

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

stability (Allesina & Tang, 2012; Delmas et al., 2018; Poisot et al., 2015). If reconstruction models encode distinct structural priors over interaction topology, then differences among communities may reflect modelling assumptions rather than ecological processes. We therefore test whether macroecological inference derived from ecological networks is robust to variation in reconstruction framework, asking which aspects of network-based inference are stable across plausible representations of interaction structure and which are intrinsically model dependent.

Deep-time ecosystems provide an especially stringent test of this issue because interactions are not observed directly and must be reconstructed explicitly (Dunhill et al., 2024; Dunne et al., 2008; Dunne et al., 2014; Karapunar et al., 2026; Roopnarine, 2006), rendering modelling assumptions transparent. Against this stringency, here we re-evaluate inferences made by Dunhill et al. (2024) on community structure and extinction dynamics during the early Toarcian extinction event (~183 Ma), a volcanic-driven hyperthermal and marine crisis in the Early Jurassic (Kemp et al., 2024). Crucially, this re-evaluation allows us to test a pivotal but often overlooked possibility - that the ecological narratives regarding community stability or collapse might be as much a product of the specific reconstruction method chosen as they are of the fossil data itself. By applying alternative models, we can determine if Dunhill et al. (2024) conclusions remain robust or if a different choice of reconstruction method would have led to fundamentally different inferences about extinction dynamics. Using four successive communities, we reconstruct ecological networks under six contrasting model classes spanning feasible, realised, and structural representations. For each reconstruction framework, we quantify emergent topology across scales, measure interaction turnover, and simulate disturbance-driven collapse. By holding species composition constant while varying the food web model used, this design isolates the influence of model constrained structure on inferred food web organisation and extinction dynamics, allowing us to distinguish ecological signals that are robust from those that are reconstruction contingent.

2 Methods

2.1 Study system and fossil data

We used fossil occurrence data from the Cleveland Basin spanning the upper Pliensbachian to the upper Toarcian. This interval encompasses a major volcanic-driven hyperthermal and marine extinction event. To capture network dynamics across this transition, we defined four successive paleo-communities: pre-extinction (Pliensbachian), post-extinction (Lower Toarcian), early recovery, and late recovery (Middle/Upper Toarcian). Each taxon was characterized using their size and Bambach's ecospace framework (Bambach et al., 2007), coding for tiering, motility, and feeding mode as per Dunhill et al. (2024). Each assemblage was treated

as a community of potentially interacting taxa. The dataset includes 57 taxa across diverse groups (*e.g.*, cephalopods, bivalves, and gastropods). By restricting our analysis to a single basin with consistent lithofacies, we controlled for biogeographic noise, ensuring that structural shifts across the four time-bins reflect localised ecological responses to environmental stress rather than sampling or facies bias.

2.2 Network reconstruction approaches

2.2.1 Conceptual classification of network types

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

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

84 **2.2.2 Network generation and replication**

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

98 **2.3 Network metrics and structural analyses**

99 We quantified network structure using a suite of macro-, meso-, and micro-scale metrics Table 2, capturing
100 global properties, motif structure, and species-level variability. Differences among reconstruction approaches
101 were assessed using a multivariate analysis of variance (MANOVA), with model identity as a fixed factor
102 and the full set of network metrics as response variables. Variance partitioning was further assessed using
103 permutational multivariate analysis of variance (PERMANOVA). Pairwise interaction turnover was quantified
104 using link-based -diversity was calculated following the framework of Poisot et al. (2012) among the four of
105 the reconstruction frameworks (ADBM, ATN, body-size ratio, and PFIM). We excluded the purely structural
106 random and niche models as they are inherently species agnostic. For each pair of reconstructed networks, we
107 represented trophic interactions as binary adjacency matrices and calculated their dissimilarity. Specifically
108 we looked at interaction rewiring among shared species (β_{OS}), which allows separation of differences arising
109 from altered interaction identities among species common to both networks. All calculations were performed
110 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	
Maximum 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)

111 2.4 Extinction simulations and model evaluation

112 Following Dunhill et al. (2024), we simulated species loss from pre-extinction networks under trait-based,
 113 network-position-based, and random removal scenarios. Species were deleted sequentially, with cascading
 114 secondary extinctions allowed to propagate. Simulated post-extinction states were compared to observed (*i.e.*,
 115 reconstructed from fossil occurrence data) networks using mean absolute differences (MAD) of food-web metrics

¹¹⁶ Table 2 and modified true skill statistics (TSS) calculated separately at the node level (species presence/absence)
¹¹⁷ and link level (presence/absence of interactions between species pairs). Scenarios were ranked within each
¹¹⁸ reconstruction framework based on MAD and TSS performance, and Kendall's rank correlation coefficient ()
¹¹⁹ was used to quantify concordance in scenario ordering across models. Full methodological details are provided
¹²⁰ in the Supplementary Materials.

