










# Are We Mapping Ecosystems or Models? Framework Choices Dominate Food Web Topology and Extinction Inferences

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## Abstract: Aim

Ecological networks are widely used to assess community structure, stability, and responses to disturbance. Such networks often require model-based reconstructions (*e.g.*, based on traits or theoretical constraints); however, the extent to which these frameworks influence ecological inference remains unexplored. Here, we assess whether macroecological inference derived from ecological networks is robust to variation in reconstruction framework.

## Location

Cleveland Basin, United Kingdom.

## Time period

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

## Major taxa studied

Marine macrofossils.

## Methods

We reconstructed four successive assemblages from an identical species pool using six contrasting food web reconstruction approaches spanning feasible (trait-based), realised (allometric and energetic), and structural (topological) network representations. For each community and reconstruction approach, 100 replicate networks were generated. We quantified several network properties and assessed differences among reconstruction approaches 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 reconstruction approaches.

## Results

Reconstruction framework strongly influenced inferred network topology, generating distinct structural signatures independent of species composition. Reconstruction approaches that were similar in network metrics often diverged in species-level interactions, with high -turnover among inferred link sets. During extinction simulations, scenario rankings were broadly consistent at the network level, but interaction-level outcomes and cascade dynamics varied substantially.

## Main conclusions

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

**Keywords:** Network reconstruction, Macroecology, Ecological networks, Interaction turnover, Trophic organisation, Palaeoecology, Ecosystem resilience

# 1 Introduction

Understanding how biological communities are organised and how species interact with each other is a central goal of ecology. 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  $\beta$ -diversity in interaction structure, to evaluate stability–complexity relationships, and to infer vulnerability under global change (Poisot *et al.*, 2015; Trøjelsgaard & Olesen, 2016; Tylianakis & Morris, 2017; Gravel *et al.*, 2019).

As a result, ecological networks now play a central role in comparative analyses spanning latitudinal gradients, disturbance regimes, and deep time environmental transitions (Roopnarine, 2006; Poisot & Gravel, 2014; Michalska-Smith & Allesina, 2019; Dunhill *et al.*, 2024; Hao *et al.*, 2025). Implicit in this expansion is the critical assumption that network properties estimated across systems using various models are structurally comparable, and that differences among network properties reflect ecological signal rather than methodological artefact (Fründ *et al.*, 2016; Jordano, 2016). However, most ecological networks are not fully observed as interaction data are incomplete and sampling is uneven across historical and biogeographic contexts, across both present day and deep time (Poisot *et al.*, 2021; Sandra *et al.*, 2025).

Interactions must often be inferred indirectly from traits (*e.g.*, body size), phylogeny, 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 observational 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 (Petchey *et al.*, 2011; Guimarães, 2020; Gauzens *et al.*, 2025; Strydom *et al.*, 2026). If alternative reconstruction approaches systematically generate different trophic configurations, then comparative analyses risk conflating ecological differences among communities with artefacts introduced by reconstruction choice. The reliability of macroecological inference therefore depends not only on ecological data, but on the structural assumptions embedded in network reconstruction approaches.

34 Despite rapid methodological development in interaction inference, few studies have  
35 directly evaluated how alternative approaches to constructing networks influence macroe-  
36 cological conclusions when applied to the same species pool. This gap is particularly  
37 consequential for comparative research, where network metrics are routinely interpreted  
38 as indicators of environmental filtering, disturbance intensity, evolutionary history, or  
39 community stability (Allesina & Tang, 2012; Poisot *et al.*, 2015; Delmas *et al.*, 2018). If  
40 reconstruction approaches encode distinct structural constraints over interaction topology,  
41 then differences among communities may reflect reconstruction assumptions rather than  
42 ecological processes.

43 Deep time ecosystems provide an especially useful test of this issue because trophic  
44 interactions are not observed directly and must be inferred from traits, co-occurrence, and  
45 theoretical constraints (Roopnarine, 2006; Dunne *et al.*, 2008; Dunne *et al.*, 2014; Dunhill  
46 *et al.*, 2024; Karapınar *et al.*, 2026). As a result, ecological networks in these systems are  
47 inherently reconstruction-dependent, rendering the assumptions embedded within different  
48 reconstruction frameworks both explicit and consequential. Among such systems, the  
49 Early Toarcian Extinction Event (E<sub>TEE</sub>; ~183 Ma) provides a particularly informative  
50 case study. The E<sub>TEE</sub> was a major Early Jurassic biotic crisis associated with rapid  
51 climatic warming, widespread marine oxygen depletion, and substantial ecological turnover  
52 (Kemp *et al.*, 2024). Although considered a second-order extinction event globally, it  
53 nevertheless resulted in the loss of approximately 26% of marine genera worldwide (Little  
54 & Benton, 1995). Ecological disruption was especially severe in shallow marine ecosystems,  
55 where environmental stress drove extensive restructuring of benthic communities and food  
56 webs. In the Cleveland Basin of Yorkshire, the E<sub>TEE</sub> caused the extinction of around  
57 60% of marine species, including up to 87% of benthic taxa (Caswell *et al.*, 2009). Fossil  
58 assemblages from this interval therefore record both the collapse of established communities  
59 and the subsequent recovery and reassembly of marine ecosystems under rapidly changing  
60 environmental conditions. Recent work has shown that the event selectively impacted  
61 specialist and infaunal organisms, leading to simplified ecosystems increasingly dominated  
62 by ecological generalists and opportunistic taxa (Dunhill *et al.*, 2024). These changes were  
63 accompanied by major shifts in community structure, trophic interactions, and ecosystem  
64 connectivity, with evidence suggesting that ecological recovery following the extinction  
65 was both prolonged and uneven across marine habitats.

66 Ecological networks have previously been used to infer patterns of community organisation

67 and extinction dynamics across this transition, providing an ideal test case for evaluating  
68 the robustness of network-based inferences of community response. Recent work by  
69 Dunhill *et al.* (2024) has used reconstructed food webs to draw ecological conclusions  
70 about community stability and collapse during this event. This creates a rare opportunity  
71 to ask a more general question - to what extent are such inferences contingent on the  
72 specific reconstruction framework used to generate the network?

73 Here, we reconstruct ecological networks for four successive assemblages across the ETEE  
74 using six contrasting reconstruction frameworks spanning feasibility-based, realised, and  
75 structural models. By holding species composition constant while varying only the  
76 reconstruction approach, we isolate the influence of structural assumptions on inferred  
77 food web organisation, interaction turnover, and extinction dynamics. This design allows  
78 us to explicitly evaluate whether conclusions drawn from a single reconstruction approach  
79 (such as those of Dunhill *et al.* (2024)) are robust to alternative, equally plausible  
80 representations of interaction structure, or whether different reconstruction choices would  
81 lead to fundamentally different ecological inferences. More broadly, our study tests whether  
82 macroecological conclusions derived from ecological networks reflect underlying biological  
83 processes or are conditioned by the assumptions embedded within the reconstruction  
84 framework itself.

