations will be essential for strength-
347 ening the interpretability of network analyses across spatial and temporal gradients, including efforts to
348 use deep-time systems to inform expectations under contemporary climate change. As ecological networks
349 increasingly inform global change research, recognising model reconstruction as fundamental determinants of
350 inference is critical for advancing food web ecology from descriptive reconstruction toward rigorous comparative
351 synthesis.

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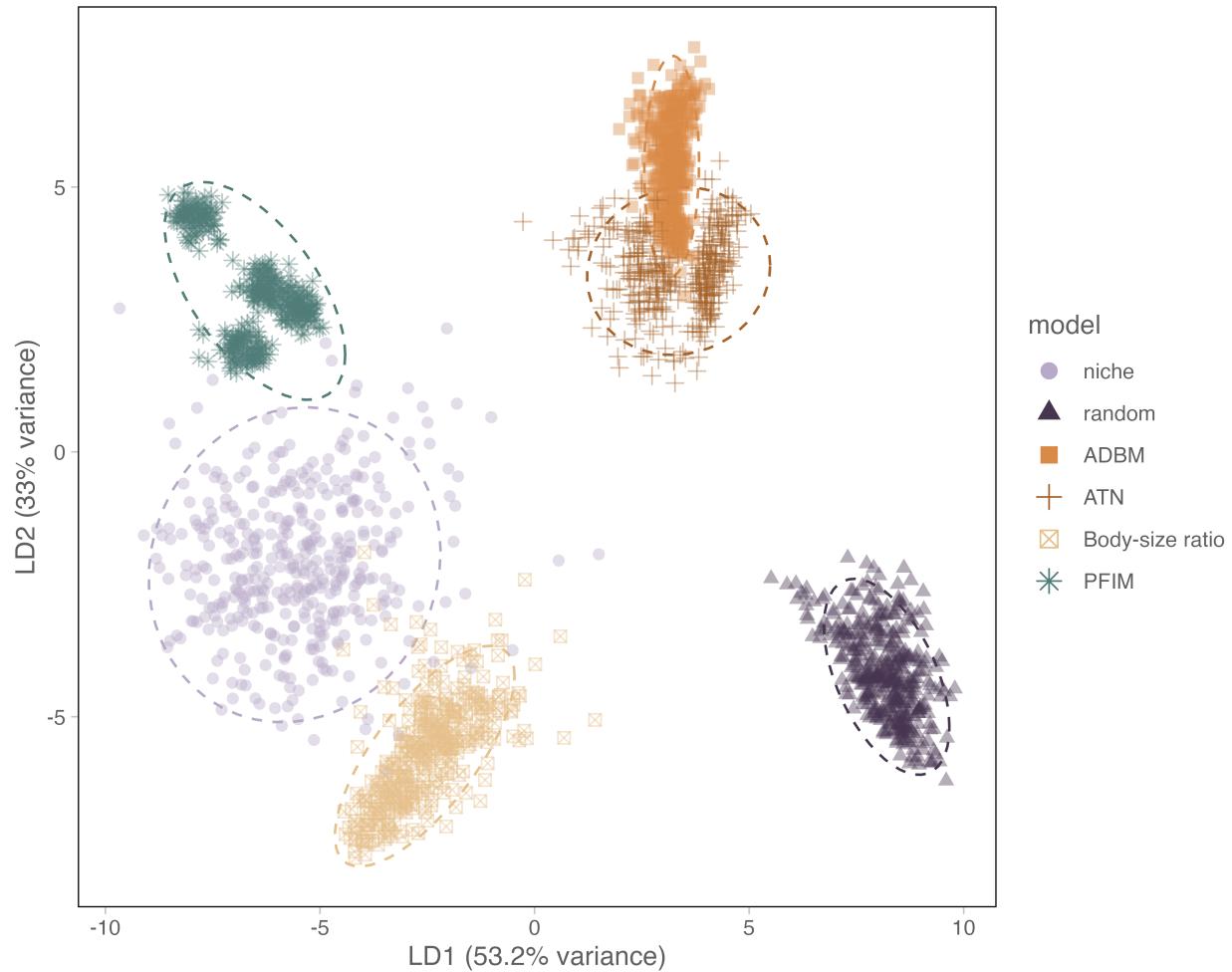


