Reconstructing food webs in deep time: why model choice matters for ecological inference

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Abstract: Food webs provide a powerful framework for understanding ecosystem structure and function, yet reconstructing them in paleoecological contexts remains challenging because direct evidence of species interactions is rarely preserved. A growing array of models exists for predicting interactions and inferring network structure, but these approaches differ markedly in their assumptions, mechanisms, and data requirements. Here, we evaluate how network reconstruction model choice shapes ecological inference in deep time and which approaches are most appropriate given the constraints of the fossil record. Using the Toarcian Oceanic Anoxic Event (Early Jurassic, ~183 Ma) as a case study, we reconstruct food webs for four successive community states using six contrasting modelling approaches spanning mechanistic, trait-based, and structural network representations. Despite identical taxon pools, models produced strikingly different network structures and species-level interactions, and these differences propagated into divergent inferences about extinction dynamics, interaction loss, and cascading effects. By framing food-web reconstructions as alternative ecological hypotheses (rather than interchangeable representations) this study bridges paleoecology and modern network theory, and demonstrates how model choice fundamentally conditions inference about extinction dynamics in deep time.

1 Introduction

There is growing interest in using deep-time fossil data and evidence of species interactions in past ecosystems (*e.g.,* Dunne et al. (2008); Dunne et al. (2014)) as a foundation for understanding how ecological communities respond to multi-stressor environmental change, such as temperature increase, ocean acidification, and hypoxia (Dillon et al., 2022; Kiessling et al., 2019). Paleoecological networks therefore represent a particularly valuable opportunity to investigate community responses to major environmental transitions as they allow for the explicit construction of pre- and post-extinction interaction networks and enable the disentangling of extinction drivers as well as broader cascading effects (Dunhill et al., 2024; Roopnarine, 2006; Yeakel et al., 2014). Insights gained from these deep-time systems provide a critical context for interpreting present day ecological change and anticipating the impacts of ongoing anthropogenic stressors (Barnosky et al., 2012; Roopnarine & Dineen, 2018).

Inference from ecological networks regarding structure and complexity is (at its core) a mathematical task and is therefore relatively independent of biological assumptions (Delmas et al., 2019). While these structural properties can be analysed independently of biological detail, their implications for stability and dynamics depend critically on assumptions about the distribution and strength of interaction (Allesina & Tang, 2012; Poisot et al., 2015). Thus, assumptions become meaningful once network structure and complexity are interpreted in functional terms or used as templates for simulating community and extinction dynamics. While there is a well-developed theoretical framework describing what can be inferred from network properties, a central challenge (particularly in paleoecology) lies in how networks are constructed. Unlike modern systems, paleoecological interactions are rarely directly observed, with only exceptional cases preserving explicit evidence of trophic interactions (*e.g.,* Jenny et al. (2019); Vullo (2011)). As a result, paleo food web reconstruction depends on indirect inference, drawing on preserved traits, analogies with modern taxa, and ecological theory. Simply put, network reconstruction is not a data recovery process, but rather hypothesis generation under constraints.

Although numerous tools exist for inferring species interactions (see Morales-Castilla et al., 2015; Pichler & Hartig, 2023; Strydom et al., 2021; Allesina et al., 2008 for reviews), only a subset can be reliably applied in paleo contexts, where data on traits, abundances, and community composition are incomplete and systematically biased. This makes it essential to clearly articulate which reconstruction approaches are appropriate for which inferential purposes. Recent work has shown that reconstruction approaches (*e.g.,* models based on traits, abundances, or co-occurrence) can be categorised by the type of network that they predict (Strydom et al., 2026). These include feasible networks (derived from trait matching and phylogenetic inference that produce metawebs of plausible interactions), realised networks, (constrained by ecological rules

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and evidence of actual feeding relationships), and purely structural networks (which reproduce ecologically plausible topologies but lack species-level node identities). In this sense, food-web reconstructions are not empirical recoveries of a single past ecosystem, but rather represent alternative, model-based, hypotheses about interaction structure constrained by the fossil record.

Each of these reconstruction approaches carries distinct assumptions that influence inferred network size, complexity, structure, and node-level properties, with direct consequences for ecological interpretations of extinction dynamics, stability, resilience, and ecosystem function (Dunne et al., 2002; Gravel et al., 2019; Roopnarine, 2006; Solé & Montoya, 2001). Despite this, most paleo food web studies default to constructing networks using expert knowledge (*e.g.,* Dunne et al. (2008)) or mechanistic feeding rules (*e.g.,* Dunhill et al. (2024); Roopnarine (2017); Fricke et al. (2022)), approaches that typically result in metawebs. This raises a critical but underexplored question: to what extent does the choice of network type (and particularly the use of alternatives to metawebs) control not only inferred food web structure but also conclusions about system behaviour, especially with respect to extinction cascades and vulnerability.

