

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 for models that infer species-specific
 100 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)

101 2.4 Extinction simulations and model evaluation

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

108 3 Results

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

118 **3.1 Network structure differs among reconstruction approaches**

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

134 [Figure 1 about here.]

135 **3.1.1 Inferred pairwise interactions vary widely among models**

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

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

147 [Figure 2 about here.]

¹⁴⁸ **3.2 Model choice influences inferred extinction dynamics**

¹⁴⁹ To quantify how network structure changed over time during extinction simulations and whether these
¹⁵⁰ dynamics differed among reconstruction models, we fit generalized additive models (GAMs) to time series of
¹⁵¹ network-level metrics. GAMs capture nonlinear temporal trajectories, allowing formal tests of whether the
¹⁵² shape of these trajectories differs among models. These model-specific temporal trajectories are shown in
¹⁵³ Figure 3. For connectance, the model-specific smooth terms were all significant (*e.g.*, PFIM: EDF = 2.99, F
¹⁵⁴ = 113.8, $p < 0.001$; ADBM: EDF = 2.92, F = 22.6, $p < 0.001$), indicating distinct temporal patterns across
¹⁵⁵ reconstruction approaches. Trophic level trajectories also differed among models (PFIM: EDF = 2.96, F =
¹⁵⁶ 36.7, $p < 0.001$; Niche: EDF = 2.96, F = 94.9, $p < 0.001$). Deterministic approaches, such as PFIM, produced
¹⁵⁷ more consistent and smooth trajectories, whereas stochastic, theory-driven models (niche, ADBM, ATN)
¹⁵⁸ displayed greater variability in timing and magnitude of structural change. These results demonstrate that
¹⁵⁹ inferred pathways of collapse, trophic bottlenecks, and secondary extinctions are highly sensitive to model
¹⁶⁰ choice. Corresponding raw temporal trajectories are shown in Fig. S3.

¹⁶¹ [Figure 3 about here.]

¹⁶² To evaluate how model choice affects inferred extinction dynamics, we compared simulated post-extinction
¹⁶³ networks to observed networks using mean absolute differences (MAD) for network-level metrics and total
¹⁶⁴ sum-of-squares (TSS) for node- and link-level outcomes Figure 4. Overall, models were more consistent in
¹⁶⁵ ranking extinction scenarios at the network level: Kendall's τ values for MAD-based rankings were generally
¹⁶⁶ positive, with strong agreement between ADBM and ATN models ($\tau = 0.82$) and weaker or inconsistent
¹⁶⁷ correlations involving stochastic models such as log ratio or random (τ ranging from -0.26 to 0.44). Node-level
¹⁶⁸ TSS scores similarly showed broad consistency across models, reflecting comparable species removal sequences
¹⁶⁹ ($\tau = 0.38\text{--}0.46$ between ADBM and niche or PFIM). In contrast, link-level outcomes were more variable:
¹⁷⁰ deterministic models like PFIM maintained moderate agreement with observed post-extinction links ($\tau = 0.44$),
¹⁷¹ whereas stochastic, theory-driven models exhibited low or inconsistent correlations (τ as low as -0.44). These
¹⁷² results indicate that while different models often recover similar species-level extinction patterns, inferred
¹⁷³ interaction loss and cascade dynamics are highly sensitive to model choice.

¹⁷⁴ [Figure 4 about here.]

₁₇₅ **4 Discussion**

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

₁₇₇ Reconstructing food webs from fossil data is inherently an exercise in inference under uncertainty, where
₁₇₈ ecological conclusions depend as much on modelling assumptions as on preserved evidence (Dunne et al., 2008;
₁₇₉ Morales-Castilla et al., 2015). Our results demonstrate that the choice of network reconstruction model is
₁₈₀ itself a major ecological decision, shaping not only the structural properties of inferred networks but also
₁₈₁ downstream interpretations of extinction dynamics (Allesina & Tang, 2012; Solé & Montoya, 2001). Even with
₁₈₂ identical taxon pools, different models yield networks that diverge in global metrics, species-level interactions,
₁₈₃ and temporal patterns of collapse. These divergences do not stem from differences in fossil evidence or taxon
₁₈₄ composition, but from the assumptions embedded within each reconstruction approach (Pichler & Hartig,
₁₈₅ 2023; Strydom et al., 2021). Consequently, network reconstruction is not a neutral methodological step; model
₁₈₆ choice shapes the ecological narratives we extract from ancient ecosystems.

