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.

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

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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. 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). 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 approaches (e.g., Fricke et al. (2022); Roopnarine (2006); Shaw et al. (2024)) currently operate within the feasibility space. That is, these approaches identify and encode the entire diet of a species and thus represent all feasible interactions within the network. Although well suited for reconstructing feasible interactions, these methods represent only a subset of the broader spectrum of network construction approaches. Here, we present a suite of models (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. For example, some tools require quantitative estimates of body size, which must often be inferred from size classes or functional morphology in the fossil record. Structural models, such as the niche model, rely only on species richness and estimates/specification of connectance, but their species-agnostic nature limits their applicability to trait-based or diet-specific questions, although they do still accurately recover network structure (Stouffer et al., 2005) . Mechanistic approaches, by contrast, depend on accurate assignment of feeding traits or robust phylogenetic support. Recognizing how these methodological requirements intersect with the limits of fossil evidence is essential for selecting an appropriate modelling framework.

Table 1: Six different models that can be used to construct food webs for both this specific community but are also broadly suited to paleo network prediction. These models span all facets of the network representation space (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/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.

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.

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 beta diversity, which measures dissimilarity in the identity of trophic links between networks, capturing differences due to species turnover or changes in interactions among shared species (Poisot et al., 2012).

Table 2: Network properties used for analysis.

Metric	Definition	Scale	Reference (for maths), can make footnotes probs
Richness	Number of nodes in the network	Macro	

Metric	Definition	Scale	Reference (for maths), can make footnotes probs
Links	Normalized standard deviation of links (number of consumers plus resources per taxon)	Micro	
Connectance	L/S^2, where S is the number of species and L the number of links	Macro	
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) and using the pre-extinction and post-extinction networks, we simulated species loss under multiple extinction scenarios. We simulated species loss under multiple scenarios, including trait-based, network-position-based, and random removals, allowing cascading extinctions to propagate. Simulated outcomes were compared to observed or expected community states using mean absolute differences (MAD) and modified true skill statistics (TSS) at node and link levels. Kendall's rank correlation coefficient was used to evaluate concordance in scenario rankings across reconstruction models, providing a measure of robustness in inferred community responses.

3 Results

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 scale - approaches that were statistically similar in multivariate structural space often diverged in inferred interactions or extinction dynamics. This demonstrates that structural similarity does not guarantee concordance in species-level diets or trophic roles. Model choice also 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. Importantly, agreement among models was not consistent across analytical scales - models that were statistically indistinguishable in multivariate structural space often diverged in inferred interactions or extinction dynamics. Together these 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.

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 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, 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 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 2. 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 2 about here.]

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3.2 Model choice influences inferred extinction dynamics

To quantify how network structure changed over time during extinction simulations and whether these dynamics differed among reconstruction models, we fit generalized additive models (GAMs) to time series of network-level metrics. GAMs capture non-linear temporal trajectories, allowing formal tests of whether the shape of these trajectories differs among models. These model-specific temporal trajectories are shown in Figure 3. For all metrics examined, the inclusion of model-specific smooth terms significantly improved model fit (ANOVA model comparison: $p < 0.001$ for all metrics). Model-specific smooths differed not only in magnitude but also in the timing and abruptness of change, indicating distinct modes of collapse across reconstruction approaches (Tables S3–S4). Deterministic, data-driven approaches (PFIM) and allometric models (ADBM, ATN) exhibited highly non-linear trajectories, showing structural shifts in connectivity and motif frequency. In contrast, the Niche model produced the most consistent and gradual trajectories, effectively smoothing the perceived magnitude of structural change during community collapse. These results demonstrate that inferred pathways of collapse, trophic bottlenecks, and secondary extinctions are highly sensitive to model choice. Corresponding raw temporal trajectories are shown in Figure S2.

[Figure 3 about here.]

To evaluate how model choice affects inferred extinction dynamics, we compared simulated post-extinction networks to observed networks using mean absolute differences (MAD) for network-level metrics and 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.]