In this study, we address this question by explicitly evaluating how network reconstruction model choice shapes ecological inference in deep time. We link recent advances in food-web reconstruction methods to a comparative re-evaluation of primary and secondary, trait-based extinction dynamics during the early Toarcian extinction event, a volcanic-driven hyperthermal and marine crisis in the Early Jurassic (~183 Ma) (Dunhill et al., 2024). We reconstruct four successive communities (pre-extinction, post-extinction, early recovery, and late recovery) from the Cleveland Basin of North Yorkshire, UK, using six contrasting network reconstruction approaches spanning feasible, realised, and structural network representations - as recognised in recent network inference frameworks (Morales-Castilla et al., 2015; Strydom et al., 2026). For each community, we compare network-level structure, species-level properties, and inferred interactions across models, allowing us to assess how reconstruction assumptions propagate into ecological interpretations. Finally, we replicate the secondary extinction analyses of Dunhill et al. across all six reconstruction methods to explicitly test how model choice influences inference about extinction drivers, interaction loss, and cascading dynamics. By explicitly comparing multiple reconstruction approaches within a single paleoecological system, this study provides a framework for evaluating how methodological assumptions shape interpretations of ancient food-web structure and dynamics.

2 Materials and 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, following Dunhill et al. (2024). Four paleo-communities were defined: pre-extinction, post-extinction, early recovery, and late recovery. Each assemblage was treated as a community of potentially interacting taxa. Modes of life were assigned following Dunhill et al. (2024) using the Bambach ecospace framework. Traits included motility, tiering, feeding mode, and size class, with size defined categorically based on maximum linear dimensions.

2.2 Network reconstruction approaches

2.2.1 Conceptual classification of network types

Most paleo-specific approaches currently operate within the feasibility space (*e.g.,* Shaw et al., 2024; Fricke et al., 2022; Roopnarine, 2006). 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 (metaweb, 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 family	Assumptions	Data needs	'Limitation'	Network type	Key reference	Usage examples
random	Links are randomly distributed within a network	richness, number of links	parameter assumptions, species agnostic	structural network	Erdős & Rényi (1959)	
niche	Networks are interval, species can be ordered on a 'niche axis'	richness, connectance	parameter assumptions, species agnostic	structural network	Williams & Martinez (2008)	
allometric diet breadth model (ADBM)	Interactions are determined by energetic costs (foraging ecology)	body mass, biomass (abundance)	does not account for forbidden links in terms of trait compatibility, assumptions on body size and biomass (abundance) from fossil data	realised network	Petchey et al. (2008)	

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Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference	Usage examples
Allometric trophic network (ATN)	Interactions inferred using allometric rules (ratio of body sizes between predator and prey), with links being constrained by a Ricker function	body mass, number of producer species	does not account for forbidden links in terms of trait compatibility, assumptions on body size from fossil data, assumptions as to the number of producer species	realised network	Brose et al. (2006); Gauzens et al. (2023)	
paleo food web inference model (PFIM)	Interactions can be inferred by a mechanistic frame-work/rela-tionships	feeding traits for taxa, mechanistic feeding rules	Assumption made as to the feeding mechanisms, need to elucidate traits from models (although this is a way smaller issue)	feasibility web	Shaw et al. (2024)	Secondary extinctions (Dunhill et al., 2024)

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference	Usage examples
body size ratio model	Interactions inferred using allometric rules (ratio of body sizes between predator and prey). Logit of the linking probability used to further constrain links to an 'optimal size range' for prey.	body mass	does not account for forbidden links in terms of evolutionary compatibility, assumptions on body size from fossil data	realised network	Rohr et al. (2010)	Network collapse (Yeakel et al., 2014)

2.2.2 Network generation and replication

We evaluated six models spanning this space Table 1: random and niche models (structural network); allometric diet breadth (ADBM), allometric trophic network (ATN), and body-size ratio models (realised network); and a paleo food-web inference model (PFIM; feasibility web). More details on parameters can be found in the Supplementary Materials. For each of the four communities, we constructed 100 replicate networks using each of the six models (2400 networks total). Networks were simplified by removing disconnected species. For size-based models, body masses were drawn from uniform distributions bounded by size-class limits,allowing for variance between replicates but preserving relative sizes within replicates. Structural models were parameterised using connectance values drawn from an empirically realistic range $(0.07 - 0.34)$ while holding richness constant. The same parameter draws were used across comparable models within each replicate.

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 models were assessed using MANOVA, followed by univariate ANOVAs, post-hoc comparisons, and linear discriminant analysis. Pairwise interaction turnover was quantified using link-based beta diversity for models that infer species-specific interactions (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	
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)

Metric	Definition	Scale	Reference (for maths), can make footnotes probs
Generality	Normalized standard deviation of generality of a species standardized by L/S	Micro	Williams & Martinez (2000)
Vulnerability	Normalized standard deviation of vulnerability of a species standardized 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, including trait-based, network-position-based, and random removals, allowing for secondary extinctions. Simulated post-extinction networks were compared to empirical post-extinction communities using mean absolute differences (MAD) in network metrics and a modified true skill statistic (TSS) at both node and link levels. Scenario rankings were compared across models using Kendall's rank correlation coefficient.

