

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 |
|--------------|---|---------------------------|--------------------------------|--------------------|----------------------------|--|
| random | Links are randomly distributed within a network | richness, number of links | parameter assumptions, species | structural network | Erdős & Rényi (1959) | Null-model comparisons; testing whether observed network structure (connectance, motifs) deviates from random expectations |
| niche | Networks are interval, species can be ordered on a 'niche axis' | richness, connectance | parameter assumptions, species | structural network | Williams & Martinez (2008) | Evaluating the influence of trophic hierarchy or intervality on network topology; generating baseline predictions for motifs and connectance |

| Model family | Assumptions | Data needs | 'Limitation' | Network type | Key reference | Usage examples |
|--------------------------------------|---|---------------------------------------|---|------------------|--|---|
| 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) | Predicting realised predator diets under energy-maximization rules; exploring secondary extinctions and trophic bottlenecks |
| 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 and biomass (abundance) from fossil data, assumptions as to the number of producer species | realised network | Brose et al. (2006); Gauzens et al. (2023) | Simulating effects of species loss on network structure; examining consequences of mechanical constraints on predator-prey interactions |

| Model family | Assumptions | Data needs | 'Limitation' | Network type | Key reference | Usage examples |
|---------------------------------------|--|--|---|-----------------|--------------------|--|
| 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) | Mapping feasible trophic interactions based on trait compatibility; assessing vulnerability and secondary extinctions in paleo-communities (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) | Estimating likely interaction networks from body-size constraints; evaluating cascading effects and network collapse under extinction scenarios [Yeakel et al. (2014)]. |

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

90 **2.2.2 Network generation and replication**

91 We evaluated six models spanning this space Table 1: random and niche models (structural network); allometric
 92 diet breadth (ADBM), allometric trophic network (ATN), and body-size ratio models (realised network);
 93 and a paleo food-web inference model (PFIM; feasibility web). Expanded descriptions of model assumptions,

94 parameterisation, and link-generation rules are provided in Supplementary Material S1. For each of the
 95 four communities, we constructed 100 replicate networks using each of the six models (2400 networks total).
 96 Networks were simplified by removing disconnected species. For size-based models, body masses were drawn
 97 from uniform distributions bounded by size-class limits, allowing for variance between replicates but preserving
 98 relative sizes within replicates. Structural models were parameterised using connectance values drawn from
 99 an empirically realistic range (0.07 – 0.34) while holding richness constant. The same parameter draws were
 100 used across comparable models within each replicate.

101 2.3 Network metrics and structural analyses

102 We quantified network structure using a suite of macro-, meso-, and micro-scale metrics Table 2, capturing
 103 global properties, motif structure, and species-level variability. Differences among models were assessed using
 104 MANOVA, followed by univariate ANOVAs, post-hoc comparisons, and linear discriminant analysis. Pairwise
 105 interaction turnover was quantified using link-based beta diversity, which measures dissimilarity in the identity
 106 of trophic links between networks, capturing differences due to species turnover or changes in interactions
 107 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) |

| Metric | Definition | Scale | Reference (for maths), can make footnotes probs |
|---------------|--|-------|---|
| S1 | Number of linear chains, normalised | Meso | Milo et al. (2002); Stouffer et al. (2007) |
| S2 | Number of omnivory motifs, normalised | Meso | Milo et al. (2002); Stouffer et al. (2007) |
| S4 | Number of apparent competition motifs, normalised | Meso | Milo et al. (2002); Stouffer et al. (2007) |
| S5 | Number of direct competition motifs, normalised | Meso | Milo et al. (2002); Stouffer et al. (2007) |
| Generality | Normalized standard deviation of generality of a species 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) |

¹⁰⁸ **2.4 Extinction simulations and model evaluation**

¹⁰⁹ Following Dunhill et al. (2024) and using the pre-extinction and post-extinction networks, we simulated
¹¹⁰ species loss under multiple extinction scenarios, including trait-based, network-position-based, and random
¹¹¹ removals, allowing for secondary extinctions. Simulated post-extinction networks were compared to empirical
¹¹² post-extinction communities using mean absolute differences (MAD) in network metrics and a modified true
¹¹³ skill statistic (TSS) at both node and link levels. Scenario rankings were compared across models using
¹¹⁴ Kendall's rank correlation coefficient.