## 85 2 Methods

### 86 2.1 Study system and fossil data

87 We used fossil occurrence data from the Cleveland Basin, UK, spanning the late Pliens-  
88 bachian to the late Toarcian. This interval encompasses a major volcanic-driven hyperther-  
89 mal and marine extinction event. To capture network dynamics across this transition, we  
90 defined four successive palaeo-assemblages: pre-extinction (Pliensbachian), post-extinction  
91 (early Toarcian), early recovery (early–middle Toarcian) and late recovery (late Toar-  
92 cian). Each taxon was characterised using their size and Bambach’s ecospace framework  
93 (Bambach *et al.*, 2007), coding for tiering, motility, and feeding mode as per Dunhill  
94 *et al.* (2024). Each assemblage was treated as a community of potentially interacting  
95 taxa. The dataset includes 57 taxa across diverse groups (*e.g.*, cephalopods, bivalves, and  
96 gastropods). See Dunhill *et al.* (2024) for detailed descriptions of the dataset, including  
97 taxonomic composition, trait coding, and temporal resolution.

## 2.2 Network reconstruction approaches

### 2.2.1 Conceptual classification of network types

Ecological network reconstruction encompasses a range of approaches that differ in how trophic interactions are inferred and in the ecological assumptions they encode. These approaches can be broadly grouped into three classes: feasibility-based, realised, and structural models. Together, these classes represent distinct hypotheses about how interactions arise and constrain the space of possible food web structure.

Feasibility-based models infer the set of potential interactions among species based on trait compatibility or mechanistic rules. These approaches define a feasible interaction space by identifying which consumer–resource pairs are biologically possible, without specifying which interactions are realised in each community. In palaeoecological contexts, where direct observation of interactions is not possible, such models provide a biologically grounded, formalised representation, of ‘expert knowledge’ based rules that can be used to infer interactions (*e.g.*, Fricke *et al.* (2022); Roopnarine (2006); Shaw *et al.* (2024)).

Realised models aim to approximate the subset of interactions that are expected to occur in practice. These approaches impose additional constraints (such as energetic optimisation, mechanical limits, or probabilistic niche structure) on top of feasibility, thereby generating networks that represent putative realised diets (Brose *et al.*, 2006; Schneider *et al.*, 2016). Although often parameterised using body size or related traits, realised models differ in their underlying ecological assumptions about how consumers select resources and how trophic interactions are structured.

Structural models, in contrast, do not attempt to reconstruct empirical trophic interactions from species-level data. Instead, they generate networks based on general topological constraints such as species richness, connectance, or trophic ordering (Allesina *et al.*, 2008). These models are species-agnostic and therefore cannot be interpreted as reconstructions of specific ecological communities. Rather, they have the potential to serve as ‘null hypotheses’, providing reference expectations against which the structure and dynamics of data-informed reconstructions can be evaluated.

In this study, we selected models to span these three conceptual classes (Table 1) to sample distinct mechanistic interpretations of trophic interactions rather than exhaustively include all available implementations. Specifically, we include: a feasibility-based model (PFWIM), representing trait-constrained interactions; multiple realised models (ADBIM,

130 ATN, and Body-size ratio), capturing energetic optimisation, mechanical constraints,  
131 and probabilistic allometric structure, respectively; and structural models (Random and  
132 Niche), providing theoretical reference points. Notably some approaches share common  
133 inputs (*e.g.*, body mass for ADBM, ATN, and Body-size ratio), they encode fundamentally  
134 different assumptions about how interactions arise. Additionally, although other feasibility-  
135 based approaches exist (*e.g.*, Roopnarine (2006)), they are conceptually similar to PFWIM  
136 in that they infer interactions from biologically feasible consumer–resource combinations.  
137 We therefore selected PFWIM as a representative feasibility-based framework because it  
138 formalises these rules in a transferable model that can be parameterised across datasets,  
139 rather than relying on system-specific expert assignment of links.

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

Recon- struction Approach	Assump- tions	Data needs	Limita- tion	Network type	Key reference	Usage examples
Random	Links assigned randomly	Species richness, number of links	Parameter assump- tions, species agnostic	Structural	Erdős & Rényi (1959)	Null- model compar- isons; testing whether observed network structure (con- nectance, motifs) deviates from random expecta- tions

Reconstruction Approach	Assumptions	Data needs	Limitation	Network type	Key reference	Usage examples
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/biomass	Assumes optimal foraging; does not account for forbidden links	Realised	Petchey <i>et al.</i> (2008)	Predicting realized predator diets; exploring secondary extinctions
Allometric trophic network (ATN)	Links constrained by body-size ratios and functional response	Body mass, number of basal species	Assumes only mechanical/energetic constraints	Realised	Brose <i>et al.</i> (2006); Gauzens <i>et al.</i> (2023)	Simulating species loss; evaluating network collapse dynamics

Reconstruction Approach	Assumptions	Data needs	Limitation	Network type	Key reference	Usage examples
Paleo food web inference model (PFWIM)	Interactions inferred using trait-based mechanistic rules	Feeding traits	Assumes feeding mechanisms; trait resolution required	Feasibility	Shaw <i>et al.</i> (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 <i>et al.</i> (2010)	Estimating likely interactions; simulating cascading effects.

140 This classification allows us to distinguish variation arising from ecological assumptions  
141 embedded in reconstruction frameworks from variation attributable to species composition.  
142 By comparing networks generated from the same species pool across these complementary  
143 model classes, we explicitly evaluate how different representations of interaction structure  
144 condition ecological inference.

