

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.

Keywords: Paleoecological networks, Food-web reconstruction, Ecological networks, Extinction dynamics, Trophic interactions, Toarcian Oceanic Anoxic Event

¹ 1 Introduction

² There is growing interest in using deep-time fossil data and evidence of species interactions in past ecosystems
³ (*e.g.*, Dunne et al. (2008); Dunne et al. (2014)) as a foundation for understanding how ecological communities
⁴ respond to multi-stressor environmental change, such as temperature increase, ocean acidification, and hypoxia
⁵ (Dillon et al., 2022; Kiessling et al., 2019). Paleoecological networks therefore represent a particularly valuable
⁶ opportunity to investigate community responses to major environmental transitions as they allow for the
⁷ explicit construction of pre- and post-extinction interaction networks and enable the disentangling of extinction
⁸ drivers as well as broader cascading effects (Dunhill et al., 2024; Roopnarine, 2006; Yeakel et al., 2014).
⁹ Insights gained from these deep-time systems provide a critical context for interpreting present day ecological
¹⁰ change and anticipating the impacts of ongoing anthropogenic stressors (Barnosky et al., 2012; Roopnarine &
¹¹ Dineen, 2018).

¹² Inference from ecological networks regarding structure and complexity is (at its core) a mathematical task
¹³ and is therefore relatively independent of biological assumptions (Delmas et al., 2019). While these structural
¹⁴ properties can be analysed independently of biological detail, their implications for stability and dynamics
¹⁵ depend critically on assumptions about the distribution and strength of interaction (Allesina & Tang, 2012;
¹⁶ Poisot et al., 2015). Thus, assumptions become meaningful once network structure and complexity are
¹⁷ interpreted in functional terms or used as templates for simulating community and extinction dynamics. While
¹⁸ there is a well-developed theoretical framework describing what can be inferred from network properties,
¹⁹ a central challenge (particularly in paleoecology) lies in how networks are constructed. Unlike modern
²⁰ systems, paleoecological interactions are rarely directly observed, with only exceptional cases preserving
²¹ explicit evidence of trophic interactions (*e.g.*, Jenny et al. (2019); Vullo (2011)). As a result, paleo food web
²² reconstruction depends on indirect inference, drawing on preserved traits, analogies with modern taxa, and
²³ ecological theory. Simply put, network reconstruction is not a data recovery process, but rather hypothesis
²⁴ generation under constraints.

²⁵ Although numerous tools exist for inferring species interactions (see Morales-Castilla et al., 2015; Pichler
²⁶ & Hartig, 2023; Strydom et al., 2021; Allesina et al., 2008 for reviews), only a subset can be reliably
²⁷ applied in paleo contexts, where data on traits, abundances, and community composition are incomplete
²⁸ and systematically biased. This makes it essential to clearly articulate which reconstruction approaches are
²⁹ appropriate for which inferential purposes. Recent work has shown that reconstruction approaches (*e.g.*,
³⁰ models based on traits, abundances, or co-occurrence) can be categorised by the type of network that they
³¹ predict (Strydom et al., 2026). These include feasible networks (derived from trait matching and phylogenetic
³² inference that produce metawebs of plausible interactions), realised networks, (constrained by ecological rules

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

37 Each of these reconstruction approaches carries distinct assumptions that influence inferred network size,
38 complexity, structure, and node-level properties, with direct consequences for ecological interpretations of
39 extinction dynamics, stability, resilience, and ecosystem function (Dunne et al., 2002; Gravel et al., 2019;
40 Roopnarine, 2006; Solé & Montoya, 2001). Despite this, most paleo food web studies default to constructing
41 networks using expert knowledge (*e.g.*, Dunne et al. (2008)) or mechanistic feeding rules (*e.g.*, Dunhill et al.
42 (2024); Roopnarine (2017); Fricke et al. (2022)), approaches that typically result in metawebs. This raises a
43 critical but underexplored question: to what extent does the choice of network type (and particularly the use
44 of alternatives to metawebs) control not only inferred food web structure but also conclusions about system
45 behaviour, especially with respect to extinction cascades and vulnerability.

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

61 2 Materials and Methods

62 2.1 Study system and fossil data

63 We used fossil occurrence data from the Cleveland Basin spanning the upper Pliensbachian to the upper
64 Toarcian, following Dunhill et al. (2024). Four paleo-communities were defined: pre-extinction, post-extinction,
65 early recovery, and late recovery. Each assemblage was treated as a community of potentially interacting taxa.
66 Modes of life were assigned following Dunhill et al. (2024) using the Bambach ecospace framework. Traits
67 included motility, tiering, feeding mode, and size class, with size defined categorically based on maximum
68 linear dimensions.