¹²¹ 2.5 Software and Reproducibility

¹²² Ecological network reconstruction and extraction of structural metrics were conducted in Julia v1.11.4
¹²³ (Bezanson et al., 2017). All statistical analyses, model fitting (MANOVA, PERMANOVA, GAMs), and figure
¹²⁴ production were performed in R v4.5.2 (R Core Team, 2024). The empirical data, derived network datasets
¹²⁵ and code implementing network reconstruction, extinction simulations, and all analytical workflows is archived
¹²⁶ at [Zenodo DOI].

¹²⁷ 3 Results

¹²⁸ Results show that reconstruction approaches that appear similar when evaluated using global network metrics
¹²⁹ can yield fundamentally different ecological narratives when interrogated at the level of interactions and
¹³⁰ extinction dynamics. Across six network reconstruction approaches, inferred food web structure, species
¹³¹ interactions, and extinction dynamics differed consistently. Multivariate analyses showed pronounced separation
¹³² among models in network metric space. Reconstruction approach explained most of the variance in structural
¹³³ properties, leaving a distinct signature independent of community composition. Notably, agreement among
¹³⁴ models depended on the scale at which the comparison was made- approaches that were statistically similar in
¹³⁵ multivariate structural space (scale 1) often diverged in inferred interactions (scale 2) or extinction dynamics
¹³⁶ (scale 3). This demonstrates that structural similarity does not guarantee concordance in species-level diets or
¹³⁷ trophic roles.

¹³⁸ Model choice substantially influenced inferred extinction dynamics. Temporal trajectories of network collapse,
¹³⁹ interaction loss, and motif reorganisation differed among approaches. Although node-level extinction ranking
¹⁴⁰ were often broadly consistent, link-level outcomes and extinction inferences were highly sensitive to recon-
¹⁴¹ struction assumptions. Together, these results show that ecological inferences drawn from networks depend
¹⁴² critically on the reconstruction framework employed.

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

¹⁴⁴ Across six reconstruction approaches, network structure (network properties listed in Table 2) differed
¹⁴⁵ significantly (MANOVA, Pillai's trace = 3.84, approximate $F_{40,11955} = 987.35$, $p < 0.001$), indicating that
¹⁴⁶ model choice systematically alters inferred food web topology. Canonical discriminant analysis identified two
¹⁴⁷ dominant axes of variation, explaining 86% of between-model variance. LD1 correlated with vulnerability,
¹⁴⁸ direct competition motifs, and connectance. LD2 correlated with maximum trophic level and apparent
¹⁴⁹ competition motifs, reflecting vertical trophic structure (Figure 1; Table S1, Figure S1). All higher-order
¹⁵⁰ canonical variates each explained less than 9% of the remaining variance.

¹⁵¹ [Figure 1 about here.]

¹⁵² **3.1.1 Variance partitioning of network structure**

¹⁵³ Permutational multivariate analysis of variance revealed that reconstruction framework accounted for the
¹⁵⁴ majority of variation in multivariate network structure ($R^2 = 0.795$, $p < 0.001$), whereas temporal turnover
¹⁵⁵ across extinction phases explained a comparatively small proportion of variance ($R^2 = 0.064$, $p < 0.001$).
¹⁵⁶ The model \times time interaction contributed a further 7.1% of variance ($R^2 = 0.071$, $p < 0.001$), indicating
¹⁵⁷ limited but significant time-dependent divergence among reconstruction frameworks. Thus, differences among
¹⁵⁸ modelling approaches were more than an order of magnitude greater than structural differences associated
¹⁵⁹ with ecological turnover through the extinction sequence, even if the Toarcian dataset was characterized with
¹⁶⁰ a significant community turnover.