115 **3 Results**

116 Across six network reconstruction approaches, inferred food-web structure, species interactions, and extinction
117 dynamics differed strongly and consistently. Multivariate analyses revealed pronounced separation among
118 models in network metric space, with reconstruction approach explaining the majority of variance in structural
119 properties and leaving a distinct signature independent of community composition. While some models
120 converged on similar global metrics, they often disagreed on inferred pairwise interactions, demonstrating
121 that structural similarity does not imply concordance in species-level diets or trophic roles. Model choice also
122 substantially influenced inferred extinction dynamics: temporal trajectories of network collapse, interaction
123 loss, and motif reorganization differed among approaches, and although species-level extinction rankings were
124 often broadly consistent, link-level outcomes and extinction inferences were highly sensitive to reconstruction
125 assumptions. Together, these results show that ecological inferences drawn from paleo networks depend
126 critically on the reconstruction framework employed.

127 **3.1 Network structure differs among reconstruction approaches**

128 To test whether network reconstruction approach influences inferred food-web structure, we compared
129 multivariate patterns of network metrics across all six models using a MANOVA. Network structure differed
130 strongly among reconstruction approaches (MANOVA, Pillai's trace = 3.84, approximate $F_{40,11955} = 987.35$, p
131 < 0.001). Univariate analyses showed that model choice explained a large proportion of variance in most network
132 metrics, with high partial η^2 values for all network structural metrics ($\eta^2 = 0.65\text{--}0.92$). Estimated marginal
133 means and Tukey-adjusted comparisons indicated consistent differences among reconstruction approaches, with
134 PFIM differing significantly from all other models ($p < 0.0001$). Within the allometric frameworks we observed
135 a notable divergence between the ADBM and ATN models ($p < 0.0001$), demonstrating that bioenergetic
136 ranking and mechanical-efficiency rules do not converge on a single structural solution. Interestingly, the only
137 pair to exhibit statistical consensus in multivariate space was the ADBM and the log-ratio model ($p = 0.99$).
138 Linear discriminant analysis (LDA) further helped visualise distinctions among reconstruction approaches in
139 multivariate network space Figure 1, with the first two axes explaining 86% of between-model variance (LD1
140 = 53%, LD2 = 33%). LD1 was most strongly correlated with vulnerability ($r = 0.86$), direct competition
141 motifs ($r = 0.81$), and connectance ($r = 0.75$), whereas LD2 was associated primarily with maximum trophic
142 level ($r = -0.76$) and a positive correlation with apparent competition motifs ($r = 0.73$). Higher-order axes
143 each explained less than 9% of the remaining variance. This demonstrates that the reconstruction approach
144 leaves a strong multivariate signature independent of community composition.

145 [Figure 1 about here.]

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

¹⁴⁷ Building on differences in global network structure, we next examined how reconstruction approach influences
¹⁴⁸ species-level ecological inference by quantifying turnover in inferred pairwise interactions among networks
¹⁴⁹ constructed from the same taxon pool. While models that produced similar global metrics sometimes agreed
¹⁵⁰ broadly on network structure, they often differed in the specific interactions they inferred.

¹⁵¹ Pairwise -turnover revealed that some model pairs shared very few links despite comparable macro- or
¹⁵² meso-scale properties Figure 2. ADBM and ATN were highly concordant, reflecting similar underlying
¹⁵³ assumptions despite different generative rules, whereas the body-size ratio model consistently exhibited high
¹⁵⁴ differences in pairwise interactions relative to all other approaches. PFIM showed intermediate overlap with
¹⁵⁵ size-based theoretical models. These patterns indicate that agreement in global network metrics does not
¹⁵⁶ guarantee agreement in species-level diets or trophic roles, highlighting the importance of evaluating both
¹⁵⁷ network- and species-level outcomes when comparing reconstruction methods.