69 2.2 Network reconstruction approaches

70 2.2.1 Conceptual classification of network types

71 Most paleo-specific approaches currently operate within the feasibility space (*e.g.*, Shaw et al., 2024; Fricke et
72 al., 2022; Roopnarine, 2006). Although well suited for reconstructing feasible interactions, these methods
73 represent only a subset of the broader spectrum of network construction approaches. Here, we present a suite
74 of models (Table 1) that enable the construction of a wider range of ecological networks and the exploration
75 of a broader set of ecological questions, provided that their underlying assumptions are compatible with
76 the constraints of fossil data. For example, some tools require quantitative estimates of body size, which
77 must often be inferred from size classes or functional morphology in the fossil record. Structural models,
78 such as the niche model, rely only on species richness and estimates/specification of connectance, but their
79 species-agnostic nature limits their applicability to trait-based or diet-specific questions, although they do still
80 accurately recover network structure (Stouffer et al., 2005) . Mechanistic approaches, by contrast, depend on
81 accurate assignment of feeding traits or robust phylogenetic support. Recognizing how these methodological
82 requirements intersect with the limits of fossil evidence is essential for selecting an appropriate modelling
83 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 | structural network | Erdős & Rényi (1959) | |
| niche | Networks are interval, species can be ordered on a 'niche axis' | richness, connectance | parameter assumptions, species | structural network | Williams & Martinez (2008) | |
| allometric | Interactions are determined by energetic costs | body mass, biomass | 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) | |
| diet breadth model (ADBM) | (foraging ecology) | (abundance) | | | | |

| 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/relationships | 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) |

⁸⁴ 2.2.2 Network generation and replication

⁸⁵ We evaluated six models spanning this space Table 1: random and niche models (structural network); allometric
⁸⁶ diet breadth (ADBM), allometric trophic network (ATN), and body-size ratio models (realised network);
⁸⁷ and a paleo food-web inference model (PFIM; feasibility web). More details on parameters can be found
⁸⁸ in the Supplementary Materials. For each of the four communities, we constructed 100 replicate networks
⁸⁹ using each of the six models (2400 networks total). Networks were simplified by removing disconnected
⁹⁰ species. For size-based models, body masses were drawn from uniform distributions bounded by size-class
⁹¹ limits, allowing for variance between replicates but preserving relative sizes within replicates. Structural
⁹² models were parameterised using connectance values drawn from an empirically realistic range (0.07 – 0.34)
⁹³ while holding richness constant. The same parameter draws were used across comparable models within each
⁹⁴ replicate.

95 2.3 Network metrics and structural analyses

96 We quantified network structure using a suite of macro-, meso-, and micro-scale metrics Table 2, capturing
 97 global properties, motif structure, and species-level variability. Differences among models were assessed using
 98 MANOVA, followed by univariate ANOVAs, post-hoc comparisons, and linear discriminant analysis. Pairwise
 99 interaction turnover was quantified using link-based beta diversity, which measures dissimilarity in the identity
 100 of trophic links between networks, capturing differences due to species turnover or changes in interactions
 101 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 | |
| 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) |

| Metric | Definition | Scale | Reference (for maths), can make footnotes probs |
|---------------|---|-------|---|
| 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 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) |

102 2.4 Extinction simulations and model evaluation

103 Following Dunhill et al. (2024) and using the pre-extinction and post-extinction networks, we simulated
 104 species loss under multiple extinction scenarios, including trait-based, network-position-based, and random
 105 removals, allowing for secondary extinctions. Simulated post-extinction networks were compared to empirical
 106 post-extinction communities using mean absolute differences (MAD) in network metrics and a modified true
 107 skill statistic (TSS) at both node and link levels. Scenario rankings were compared across models using
 108 Kendall's rank correlation coefficient.

109 3 Results

110 Across six reconstruction approaches, both global network structure and species-level interactions differed
 111 substantially, with implications for interpreting past extinction dynamics. Deterministic models (e.g., PFIM)
 112 tended to produce more consistent network-level patterns and smoother extinction trajectories, whereas
 113 stochastic or theory-driven models (e.g., ADBM, niche, ATN) showed greater variability in inferred interactions
 114 and temporal extinction dynamics. Models with similar macro-level metrics sometimes differed in their
 115 specification of pairwise interactions, highlighting that agreement in global structure does not guarantee
 116 concordance at the species level. Consequently, inferred extinction pathways and secondary extinctions were

¹¹⁷ highly sensitive to model choice, emphasizing the importance of evaluating multiple network reconstructions
¹¹⁸ when interpreting ecological dynamics in deep time.

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

¹²⁰ To test whether network reconstruction approach influences inferred food-web structure, we compared
¹²¹ multivariate patterns of network metrics across all six models using a MANOVA. Network structure differed
¹²² strongly among reconstruction approaches (MANOVA, Pillai's trace = 3.81, approximate $F_{40,11955} = 962.12$,
¹²³ $p < 0.001$). Univariate analyses showed that model choice explained a large proportion of variance in most
¹²⁴ network metrics, with high partial η^2 values for connectance, generality, vulnerability, and motif frequencies
¹²⁵ ($\eta^2 = 0.66\text{--}0.92$). In contrast, maximum trophic level exhibited a much smaller effect of model choice ($\eta^2 =$
¹²⁶ 0.04). Estimated marginal means and Tukey-adjusted comparisons indicated consistent differences among
¹²⁷ reconstruction approaches, with PFIM differing significantly from all other models ($p = 0.026$), while ADBM
¹²⁸ and ATN did not differ from one another ($p = 1.00$). Linear discriminant analysis (LDA) further helped
¹²⁹ visualise distinctions among reconstruction approaches in multivariate network space Figure 1, with the first
¹³⁰ two axes explaining 86.5% of between-model variance (LD1 = 53.9%, LD2 = 32.6%). LD1 was most strongly
¹³¹ correlated with vulnerability, connectance, and the number of direct competition motifs (S4), whereas LD2 was
¹³² associated primarily with generality, number of omnivory motifs (S2), and number of apparent competition
¹³³ motifs (S5). Higher-order axes each explained less than 9% of the remaining variance. This demonstrates that
¹³⁴ the reconstruction approach leaves a strong multivariate signature independent of community composition.