3 Results

Across six reconstruction approaches, both global network structure and species-level interactions differed substantially, with implications for interpreting past extinction dynamics. Deterministic models (e.g., PFIM) tended to produce more consistent network-level patterns and smoother extinction trajectories, whereas stochastic or theory-driven models (*e.g.,* ADBM, niche, ATN) showed greater variability in inferred interactions and temporal extinction dynamics. Models with similar macro-level metrics sometimes differed in their specification of pairwise interactions, highlighting that agreement in global structure does not guarantee concordance at the species level. Consequently, inferred extinction pathways and secondary extinctions were highly sensitive to model choice, emphasizing the importance of evaluating multiple network reconstructions when interpreting ecological dynamics in deep time.

3.1 Network structure differs among reconstruction approaches

To test whether network reconstruction approach influences inferred food-web structure, we compared multivariate patterns of network metrics across all six models using a MANOVA. Network structure differed strongly among reconstruction approaches (MANOVA, Pillai's trace = 3.81, approximate $F_{40,11955} = 962.12$, p < 0.001). Univariate analyses showed that model choice explained a large proportion of variance in most network metrics, with high partial η^2 values for connectance, generality, vulnerability, and motif frequencies ($\eta^2 = 0.66$–0.92). In contrast, maximum trophic level exhibited a much smaller effect of model choice ($\eta^2 = 0.04$). Estimated marginal means and Tukey-adjusted comparisons indicated consistent differences among reconstruction approaches, with PFIM differing significantly from all other models (p $\leq$ 0.026), while ADBM and ATN did not differ from one another (p = 1.00). Linear discriminant analysis (LDA) further helped visualise distinctions among reconstruction approaches in multivariate network space Figure 1, with the first two axes explaining 86.5% of between-model variance (LD1 = 53.9%, LD2 = 32.6%). LD1 was most strongly correlated with vulnerability, connectance, and the number of direct competition motifs (S4), whereas LD2 was associated primarily with generality, number of omnivory motifs (S2), and number of apparent competition motifs (S5). Higher-order axes each explained less than 9% of the remaining variance. This demonstrates that the reconstruction approach leaves a strong multivariate signature independent of community composition.

[Figure 1 about here.]

3.1.1 Inferred pairwise interactions vary widely among models

Building on differences in global network structure, we next examined how reconstruction approach influences species-level ecological inference by quantifying turnover in inferred pairwise interactions among networks constructed from the same taxon pool. While models that produced similar global metrics sometimes agreed broadly on network structure, they often differed sharply in the specific interactions they inferred.

Pairwise β-turnover revealed that some model pairs shared very few links despite comparable macro- or meso-scale properties Figure 2. ADBM and ATN were highly concordant, reflecting similar underlying assumptions despite different generative rules, whereas the body-size ratio model consistently exhibited high differences in pairwise interactions relative to all other approaches. PFIM showed intermediate overlap with size-based theoretical models. These patterns indicate that agreement in global network metrics does not guarantee agreement in species-level diets or trophic roles, highlighting the importance of evaluating both network- and species-level outcomes when comparing reconstruction methods.

[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 nonlinear temporal trajectories, allowing formal tests of whether the shape of these trajectories differs among models. For connectance, the model-specific smooth terms were all significant (*e.g.,* PFIM: EDF = 2.99, F = 113.8, p < 0.001; ADBM: EDF = 2.92, F = 22.6, p < 0.001), indicating distinct temporal patterns across reconstruction approaches. Trophic level trajectories also differed among models (PFIM: EDF = 2.96, F = 36.7, p < 0.001; Niche: EDF = 2.96, F = 94.9, p < 0.001). Deterministic approaches, such as PFIM, produced more consistent and smooth trajectories, whereas stochastic, theory-driven models (niche, ADBM, ATN) displayed greater variability in timing and magnitude of structural change. These results demonstrate that inferred pathways of collapse, trophic bottlenecks, and secondary extinctions are highly sensitive to model choice.

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 total sum-of-squares (TSS) for node- and link-level outcomes Figure 3. Overall, models were more consistent in ranking extinction scenarios at the network level: Kendall's τ values for MAD-based rankings were generally positive, with strong agreement between ADBM and ATN models (τ 0.82) and weaker or inconsistent correlations involving stochastic models such as log ratio or random (τ ranging from -0.26 to 0.44). Node-level TSS scores similarly showed broad consistency across models, reflecting comparable species removal sequences (τ 0.38–0.46 between ADBM and niche or PFIM). In contrast, link-level outcomes were more variable: deterministic models like PFIM maintained moderate agreement with observed post-extinction links (τ 0.44), whereas stochastic, theory-driven models exhibited low or inconsistent correlations (τ as low as -0.44). These results indicate that while different models often recover similar species-level extinction patterns, inferred interaction loss and cascade dynamics are highly sensitive to model choice.