### 145 **2.2.2 Network generation and replication**

146 We evaluated six network reconstruction frameworks using the approaches listed in Table 1:  
147 Random and Niche models (structural networks); allometric diet breadth (ADBM),  
148 allometric trophic network (ATN), and Body-size ratio models (realised networks); and a  
149 paleo food web inference model (PFWIM; feasibility network). Expanded descriptions  
150 of reconstruction approach assumptions, parameterisation, and link-generation rules are  
151 provided in Supplementary Material S1, including full mathematical formulations and

152 parameter definitions. For each community, 100 stochastic network realisations were  
153 generated per reconstruction approach ( $n = 2400$  per time bin in total, 600 per time bin)  
154 to capture uncertainty in link assignment. Where reconstruction approaches required  
155 species body mass or trait values, these were uniformly sampled within the different size  
156 classes, we adopted a uniform sampling by default, as alternative distributions (lognormal,  
157 truncated lognormal) have negligible impact on topology (Supplementary Material S1;  
158 Figure S1). Random and Niche models were parameterised using connectance values  
159 drawn from an empirically realistic range (0.05–0.25; Curtsdotter *et al.* (2011)). For  
160 the Random model, which requires link number explicitly, connectance ( $C_o$ ) was first  
161 converted to expected link number ( $L$ ) using  $L = C_o \times S^2$ , ensuring consistency in network  
162 density across all reconstruction approaches. Richness ( $S$ ) was determined by the number  
163 of species for each time bin. For the Body-size ratio model, we followed the approach of  
164 Yeakel *et al.* (2014) using only the body-mass scaling to determine links between species.  
165 Sensitivity of network structure to these parameter choices is evaluated in Supplementary  
166 Material S1. The PFWIM generates a deterministic feasible metaweb for a given trait  
167 configuration. To allow for statistical analyses we introduced controlled variation in  
168 interaction subsets by applying a downsampling procedure that stochastically samples  
169 feasible interactions. This step allowed us to introduce statistical variation while still  
170 preserving most of the metaweb structure. The choice of downsampling parameter and its  
171 effects on network structure are evaluated in Supplementary Material S1.

## 172 **2.3 Network metrics and structural analyses**

173 We quantified network structure using a suite of network metrics Table 2, capturing  
174 overall network properties, motif structure, and species-level variability. Differences  
175 among reconstruction approaches were assessed using a multivariate analysis of variance  
176 (MANOVA), with reconstruction approach identity as a fixed factor and the full set of  
177 network metrics as response variables. Variance partitioning was further assessed using  
178 permutational multivariate analysis of variance (PERMANOVA). Pairwise interaction  
179 turnover was quantified using link-based  $\beta$ -diversity and was calculated following the  
180 framework of Poisot *et al.* (2012) among the four of the reconstruction frameworks (ADBM,  
181 ATN, body-size ratio, and PFWIM). Random and Niche models were excluded because  
182 they are species-agnostic reconstruction approaches that generate networks matching  
183 broad topological properties (*e.g.*, connectance and degree distributions) rather than  
184 predicting biologically realistic species-specific interactions. Specifically, we looked at

185 interaction rewiring among shared species ( $\beta_{OS}$ , see S1 for additional details on the  
186 decomposition of interaction -diversity and its implementation), which allows separation  
187 of differences arising from altered interaction identities among species common to both  
188 networks. Because all networks within a given assemblage are constructed from the same  
189 species pool, differences in interaction structure primarily reflect ‘rewiring’ of trophic  
190 links due to stochasticity in the reconstruction approach rather than species turnover.  
191 All calculations were performed for all reconstruction combinations within the same  
192 assemblage (time bin).

Table 2: Network properties used for analysis.

Metric	Definition	Reference
Connectance	$L/S^2$ , where $S$ is the number of species and $L$ the number of links	Williams & Martinez (2004)
Maximum trophic level	Prey-weighted trophic level averaged across taxa	Williams & Martinez (2004)
No. of linear chains (S1)	Number of linear chains, normalised by $L/S$	Milo <i>et al.</i> (2002); Stouffer <i>et al.</i> (2007)
No. of omnivory motifs (S2)	Number of omnivory motifs, normalised by $L/S$	Milo <i>et al.</i> (2002); Stouffer <i>et al.</i> (2007)
No. of apparent competition motifs (S4)	Number of apparent competition motifs, normalised by $L/S$	Milo <i>et al.</i> (2002); Stouffer <i>et al.</i> (2007)
No. of direct competition motifs (S5)	Number of direct competition motifs, normalised by $L/S$	Milo <i>et al.</i> (2002); Stouffer <i>et al.</i> (2007)
Generality	Standard deviation of normalised generality of all species within network, normalised by $L/S$	Williams & Martinez (2000)
Vulnerability	Standard deviation of normalised vulnerability of all species within network, normalised by $L/S$	Williams & Martinez (2000)

## 2.4 Extinction simulations and their evaluation

Following Dunhill *et al.* (2024), we simulated species loss from pre-extinction networks under trait-based, network-position-based, and random removal scenarios. Species were deleted sequentially, with cascading secondary extinctions allowed to propagate. Simulated post-extinction states were compared to observed (*i.e.*, reconstructed from fossil occurrence data) networks using mean absolute differences (MAD) of food web metrics (Table 2) and modified true skill statistics (TSS) calculated separately at the node level (species presence/absence) and link level (presence/absence of interactions between species pairs). Scenarios were ranked within each reconstruction framework based on MAD and TSS performance, and Kendall’s rank correlation coefficient ( $\tau$ ) was used to quantify concordance in scenario ordering across reconstruction approaches. Detailed implementation of extinction sequences and secondary extinction rules is provided in Supplementary Material S1.

## 2.5 Software and Reproducibility

Ecological network reconstruction and extraction of structural metrics were conducted in Julia v1.11.4 (Bezanson *et al.*, 2017) using the model implementations provided in Supplementary Material S1. All statistical analyses, including MANOVA, PERMANOVA, and post hoc comparisons, were performed in R v4.5.2 (R Core Team, 2024). The full analytical workflow, including data preprocessing, network generation, extinction simulations, and metric calculation, is fully reproducible from the archived codebase.

## 3 Results

We found that different reconstruction approaches, even those that appeared structurally similar, yielded fundamentally different ecological inferences. Across six reconstruction approaches, inferred food web structure, species interactions, and extinction dynamics differed consistently. Multivariate analyses showed pronounced separation among reconstruction approaches in network metric space (Figure 1), with reconstruction approach explaining most of the variance in structural properties (Figure 2). Notably, approaches that were statistically similar in multivariate structural space often diverged in inferred interactions (Figure 3) or extinction dynamics (Figure 4), demonstrating that structural similarity does not guarantee concordance in species-level diets or inferred behaviour of the system.

224 Reconstruction approach substantially influenced inferred extinction dynamics. Temporal  
225 trajectories of network collapse, interaction loss, and motif reorganisation differed among  
226 approaches (Figure 2). Although node-level extinction rankings were often broadly consis-  
227 tent, link-level outcomes and extinction inferences were highly sensitive to reconstruction  
228 assumptions (Figure 4). Together, these results show that ecological inferences drawn  
229 from networks depend critically on the reconstruction framework used.