¹⁶¹ To determine whether the dominance of the reconstruction framework reflected absolute mean shifts among
¹⁶² time bins, we repeated the analysis after centring network metrics within each extinction phase. This procedure
¹⁶³ removes between-phase differences while retaining within-phase structural variation. Even after temporal
¹⁶⁴ bin-standardised centring, the reconstruction framework explained 84.8% of multivariate variance ($R^2 = 0.848$,
¹⁶⁵ $p < 0.001$). These results demonstrate that the influence of model choice is not driven by temporal mean
¹⁶⁶ differences, but reflects intrinsic divergence among reconstruction frameworks in how ecological interactions
¹⁶⁷ are organised.

¹⁶⁸ **3.1.2 Statistical Drivers of Network Variation**

¹⁶⁹ To identify which specific structural properties drive the multivariate separation observed above, we partitioned
¹⁷⁰ variance at the level of individual network metrics. Results show that reconstruction choice exerted a
¹⁷¹ significantly stronger influence on network topology than the ecological signal of species loss. A two-way
¹⁷² factorial ANOVA across all eight network metrics confirmed that the reconstruction approach was the dominant

173 driver of variance, with partial eta-squared values (η_p^2) consistently exceeding 0.82 and reaching 0.97 for
174 meso-scale motifs (Figure 2; Table S3). While the extinction event (time bin) significantly altered network
175 structure ($p < 0.001$), its relative importance remained secondary, typically explaining a smaller fraction
176 of the total topological variation. This is clear in Figure 2 where all metrics are within the bottom-right
177 (model-dominated) quadrant of this space, emphasising that framework assumptions outweigh the ecological
178 signal of species loss. Furthermore, the high inter-model Coefficient of Variation (CV) observed for some
179 metrics (Table S4, Figure S4) highlights a sensitivity. The properties that are influenced by time are also
180 those upon which the models disagree most profoundly. Demonstrating that our understanding of structural
181 food web collapse in the fossil record is highly contingent on the chosen reconstruction framework, particularly
182 when examining complex trophic pathways beyond simple macro-scale properties like connectance.

183 [Figure 2 about here.]

184 3.1.3 Inferred pairwise interactions vary widely among models

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

191 [Figure 3 about here.]

192 3.2 Model choice influences inferred extinction dynamics

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

200 Node-level TSS rankings were similarly consistent across models (Kendall's $\tau = 0.26\text{--}0.90$), reflecting broadly
201 comparable node-level removal sequences. In contrast, link-level outcomes were far more variable (Kendall's τ
202 = $-0.48\text{--}0.29$), highlighting that inferences about which interactions are lost, retained, or re-established during

203 collapse and recovery are highly model contingent. Together, these results suggest that while alternative
204 models converge on similar species-level extinction patterns, the inferred pathways of interaction loss and
205 cascading dynamics depend strongly on both reconstruction approaches.

206 [Figure 4 about here.]

207 4 Discussion

208 4.1 Network reconstruction is not neutral: structural priors shape ecological 209 theory

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

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

225 Reconstruction framework explained the overwhelming majority of variance in inferred food web topology,
226 far outweighing the influence of temporal turnover across extinction phases. Across an identical regional
227 taxon pool, alternative reconstruction approaches generated distinct structural signatures that occupied
228 non-overlapping regions of multivariate space Figure 1, demonstrating that divergence among models reflects
229 intrinsic differences in how interactions are organised rather than temporal shifts in community composition.
230 Even after centring metrics within extinction phases to remove between-bin mean differences, model identity
231 remained the dominant driver of structural variation. These results indicate that reconstruction approaches

²³² impose distinct ‘structural priors’ on ecological inference. These priors are not subtle; they propagate into
²³³ emergent topology, species roles, and predictions of disturbance dynamics. Network structure is therefore not
²³⁴ solely a property of ecological communities, but jointly determined by ecological data, modelling assumptions,
²³⁵ and level of organisation (Gauzens et al., 2025; Guimarães, 2020; Pichler & Hartig, 2023; Strydom et al., 2021;
²³⁶ Strydom et al., 2026).