[Figure 3 about here.]

4 Discussion

5 Model choice as a component of ecological inference

Reconstructing food webs from fossil data is inherently an exercise in inference under uncertainty, where ecological conclusions depend as much on modelling assumptions as on preserved evidence (Dunne et al., 2008;

Morales-Castilla et al., 2015). Our results demonstrate that the choice of network reconstruction model is itself a major ecological decision, shaping not only the structural properties of inferred networks but also downstream interpretations of extinction dynamics (Allesina & Tang, 2012; Solé & Montoya, 2001). Even with identical taxon pools, different models yield networks that diverge in global metrics, species-level interactions, and temporal patterns of collapse. These divergences do not stem from differences in fossil evidence or taxon composition, but from the assumptions embedded within each reconstruction approach (Pichler & Hartig, 2023; Strydom et al., 2021). Consequently, network reconstruction is not a neutral methodological step; model choice shapes the ecological narratives we extract from ancient ecosystems.

While previous studies have emphasized the role of model assumptions in metaweb reconstruction (Dunhill et al., 2024; Roopnarine, 2006), our results demonstrate that these assumptions create distinct, predictable clusters of network properties. These clusters map directly onto the conceptual divide between feasible, realised, and structural network types (Strydom et al., 2026). Specifically, mechanistic models (PFIM) identify a broad landscape of trait-compatible interactions, theoretical models (ADBM, ATN) impose energetic filters to approximate realised energy flow, and structural models (niche, random) prioritise topological patterns over species identity. Our Pairwise -turnover analysis confirms that these differences are not merely quantitative; models fundamentally disagree on link identity, reinforcing concerns that traditional metawebs may significantly overestimate realised interaction diversity (Fricke et al., 2022; Shaw et al., 2024). This distinction is central to paleoecological inference, where feasible interactions are often mistaken for realised trophic relationships.

The downstream consequences of model choice are most pronounced when evaluating extinction dynamics (Dunne et al., 2002; Sahasrabudhe & Motter, 2011). While broad, trait-driven patterns of species loss are relatively robust across models, the identity of lost interactions, secondary extinctions, and cascade dynamics are sensitive to the type of network reconstructed. Node-level patterns tend to be more consistent across models because they primarily reflect intrinsic species traits, whereas link-level outcomes are emergent properties of model assumptions. This distinction mirrors findings in modern food-web studies, where deterministic and stochastic model assumptions influence the magnitude and timing of secondary extinctions (Allesina & Tang, 2012; Curtsdotter et al., 2011; Dunne et al., 2002; Yeakel et al., 2014). Our results suggest that interpretations of trophic collapse, bottlenecks, and recovery trajectories are shaped not only by the fossil record but also by the choice of network model. Consequently, paleoecologists must carefully consider which ecological signals they aim to recover (potential interactions, realized diets, or macro-scale structural properties) before selecting a reconstruction approach. Importantly, disagreement among models does not imply that any single approach is 'wrong', but rather reflects the fact that different models capture different ecological signals (Stouffer, 2019).

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The challenge therefore lies not in identifying a universally correct model, but rather in aligning model choice with the ecological question being asked.

5.1 Aligning ecological questions with model choice

A central insight from our study is that different ecological questions require different network representations. Feasibility networks are most appropriate for evaluating potential trophic links or dietary breadth; realised networks capture energetically constrained, ecologically plausible interactions; and structural networks are suited for exploring generic topological patterns such as connectance or trophic depth. Link-level dynamics and cascade sensitivity are particularly sensitive to network choice, whereas higher-level patterns of species loss are less so.

This alignment between question and model type reflects a broader trend in network ecology emphasizing the role of assumptions in determining which inferences are valid (Delmas et al., 2019; Petchey et al., 2008; Schneider et al., 2016). By explicitly matching network representation to research question, paleoecologists can avoid overinterpreting model-dependent artifacts as biological signals.

Below is a conceptual summary:

Ecological question	Recommended network type	Rationale
What *could* have eaten what? (feasible interactions; trophic potential)	Feasibility web (PFIM, trait-based, evolutionary-signal models)	Captures all trait-feasible links; appropriate for reconstructing dietary breadth or assessing potential niches.
What interactions were *likely realised*?	Realised network (ADBM, ATN)	Encodes foraging ecology and energetic constraints; provides ecologically plausible 'realised' networks.
How do global macro structural properties vary?	Structural network (niche, random as baseline)	Useful for understanding generic patterns (connectance, trophic depth) without trait reliance.
How do traits influence dynamics (e.g., cascade sensitivity)?	Realised network	Capture body-size scaling, energetic constraints, and trophic dependencies.

Ecological question	Recommended network type	Rationale
How robust are inferences to uncertainty?	Ensembles across multiple network types	Allows quantifying how conclusions depend on assumptions.