¹³⁵ [Figure 1 about here.]

¹³⁶ **3.1.1 Inferred pairwise interactions vary widely among models**

¹³⁷ Building on differences in global network structure, we next examined how reconstruction approach influences
¹³⁸ species-level ecological inference by quantifying turnover in inferred pairwise interactions among networks
¹³⁹ constructed from the same taxon pool. While models that produced similar global metrics sometimes agreed
¹⁴⁰ broadly on network structure, they often differed sharply in the specific interactions they inferred.

¹⁴¹ Pairwise -turnover revealed that some model pairs shared very few links despite comparable macro- or
¹⁴² meso-scale properties Figure 2. ADBM and ATN were highly concordant, reflecting similar underlying
¹⁴³ assumptions despite different generative rules, whereas the body-size ratio model consistently exhibited high
¹⁴⁴ differences in pairwise interactions relative to all other approaches. PFIM showed intermediate overlap with
¹⁴⁵ size-based theoretical models. These patterns indicate that agreement in global network metrics does not
¹⁴⁶ guarantee agreement in species-level diets or trophic roles, highlighting the importance of evaluating both

¹⁴⁷ network- and species-level outcomes when comparing reconstruction methods.

¹⁴⁸ [Figure 2 about here.]

¹⁴⁹ 3.2 Model choice influences inferred extinction dynamics

¹⁵⁰ To quantify how network structure changed over time during extinction simulations and whether these
¹⁵¹ dynamics differed among reconstruction models, we fit generalized additive models (GAMs) to time series of
¹⁵² network-level metrics. GAMs capture nonlinear temporal trajectories, allowing formal tests of whether the
¹⁵³ shape of these trajectories differs among models. These model-specific temporal trajectories are shown in
¹⁵⁴ Figure 3. For connectance, the model-specific smooth terms were all significant (*e.g.*, PFIM: EDF = 2.99, F
¹⁵⁵ = 113.8, $p < 0.001$; ADBM: EDF = 2.92, F = 22.6, $p < 0.001$), indicating distinct temporal patterns across
¹⁵⁶ reconstruction approaches. Trophic level trajectories also differed among models (PFIM: EDF = 2.96, F =
¹⁵⁷ 36.7, $p < 0.001$; Niche: EDF = 2.96, F = 94.9, $p < 0.001$). Deterministic approaches, such as PFIM, produced
¹⁵⁸ more consistent and smooth trajectories, whereas stochastic, theory-driven models (niche, ADBM, ATN)
¹⁵⁹ displayed greater variability in timing and magnitude of structural change. These results demonstrate that
¹⁶⁰ inferred pathways of collapse, trophic bottlenecks, and secondary extinctions are highly sensitive to model
¹⁶¹ choice. Corresponding raw temporal trajectories are shown in Fig. S3.

¹⁶² [Figure 3 about here.]

¹⁶³ To evaluate how model choice affects inferred extinction dynamics, we compared simulated post-extinction
¹⁶⁴ networks to observed networks using mean absolute differences (MAD) for network-level metrics and total
¹⁶⁵ sum-of-squares (TSS) for node- and link-level outcomes Figure 4. Overall, models were more consistent in
¹⁶⁶ ranking extinction scenarios at the network level: Kendall's τ values for MAD-based rankings were generally
¹⁶⁷ positive, with strong agreement between ADBM and ATN models ($\tau \approx 0.82$) and weaker or inconsistent
¹⁶⁸ correlations involving stochastic models such as log ratio or random (τ ranging from -0.26 to 0.44). Node-level
¹⁶⁹ TSS scores similarly showed broad consistency across models, reflecting comparable species removal sequences
¹⁷⁰ ($\tau \approx 0.38\text{--}0.46$ between ADBM and niche or PFIM). In contrast, link-level outcomes were more variable:
¹⁷¹ deterministic models like PFIM maintained moderate agreement with observed post-extinction links ($\tau \approx 0.44$),
¹⁷² whereas stochastic, theory-driven models exhibited low or inconsistent correlations (τ as low as -0.44). These
¹⁷³ results indicate that while different models often recover similar species-level extinction patterns, inferred
¹⁷⁴ interaction loss and cascade dynamics are highly sensitive to model choice.

¹⁷⁵ [Figure 4 about here.]

₁₇₆ **4 Discussion**

₁₇₇ **5 Model choice as a component of ecological inference**

₁₇₈ Reconstructing food webs from fossil data is inherently an exercise in inference under uncertainty. It involves
₁₇₉ not only assembling data but also making explicit assumptions about how species interact and how those
₁₈₀ interactions are represented mathematically (Dunne et al., 2008; Morales-Castilla et al., 2015; Strydom et
₁₈₁ al., 2026). This process has parallels in modern ecological network studies, where the tension between data
₁₈₂ limitations and the goal of meaningful ecological inference is well recognised (Delmas et al., 2019; Poisot et
₁₈₃ al., 2021). Results demonstrate that the choice of network reconstruction model is itself a major ecological
₁₈₄ decision, shaping not only the structural properties of inferred networks but also downstream interpretations
₁₈₅ of extinction dynamics (Allesina & Tang, 2012; Solé & Montoya, 2001).