### 230 **3.1 Network structure differs among reconstruction approaches**

231 Across six reconstruction approaches, network structure (network properties listed in  
232 Table 2) differed significantly (MANOVA, Pillai’s trace = 3.84, approximate  $F_{40,11955}$   
233 = 987.35,  $p < 0.001$ ), indicating that the reconstruction approach systematically alters  
234 inferred food web topology. Linear discriminant (LD) analysis identified two dominant  
235 axes of variation, explaining 86% of the differences between reconstruction approach. LD1  
236 axis correlated with vulnerability, direct competition motifs, and connectance. LD2 axis  
237 correlated with maximum trophic level and apparent competition motifs, reflecting vertical  
238 trophic structure (Figure 1; Table S1, Figure S1). The higher-order variates explained less  
239 than 9% of the remaining variance.

240 [Figure 1 about here.]

#### 241 **3.1.1 Variance partitioning of network structure**

242 Permutational multivariate analysis of variance (PERMANOVA) revealed that reconstruc-  
243 tion framework accounted for most of the variation in multivariate network structure  
244 ( $R^2 = 0.795$ ,  $p < 0.001$ ), whereas temporal turnover across extinction phases explained a  
245 comparatively small proportion of variance ( $R^2 = 0.064$ ,  $p < 0.001$ ). The reconstruction  
246 approach  $\times$  time interaction contributed a further 7.1% of variance ( $R^2 = 0.071$ ,  $p <$   
247  $0.001$ ), indicating limited but significant time-dependent divergence among reconstruction  
248 frameworks. Thus, differences among reconstruction approaches were more than an order of  
249 magnitude greater than structural differences associated with ecological turnover through  
250 the extinction sequence, even if the Pliensbachian–Toarcian dataset was characterised  
251 with a significant community turnover.

252 To determine whether the dominance of the reconstruction framework reflected absolute  
253 mean shifts among time bins, we repeated the analysis after centring network metrics  
254 within each extinction phase. This procedure removes between-phase differences while

255 retaining within-phase structural variation. Even after temporal bin-standardised centring,  
256 the reconstruction framework explained 84.8% of multivariate variance ( $R^2 = 0.848$ ,  $p <$   
257  $0.001$ ). These results demonstrate that the influence of reconstruction approach is not  
258 driven by temporal mean differences but reflects intrinsic divergence among reconstruction  
259 frameworks in how ecological interactions are organised.

### 260 **3.1.2 Statistical Drivers of Network Variation**

261 To identify which specific structural properties drive the multivariate separation observed  
262 above, we partitioned variance at the level of individual network metrics. Results show  
263 that reconstruction choice had a significantly stronger influence on network topology than  
264 the ecological signal of species loss. In panel A of Figure 2 for certain network metrics  
265 reconstruction approaches predict different responses across time (*e.g.*, connectance),  
266 as well as differing magnitudes of change (*e.g.*, the number of apparent competition  
267 motifs). A two-way factorial ANOVA across all eight network metrics confirmed that the  
268 reconstruction approach was the dominant driver of variance, with partial eta-squared  
269 values ( $\eta_p^2$ ) consistently exceeding 0.82 and reaching 0.97 for motifs (Figure 2, panel B;  
270 Table S3). While the extinction event (time bin) significantly altered network structure  
271 ( $p < 0.001$ ), its relative importance remained secondary, typically explaining a smaller  
272 fraction of the total topological variation. This is clear in panel B of Figure 2 where  
273 all metrics are within the bottom-right (reconstruction approach-dominated) triangle  
274 (below the dashed line), emphasising that framework assumptions outweigh the ecological  
275 signal of species loss. Furthermore, the high inter-reconstruction approach Coefficient of  
276 Variation (CV) observed for some metrics (Table S4, Figure S4) highlights a sensitivity.  
277 The properties that are influenced by time are also those upon which the reconstruction  
278 approaches disagree most profoundly. Demonstrating that our understanding of structural  
279 food web collapse in the fossil record is highly contingent on the chosen reconstruction  
280 framework, particularly when examining complex trophic pathways beyond simple macro-  
281 scale properties like connectance.

282 [Figure 2 about here.]

### 283 **3.1.3 Inferred pairwise interactions vary widely among reconstruction ap-** 284 **proaches**

285 Despite some network reconstruction approaches showing similar network metrics, specific  
286 pairwise interactions often differed. Pairwise  $\beta_{OS}$  revealed that certain reconstruction

287 approach pairs shared very few links (Figure 3). Size-based models (ADBM, ATN)  
288 were broadly similar due to shared sole reliance on body-size constraints, whereas the  
289 Body-size ratio model exhibited consistently higher differences to other reconstruction  
290 approaches. PFWIM showed intermediate overlap with body mass-based models. These  
291 results demonstrate that agreement in overall network structure does not guarantee  
292 concordance in species-level interactions.

293 [Figure 3 about here.]

### 294 **3.2 Reconstruction approach choice influences inferred extinction** 295 **dynamics**

296 To evaluate how reconstruction approach choice affects inferred extinction dynamics, we  
297 compared simulated post-extinction networks to observed networks using mean absolute  
298 differences (MAD) for network-level metrics and true skills statistics (TSS) for node- and  
299 link-level outcomes Figure 4. Across reconstruction approaches, MAD-based rankings were  
300 generally positively correlated (Kendall's  $\tau = 0.13$  across structural metrics), indicating weak  
301 but generally positive agreement on the relative importance of extinction drivers despite  
302 substantial differences in reconstructed network structure. However, agreement within  
303 the allometric models (ADMB, ATN) differed from patterns observed for reconstructed  
304 network structure.

305 Node-level TSS rankings were similarly consistent across network reconstruction approaches  
306 (Kendall's  $\tau = 0.26 - 0.90$ ), reflecting broadly comparable node-level removal sequences.  
307 In contrast, link-level outcomes were far more variable (Kendall's  $\tau = -0.48 - 0.29$ ),  
308 highlighting that inferences about which interactions are lost or retained during collapse  
309 and recovery are highly reconstruction approach contingent. Together, these results  
310 suggest that while alternative reconstruction approaches converge on similar species-level  
311 extinction patterns, the inferred pathways of interaction loss and cascading dynamics  
312 depend strongly on both reconstruction approaches.

313 [Figure 4 about here.]

## 4 Discussion

### 4.1 Network reconstruction is not neutral: structural priors shape ecological theory

Food web ecology has long treated network reconstruction as a methodologically neutral step preceding ecological analysis, with limited attention to how methodological choices might influence outcomes. Once assembled, network properties are generally interpreted as reflections of underlying ecological organisation. This workflow assumes that reconstructed networks provide structurally comparable representations of ecological communities. As a result, differences in connectance, trophic structure, motif composition, or robustness are interpreted as primarily reflecting biological variation, rather than the effects of reconstruction approach.