²³⁷ Crucially, this dominance was not confined to multivariate summaries. Variance partitioning at the level
²³⁸ of individual network properties revealed that model identity overwhelmingly structured specific ecological
²³⁹ metrics, with partial η^2 values exceeding 0.9 for meso-scale motif composition and remaining consistently high
²⁴⁰ across macro- and micro-scale properties. Thus the imprint of reconstruction framework is visible not only
²⁴¹ in aggregate topology but in the very structural features often interpreted as ecological signals — trophic
²⁴² height, competition, and variability in species roles. Notably, the few properties that exhibited detectable
²⁴³ temporal sensitivity were also those with the greatest inter-model disagreement, indicating that temporal
²⁴⁴ trends is most difficult to disentangle when reconstruction frameworks diverge most strongly. These results
²⁴⁵ suggest that structural assumptions do not merely shift networks within a shared architectural space; they
²⁴⁶ condition the specific patterns through which ecological change is perceived and interpreted.

²⁴⁷ This has direct implications for the interpretation of comparative network studies. Feasible, realised, and
²⁴⁸ structural models encode different assumptions about constraint, optimisation, and topology, with these
²⁴⁹ assumptions propagating into emergent metrics and dynamical predictions (Allesina & Tang, 2012; Dunne
²⁵⁰ et al., 2002; Michalska-Smith & Allesina, 2019; Poisot & Gravel, 2014; Solé & Montoya, 2001). When
²⁵¹ networks reconstructed under different classes are compared across spatial gradients, disturbance regimes, or
²⁵² evolutionary transitions, part of the observed variation may derive from reconstruction choice rather than
²⁵³ ecological process. Without explicit standardisation or sensitivity analysis, methodological heterogeneity can
²⁵⁴ be mistaken for biological signal. Food web ecology has devoted substantial effort to understanding how
²⁵⁵ topology shapes dynamics; comparatively less attention has been paid to how reconstruction method shapes
²⁵⁶ topology. Our findings indicate that these two questions cannot be separated.

²⁵⁷ 4.2 Scale-dependent robustness in network-based inference

²⁵⁸ Importantly, reconstruction sensitivity was not uniform across network scales (macro-, meso-, micro- level
²⁵⁹ properties). Node-level extinction rankings were broadly consistent among model classes, whereas interaction-
²⁶⁰ level outcomes and cascade trajectories were highly contingent on reconstruction approach. The predominance
²⁶¹ of reconstruction framework over temporal turnover (~80% vs. 6% variance explained) illustrates why coarse-
²⁶² grained patterns like node-level extinction rankings are more robust. Model-imposed structure dominates

263 the overall topology, leaving interaction dynamics highly contingent on framework choice. This asymmetry
264 reveals a context-dependent pattern of robustness. Coarse-grained macroecological patterns (such as the
265 vulnerability of a community to collapse) can emerge from multiple plausible interaction architectures. By
266 contrast, fine-grained inferences about which links are lost, retained, or reorganised depend strongly on how
267 interactions are inferred.

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

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

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

291 This perspective reframes reconstruction choice as part of hypothesis specification. Researchers must align
292 reconstruction approaches with the ecological signals of interest (whether potential interactions, realised
293 diets, or macro-scale structural properties) rather than treating model selection as a technical convenience.

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

301 4.3 Implications for comparative biogeography and global change research

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

312 Deep-time paleo-food webs provide a complementary perspective because they capture ecosystem responses
313 to large-scale environmental perturbations and extinction events under past climate change (*e.g.*, Dunhill
314 et al. (2024); Karapunar et al. (2026); Smith et al. (2025)). Fossil networks therefore represent natural
315 experiments for evaluating resilience, trophic reorganisation, and recovery following extreme environmental
316 change. Studies of fossil food webs have demonstrated how network structure mediates extinction cascades
317 and post-disturbance reassembly (Dunne et al., 2008; Roopnarine, 2006), providing empirical constraints on
318 long-term ecological stability.

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

323 **4.4 Toward a more explicit modelling paradigm in food web ecology**

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

329 A mature modelling paradigm in food web ecology would treat model based assumptions as testable, incorpo-
330 rate probabilistic link inference where possible, and quantify the sensitivity of macroecological conclusions to
331 alternative representations of interaction structure. Such an approach aligns with recent advances in proba-
332 bilistic and ensemble network modelling and would strengthen the interpretability of network-based inference
333 under global change (Banville et al., 2025; Baskerville et al., 2011; Elmasri et al., 2020; Perez-Lamarque et al.,
334 2026; Poisot et al., 2016).