₁₈₇ While previous studies have emphasized the role of model assumptions in metaweb reconstruction (Dunhill
₁₈₈ et al., 2024; Roopnarine, 2006), our results demonstrate that these assumptions create distinct, predictable
₁₈₉ clusters of network properties. These clusters map directly onto the conceptual divide between feasible,
₁₉₀ realised, and structural network types (Strydom et al., 2026). Specifically, mechanistic models (PFIM)
₁₉₁ identify a broad landscape of trait-compatible interactions, theoretical models (ADBM, ATN) impose energetic
₁₉₂ filters to approximate realised energy flow, and structural models (niche, random) prioritise topological
₁₉₃ patterns over species identity. Our Pairwise -turnover analysis confirms that these differences are not merely
₁₉₄ quantitative; models fundamentally disagree on link identity, reinforcing concerns that traditional metawebs
₁₉₅ may significantly overestimate realised interaction diversity (Fricke et al., 2022; Shaw et al., 2024). This
₁₉₆ distinction is central to paleoecological inference, where feasible interactions are often mistaken for realised
₁₉₇ trophic relationships.

₁₉₈ The downstream consequences of model choice are most pronounced when evaluating extinction dynamics
₁₉₉ (Dunne et al., 2002; Sahasrabudhe & Motter, 2011). While broad, trait-driven patterns of species loss are
₂₀₀ relatively robust across models, the identity of lost interactions, secondary extinctions, and cascade dynamics
₂₀₁ are sensitive to the type of network reconstructed. Node-level patterns tend to be more consistent across models
₂₀₂ because they primarily reflect intrinsic species traits, whereas link-level outcomes are emergent properties of
₂₀₃ model assumptions. This distinction mirrors findings in modern food-web studies, where deterministic and
₂₀₄ stochastic model assumptions influence the magnitude and timing of secondary extinctions (Allesina & Tang,
₂₀₅ 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). 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 <i>could</i> 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 <i>likely realised</i> ?	Realised network (ADBM, ATN)	Encodes foraging ecology and energetic constraints; provides ecologically plausible ‘realised’ networks.

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

225 5.2 Implications for paleoecological network studies

226 Our analysis underscores three important implications for the broader field:

- 227 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.
- 230 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.
- 233 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).

237 5.3 Recommendations for network reconstruction in paleoecology

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

- 240 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

243 realisations.

- 244 2. **Implement an Ensemble Modelling Framework:** Rather than just using multiple models, advocate
245 for an ensemble approach. Evaluating a suite of models allows researchers to quantify model uncertainty
246 identifying which ecological conclusions are robust biological signals and which are methodological
247 artifacts.
- 248 3. **Standardise Comparative Analyses:** To avoid misleading comparisons across studies, researchers
249 should only compare networks constructed within the same model family. If comparing a new metaweb
250 to a published realised web, the differences must be explicitly attributed to the representation gap rather
251 than environmental change.
- 252 4. **Prioritize Scale-Specific Interpretation:** Distinguish clearly between node- and link-level results.
253 Since node-level patterns (who goes extinct) are generally more robust to model choice, they can be
254 interpreted with higher confidence than specific link-level pathways (the exact cascade route), which are
255 highly sensitive to model assumptions.