Assuming that reconstructed food webs are independent of model choice is particularly critical to evaluate within the context of deep time palaeoecological data. Because interactions in fossil ecosystems are never observed directly, and direct inferences (such as gut contents) are limited, hence they must explicitly be formed through some form of reconstruction approach. This necessity renders the underlying assumptions transparent but also makes the resulting ecological narratives highly susceptible to the constraints inherent in the chosen reconstruction framework. In these settings the risk is not just incomplete data, but the potential for methodological artefacts to be misinterpreted as genuine macroevolutionary or palaeoecological signals. Consequently, deep time studies offer a unique and stringent testing ground for determining whether community-level responses (such as stability or collapse during mass extinctions) are robust features of the ecosystem or merely byproducts of how we choose to construct the links between species.

Reconstruction framework explained far more variation in food-web topology than temporal turnover across extinction and recovery phases. Across an identical regional taxon pool, alternative reconstruction approaches generated distinct structural signatures that occupied non-overlapping regions of multivariate space Figure 1, demonstrating that divergence among reconstruction approaches reflects intrinsic differences in how interactions are organised rather than temporal shifts in community composition. Even after centring metrics within time bins to remove between-bin mean differences, reconstruction approach remained the dominant driver of structural variation. These results indicate that reconstruction approaches impose distinct ‘structural priors’ on ecological inference, shaping

346 emergent topology, species roles, and predictions of disturbance dynamics. Network struc-  
347 ture is therefore not solely a property of ecological communities but jointly determined by  
348 ecological data and assumptions made when inferring/reconstructing interactions (Gauzens  
349 *et al.*, 2025; Strydom *et al.*, 2026).

350 Crucially, this dominance was not confined to multivariate summaries. Variance partition-  
351 ing at the level of individual network properties revealed that reconstruction approach  
352 overwhelmingly structured specific ecological metrics, thus the imprint of the recon-  
353 struction framework is visible not only in aggregate topology but in the very structural  
354 features often interpreted as ecological signals. Notably, the few properties that exhibited  
355 detectable temporal sensitivity were also those with the greatest inter-reconstruction  
356 approach disagreement (*i.e.*, motif distributions), indicating that temporal trends are  
357 most difficult to disentangle when reconstruction frameworks diverge most strongly. These  
358 results suggest that structural assumptions do not merely shift networks within a shared  
359 architectural space; they condition the specific patterns through which ecological change  
360 is perceived and interpreted.

361 This has direct implications for the interpretation of comparative network studies. Feasible,  
362 realised, and structural reconstruction approaches encode different assumptions about  
363 constraint, optimisation, and topology, with these assumptions propagating into emergent  
364 metrics and dynamical predictions (Dunne *et al.*, 2002; Curtsdotter *et al.*, 2011; Allesina  
365 & Tang, 2012; Poisot & Gravel, 2014; Michalska-Smith & Allesina, 2019). When networks  
366 reconstructed under different classes are compared across spatial gradients, disturbance  
367 regimes, or evolutionary transitions, part of the observed variation may derive from  
368 reconstruction choice rather than ecological process. Without explicit standardisation or  
369 sensitivity analysis, methodological heterogeneity can be mistaken for biological signal.  
370 Food web ecology has devoted substantial effort to understanding how topology shapes  
371 dynamics; comparatively less attention has been paid to how reconstruction method shapes  
372 topology. Our findings indicate that these two questions cannot be separated.

## 373 **4.2 Scale-dependent robustness in network-based inference**

374 Importantly, reconstruction sensitivity was not uniform across levels of inference. Node-  
375 level extinction rankings were broadly consistent among reconstruction approaches, whereas  
376 interaction-level outcomes and cascade trajectories were highly contingent on reconstruc-  
377 tion methods. The predominance of the reconstruction framework over temporal turnover

378 helps explain this pattern. Different reconstruction approaches often converged on similar  
379 patterns of community vulnerability yet diverged substantially in the mechanisms through  
380 which collapse unfolded. Broad ecological patterns may be robust across plausible interac-  
381 tion architectures, whereas conclusions about interaction loss, retention, or reorganisation  
382 depend strongly on how interactions are inferred.

383 This distinction challenges a central ambition of food web ecology: using interaction  
384 structure to identify the mechanisms underlying stability and collapse. Our findings suggest  
385 that while broad patterns may be robust across reconstruction approaches, mechanistic  
386 explanations are far less secure. Had Dunhill *et al.* (2024) used a reconstruction approach  
387 other than PFWIM, the inferred drivers of extinction and recovery may have differed  
388 substantially. If cascade pathways vary across equally plausible reconstructions, then  
389 mechanistic narratives derived from a single inferred topology may overstate their precision  
390 (Dunne *et al.*, 2002; Curtsdotter *et al.*, 2011; Allesina & Tang, 2012). The apparent  
391 determinism of extinction cascades may therefore reflect reconstruction-imposed structure  
392 as much as ecological inevitability.

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

398 Taken together, these results underscore that network reconstruction is not a neutral  
399 preprocessing step but an additional part of the hypothesis-generating process in which  
400 each reconstruction approach encodes a distinct set of ecological assumptions. The inferred  
401 topology and dynamics of a food web therefore reflect not only ecological data, but the  
402 theoretical assumptions embedded in the reconstruction framework. Disagreement among  
403 reconstruction approaches does not imply that any single approach is ‘wrong’ (Petchey  
404 *et al.*, 2011; Stouffer, 2019). Rather, different frameworks emphasise different ecological  
405 constraints, such as trait compatibility, energetic optimisation, or topological regularity  
406 and it is a case of matching the ‘correct’ reconstruction approach to the task at hand.

407 This perspective reframes reconstruction choice as part of hypothesis specification. Re-  
408 searchers must align reconstruction approaches with the ecological signals of interest  
409 (whether potential interactions, realised diets, or macro-scale structural properties) rather  
410 than treating network reconstruction as a technical convenience. Viewed through the lens

411 of accuracy and precision, our results indicate that some network-based inferences are  
412 relatively robust across reconstruction approaches, whereas others remain intrinsically  
413 uncertain. High-level extinction rankings were broadly convergent, suggesting relative  
414 accuracy at coarse resolution, but interaction-level details and temporal cascade dynamics  
415 diverged substantially, indicating limited precision in reconstructing the fine structure  
416 of collapse. Recognising and explicitly accounting for this distinction is essential if food  
417 web ecology is to move beyond descriptive reconstruction toward rigorous comparative  
418 inference.