₁₈₆ These differences arise not from the fossil evidence per se, but from the assumptions embedded in each model
₁₈₇ family (Pichler & Hartig, 2023; Strydom et al., 2021), such as how trophic links are defined (trait compatibility
₁₈₈ versus energetic constraints), how interaction probability is parameterised, and whether network topology is
₁₈₉ informed by macroecological theory (*e.g.*, niche structure) or by mechanistic rules (*e.g.*, body-size ratios).
₁₉₀ Consequently, network reconstruction is not a neutral methodological step; model choice shapes the ecological
₁₉₁ narratives we extract from ancient ecosystems. This sensitivity mirrors challenges faced in modern network
₁₉₂ ecology, where the choice of model and metric influences the interpretation of patterns such as connectance,
₁₉₃ modularity, or motif distributions (Michalska-Smith & Allesina, 2019; Poisot & Gravel, 2014) .

₁₉₄ While previous studies have emphasized the role of model assumptions in metaweb reconstruction (Dunhill
₁₉₅ et al., 2024; Roopnarine, 2006), our results demonstrate that these assumptions create distinct, predictable
₁₉₆ clusters of network properties. These clusters map directly onto the conceptual divide between feasible,
₁₉₇ realised, and structural network types (Strydom et al., 2026). Specifically, mechanistic models (PFIM) identify
₁₉₈ a broad landscape of trait-compatible interactions, theoretical models (ADBM, ATN) impose energetic filters
₁₉₉ to approximate realised energy flow, and structural models (niche, random) prioritise topological patterns
₂₀₀ over species identity.

₂₀₁ Pairwise -turnover analysis underscores that disagreements among reconstruction approaches are not merely
₂₀₂ quantitative differences in metrics, but qualitative differences in the identity of inferred interactions. Models
₂₀₃ that may produce similar aggregate properties (*e.g.*, connectance) can still disagree strongly on species-level
₂₀₄ diets and trophic roles. This reinforces concerns raised in both paleoecological and modern studies that
₂₀₅ metrics alone can mask substantive differences in network structure and function (Fricke et al., 2022; Shaw et

²⁰⁶ al., 2024).

²⁰⁷ The implications of these differences are most pronounced when interpreting extinction dynamics (Dunne
²⁰⁸ et al., 2002; Sahasrabudhe & Motter, 2011). While broad, trait-driven patterns of species loss are relatively
²⁰⁹ robust across models, the identity of lost interactions, secondary extinctions, and cascade dynamics are
²¹⁰ sensitive to the type of network reconstructed. Node-level patterns of species loss (such as which taxa are
²¹¹ more likely to go extinct under certain scenarios) tend to be relatively robust across models, likely because
²¹² they reflect consistent trait-based vulnerabilities. However, inferred link-level outcomes vary markedly with
²¹³ reconstruction assumptions as extinctions are determined by network structure, *i.e.*, are emergent properties
²¹⁴ of model assumptions. This distinction mirrors findings in modern food-web studies, where deterministic and
²¹⁵ stochastic model assumptions influence the magnitude and timing of secondary extinctions (Allesina & Tang,
²¹⁶ 2012; Curtsdotter et al., 2011; Dunne et al., 2002; Yeakel et al., 2014).

²¹⁷ Taken together, these results highlight that network reconstruction is not neutral. Rather, it is a hypothesis
²¹⁸ generation process where the chosen model encodes a set of ecological assumptions. Consequently, paleoecolo-
²¹⁹ gists must carefully consider which ecological signals they aim to recover (potential interactions, realised diets,
²²⁰ or macro-scale structural properties) before selecting a reconstruction approach. Importantly, disagreement
²²¹ among models does not imply that any single approach is ‘wrong’, but rather reflects the fact that different
²²² models capture different ecological signals (Stouffer, 2019). The challenge therefore lies not in identifying
²²³ a universally correct model, but rather in aligning model choice with the ecological question being asked.
²²⁴ Recognising this is critical for advancing paleoecology beyond descriptive reconstruction toward rigorous
²²⁵ comparative inference.

²²⁶ 5.1 Aligning ecological questions with model choice

²²⁷ A central insight from our study is that different ecological questions require different network representations.
²²⁸ This conclusion parallels broader efforts in network ecology to clarify what various models and metrics
²²⁹ can validly infer about ecological systems (Gauzens et al., 2025; Strydom et al., 2026). Here we provide a
²³⁰ conceptual divide between feasible, realised, and structural network types and provides a practical framework
²³¹ for matching research goals with appropriate reconstruction approaches.

²³² **Feasibility networks:** (*e.g.*, trait- and phylogeny-based metaweb approaches) are best suited for questions
²³³ about potential trophic links and dietary breadth. These models aim to capture the range of interactions
²³⁴ that are biologically plausible given species traits, even if not all are realised in any given context. Such an
²³⁵ approach aligns with metaweb concepts in modern ecology, where large pools of potential interactions are
²³⁶ used to understand regional species interaction potentials and local assembly processes (Tylianakis & Morris,

²³⁷ 2017).

²³⁸ **Realised networks:** (*e.g.*, models incorporating energetic and foraging constraints such as body-size
²³⁹ allometry) are more appropriate when the goal is to infer the most likely realised interactions. These models
²⁴⁰ embed ecological rules that approximate energy transfer and foraging ecology, improving ecological plausibility
²⁴¹ of predicted links as compared with purely combinatorial approaches (Brose et al., 2006; Petchey et al., 2008).