256 6 Conclusions

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

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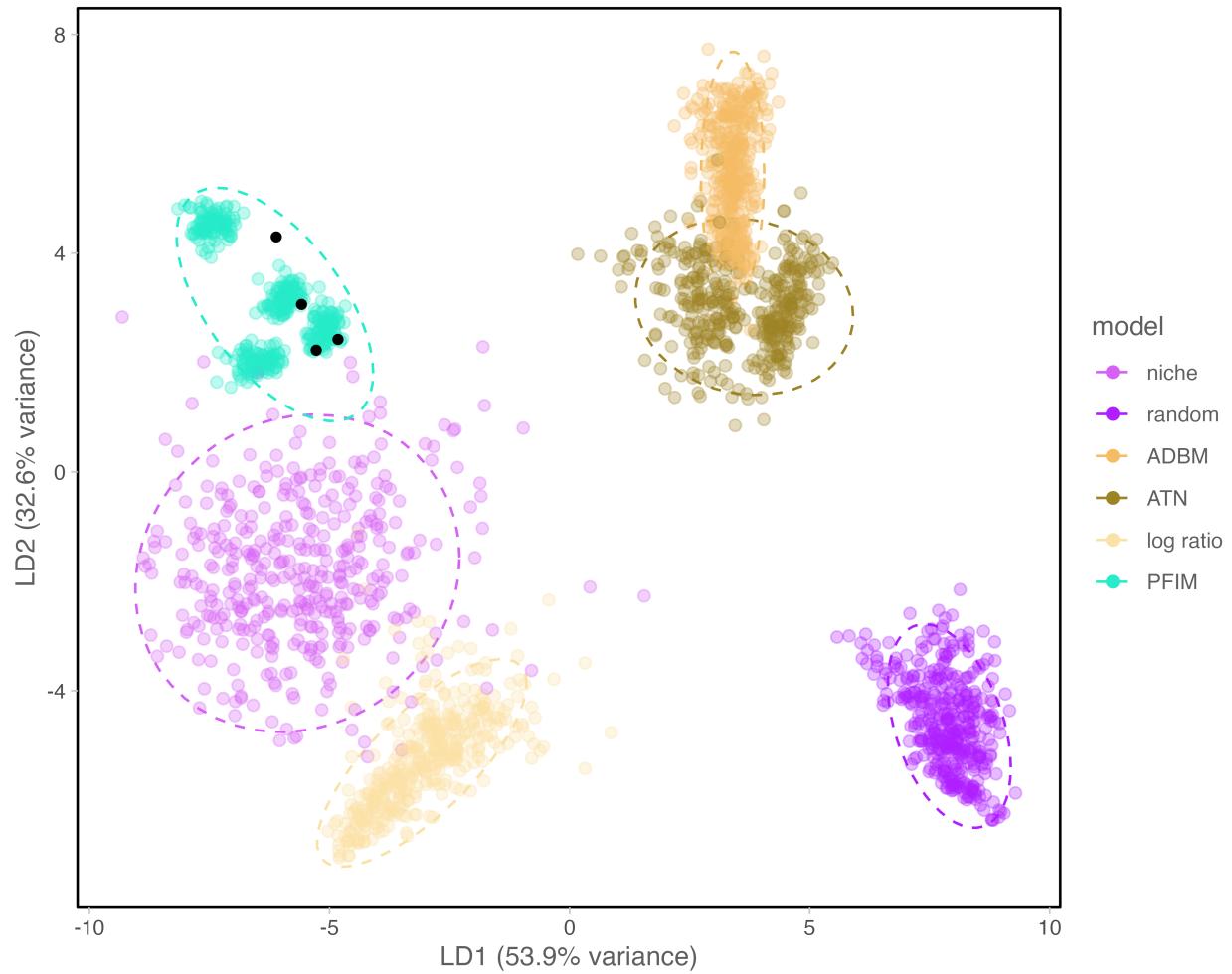