¹⁵⁸ [Figure 2 about here.]

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

¹⁶⁰ To quantify how network structure changed over time during extinction simulations and whether these
¹⁶¹ dynamics differed among reconstruction models, we fit generalized additive models (GAMs) to time series of
¹⁶² network-level metrics. GAMs capture nonlinear temporal trajectories, allowing formal tests of whether the
¹⁶³ shape of these trajectories differs among models. These model-specific temporal trajectories are shown in
¹⁶⁴ Figure 3. For all metrics examined, the inclusion of model-specific smooth terms significantly improved model
¹⁶⁵ fit (ANOVA model comparison: $p < 0.001$ for all metrics). Deterministic, data-driven approaches (PFIM)
¹⁶⁶ and allometric models (ADBM, ATN) exhibited highly non-linear trajectories, showing structural shifts in
¹⁶⁷ connectivity and motif frequency. In contrast, the Niche model produced the most consistent and gradual
¹⁶⁸ trajectories, effectively smoothing the perceived magnitude of structural change during community collapse.
¹⁶⁹ These results demonstrate that inferred pathways of collapse, trophic bottlenecks, and secondary extinctions
¹⁷⁰ are highly sensitive to model choice. Corresponding raw temporal trajectories are shown in Fig. S3.

¹⁷¹ [Figure 3 about here.]

¹⁷² To evaluate how model choice affects inferred extinction dynamics, we compared simulated post-extinction
¹⁷³ networks to observed networks using mean absolute differences (MAD) for network-level metrics and total
¹⁷⁴ sum-of-squares (TSS) for node- and link-level outcomes Figure 4. Overall, models were consistent in ranking
¹⁷⁵ extinction scenarios at the network level: Kendall's τ values for MAD-based rankings were generally positive,

176 with strong agreement between ADBM and ATN models ($\tau = 0.63$). Node-level TSS scores similarly showed
177 broad consistency across models ($\tau: 0.25 - 0.90$), reflecting comparable species removal sequences. In contrast,
178 link-level outcomes were more variable ($\tau: -0.48 - 0.29$), reflecting variance in the recovery of specific pairwise
179 links between real and simulated networks. These results indicate that while different models often recover
180 similar species-level extinction patterns, inferred interaction loss and cascade dynamics are highly sensitive to
181 model choice.

182 [Figure 4 about here.]

183 4 Discussion

184 4.1 Model choice as a component of ecological inference

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

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

202 Multivariate analyses of network metrics reveal that reconstruction approach explains a large portion of
203 variance in structural properties. These patterns demonstrate a strong, model-specific signature independent
204 of community composition. While some models occasionally converged on some global metrics (*e.g.*, ADBM
205 and log-ratio models), pairwise turnover revealed disagreements in inferred species-level interactions. Thus,

206 structural similarity does not guarantee concordance in trophic roles, highlighting that uncertainty in
207 reconstructed networks is structured and predictable rather than random. Comparing multiple reconstruction
208 approaches provides a means to identify robust ecological signals while delineating areas where inference
209 remains model-dependent.

210 Mechanistic models (PFIM) typically identify a broad landscape of trait-compatible interactions, theoretical
211 size-based models (ADBM, ATN, body size ratio) impose energetic filters to approximate realised diets, and
212 structural models (niche, random) prioritise topological patterns over species identity. These differences
213 are most evident when looking at inferred extinction dynamics. Temporal trajectories of network collapse,
214 interaction loss, and motif reorganization varied markedly among approaches. While species-level extinction
215 rankings were often broadly consistent across models, link-level outcomes and secondary extinctions were
216 highly sensitive to reconstruction assumptions, reflecting the emergent dependence of extinction pathways on
217 network structure (Allesina & Tang, 2012; Curtsdotter et al., 2011; Dunne et al., 2002; Yeakel et al., 2014)

218 Taken together, these results underscore that network reconstruction is a hypothesis-generating process where
219 each model encodes a distinct set of ecological assumptions, and the inferred structure and dynamics reflect
220 these assumptions. Accordingly, paleoecologists should carefully align reconstruction approaches with the
221 specific ecological signals of interest, whether potential interactions, realised diets, or macro scale structural
222 properties. Disagreement among models does not imply that any single approach is ‘wrong’, but rather that
223 different models capture different facets of ecological reality (Stouffer, 2019). Recognizing and explicitly
224 accounting for these differences is essential for advancing paleoecology beyond descriptive reconstruction
225 toward rigorous comparative inference.