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

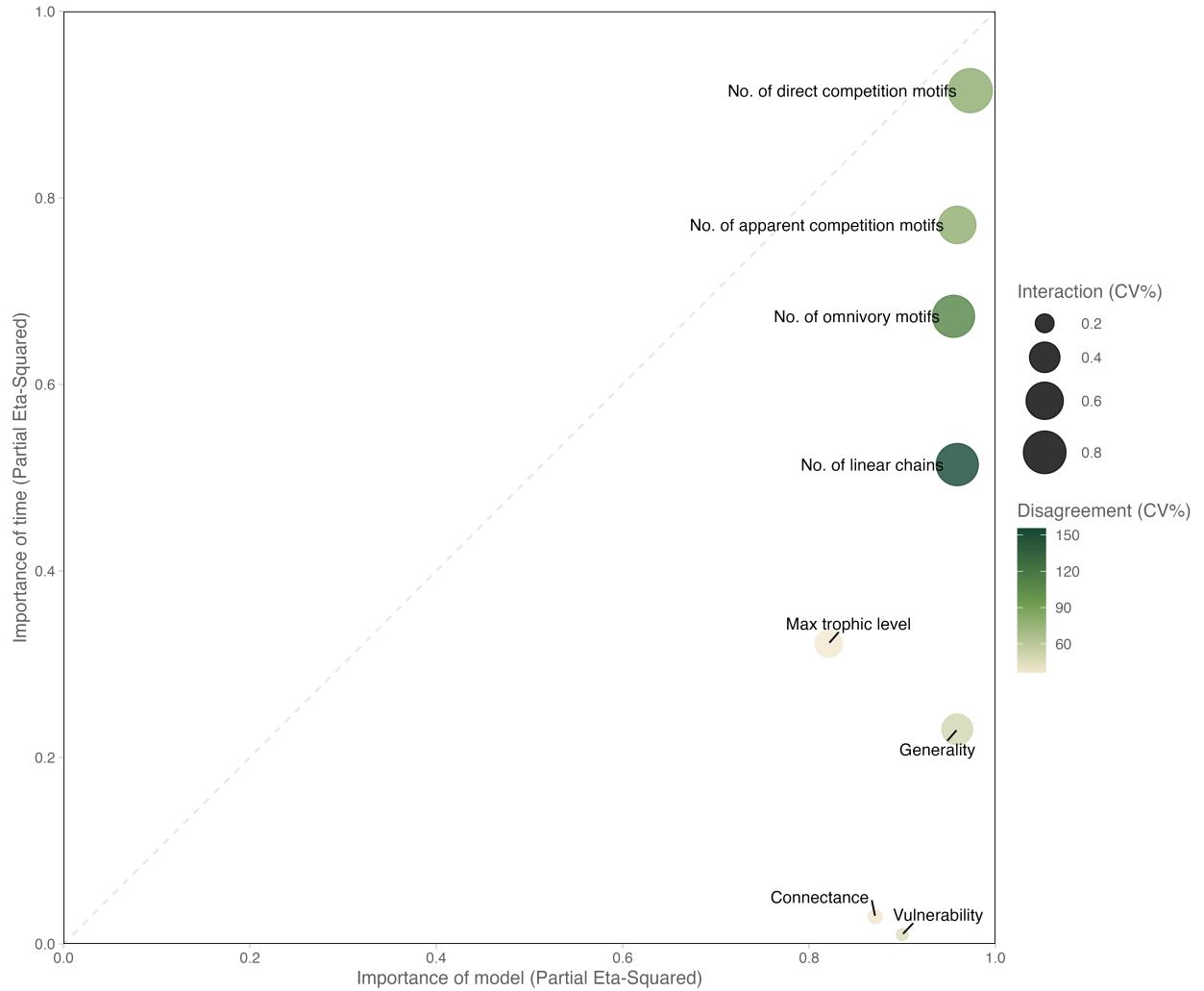


Figure 2: Scatter plot illustrating the influence of model (x-axis) and time (y-axis) across network metrics. The dashed 1:1 diagonal represents the parity of influence; metrics below this line are governed primarily by model choice and those above by time. Bubble size indicates the interaction between model and time while colour indicates inter-model disagreement (Mean CV%); greener bubbles signify metrics where models show the highest divergence in their structural predictions.