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

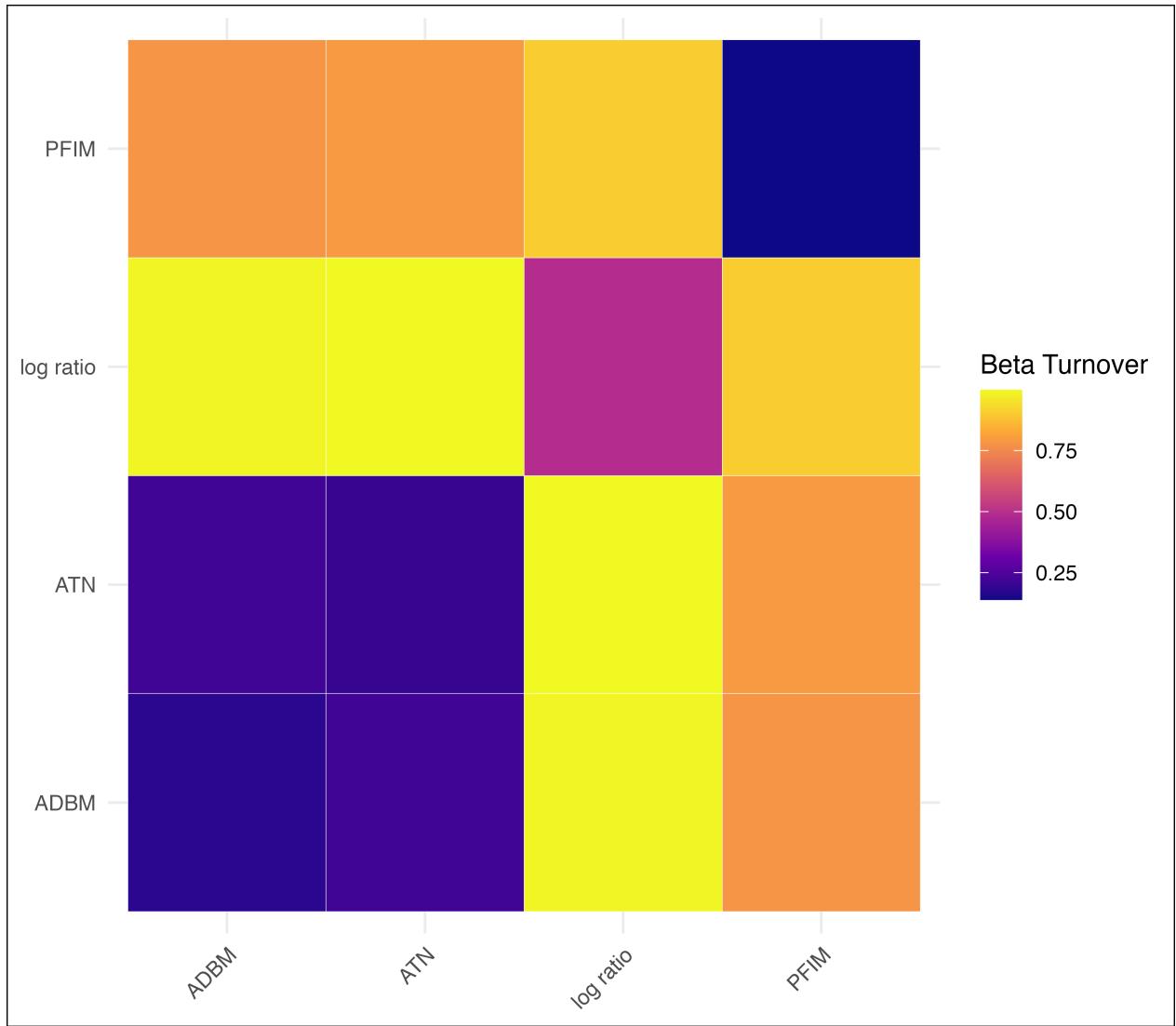


Figure 2: Pairwise beta turnover in species interactions among four ecological network models (ADBM, lmatrix, body-size ratio, and pfim). Each cell represents the mean turnover value between a pair of models, with warmer colors indicating greater dissimilarity in inferred interactions. The diagonal is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