### 419 **4.3 Implications for comparative biogeography and global change** 420 **research**

421 Network approaches are increasingly applied to examine how ecological organisation varies  
422 across latitudinal gradients, environmental filters, disturbance regimes, and climate-driven  
423 transitions (Tylianakis *et al.*, 2008; Gilman *et al.*, 2010). In global change ecology, networks  
424 are used to project vulnerability under warming, quantify rewiring of interactions, and  
425 assess stability under species loss (*e.g.*, Hao *et al.*, 2025; Marjakangas *et al.*, 2025).  
426 These studies frequently interpret variation in connectance, trophic height, interaction  
427  $\beta$ -diversity, or robustness as indicators of ecological differentiation among regions or time  
428 intervals (Trøjelsgaard & Olesen, 2016; *e.g.*, Pellissier *et al.*, 2018). Our results show that  
429 reconstruction choice can systematically alter inferred topology and disturbance dynamics  
430 even when species composition is held constant. Apparent differences in network structure  
431 across spatial or climatic gradients may therefore reflect reconstruction choices as much as  
432 ecological processes.

433 Deep time palaeo food webs provide a complementary perspective because they capture  
434 ecosystem responses to large-scale environmental perturbations and extinction events  
435 under past climate change (*e.g.*, Dunhill *et al.* (2024); Smith *et al.* (2025); Karapınar *et al.*  
436 (2026)). Fossil networks therefore represent natural experiments for evaluating resilience,  
437 trophic reorganisation, and recovery following extreme environmental change. Studies of  
438 palaeo food webs have demonstrated how network structure mediates extinction cascades  
439 and post-disturbance reassembly (Roopnarine, 2006; Dunne *et al.*, 2008), providing  
440 empirical constraints on long-term ecological stability.

441 However, our results emphasise that even in deep time systems structural conclusions  
442 remain sensitive to reconstruction approaches. Treating reconstructed networks as

443 reconstruction-dependent inferences rather than deterministic representations provides a  
444 more transparent framework for incorporating uncertainty into comparative macroecology.

#### 445 **4.4 Toward a more explicit modelling paradigm in food web ecol-** 446 **ogy**

447 No single reconstruction framework is universally correct. Instead, each represents a  
448 distinct hypothesis about how ecological interactions are constrained. (Petchey *et al.*,  
449 2011). Food web reconstruction is therefore theory-laden. Making this explicit shifts  
450 reconstruction from a preparatory step to a central component of ecological modelling.

451 A mature modelling paradigm in food web ecology would treat reconstruction approaches  
452 as testable, incorporate probabilistic link inference where possible, and quantify the  
453 sensitivity of macroecological conclusions to alternative representations of interaction  
454 structure. Such an approach aligns with recent advances in probabilistic and ensemble  
455 network modelling and would strengthen the interpretability of network-based inference  
456 under global change (Poisot *et al.*, 2016; Banville *et al.*, 2025).

## 457 **5 Conclusions**

458 Ecological network reconstruction is a theoretical choice that fundamentally shapes eco-  
459 logical inference. By applying six contrasting reconstruction frameworks to an identical  
460 species pool, we show that different reconstruction approaches systematically influence  
461 inferred food web topology, interaction identity, and disturbance dynamics. Some coarse-  
462 grained patterns, such as relative species vulnerability, are comparatively robust across  
463 representations. In contrast, fine-scale interaction structure and cascade pathways are  
464 highly contingent on reconstruction approaches. The reliability of network-based inference  
465 is therefore scale dependent.

466 These results challenge the implicit assumption that reconstructed networks are comparable  
467 across systems — whether comparing modern communities across environmental gradients  
468 or fossil assemblages across extinction intervals. When reconstruction frameworks differ,  
469 variation in connectance, trophic organisation, robustness, or interaction turnover may  
470 reflect embedded reconstruction approaches as much as ecological processes. Network  
471 reconstruction should thus be treated as an explicit component of hypothesis specification  
472 in comparative macroecology and biogeography.

473 No single reconstruction approach captures the full complexity of ecological organisation,  
474 but neither are alternative reconstruction approaches interchangeable. Aligning recon-  
475 struction framework with inferential goals, standardising approaches across comparative  
476 studies, and incorporating ensemble or probabilistic representations will be essential for  
477 strengthening the interpretability of network analyses across spatial and temporal gradi-  
478 ents, including efforts to use deep time systems to inform expectations under contemporary  
479 climate change. As ecological networks play an increasingly prominent role in global  
480 change research, recognising reconstruction as a determinant of inference will be essential  
481 for moving food web ecology from descriptive reconstruction toward rigorous comparative  
482 synthesis.

483 *Data and Code Availability Statement:* The empirical data, derived network datasets,  
484 and all analysis scripts are archived in a public Zenodo repository (DOI: [10.5281/zen-  
485 odo.20444969](https://doi.org/10.5281/zenodo.20444969)), which includes a complete README file describing software dependencies,  
486 execution order, and reproduction instructions.

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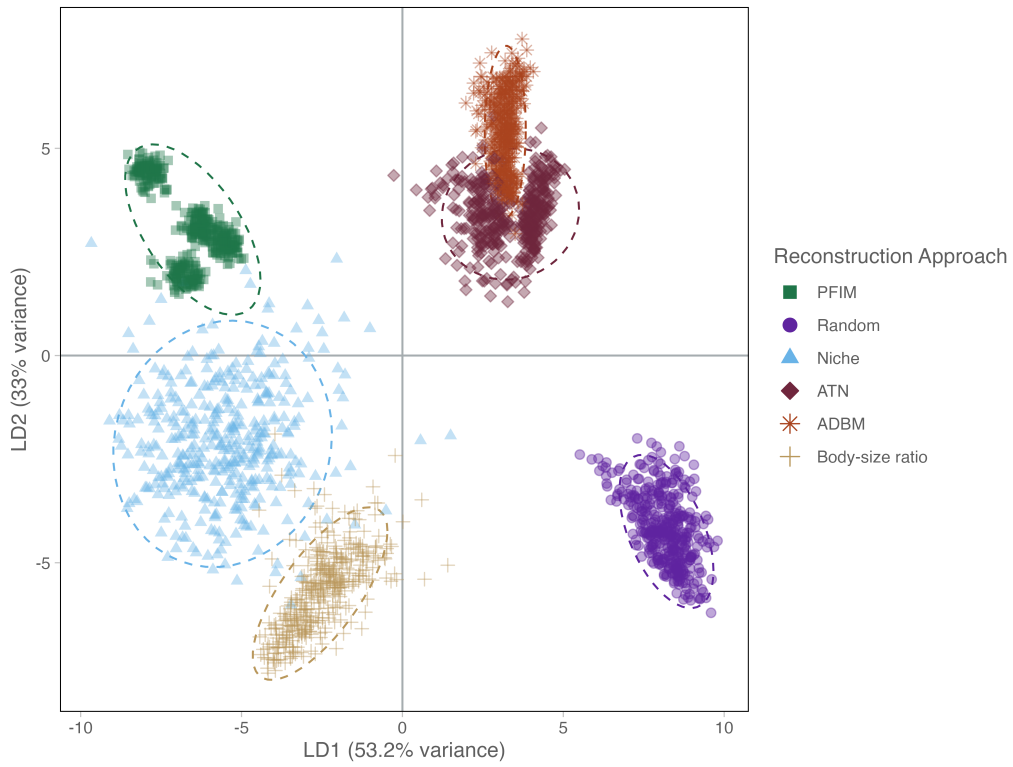