226 4.2 Aligning ecological questions with model choice

227 A central insight from this study is that different ecological questions require different network representations,
228 echoing broader efforts in network ecology to clarify what models and metrics can validly infer about ecological
229 systems (Gauzens et al., 2025; Strydom et al., 2026). Here we identify a conceptual divide among feasible,
230 realised, and structural networks, providing a practical framework to match research goals with appropriate
231 reconstruction approaches.

232 **Feasibility networks:** (*e.g.*, trait- and phylogeny-based metaweb approaches) are most suitable for exploring
233 potential trophic links and dietary breadth. These models capture the set of interactions that are biologically
234 plausible given species traits, even if not all are realised in a particular community, aligning with metaweb
235 concepts in modern ecology (Tylianakis & Morris, 2017).

236 **Realised networks:** (*e.g.*, allometric or energetic models such as ADBM, ATN, and body-size ratio
237 approaches) are appropriate when the goal is to infer the most likely interactions. By embedding energetic or
238 foraging rules, these models approximate realised diets and energy transfer, improving ecological plausibility
239 compared to purely combinatorial approaches (Brose et al., 2006; Petchey et al., 2008).

240 **Structural networks:** (*e.g.*, niche, cascade) focus on topological patterns rather than species identity,
241 making them useful when broad questions about connectance, trophic depth, or motif frequency are the focus.
242 Such models have a long history as null frameworks in network ecology (Allesina et al., 2008; Williams &
243 Martinez, 2008).

244 Recognising this alignment helps avoid misinterpretation; for instance, treating predicted metaweb links as
245 realised interactions conflates potential and actual diets, potentially exaggerating inferred interaction diversity.

246 4.3 Implications for paleoecological network studies

247 Findings carry three key implications for paleoecology:

248 1. **Explicitly acknowledge model assumptions:** Interpretations of ancient food webs must clearly
249 articulate the assumptions underlying reconstruction models. Without this, differences between networks
250 from different datasets or research groups could be misattributed to ecological variation rather than
251 methodological choice.

252 2. **Standardise comparative frameworks:** When comparing food webs across studies, networks
253 should be constructed and analysed using comparable model families. Failing to do so risks conflating
254 methodological differences with ecological or temporal variation.

255 3. **Leverage modern theory to expand inference:** Integrating modern network ecology frameworks
256 and methods enriches the paleoecological toolkit(Dunne et al., 2014; Solé & Montoya, 2001). Models
257 developed for modern systems can be adapted to the constraints of fossil data (*e.g.*, Perez-Lamarque et
258 al., 2026), enabling more nuanced insights into deep-time dynamics.

259 4.4 Recommendations for network reconstruction in paleoecology

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

262 1. **Define the Inferential Goal First:** Before reconstructing networks, researchers should articulate
263 whether they aim to infer potential interactions, likely realised diets, or general structural properties.
264 This will inform the selection of an appropriate model family consistent with the ecological question at

265 hand (*e.g.*, metaweb for complete diets, energetic models for trophic energy flows, or structural models
266 for generic topologies)

- 267 **2. Use ensemble and sensitivity frameworks:** Rather than relying on a single model output, researchers
268 should adopt ensemble approaches that generate and compare multiple network reconstructions. This
269 not only quantifies model uncertainty but also reveals which ecological conclusions are robust biological
270 signals and which are methodological artifacts.
- 271 **3. Standardise cross-study comparisons:** Comparisons of networks from different palaeoecological
272 studies should be standardised by model family. When models differ, interpretations about ecological or
273 environmental change should explicitly address how model choice may contribute to observed differences.
- 274 **4. Interpret scale-specific results with caution:** Because node-level patterns tend to be more robust
275 to model choice than link-level patterns, researchers should prioritise interpretations at the appropriate
276 scale. Structural conclusions about cascade pathways or secondary extinctions should be framed as
277 model-dependent hypotheses rather than definitive historical reconstructions.