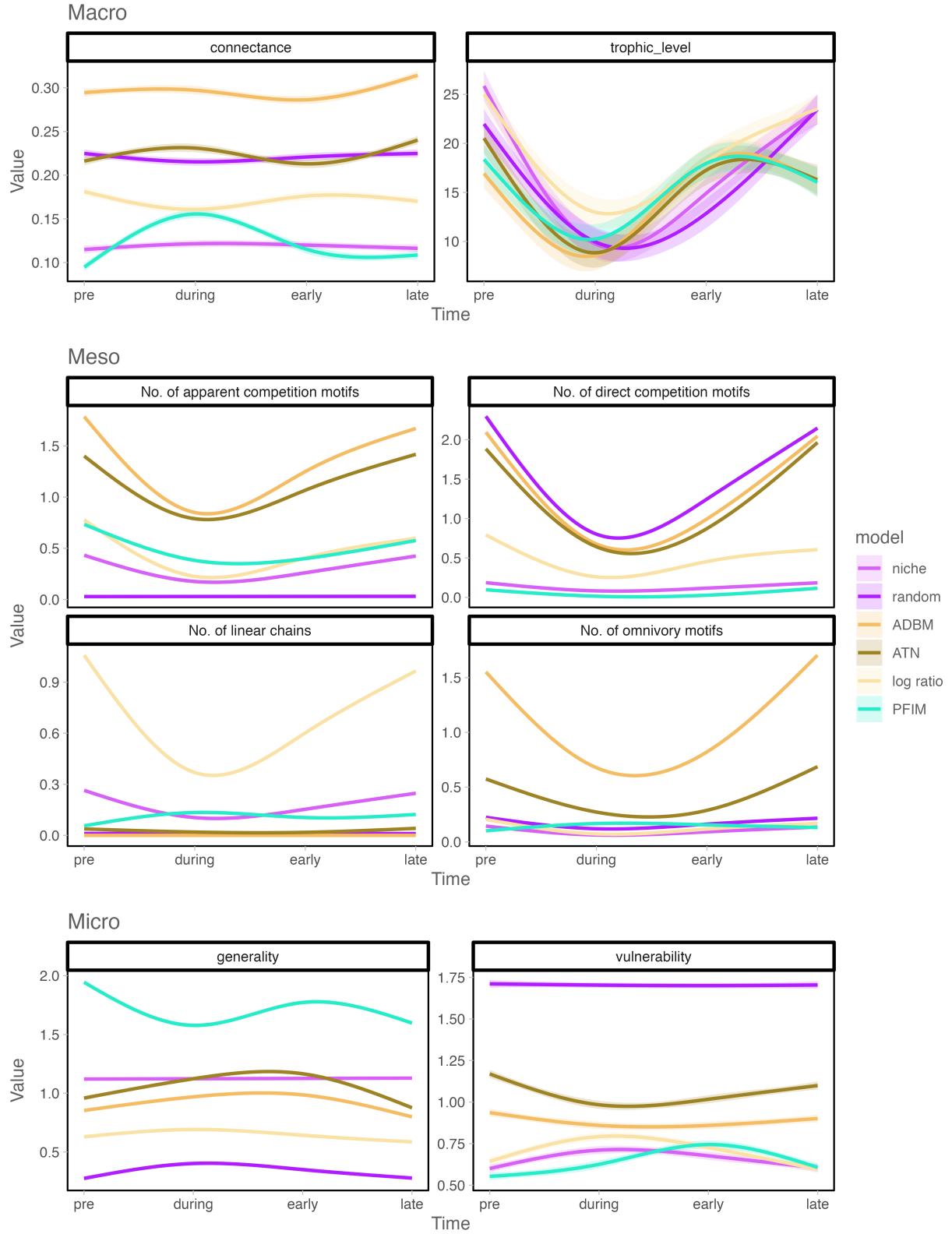
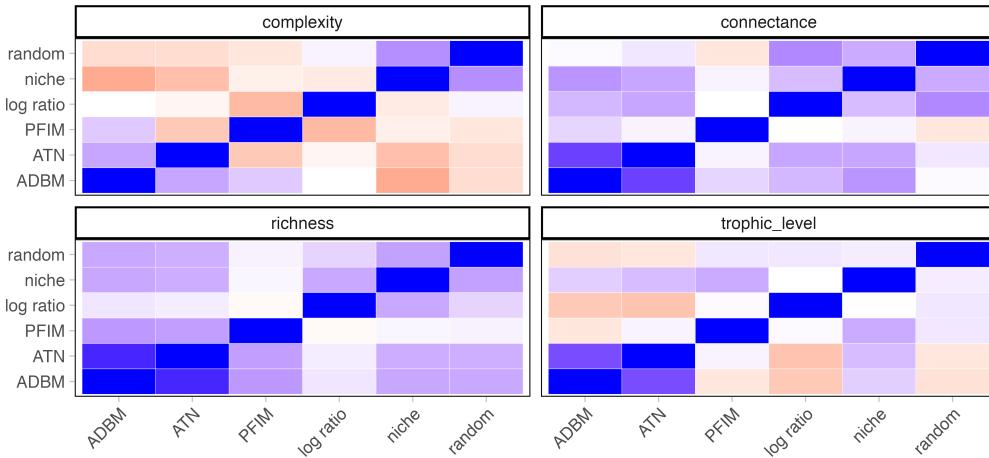
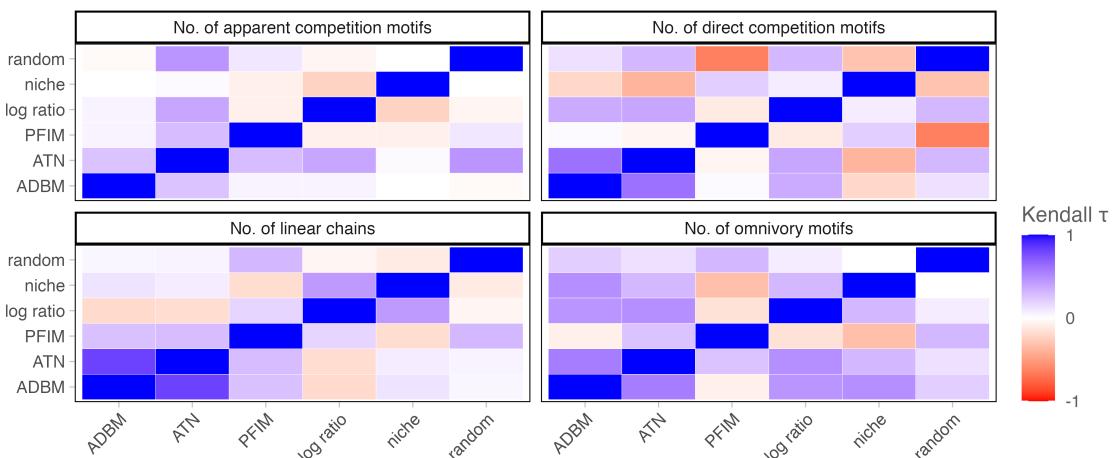