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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. Our results challenge this assumption. Across an identical species pool, reconstruction frameworks explained the majority of variance among reconstructed network topologies, generating distinct structural signatures independent of community composition. Although some model classes converged on similar global metrics, pairwise interaction turnover revealed substantial divergence in inferred trophic links. Structural similarity at the level of connectance or trophic height therefore does not guarantee concordance in species roles or interaction architecture.

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, and these assumptions propagate 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 structural priors 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

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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 structural prior. 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 finer-scale 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 (*e.g.,* Dunhill et al., 2024). 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 or trophic bottlenecks may partly reflect model-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 part of a 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. These studies frequently interpret variation in connectance, trophic height, interaction -diversity, or robustness as indicators of ecological differentiation among regions or time intervals. Yet reconstruction frameworks often differ among systems due to variation in sampling intensity, trait resolution, or modelling preference. Our results show that such differences can systematically alter inferred topology and disturbance dynamics even when species composition is held constant.

This finding has consequences for interaction biogeography. Apparent differences in network turnover across spatial gradients may reflect divergence in structural priors rather than genuine ecological reorganisation. Similarly, projected differences in vulnerability under climate change may depend on how realised interactions are modelled, not solely on community composition. Without explicit treatment of reconstruction assumptions, comparative network analyses risk conflating modelling artefact with macroecological process.

If ecological networks are to function as reliable macroecological state variables, reconstruction framework must be treated as a formal component of hypothesis specification. Cross-system comparisons should standardise modelling approaches wherever possible, or explicitly evaluate sensitivity to alternative structural priors. Ensemble reconstruction—treating networks as distributions rather than single topologies—offers a principled pathway toward incorporating structural uncertainty into comparative synthesis.

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 structurally commensurable across systems. 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. As ecological networks increasingly inform global change research, recognising structural priors as fundamental determinants of inference is critical for advancing food web ecology from descriptive reconstruction toward rigorous comparative

synthesis.

References

Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, *483*(7388), 205–208. https://doi.org/10.1038/nature10832

Bambach, R. K., Bush, A. M., & Erwin, D. H. (2007). Autecology and the filling of ecospace: Key metazoan radiations. *Palaeontology*, *50*(1), 1–22. https://doi.org/10.1111/j.1475-4983.2006.00611.x

Banville, F., Strydom, T., Blyth, P. S. A., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas, T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2025). Deciphering probabilistic species interaction networks. *Ecology Letters*, *28*(6), e70161. https://doi.org/10.1111/ele.70161

Baskerville, E. B., Dobson, A. P., Bedford, T., Allesina, S., Anderson, T. M., & Pascual, M. (2011). Spatial guilds in the serengeti food web revealed by a bayesian group model. *PLOS Computational Biology*, *7*(12), e1002321. https://doi.org/10.1371/journal.pcbi.1002321

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., … Cohen, J. E. (2006). Consumer–resource body-size relationships in natural food webs. *Ecology*, *87*(10), 2411–2417. https://doi.org/https://doi.org/10.1890/0012-9658(2006)87%5B2411:CBRINF%5D2.0.CO;2

Carstensen, D. W., Sabatino, M., Trøjelsgaard, K., & Morellato, L. P. C. (2014). Beta diversity of plant-pollinator networks and the spatial turnover of pairwise interactions. *PLOS ONE*, *9*(11), e112903. https://doi.org/10.1371/journal.pone.0112903

Catchen, M. D., Lin, M., Poisot, T., Rolnick, D., & Gonzalez, A. (2023). *Improving ecological connectivity assessments with transfer learning and function approximation*. https://ecoevorxiv.org/repository/view/5348/

Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A., & Rall, B. C. (2011). Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs. *Basic and Applied Ecology*, *12*(7), 571–580. https://doi.org/10.1016/j.baae.2011.09.008

Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Dalla Riva, G. V., Fortin, M.-J., Gravel, D., Guimarães, P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2018). Analysing ecological networks of species interactions. *Biological Reviews*, 112540. https://doi.org/10.1111/brv.12433

Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024). Extinction cascades, community collapse, and recovery across a mesozoic hyperthermal event. *Nature*

Communications, *15*(1), 8599. https://doi.org/10.1038/s41467-024-53000-2

Dunne, J. A., Labandeira, C. C., & Williams, R. J. (2014). Highly resolved early eocene food webs show development of modern trophic structure after the end-cretaceous extinction. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782), 20133280. https://doi.org/10.1098/rspb.2013.3280

Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and network analyses of cambrian food webs. *PLOS Biology*, *6*(4), e102. https://doi.org/10.1371/journal.pbio.0060102

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecol. Lett.*, *5*(4), 558–567.