278 4.5 Future directions

279 Advances in modern network ecology offer several promising directions for paleoecology. These include
280 probabilistic and Bayesian approaches to quantify uncertainty in link prediction (Baskerville et al., 2011;
281 Elmasri et al., 2020), maximum entropy methods to infer network structure under limited data (Banville et
282 al., 2023), and multi-layer network representations that integrate trophic and non-trophic interactions (Pilosof
283 et al., 2017). Combined with increasingly available trait and phylogenetic information, such developments
284 can bridge fossil constraints and ecological inference, enabling more nuanced, probabilistically grounded
285 reconstructions of deep-time ecosystems (Banville et al., 2025; Perez-Lamarque et al., 2026; Poisot et al.,
286 2016).

287 5 Conclusions

288 Ecological network reconstruction in deep time is not merely a technical step but a fundamental component
289 of ecological inference. By explicitly comparing six contrasting reconstruction approaches for a single
290 extinction event and location, we show that model choice strongly shapes inferred food-web structure, species
291 interactions, and extinction dynamics (even when the underlying fossil data are identical). While broad,
292 trait-based patterns of species loss are relatively robust, conclusions about pairwise interactions, secondary
293 extinctions, and cascading dynamics depend critically on the assumptions embedded in the chosen network

reconstruction approach. Network reconstruction is inherently hypothesis-driven: each model encodes distinct ecological assumptions that influence both network structure and inferred dynamics. No single approach captures all aspects of past ecosystems, but careful alignment of model choice with research goals, combined with ensemble or comparative frameworks, allows robust inference while quantifying uncertainty. These results underscore the need for paleoecological studies to evaluate the sensitivity of key conclusions to alternative network representations and highlight that understanding past ecosystem collapse requires not only better fossil data, but also transparent, question-driven modelling frameworks that explicitly encode 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>
- Banville, F., Gravel, D., & Poisot, T. (2023). What constrains food webs? A maximum entropy framework for predicting their structure with minimal biases. *PLOS Computational Biology*, 19(9), e1011458. <https://doi.org/10.1371/journal.pcbi.1011458>
- Banville, F., Strydom, T., Blyth, P. S. A., Brimacombe, C., Catchen, M. D., Dansereau, G., Higino, G., Malpas, T., Mayall, H., Norman, K., Gravel, D., & Poisot, T. (2025). Deciphering probabilistic species interaction networks. *Ecology Letters*, 28(6), e70161. <https://doi.org/10.1111/ele.70161>
- 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>
- Baskerville, E. B., Dobson, A. P., Bedford, T., Allesina, S., Anderson, T. M., & Pascual, M. (2011). Spatial guilds in the serengeti food web revealed by a bayesian group model. *PLOS Computational Biology*, 7(12), e1002321. <https://doi.org/10.1371/journal.pcbi.1002321>
- Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., ... Cohen, J. E. (2006). Consumer–resource body-size relationships in natural food webs. *Ecology*, 87(10), 2411–2417. [https://doi.org/10.1890/0012-9658\(2006\)87%5B2411:CBRINF%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87%5B2411:CBRINF%5D2.0.CO;2)