335 **5 Conclusions**

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

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

349 No single model captures the full complexity of ecological organisation, but neither are alternative models
350 interchangeable. Aligning reconstruction framework with inferential goals, standardising approaches across
351 comparative studies, and incorporating ensemble or probabilistic representations will be essential for strength-
352 ening the interpretability of network analyses across spatial and temporal gradients, including efforts to

353 use deep-time systems to inform expectations under contemporary climate change. As ecological networks
354 increasingly inform global change research, recognising model reconstruction as fundamental determinants of
355 inference is critical for advancing food web ecology from descriptive reconstruction toward rigorous comparative
356 synthesis.

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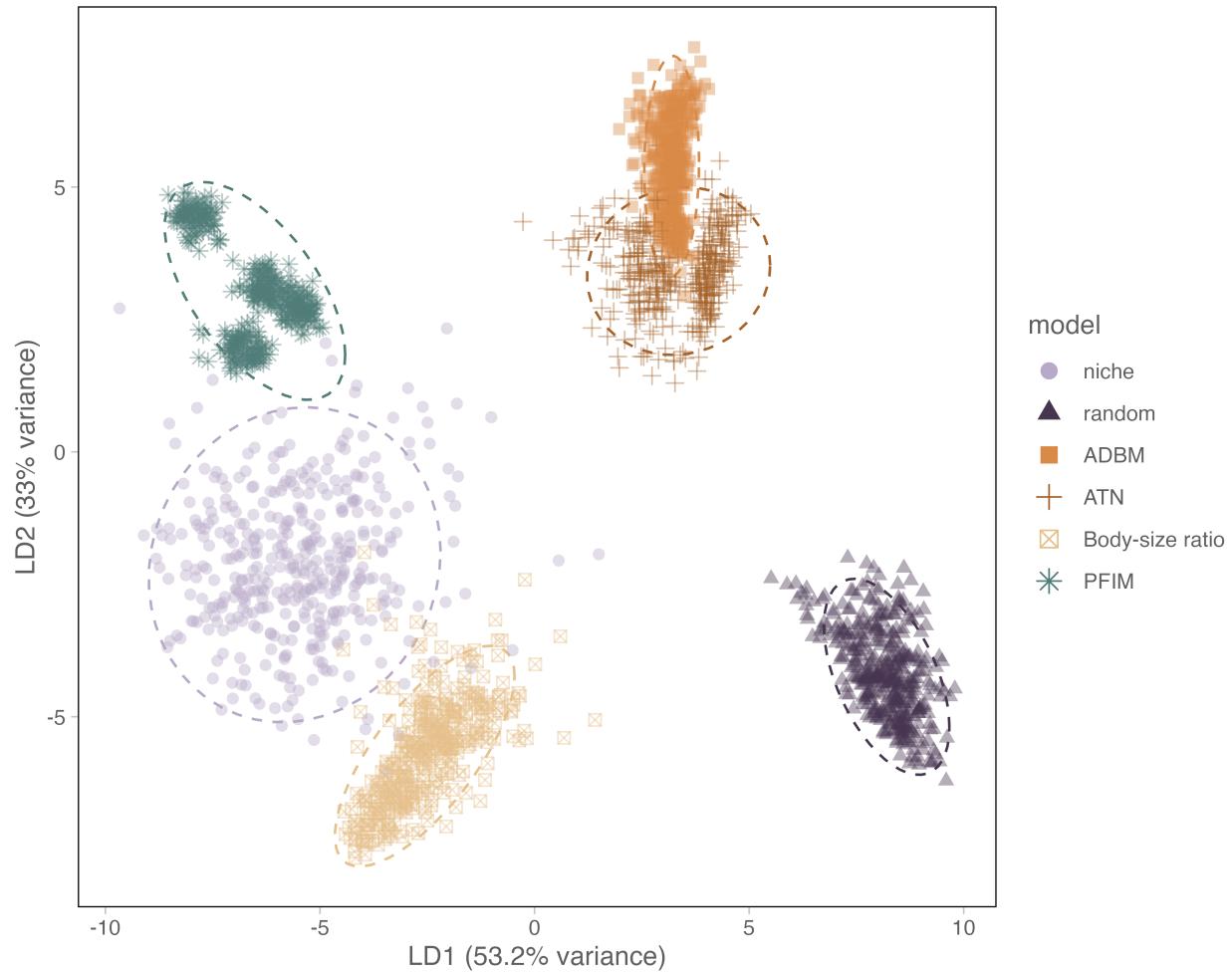