5.2 Implications for paleoecological network studies

Our analysis underscores three important implications for the broader field:

1. **Interpretations of ancient food webs must explicitly acknowledge model assumptions:** Without this, differences in reconstructed networks may be mistakenly attributed to biological change rather than methodological artifacts.

2. **Comparisons across studies must be standardised by model family:** Comparing a metaweb from one study to a realised network from another risks generating misleading conclusions about ecological differences across space or time.

3. **Integrating theory-driven models expands inference:** Mechanistic paleo-specific models alone capture only a subset of feasible networks. Incorporating modern theory-based approaches allows researchers to explore alternative network archetypes, extending the range of questions that can be addressed (Dunne et al., 2014; Solé & Montoya, 2001).

5.3 Recommendations for network reconstruction in paleoecology

To support consistent, transparent use of network reconstruction methods in paleoecology, we propose the following guidelines :

1. **Establish the Inferential Goal First:** Explicitly define whether the study aims to capture potential interactions (feasibility), energetic flows (realised), or global patterns (structural). This choice dictates the appropriate model family and prevents the common error of treating metawebs as local diet realisations.

2. **Implement an Ensemble Modelling Framework:** Rather than just using multiple models, advocate for an ensemble approach. Evaluating a suite of models allows researchers to quantify model uncertainty identifying which ecological conclusions are robust biological signals and which are methodological artifacts.

3. **Standardise Comparative Analyses:** To avoid misleading comparisons across studies, researchers should only compare networks constructed within the same model family. If comparing a new metaweb to a published realised web, the differences must be explicitly attributed to the representation gap rather than environmental change.

4. **Prioritize Scale-Specific Interpretation:** Distinguish clearly between node- and link-level results. Since node-level patterns (who goes extinct) are generally more robust to model choice, they can be interpreted with higher confidence than specific link-level pathways (the exact cascade route), which are highly sensitive to model assumptions.

6 Conclusions

Ecological network reconstruction in deep time is not merely a technical step but a fundamental component of ecological inference. By explicitly comparing six contrasting reconstruction approaches within a single extinction event and location we show that model choice strongly shapes inferred food-web structure, species interactions, and extinction dynamics, even when underlying fossil data are identical. While broad, trait-based patterns of species loss appear relatively robust, conclusions about pairwise interactions, secondary extinctions, and cascading dynamics depend critically on the assumptions embedded in the chosen network reconstruction approach. These results underscore the need for paleoecological studies to align reconstruction methods with specific ecological questions and to evaluate the sensitivity of key conclusions to alternative network representations. More broadly, our findings highlight that understanding past ecosystem collapse requires not only better fossil data, but also transparent, question-driven modelling frameworks that make explicit the assumptions underlying ecological inference.

References

Allesina, S., Alonso, D., & Pascual, M. (2008). A general model for food web structure. *Science*, *320*(5876), 658–661. https://doi.org/10.1126/science.1156269

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

Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte, J., Hastings, A., Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J. W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., … Smith, A. B. (2012). Approaching a state shift in earth's biosphere. *Nature*, *486*(7401), 52–58. https://doi.org/10.1038/nature11018

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

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., Riva, G. V. D., 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. (2019). Analysing ecological networks of species interactions. *Biological Reviews*, *94*(1), 16–36. https://doi.org/10.1111/brv.12433

Dillon, E. M., Pier, J. Q., Smith, J. A., Raja, N. B., Dimitrijević, D., Austin, E. L., Cybulski, J. D., De Entrambasaguas, J., Durham, S. R., Grether, C. M., Haldar, H. S., Kocáková, K., Lin, C.-H., Mazzini, I., Mychajliw, A. M., Ollendorf, A. L., Pimiento, C., Regalado Fernández, O. R., Smith, I. E., & Dietl, G. P. (2022). What is conservation paleobiology? Tracking 20 years of research and development. *Frontiers in Ecology and Evolution*, *10*. https://doi.org/10.3389/fevo.2022.1031483

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., 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.

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

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

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

Jenny, D., Fuchs, D., Arkhipkin, A. I., Hauff, R. B., Fritschi, B., & Klug, C. (2019). Predatory behaviour and taphonomy of a jurassic belemnoid coleoid (diplobelida, cephalopoda). *Scientific Reports*, *9*(1), 7944. https://doi.org/10.1038/s41598-019-44260-w

Kiessling, W., Raja, N. B., Roden, V. J., Turvey, S. T., & Saupe, E. E. (2019). Addressing priority questions of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1788), 20190222. https://doi.org/10.1098/rstb.2019.0222

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

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

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., 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., 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. (2017). *Ecological modelling of paleocommunity food webs* (pp. 201–226). University of Chicago Press.