Elmasri, M., Farrell, M. J., Davies, T. J., & Stephens, D. A. (2020). A hierarchical bayesian model for predicting ecological interactions using scaled evolutionary relationships. *The Annals of Applied Statistics*, *14*(1), 221–240. https://doi.org/10.1214/19-AOAS1296

Erdős, P., & Rényi, A. (1959). On random graphs. i. *Publicationes Mathematicae Debrecen*, *6*(3-4), 290–297. https://doi.org/10.5486/pmd.1959.6.3-4.12

Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning, J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the late pleistocene. *Science*, *377*(6609), 1008–1011. https://doi.org/10.1126/science.abn4012

Fründ, J., McCann, K. S., & Williams, N. M. (2016). Sampling bias is a challenge for quantifying specialization and network structure: Lessons from a quantitative niche model. *Oikos*, *125*(4), 502–513. https://doi.org/10.1111/oik.02256

Gauzens, B., Brose, U., Delmas, E., & Berti, E. (2023). ATNr: Allometric trophic network models in r. *Methods in Ecology and Evolution*, *14*(11), 2766–2773. https://doi.org/10.1111/2041-210X.14212

Gauzens, B., Thouvenot, L., Srivastava, D. S., Kratina, P., Romero, G. Q., Berti, E., O'Gorman, E. J., González, A. L., Dézerald, O., Eisenhauer, N., Pires, M., Ryser, R., Farjalla, V. F., Rogy, P., Brose, U., Petermann, J. S., Geslin, B., & Hines, J. (2025). Tailoring interaction network types to answer different ecological questions. *Nature Reviews Biodiversity*, 1–10. https://doi.org/10.1038/s44358-025-00056-7

Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B., Tylianakis, J. M., Wood, S. A., & Roslin, T. (2019). Bringing elton and grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, *42*(3), 401–415. https://doi.org/https://doi.org/10.1111/ecog.04006

Guimarães, P. R. (2020). The structure of ecological networks across levels of organization. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1). https://doi.org/10.1146/annurev-ecolsys-012220-120819

Hao, X., Holyoak, M., Zhang, Z., & Yan, C. (2025). Global projection of terrestrial vertebrate food webs under future climate and land-use changes. *Global Change Biology*, *31*(2), e70061. https://doi.org/10.

1111/gcb.70061

Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*. https://doi.org/10.1111/1365-2435.12763

Kemp, D. B., Han, Z., Hu, X., Chen, W., Jin, S., Izumi, K., Yan, Q., Baranyi, V., Jin, X., Corso, J. D., & Ge, Y. (2024). Global hydroclimate perturbations during the toarcian oceanic anoxic event. *Earth-Science Reviews*, *258*, 104946. https://doi.org/10.1016/j.earscirev.2024.104946

Michalska-Smith, M. J., & Allesina, S. (2019). Telling ecological networks apart by their structure: A computational challenge. *PLOS Computational Biology*, *15*(6), e1007076. https://doi.org/10.1371/journal.pcbi.1007076

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple building blocks of complex networks. *Science*, *298*(5594), 824–827. https://doi.org/10.1126/science.298.5594.824

Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, *30*(6), 347–356. https://doi.org/10.1016/j.tree.2015.03.014

Perez-Lamarque, B., Andréoletti, J., Morillon, B., Pion-Piola, O., Lambert, A., & Morlon, H. (2026). Darwin's entangled bank through deep time: Structural stability of mutualistic networks over large geographic and temporal scales. *EcoEvoRxiv*. https://doi.org/10.1101/2025.10.08.681159

Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences*, *105*(11), 4191–4196. https://doi.org/10.1073/pnas.0710672105

Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2011). Fit, efficiency, and biology: Some thoughts on judging food web models. *Journal of Theoretical Biology*, *279*(1), 169–171. https://doi.org/10.1016/j.jtbi.2011.03.019

Pichler, M., & Hartig, F. (2023). Machine learning and deep learning—a review for ecologists. *Methods in Ecology and Evolution*, *14*(4), 994–1016. https://doi.org/10.1111/2041-210X.14061

Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., & Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*, jbi.14127. https://doi.org/10.1111/jbi.14127

Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecology Letters*, *15*(12), 1353–1361. https://doi.org/10.1111/ele.12002

Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of probabilistic networks. *Methods in Ecology and Evolution*, *7*(3), 303312. https://doi.org/10

Poisot, T., & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree

distribution and emerging network properties. *PeerJ*, *2*, e251. https://doi.org/10.7717/peerj.251

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, *124*(3), 243–251. https://doi.org/10.1111/oik.01719

Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring unexplained structure using latent traits. *The American Naturalist*, *176*(2), 170–177. https://doi.org/10.1086/653667

Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, *32*(1), 1–19. https://www.jstor.org/stable/4096814

Sandra, H.-P., Traveset, A., Nogales, M., Heleno, R., Llewelyn, J., & Strona, G. (2025). Sampling biases across interaction types affect the robustness of ecological multilayer networks. *Ecological Informatics*, 103183. https://doi.org/10.1016/j.ecoinf.2025.103183

Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. https://doi.org/10.1101/2024.01.30.578036

Solé, R. V., & Montoya, M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1480), 2039–2045. https://doi.org/10.1098/rspb.2001.1767

Stouffer, D. B., Camacho, J., Guimerà, R., Ng, C. A., & Nunes Amaral, L. A. (2005). Quantitative patterns in the structure of model and empirical food webs. *Ecology*, *86*(5), 1301–1311. https://doi.org/10.1890/04-0957

Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*, *88*(2), 192–195. https://doi.org/https://doi.org/10.1111/1365-2656.12949

Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1621), 1931–1940. https://doi.org/10.1098/rspb.2007.0571

Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz, N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap towards predicting species interaction networks (across space and time). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1837), 20210063. https://doi.org/10.1098/rstb.2021.0063

Strydom, T., Dunhill, A. M., Dunne, J. A., Poisot, T., & Beckerman, A. P. (2026). Scaling from metawebs to realised webs: A hierarchical approach to network ecology. *EcoEvoRxiv*. https://doi.org/10.32942/X2JW8K

Thuiller, W., Calderón-Sanou, I., Chalmandrier, L., Gaüzère, P., O'Connor, L. M. J., Ohlmann, M., Poggiato,

G., & Münkemüller, T. (2024). Navigating the integration of biotic interactions in biogeography. *Journal of Biogeography*, *51*(4), 550–559. https://doi.org/10.1111/jbi.14734

Trøjelsgaard, K., & Olesen, J. M. (2016). Ecological networks in motion: Micro- and macroscopic variability across scales. *Functional Ecology*, *30*(12), 1926–1935. https://doi.org/https://doi.org/10.1111/1365-2435.12710

Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 25–48. https://doi.org/10.1146/annurev-ecolsys-110316-022821

Williams, R. J., & Martinez, N. D. (2004). Stabilization of chaotic and non-permanent food-web dynamics. *The European Physical Journal B - Condensed Matter*, *38*(2), 297–303. https://doi.org/10.1140/epjb/e2004-00122-1

Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, *404*(6774), 180–183. https://doi.org/10.1038/35004572

Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food webs. *The Journal of Animal Ecology*, *77*(3), 512–519. https://doi.org/10.1111/j.1365-2656.2008.01362.x

Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014). Collapse of an ecological network in ancient egypt. *PNAS*, *111*(40), 14472–14477. https://doi.org/10.1073/pnas.1408471111
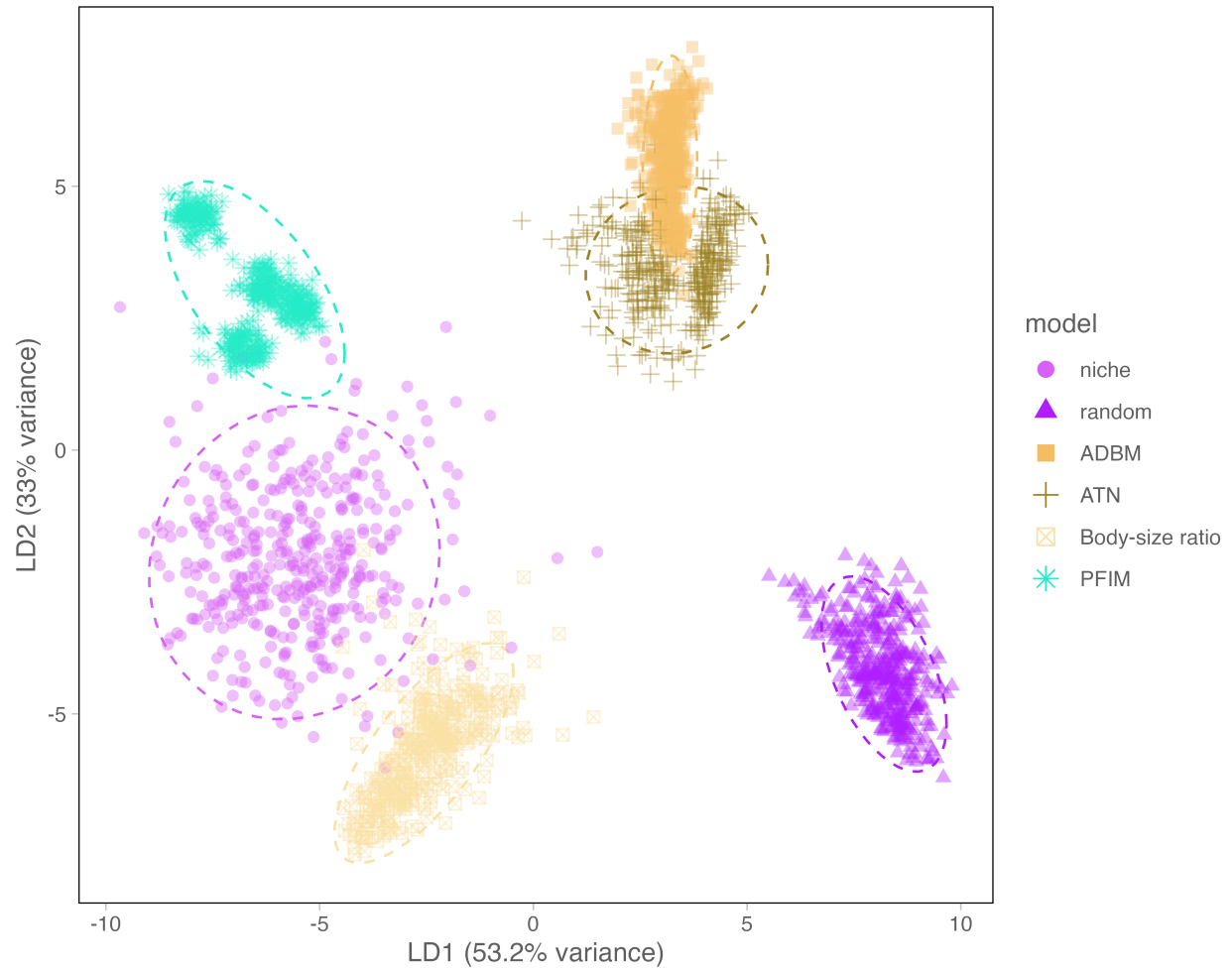
Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.
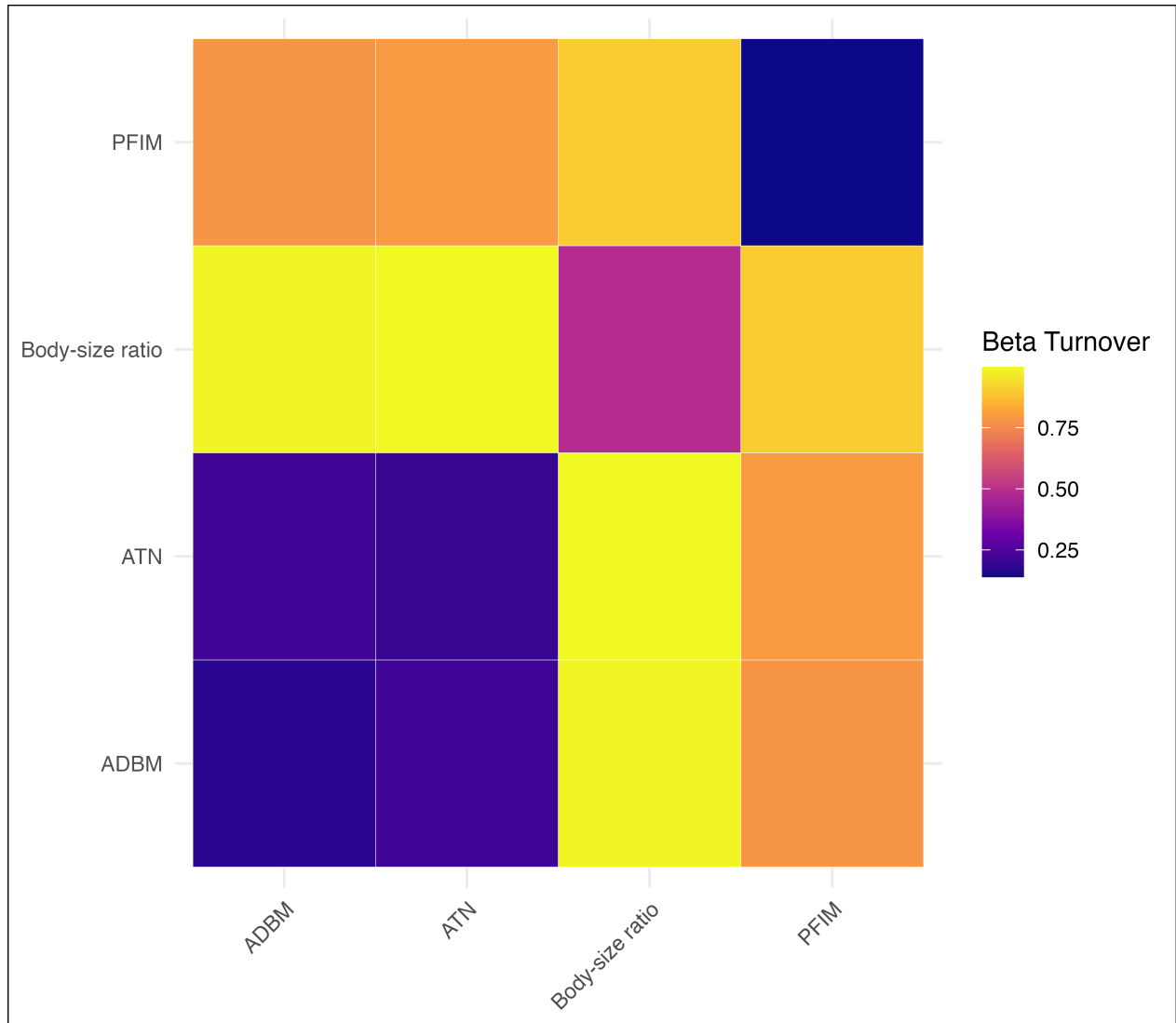
Figure 2: Pairwise -turnover in species interactions among four