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

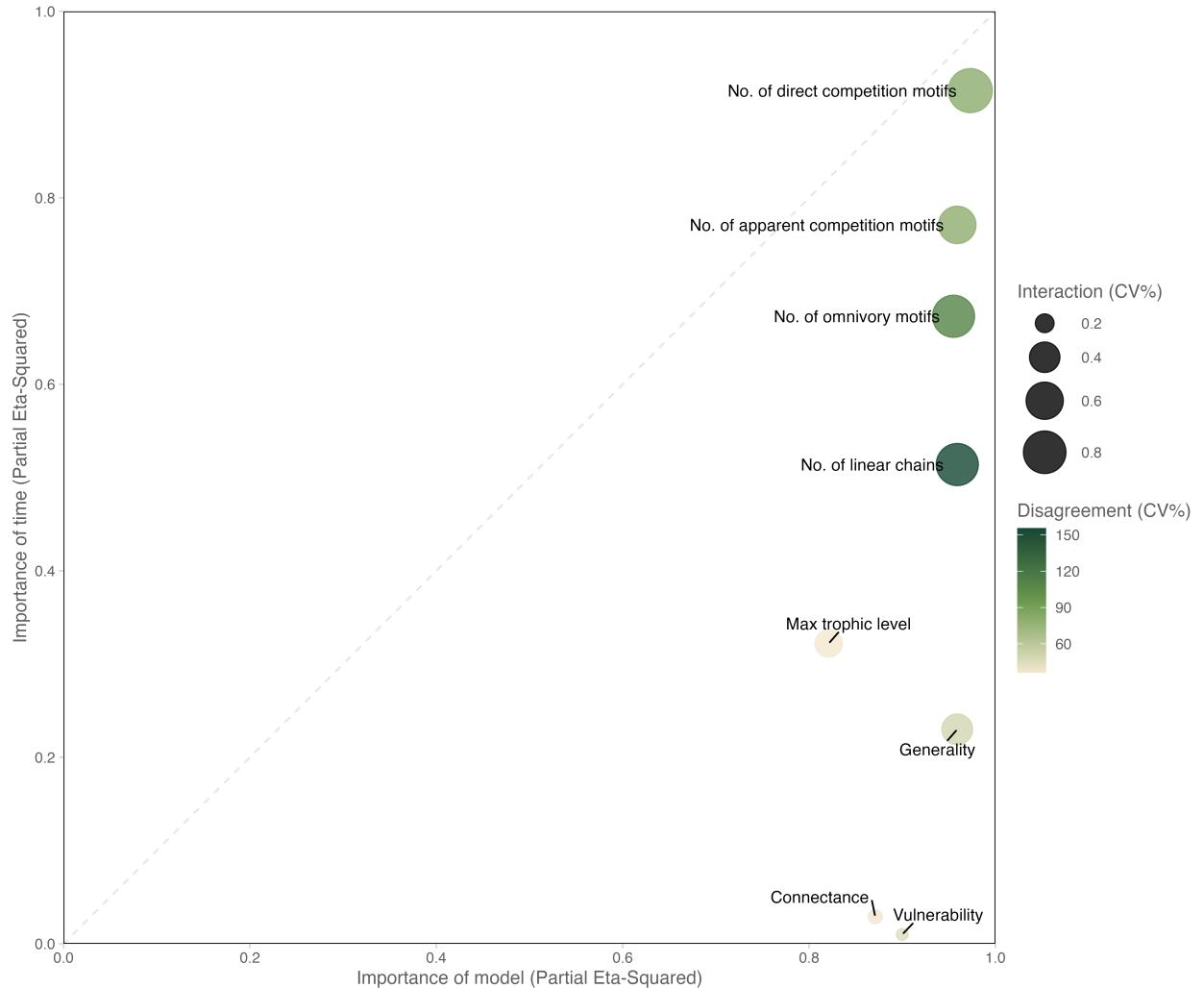


Figure 2: Scatter plot illustrating the influence of model (x-axis) and time (y-axis) across network metrics. The dashed 1:1 diagonal represents the parity of influence; metrics below this line are governed primarily by model choice and those above by time. Bubble size indicates the interaction between 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.