Figure 3: GAM-predicted trajectories of network structure during extinction simulations reveal pronounced differences in the timing and magnitude of change across reconstruction models. Lines show model-specific smooths and shaded areas indicate 95% confidence intervals. Deterministic approaches produce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

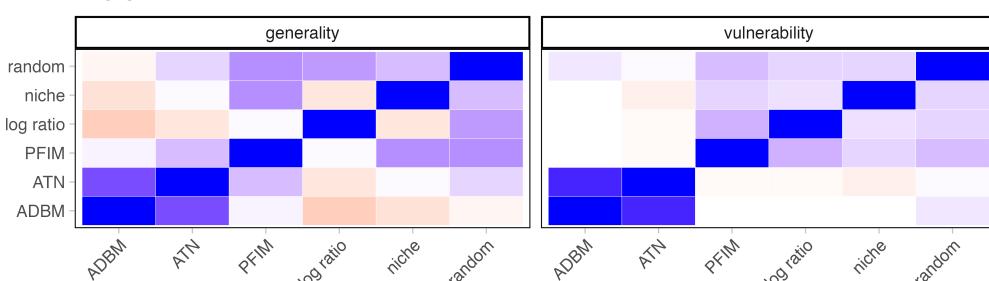
Macro



Meso



Micro



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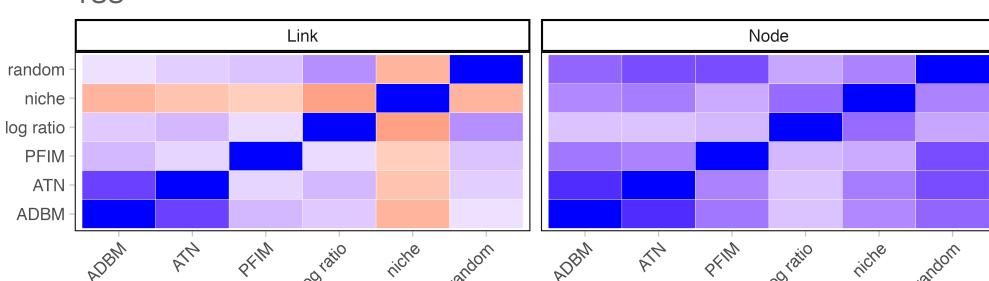


Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients (τ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between observed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