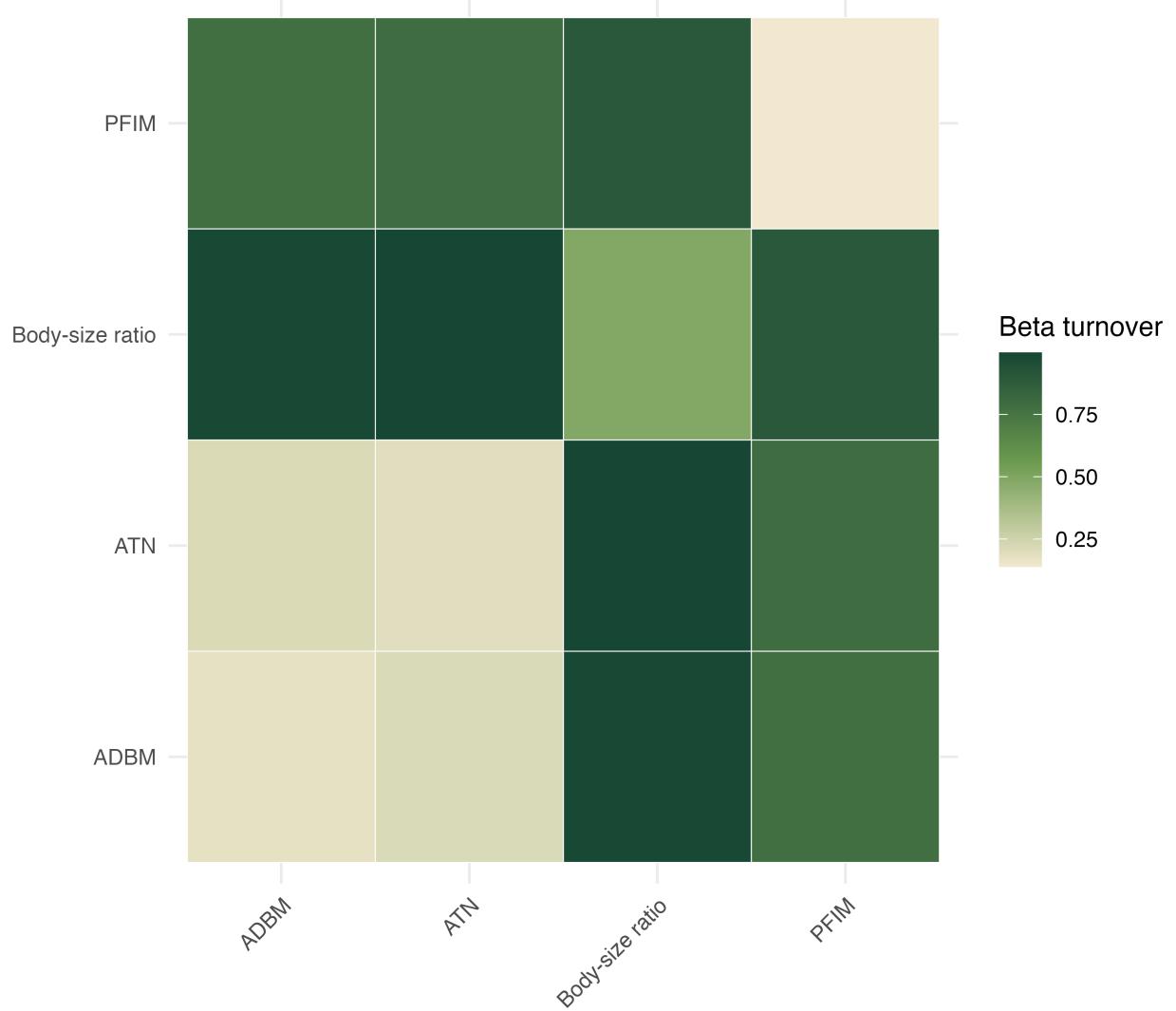


Figure 3: Pairwise β -turnover in species interactions among four ecological network models (ADBM, ATN, Body-size ratio, and PFIM). Each cell represents the mean turnover value between a pair of models, with darker colours indicating greater dissimilarity in inferred interactions. High turnover values indicate strong disagreement in pairwise interactions between models, whereas lower values indicate greater similarity.