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six reconstruction approach types. Each point represents a replicate ( $n = 100$  per approach), and ellipses indicate 95% confidence regions for each reconstruction approach.

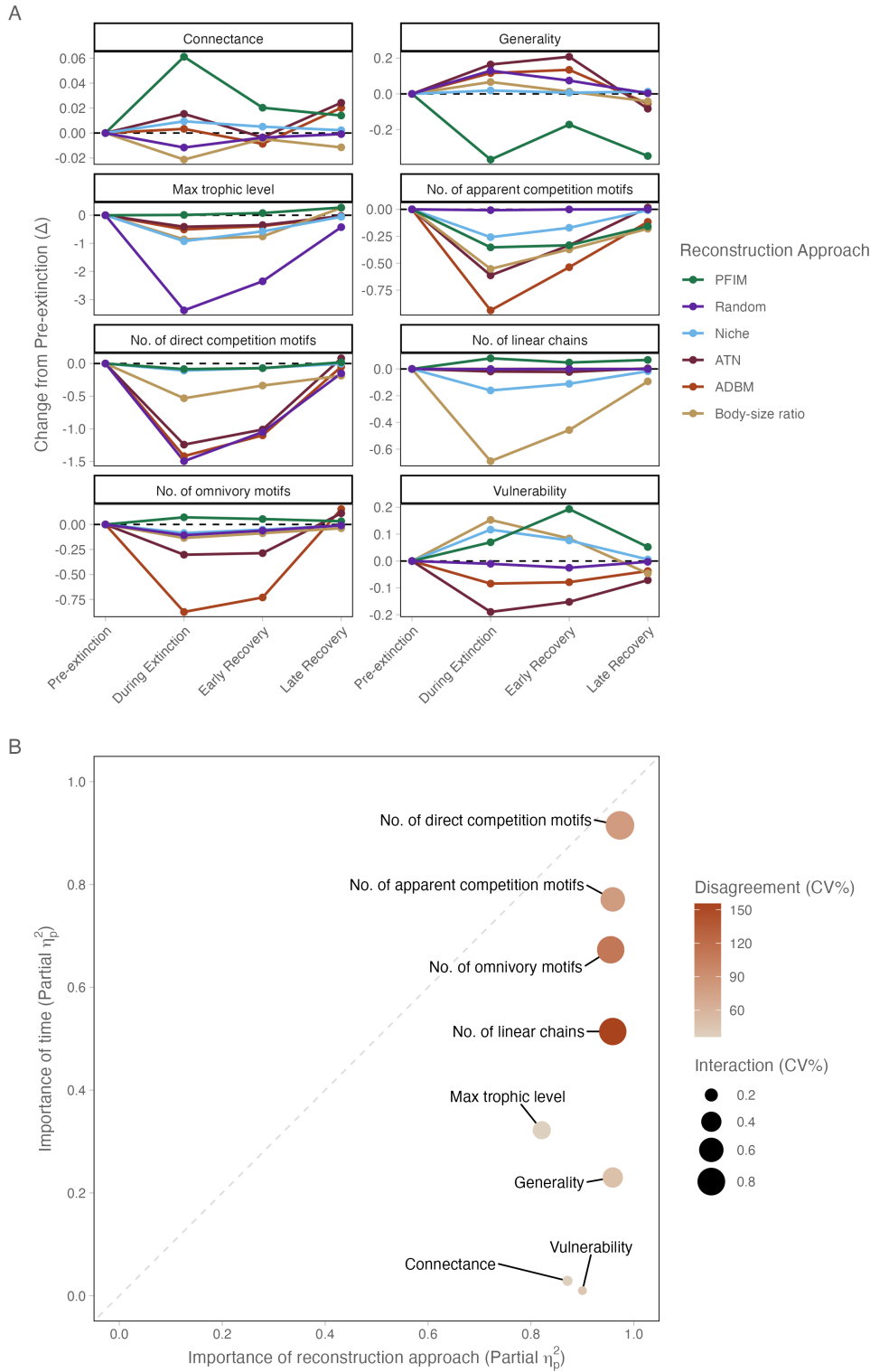


Figure 2: Figure 2: Temporal changes in food-web structure and the relative influence of reconstruction approach and ecological turnover on network properties. **(A)** Changes in network metrics through time, expressed as deviations from pre-extinction conditions ( $\delta$ ). Metrics are faceted and scaled independently to highlight differences in temporal trajectories among network properties. **(B)** Relative influence of reconstruction approach (x-axis) and time (y-axis) on individual network metrics. The dashed 1:1 line indicates equal explanatory power. Metrics below the line are more strongly influenced by reconstruction approach than by temporal turnover. Bubble size represents the reconstruction approach  $\times$  time interaction, and colour indicates disagreement among reconstruction approaches (mean CV%), with darker colours indicating greater divergence in metric estimates.