²⁴² **Structural networks:** (*e.g.*, niche, cascade, and random models) strip away species identities in favour of
²⁴³ topological patterns, and are useful when broad questions about connectance or trophic depth are the focus.
²⁴⁴ Structural models have a long history in network ecology for generating null expectations about network
²⁴⁵ topology (Allesina et al., 2008; Williams & Martinez, 2008).

²⁴⁶ Recognising this alignment helps avoid misinterpretation. For example, reconstructing a metaweb and treating
²⁴⁷ predicted links as realised trophic interactions conflates potential with actual diet, potentially exaggerating
²⁴⁸ inferred interaction diversity.

²⁴⁹ 5.2 Implications for paleoecological network studies

²⁵⁰ Our findings have three major implications for the field of paleoecological networks:

²⁵¹ 1. **Explicitly acknowledge model assumptions:** Interpretations of ancient food webs must clearly
²⁵² articulate the assumptions underlying reconstruction models. Without this, differences in networks
²⁵³ reconstructed from different datasets or by different research groups may be misattributed to ecological
²⁵⁴ differences rather than methodological choices.

²⁵⁵ 2. **Standardise comparative frameworks:** When comparing food webs across studies, researchers
²⁵⁶ should ensure that networks are constructed and analysed using comparable model families. Without
²⁵⁷ such standardisation, meta-analyses risk conflating methodological differences with ecological or temporal
²⁵⁸ variation.

²⁵⁹ 3. **Leverage modern theory to expand inference:** Integrating modern network ecology frameworks
²⁶⁰ and methods with paleo-specific approaches enriches the inferential toolkit available to paleoecologists
²⁶¹ (Dunne et al., 2014; Solé & Montoya, 2001). Models developed for modern systems (*e.g.*, allometric or
²⁶² trait-based energy models) can be adapted to the constraints of fossil data (*e.g.*, Perez-Lamarque et al.,
²⁶³ 2026), enabling novel insights into deep-time dynamics.

264 **5.3 Recommendations for network reconstruction in paleoecology**

265 Given the sensitivity of ecological inference to reconstruction model choice, we propose the following guidelines
266 to improve consistency, transparency, and ecological relevance:

- 267 **1. Define the Inferential Goal First:** Before reconstructing networks, researchers should articulate
268 whether they aim to infer potential interactions, likely realised diets, or general structural properties.
269 This will inform the selection of an appropriate model family consistent with the ecological question at
270 hand (*e.g.*, metaweb for complete diets, energetic models for trophic energy flows, or structural models
271 for generic topologies)
- 272 **2. Use ensemble and sensitivity frameworks:** Rather than relying on a single model output, researchers
273 should adopt ensemble approaches that generate and compare multiple network reconstructions. This
274 not only quantifies model uncertainty but also reveals which ecological conclusions are robust biological
275 signals and which are methodological artifacts.
- 276 **3. Standardise cross-study comparisons:** Comparisons of networks from different palaeoecological
277 studies should be standardised by model family. When models differ, interpretations about ecological or
278 environmental change should explicitly address how model choice may contribute to observed differences.
- 279 **4. Interpret scale-specific results with caution:** Because node-level patterns tend to be more robust
280 to model choice than link-level patterns, researchers should prioritise interpretations at the appropriate
281 scale. Structural conclusions about cascade pathways or secondary extinctions should be framed as
282 model-dependent hypotheses rather than definitive historical reconstructions.

283 **5.4 Future directions**

284 Looking ahead, paleoecological network reconstruction would benefit from deeper integration with advances
285 in modern network ecology. This includes incorporating probabilistic and Bayesian approaches to quantify
286 uncertainty in link prediction, such as Bayesian group models (Baskerville et al., 2011; Elmasri et al., 2020),
287 developing maximum entropy methods to predict network structure under constrained information (Banville
288 et al., 2023), and exploring multi-layer network representations that integrate trophic interactions with
289 other types of ecological relationships (Pilosof et al., 2017). Such developments, combined with increasing
290 availability of trait and phylogenetic information, can help bridge the gap between fossil constraints and
291 ecological inference, enabling more nuanced and probabilistically grounded reconstructions of deep-time
292 ecosystems (Banville et al., 2025; Perez-Lamarque et al., 2026; Poisot et al., 2016).

