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 Introduction

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

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

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

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

stability (Allesina & Tang, 2012; Delmas et al., 2018; Poisot et al., 2015). If reconstruction models encode 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; 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 drawn from an identical taxon pool, 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, abun-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 mechanical/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.

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

2.2.2 Network generation and replication

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

2.3 Network metrics and structural analyses

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

Table 2: Network properties used for analysis.

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

Metric	Definition	Scale	Reference
Max trophic level	Prey-weighted trophic level averaged across taxa	Macro	Williams & Martinez (2004)
S1	Number of linear chains, normalised	Meso	Milo et al. (2002); Stouffer et al. (2007)
S2	Number of omnivory motifs, normalised	Meso	Milo et al. (2002); Stouffer et al. (2007)
S4	Number of apparent competition motifs, normalised	Meso	Milo et al. (2002); Stouffer et al. (2007)
S5	Number of direct competition motifs, normalised	Meso	Milo et al. (2002); Stouffer et al. (2007)
Generality	Normalized standard deviation of generality of a species, standardised by L/S	Micro	Williams & Martinez (2000)
Vulnerability	Normalized standard deviation of vulnerability of a species, standardised by L/S	Micro	Williams & Martinez (2000)

2.4 Extinction simulations and model 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' 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 ( ) was used to quantify concordance in scenario ordering across models. Full methodological details are provided in the Supplementary Materials.

2.5 Software and Reproducibility

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

3 Results

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

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

3.1 Network structure differs among reconstruction approaches

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

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

[Figure 1 about here.]

3.1.1 Variance partitioning of network structure

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

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

3.1.2 Statistical Drivers of Network Variation

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

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

[Figure 2 about here.]

3.1.3 Inferred pairwise interactions vary widely among models

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

[Figure 3 about here.]

3.2 Model choice influences inferred extinction dynamics

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

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

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

This assumption is particularly critical to evaluate within the context of deep-time paleoecological data. Because interactions in fossil ecosystems are never observed directly, they must explicitly be reconstructed 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 paleoecological 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.

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

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

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

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

4.2 Scale-dependent robustness in network-based inference

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

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

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

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

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

inference.

4.3 Implications for comparative biogeography and global change research

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

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

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

4.4 Toward a more explicit modelling paradigm in food web ecology

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

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

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

5 Conclusions

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

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

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

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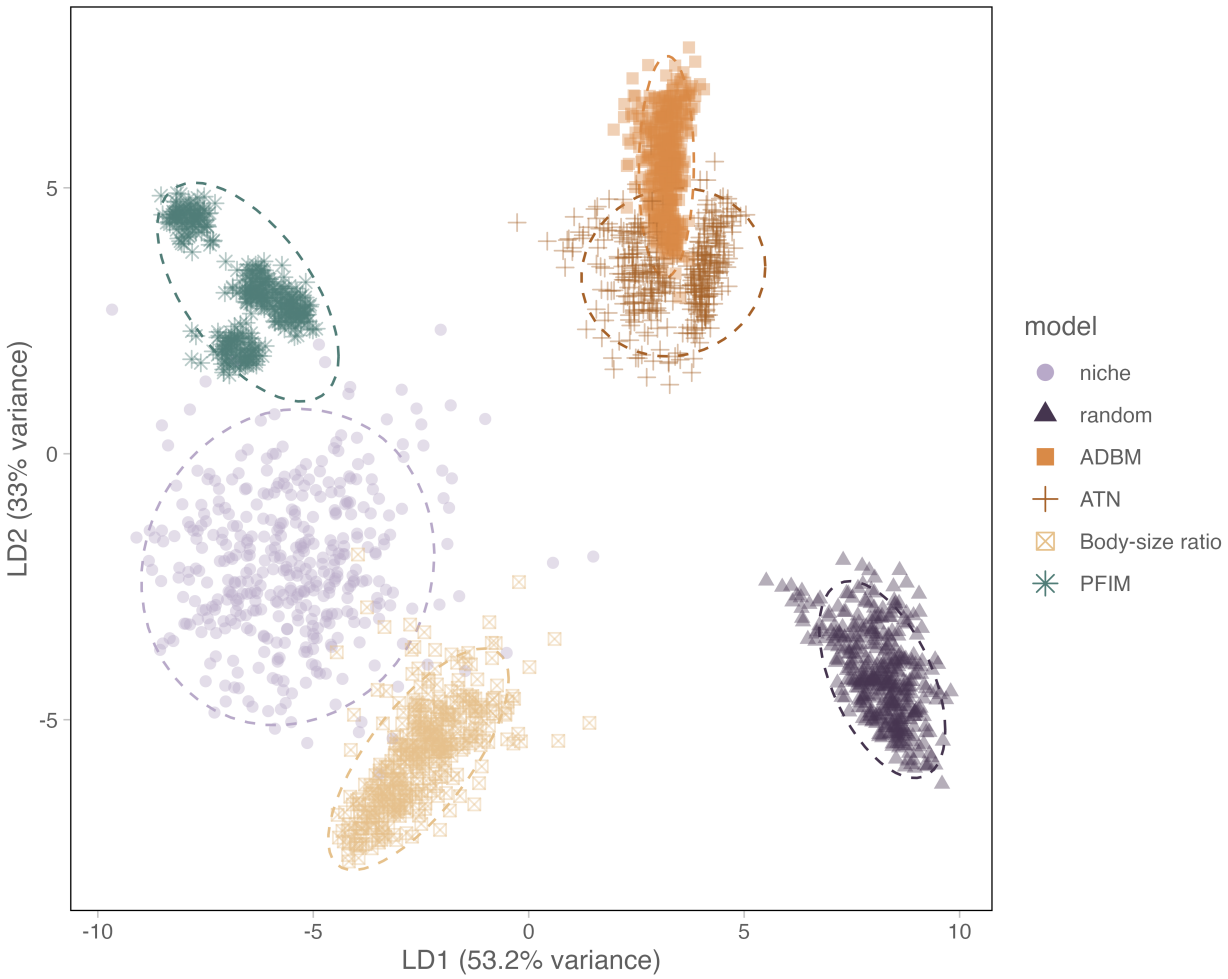

Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

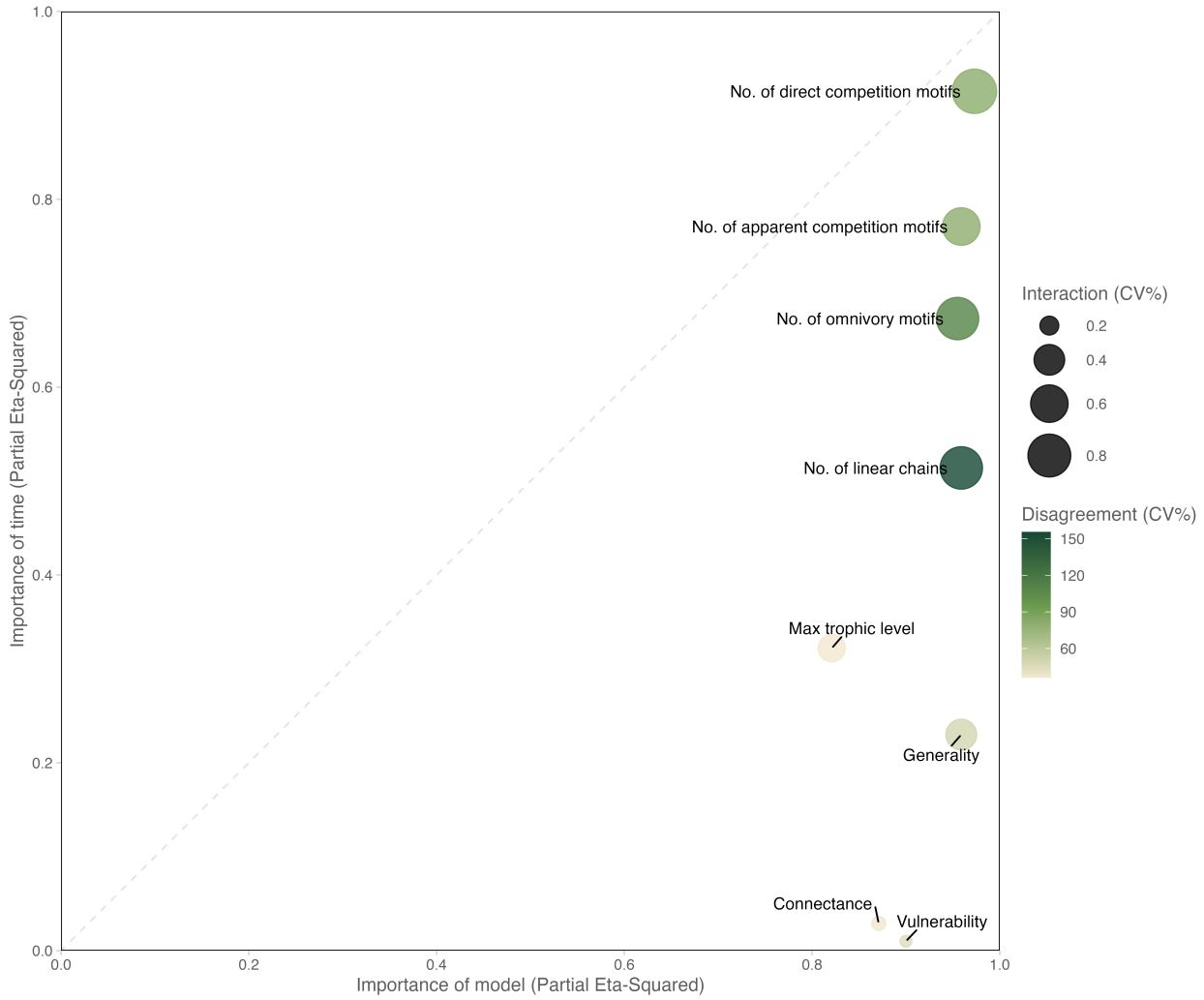

Figure 2: Scatter plot illustrating the influence of model (x-axis) and time (y-axis) across network metrics. The dashed 1:1 diagonal represents the parity of influence; metrics below this line are governed primarily by model choice and those above by time. Bubble size indicates the interaction between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