ecological network models (ADBM, ATN, Body-size ratio, and PFIM). Each cell represents the mean turnover value between a pair of models, with warmer colours indicating greater dissimilarity in inferred interactions. The diagonal is omitted. High turnover values (yellow) indicate strong disagreement in network structure between models, whereas lower values (blue–purple) indicate greater similarity.
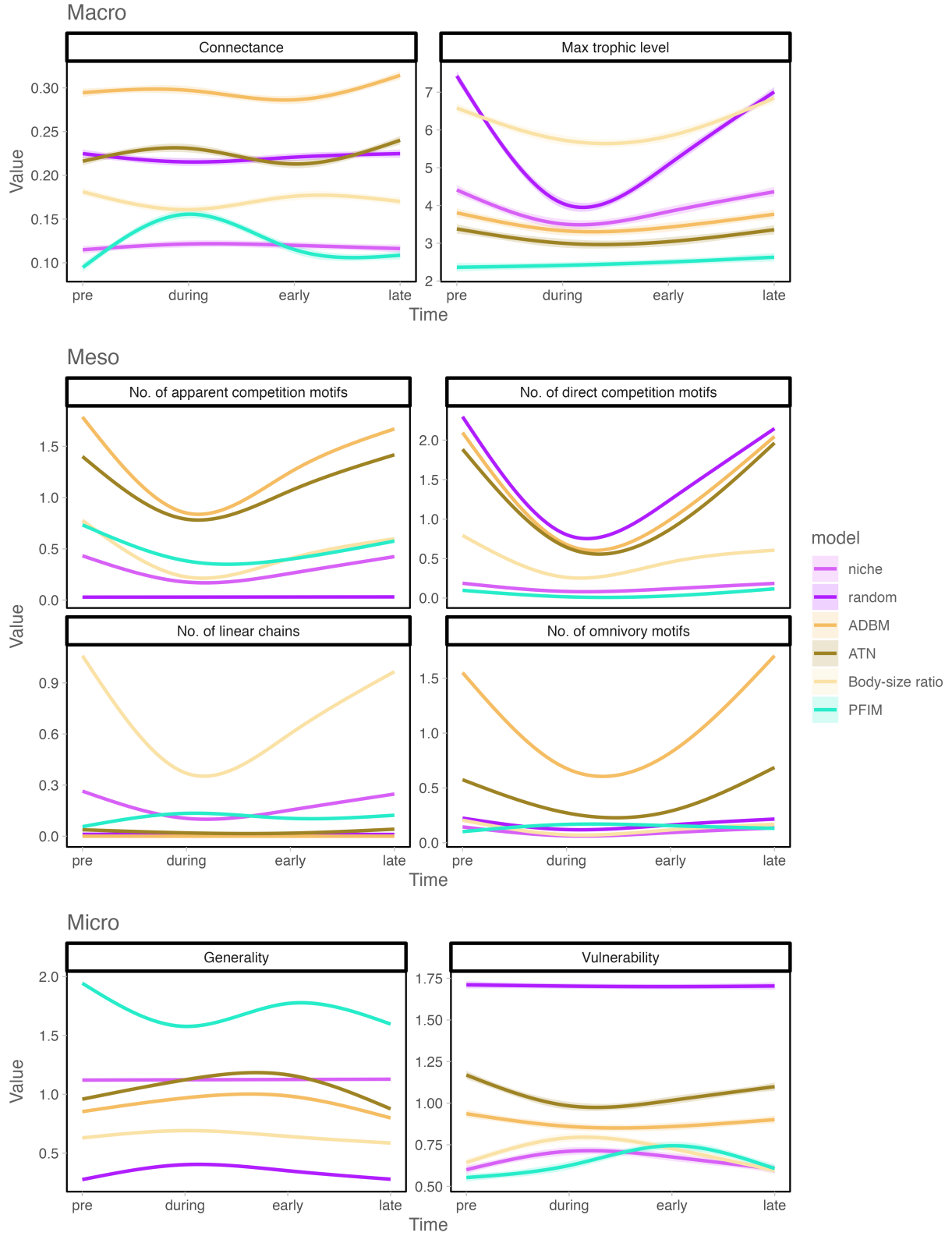
Figure 3: GAM-predicted trajectories of network structure during extinction simulations reveal pronounced differences in the timing and magnitude of change across reconstruction models. Lines show model-specific smooths and shaded areas indicate 95% confidence intervals. Deterministic approaches produce smoother, more consistent