293 **6 Conclusions**

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

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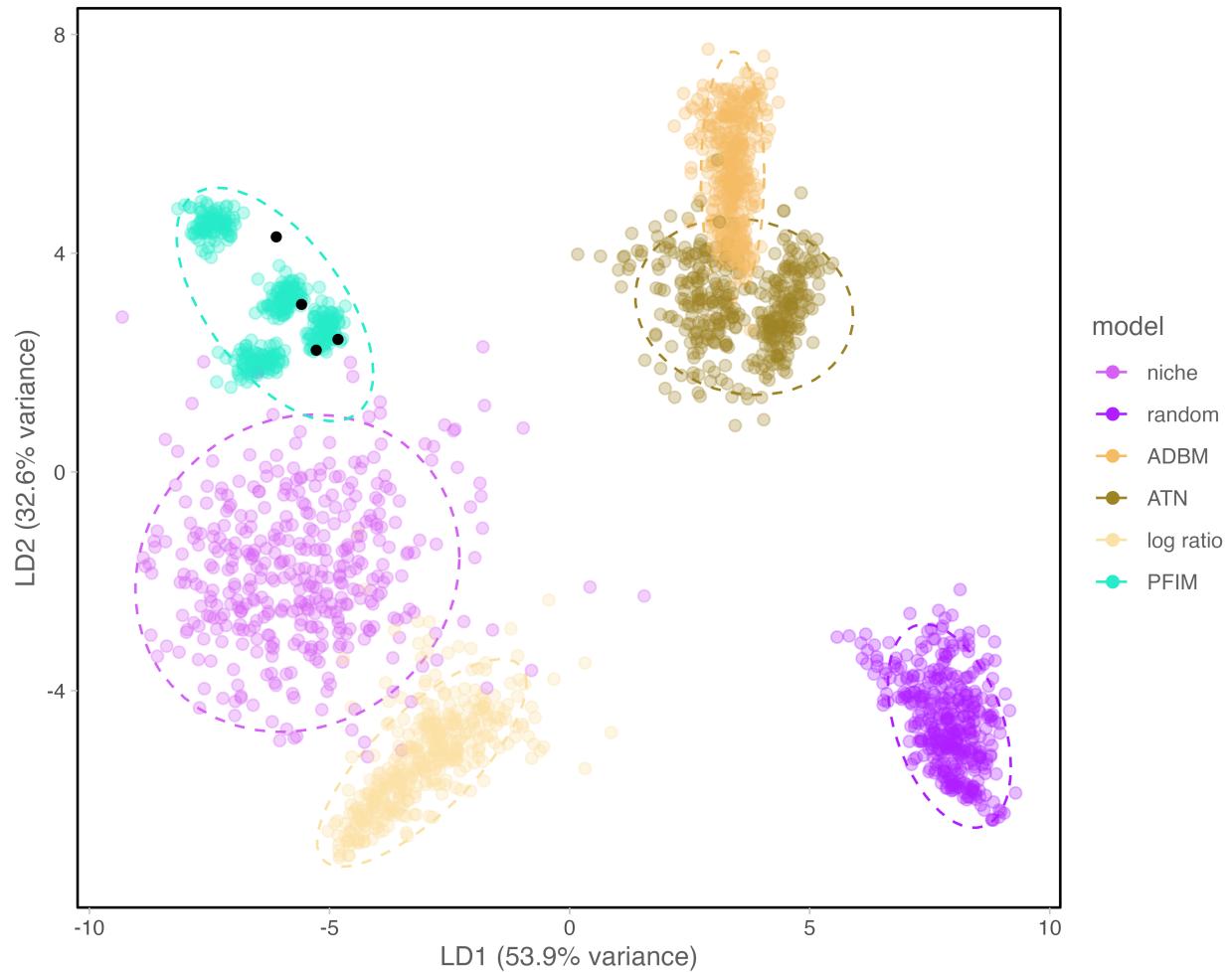