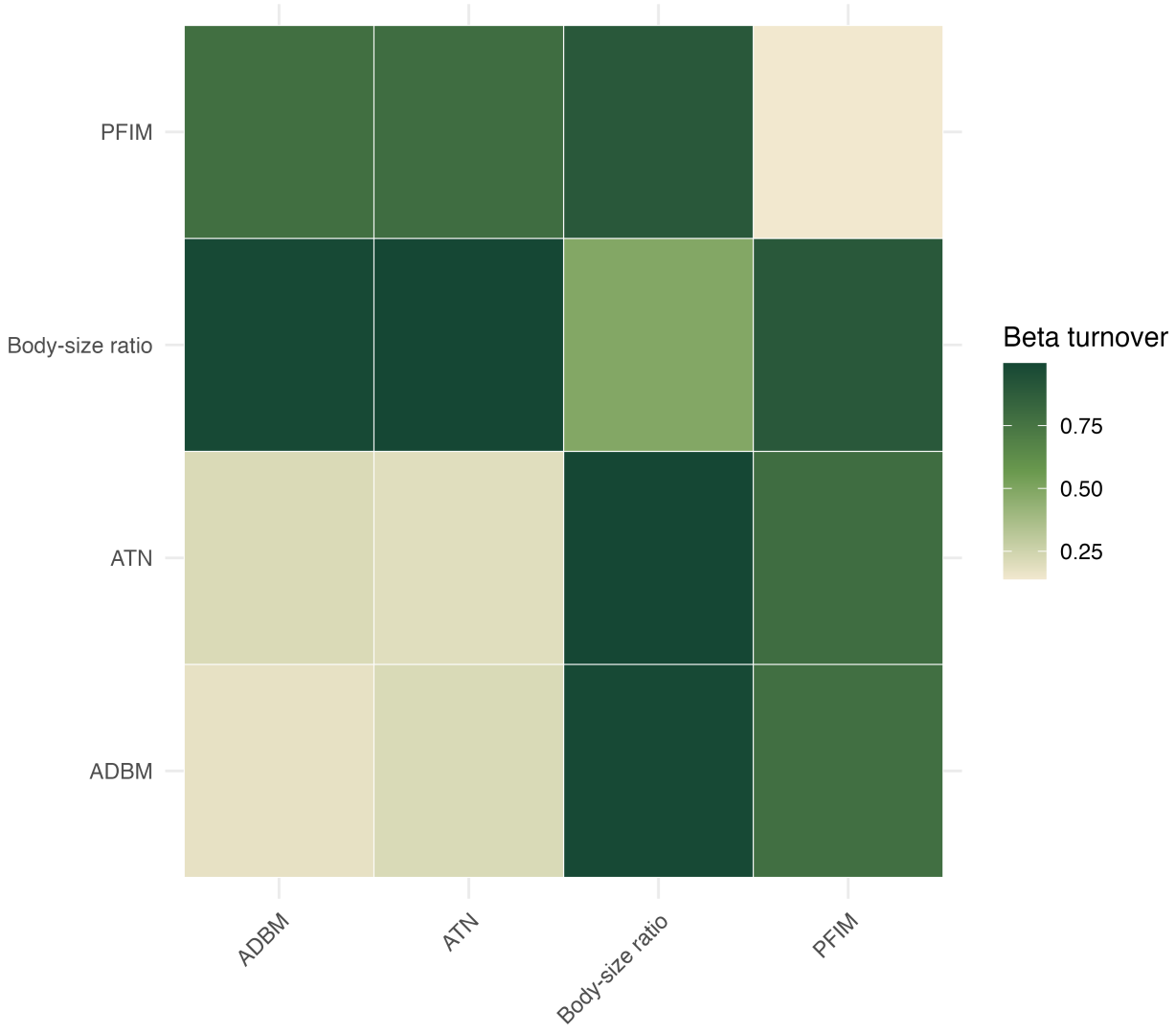

Figure 3: Pairwise -turnover in species interactions among four ecological network models (ADBM, ATN, Body-size ratio, and PFIM). Each cell represents the mean turnover value between a pair of models, with darker colours indicating greater dissimilarity in inferred interactions. High turnover values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