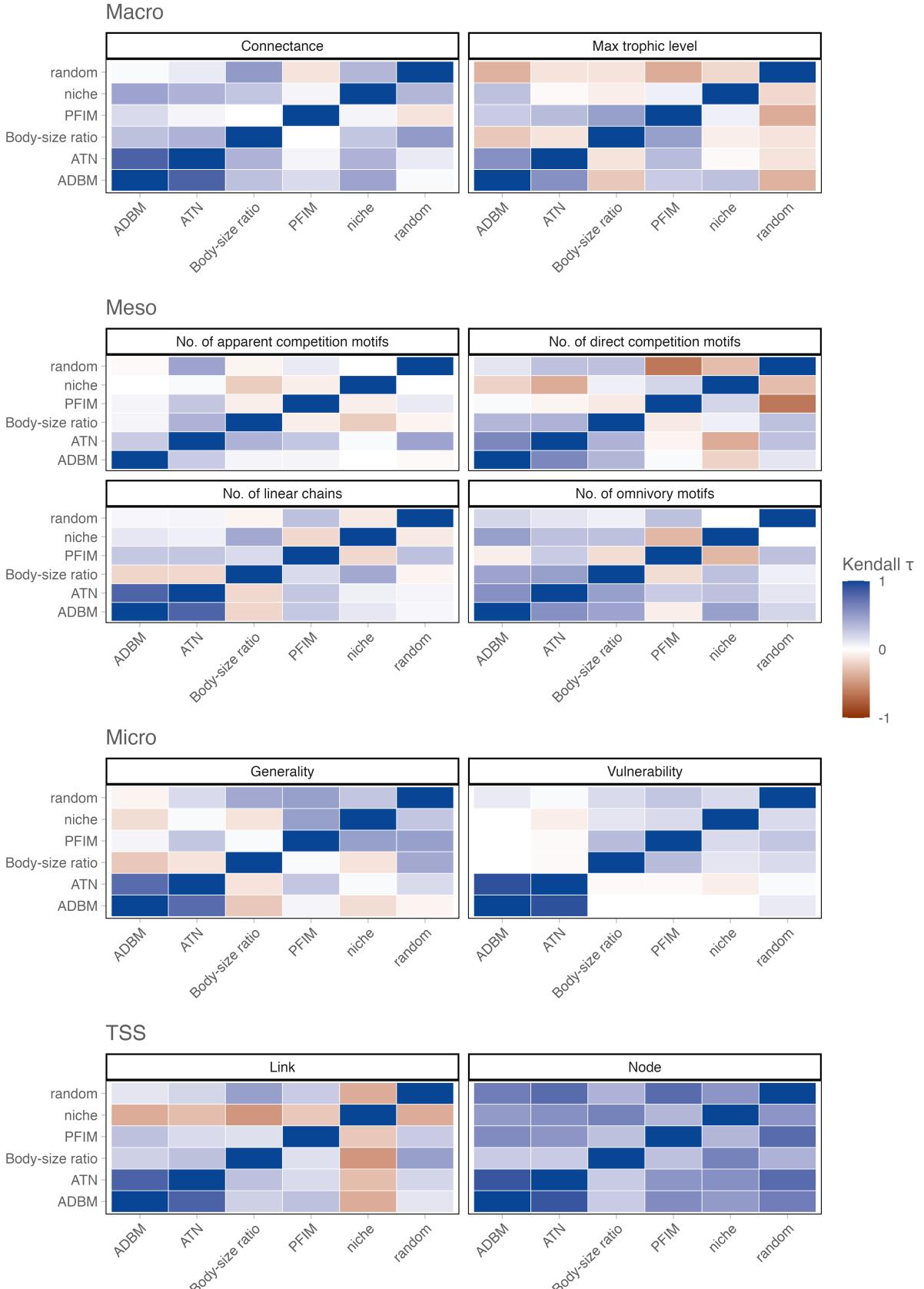


Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients (τ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between observed and predicted network values. Positive τ values (blue) indicate concordant rankings between models, whereas negative τ values (red) indicate opposing rankings. Warmer colours approaching zero represent little or no agreement.