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

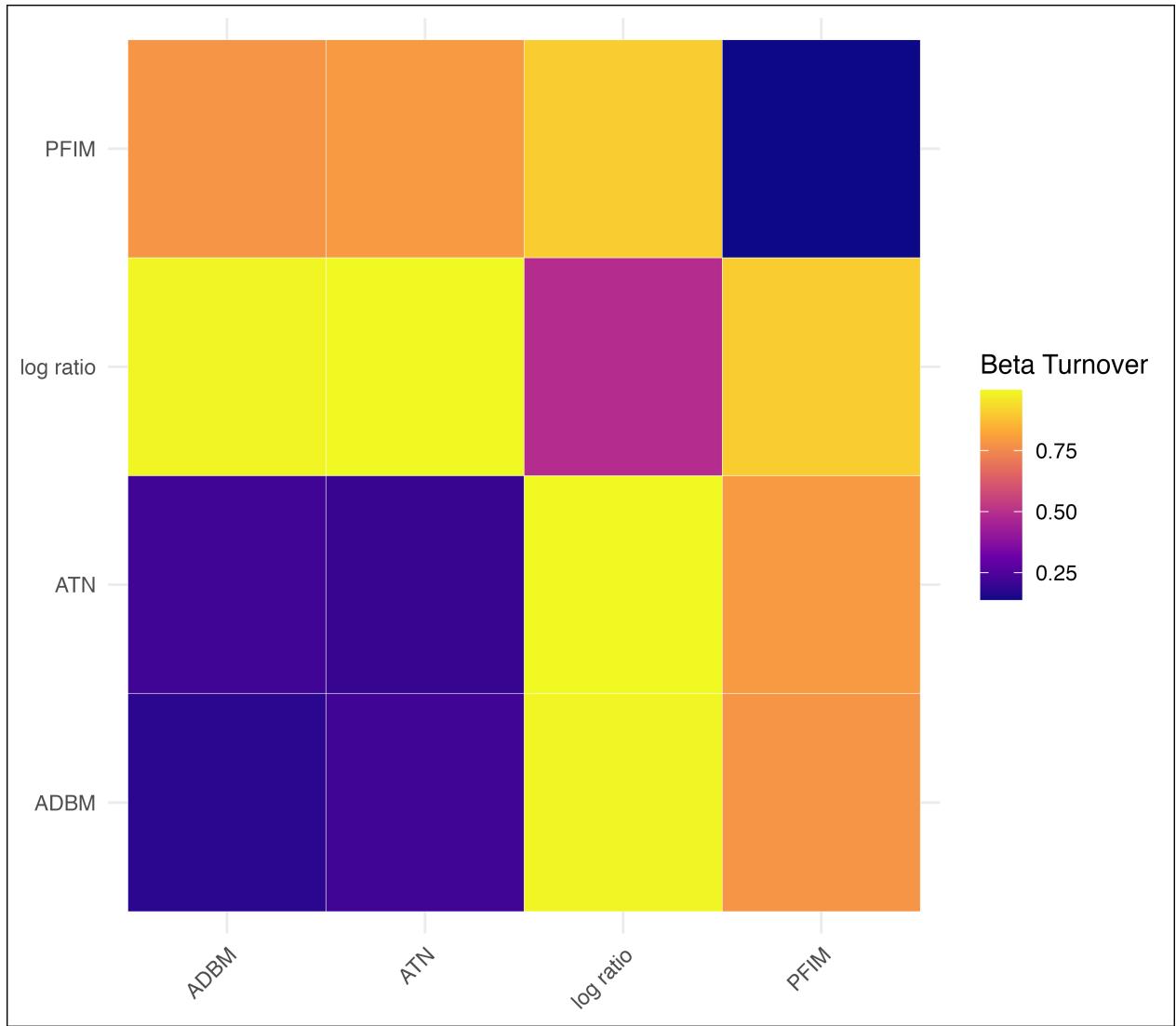


Figure 2: Pairwise beta turnover in species interactions among four ecological network models (ADBM, lmatrix, body-size ratio, and pfim). Each cell represents the mean turnover value between a pair of models, with warmer colors indicating greater dissimilarity in inferred interactions. The diagonal is omitted. High turnover values (yellow) indicate strong disagreement in network structure between models, whereas lower values (blue–purple) indicate greater similarity.

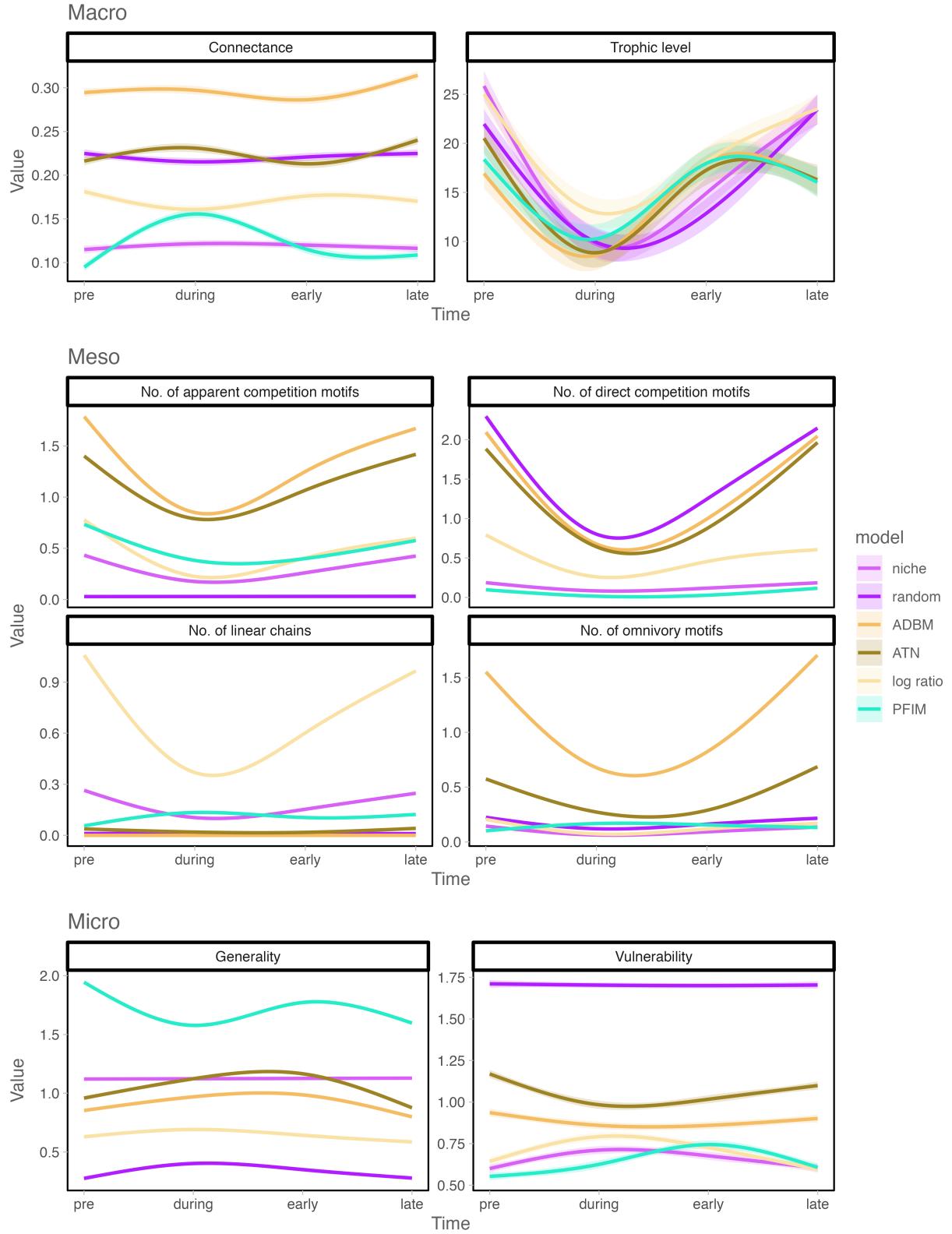
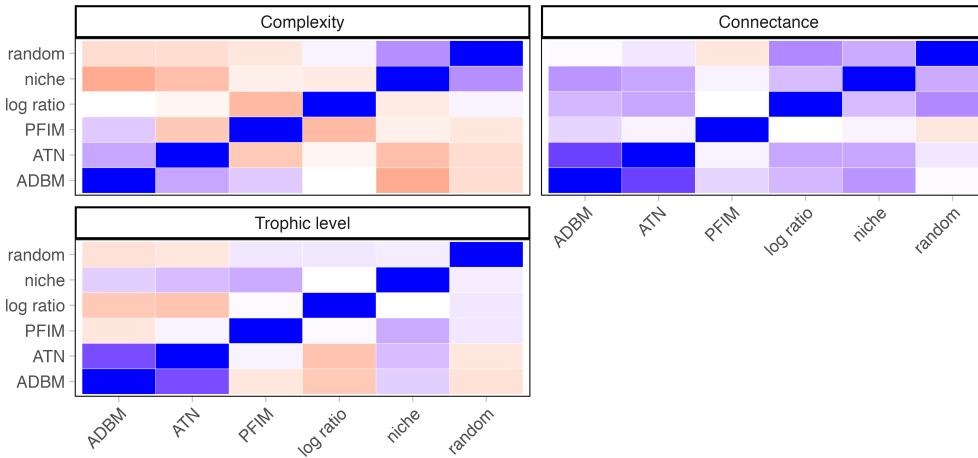
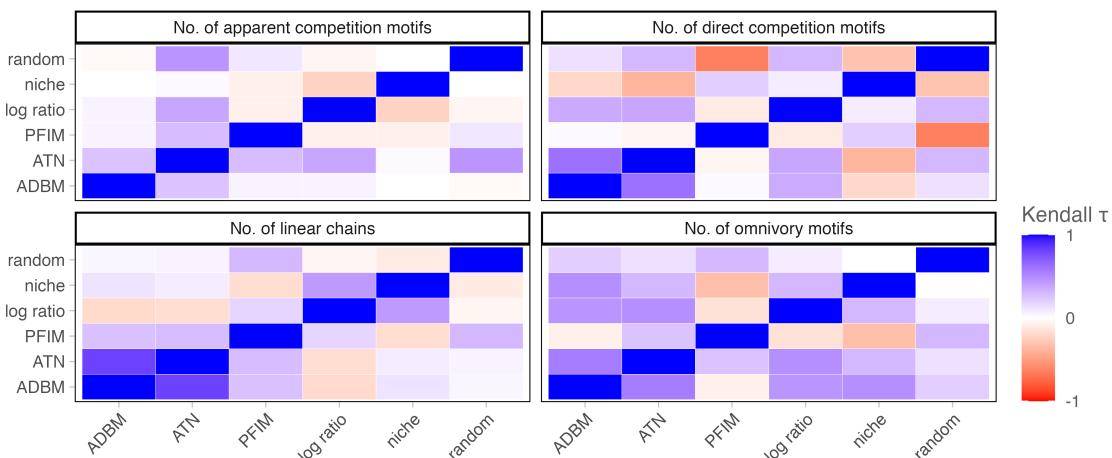