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

Roopnarine, P. D., & Dineen, A. A. (2018). *Coral reefs in crisis: The reliability of deep-time food web*

reconstructions as analogs for the present (C. L. Tyler & C. L. Schneider, Eds.; pp. 105–141). Springer International Publishing. https://doi.org/10.1007/978-3-319-73795-9_6

Sahasrabudhe, S., & Motter, A. E. (2011). Rescuing ecosystems from extinction cascades through compensatory perturbations. *Nature Communications*, *2*(1), 170. https://doi.org/10.1038/ncomms1163

Schneider, F. D., Brose, U., Rall, B. C., & Guill, C. (2016). Animal diversity and ecosystem functioning in dynamic food webs. *Nature Communications*, *7*(1), 12718. https://doi.org/10.1038/ncomms12718

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

Vullo, R. (2011). Direct evidence of hybodont shark predation on late jurassic ammonites. *Naturwissenschaften*, *98*(6), 545–549. https://doi.org/10.1007/s00114-011-0789-9

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.

374   https://doi.org/10.1038/35004572

375   Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food

376   webs. *The Journal of Animal Ecology*, *77*(3), 512–519. https://doi.org/10.1111/j.1365-2656.2008.01362.x

377   Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T.

378   (2014). Collapse of an ecological network in ancient egypt. *PNAS*, *111*(40), 14472–14477. https:

379   //doi.org/10.1073/pnas.1408471111
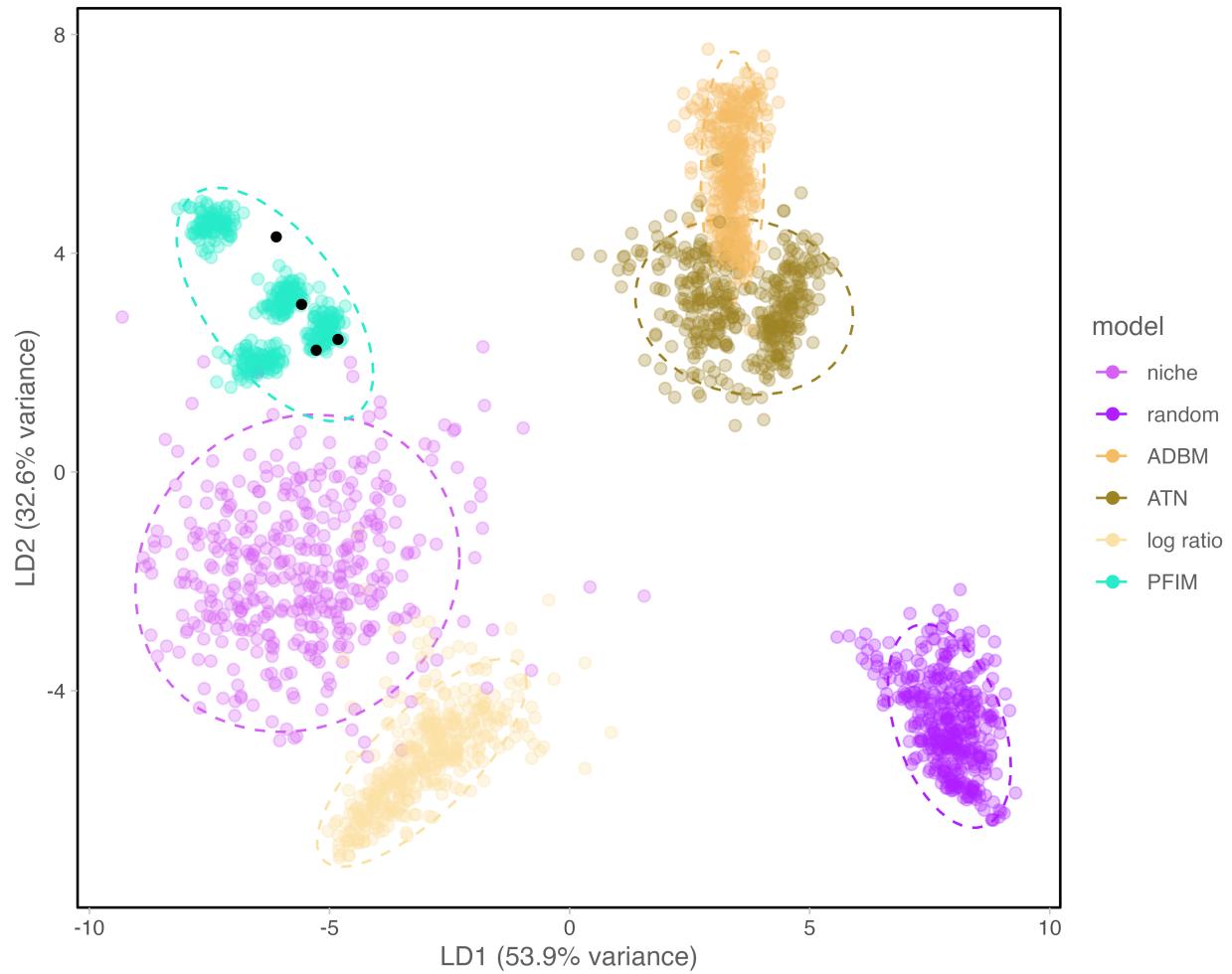
Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.
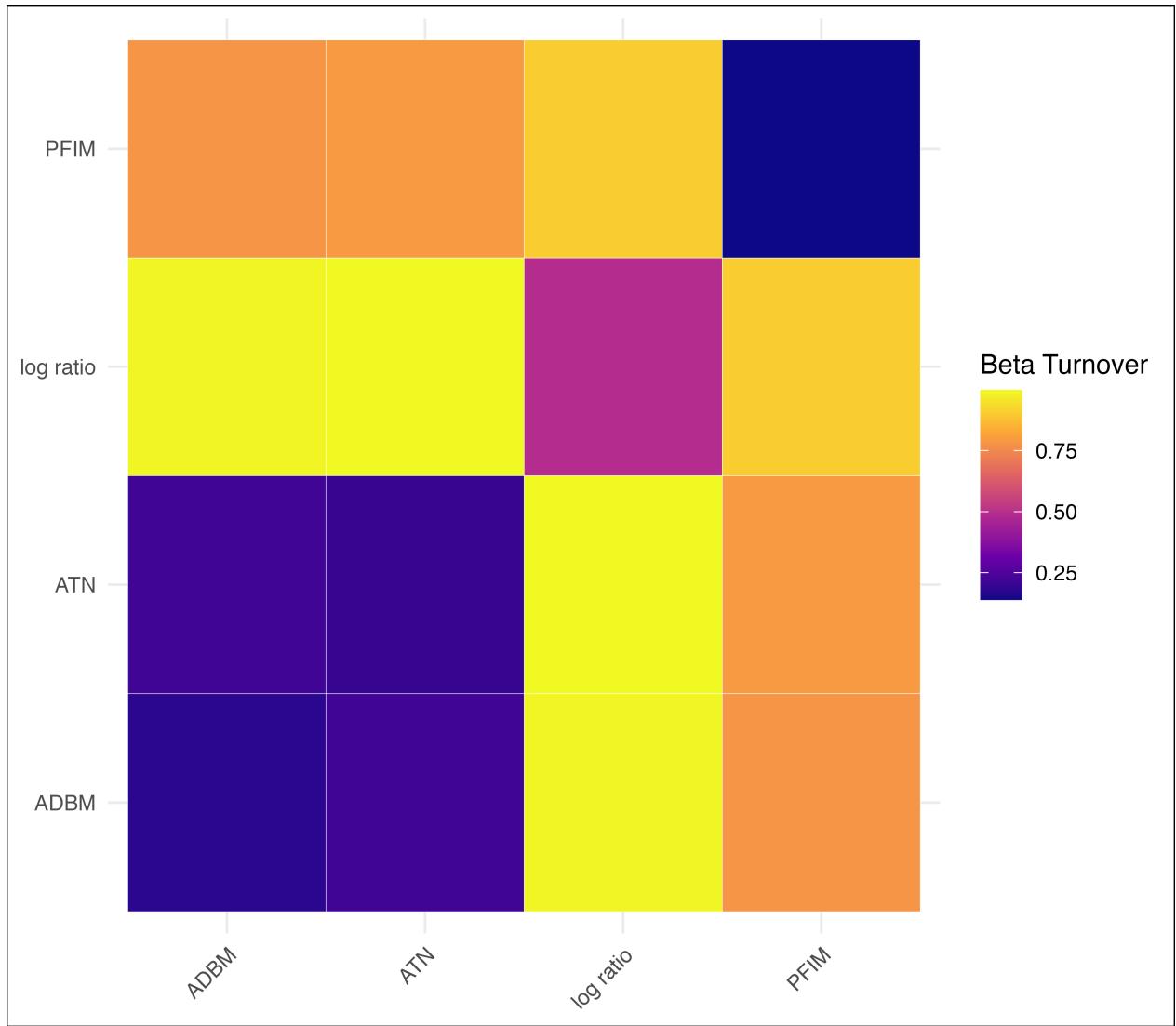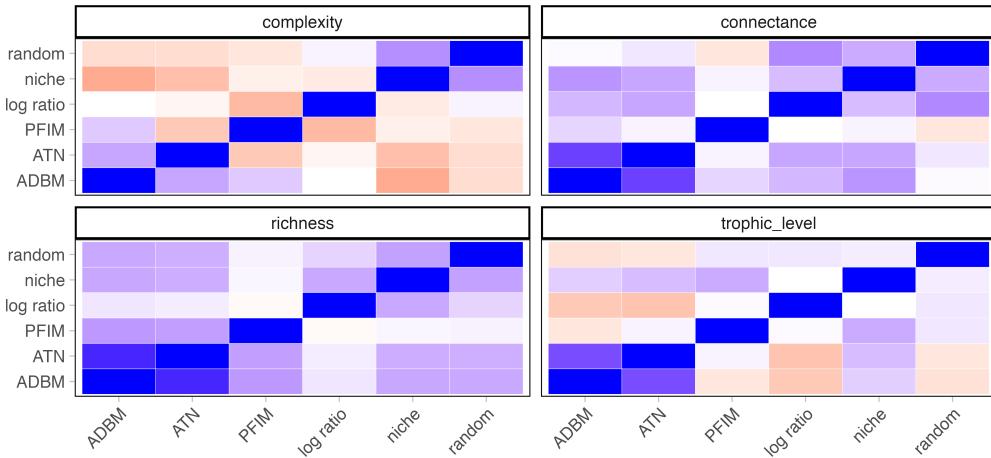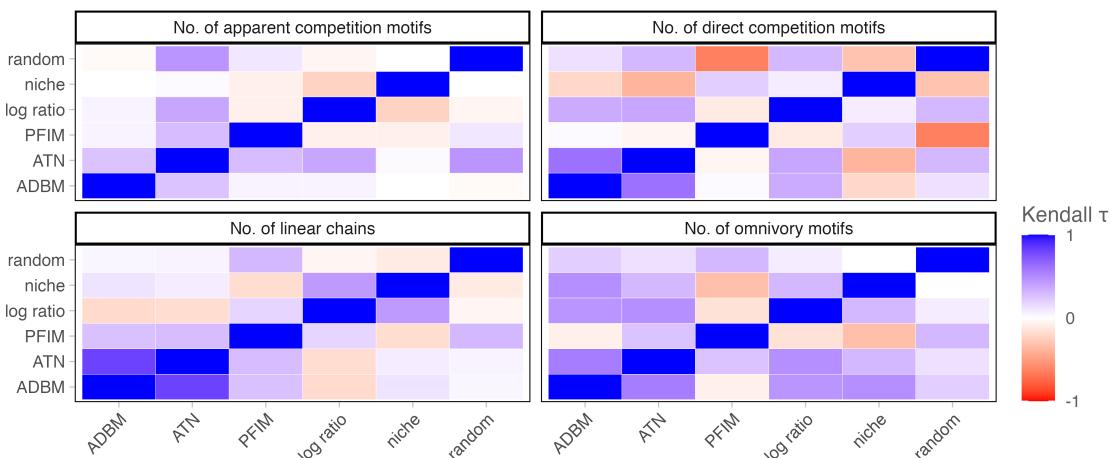
Figure 2: Pairwise beta turnover in species interactions among four ecological network models (ADBM, lmatrix, body-size ratio, and pfim). Each cell represents the mean turnover value between a pair of models, with warmer colors indicating greater dissimilarity in inferred interactions. The diagonal