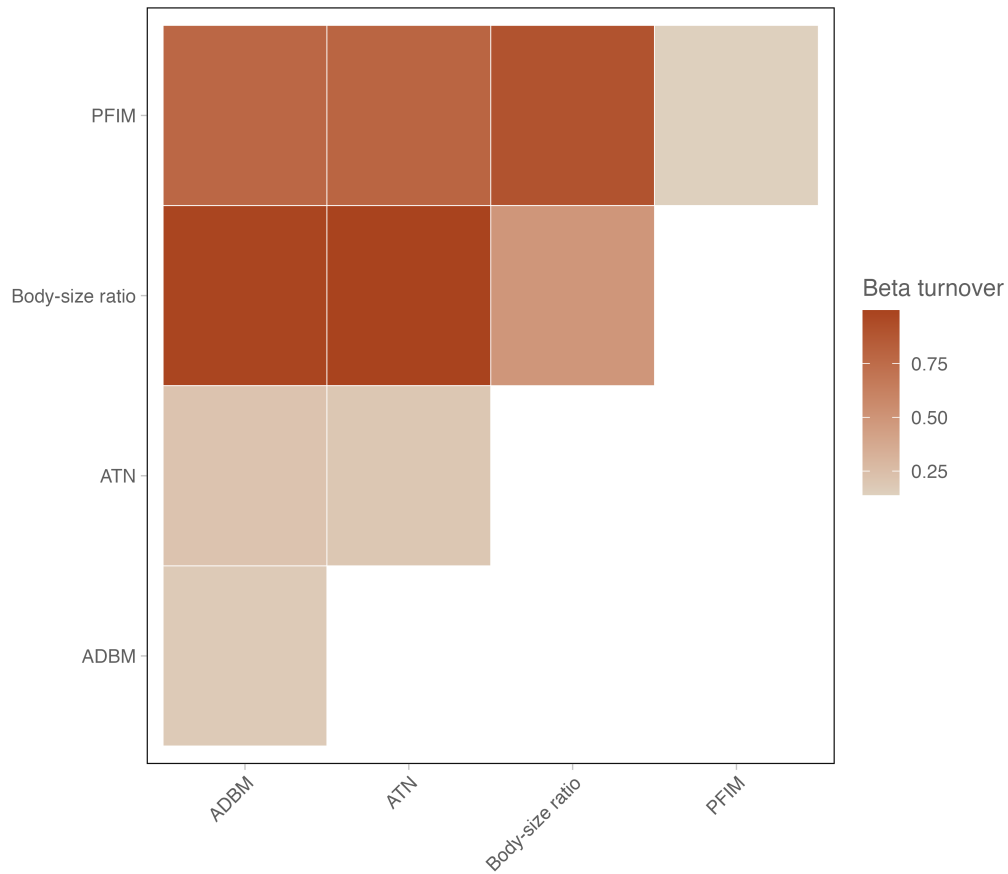


Figure 3: Pairwise interaction turnover ( $\beta_{OS}$ ) among four food-web reconstruction approaches that infer species-specific trophic interactions (ADBM, ATN, Body-size Ratio, and PFWIM). Each cell represents the mean turnover value between a pair of reconstruction approaches, with darker colours indicating greater dissimilarity in inferred interactions. High turnover values indicate strong disagreement in predicted trophic links, whereas lower values indicate greater similarity.

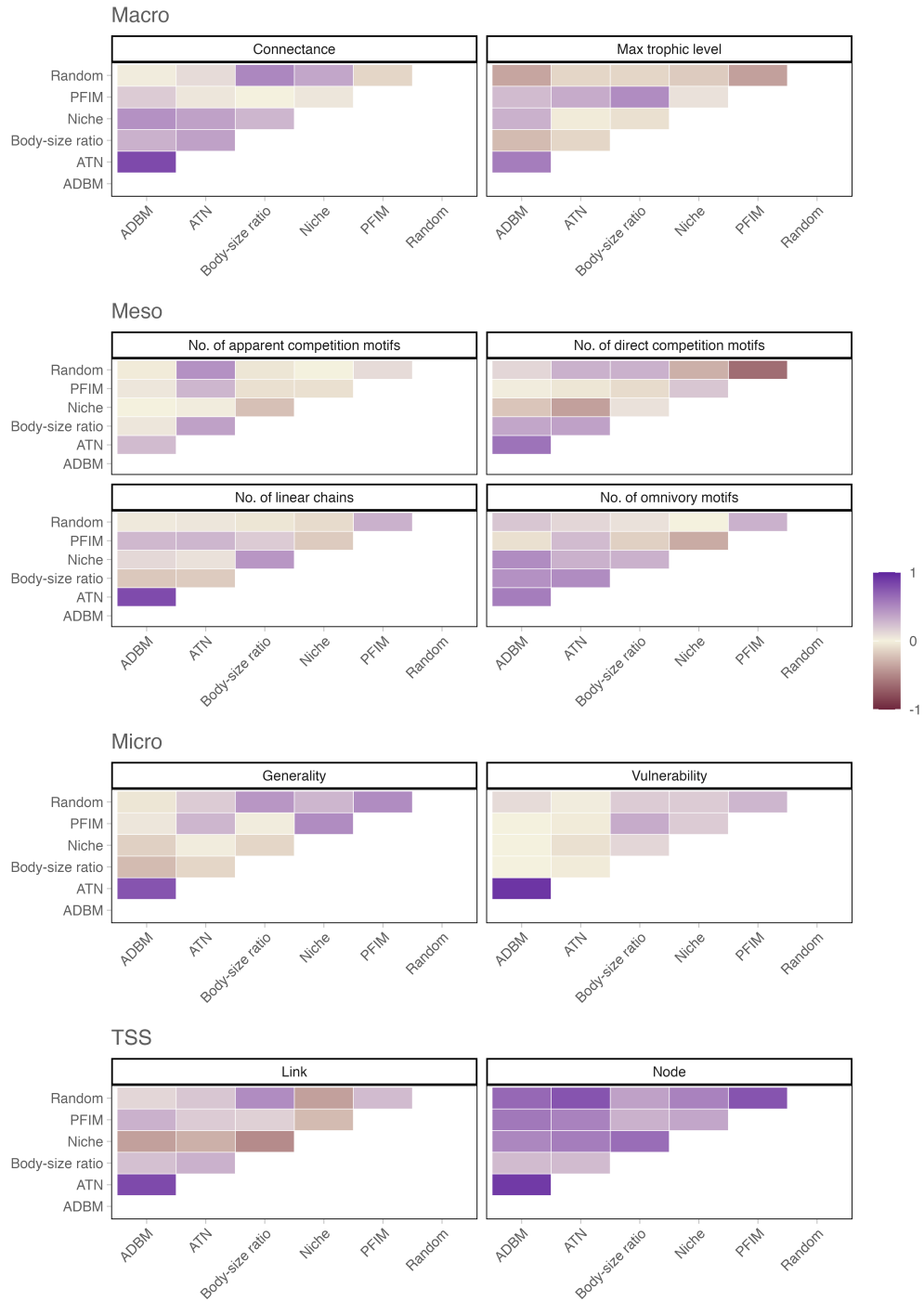


Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients ( $\tau$ ) between reconstruction approaches for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across reconstruction approaches based on mean absolute differences (MAD) between observed and predicted network values as well as differences in species links (TSS). Positive  $\tau$  values (purple) indicate concordant rankings between reconstruction approaches, whereas negative  $\tau$  values (sienna) indicate opposing rankings. Paler colours approaching zero represent little or no agreement.