Figure 3: GAM-predicted trajectories of network structure during extinction simulations reveal pronounced differences in the timing and magnitude of change across reconstruction models. Lines show model-specific smooths and shaded areas indicate 95% confidence intervals. Deterministic approaches produce smoother, more consistent dynamics, whereas stochastic models exhibit greater variability, underscoring the sensitivity of inferred collapse pathways to reconstruction assumptions.

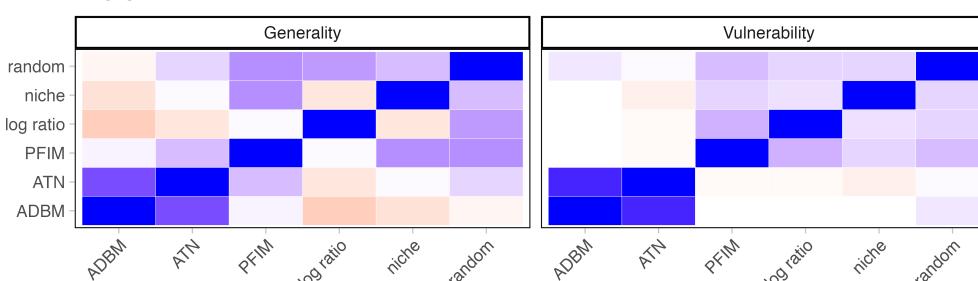
Macro



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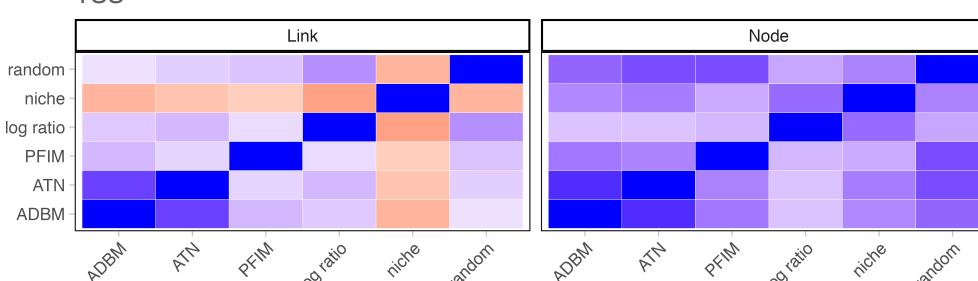


Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients (τ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between observed 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