is omitted. High turnover values (yellow) indicate strong disagreement in network structure between models, whereas lower values (blue–purple) indicate greater similarity.
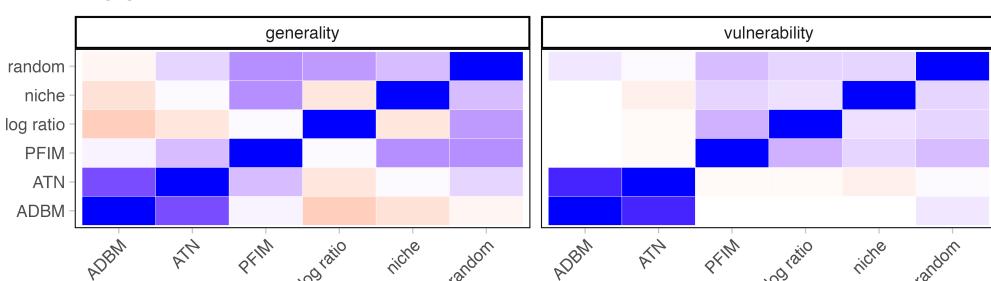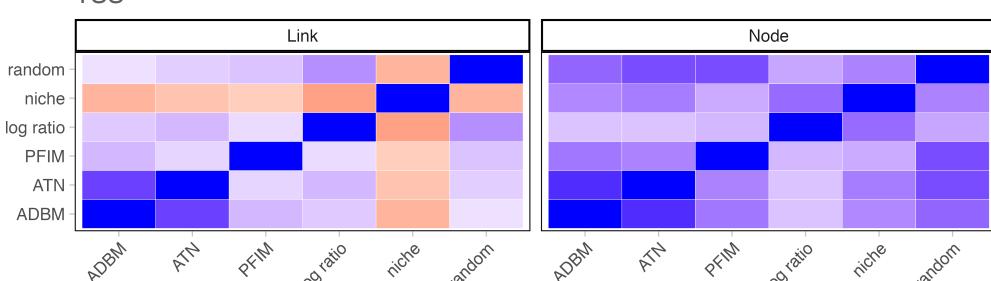
Figure 3: Heatmaps showing pairwise Kendall rank correlation coefficients (τ) between models for each network metric. Each panel corresponds to a different metric and 21 displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between observed 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