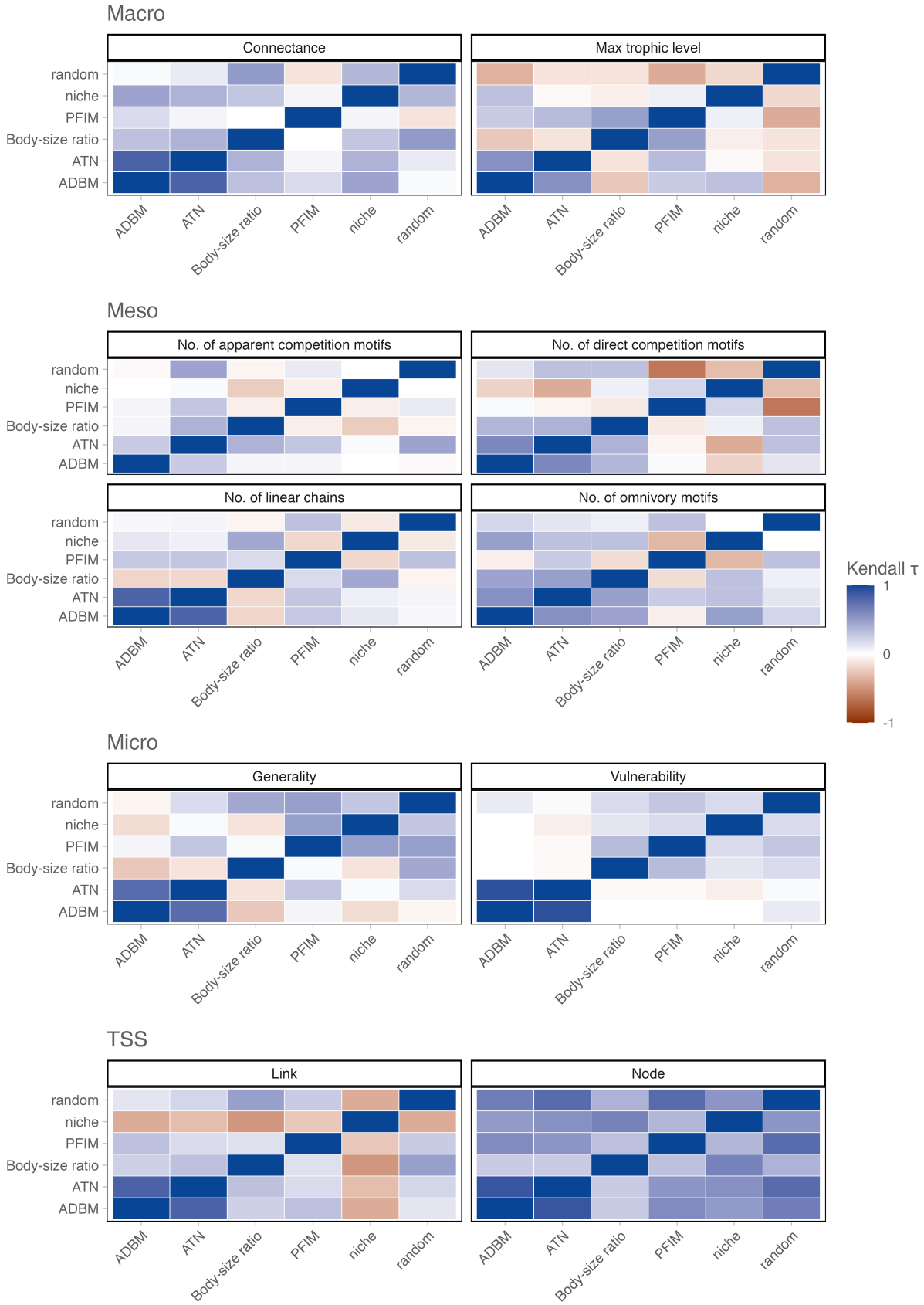

Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients (τ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between observed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