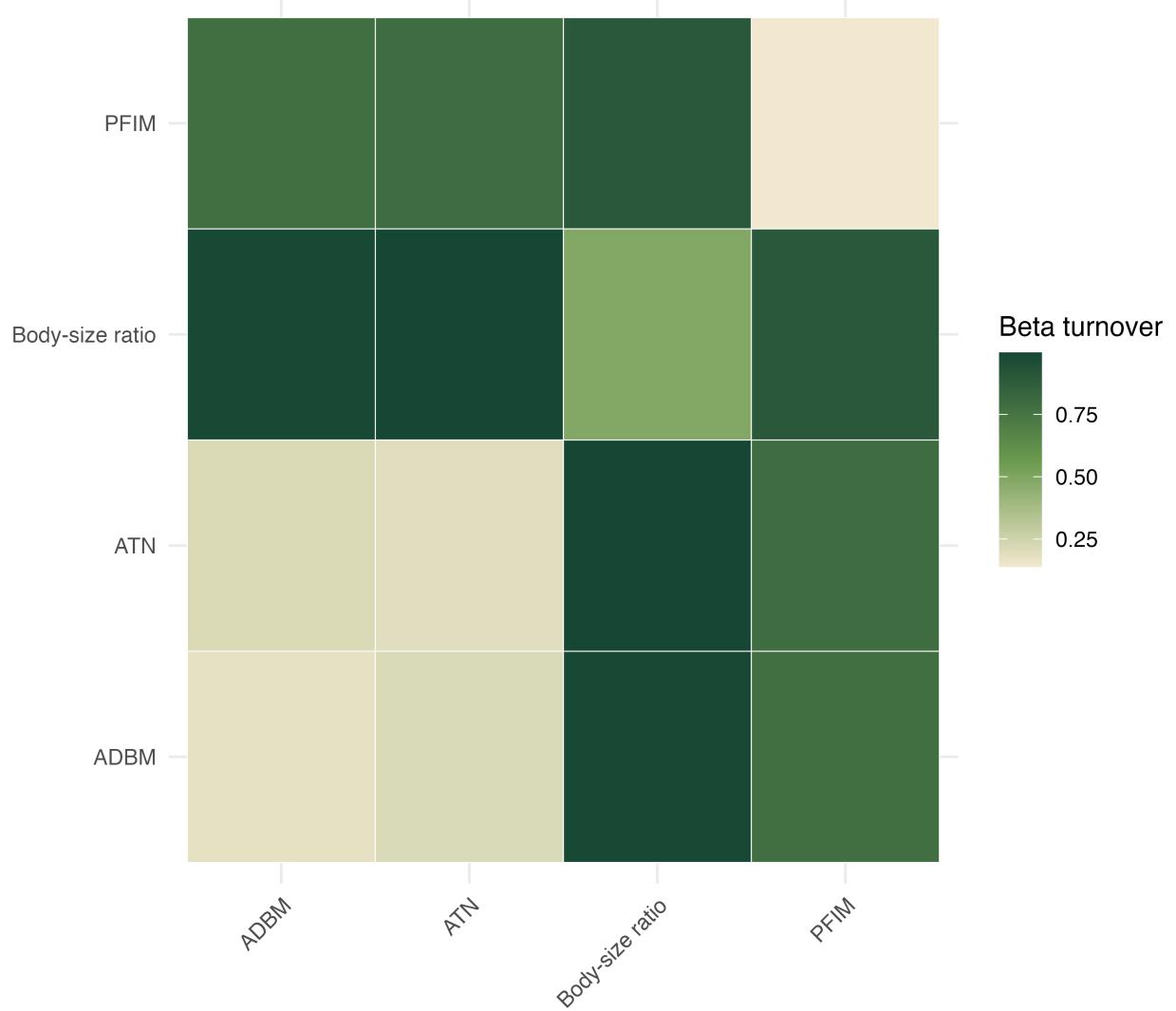


Figure 3: Pairwise β_{OS} in species interactions among four ecological network models (ADBM, ATN, Body-size ratio, and PFIM). Each cell represents the mean turnover value between a pair of models, with darker colours indicating greater dissimilarity in inferred interactions. High turnover values indicate strong disagreement in pairwise interactions between models, whereas lower values indicate greater similarity. Note that we do not include the Random or Niche model as these models are species agnostic and thus we cannot truly evaluate differences in pairwise interactions



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.