dynamics, whereas stochastic models exhibit greater variability, underscoring the sensitivity of inferred collapse pathways to reconstruction assumptions.
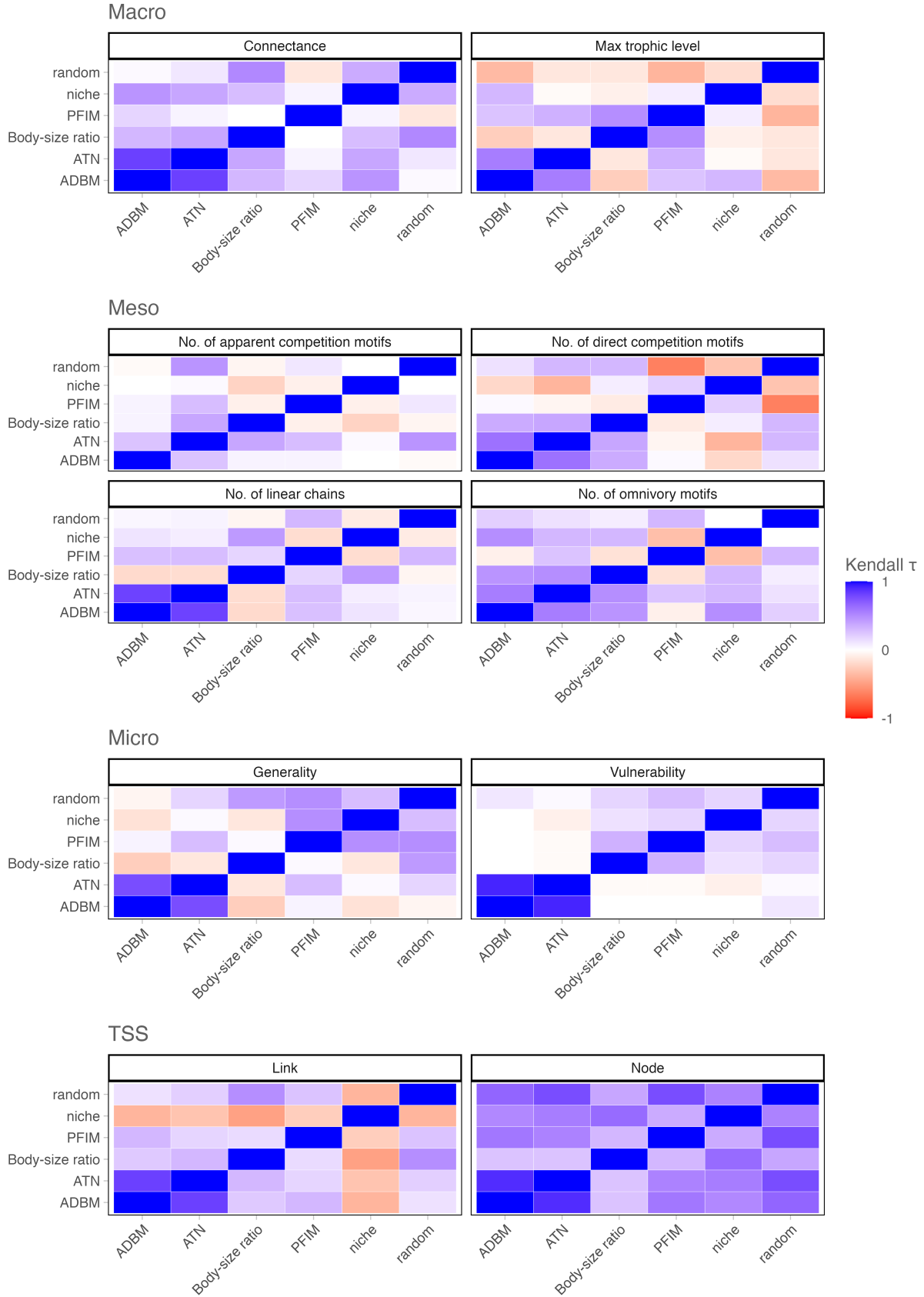
Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients (τ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between observed 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. Panels