- 325 Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A., & Rall,
326 B. C. (2011). Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and
327 dynamic food webs. *Basic and Applied Ecology*, 12(7), 571–580. <https://doi.org/10.1016/j.baae.2011.09.008>
- 328 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães,
329 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019).
330 Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brv.12433>
- 331 Dillon, E. M., Pier, J. Q., Smith, J. A., Raja, N. B., Dimitrijević, D., Austin, E. L., Cybulski, J. D., De
332 Entrambasaguas, J., Durham, S. R., Grether, C. M., Haldar, H. S., Kocáková, K., Lin, C.-H., Mazzini, I.,
333 Mychajliw, A. M., Ollendorf, A. L., Pimiento, C., Regalado Fernández, O. R., Smith, I. E., & Dietl, G. P.
334 (2022). What is conservation paleobiology? Tracking 20 years of research and development. *Frontiers in
335 Ecology and Evolution*, 10. <https://doi.org/10.3389/fevo.2022.1031483>
- 336 Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).
337 Extinction cascades, community collapse, and recovery across a mesozoic hyperthermal event. *Nature
338 Communications*, 15(1), 8599. <https://doi.org/10.1038/s41467-024-53000-2>
- 339 Dunne, J. A., Labandeira, C. C., & Williams, R. J. (2014). Highly resolved early eocene food webs show
340 development of modern trophic structure after the end-cretaceous extinction. *Proceedings of the Royal
341 Society B: Biological Sciences*, 281(1782), 20133280. <https://doi.org/10.1098/rspb.2013.3280>
- 342 Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and network
343 analyses of cambrian food webs. *PLOS Biology*, 6(4), e102. <https://doi.org/10.1371/journal.pbio.0060102>
- 344 Dunne, J., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs:
345 Robustness increases with connectance. *Ecol. Lett.*, 5(4), 558–567.
- 346 Elmasri, M., Farrell, M. J., Davies, T. J., & Stephens, D. A. (2020). A hierarchical bayesian model for
347 predicting ecological interactions using scaled evolutionary relationships. *The Annals of Applied Statistics*,
348 14(1), 221–240. <https://doi.org/10.1214/19-AOAS1296>
- 349 Erdős, P., & Rényi, A. (1959). On random graphs. i. *Publicationes Mathematicae Debrecen*, 6(3-4), 290–297.
350 <https://doi.org/10.5486/pmd.1959.6.3-4.12>
- 351 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,
352 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the late pleistocene. *Science*,
353 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 354 Gauzens, B., Brose, U., Delmas, E., & Berti, E. (2023). ATNr: Allometric trophic network models in r.
355 *Methods in Ecology and Evolution*, 14(11), 2766–2773. <https://doi.org/10.1111/2041-210X.14212>
- 356 Gauzens, B., Thouvenot, L., Srivastava, D. S., Kratina, P., Romero, G. Q., Berti, E., O'Gorman, E. J.,

- 358 González, A. L., Dézerald, O., Eisenhauer, N., Pires, M., Ryser, R., Farjalla, V. F., Rogy, P., Brose, U.,
359 Petermann, J. S., Geslin, B., & Hines, J. (2025). Tailoring interaction network types to answer different
360 ecological questions. *Nature Reviews Biodiversity*, 1–10. <https://doi.org/10.1038/s44358-025-00056-7>
- 361 Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B.,
362 Tylianakis, J. M., Wood, S. A., & Roslin, T. (2019). Bringing elton and grinnell together: A quantitative
363 framework to represent the biogeography of ecological interaction networks. *Ecography*, 42(3), 401–415.
364 [https://doi.org/https://doi.org/10.1111/ecog.04006](https://doi.org/10.1111/ecog.04006)
- 365 Jenny, D., Fuchs, D., Arkhipkin, A. I., Hauff, R. B., Fritschi, B., & Klug, C. (2019). Predatory behaviour
366 and taphonomy of a jurassic belemnoid coleoid (diplobelida, cephalopoda). *Scientific Reports*, 9(1), 7944.
367 <https://doi.org/10.1038/s41598-019-44260-w>
- 368 Kiessling, W., Raja, N. B., Roden, V. J., Turvey, S. T., & Saupe, E. E. (2019). Addressing priority questions
369 of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B:
370 Biological Sciences*, 374(1788), 20190222. <https://doi.org/10.1098/rstb.2019.0222>
- 371 Michalska-Smith, M. J., & Allesina, S. (2019). Telling ecological networks apart by their structure: A
372 computational challenge. *PLOS Computational Biology*, 15(6), e1007076. <https://doi.org/10.1371/journal.pcbi.1007076>
- 373 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple
374 building blocks of complex networks. *Science*, 298(5594), 824–827. <https://doi.org/10.1126/science.298.5594.824>
- 375 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from
376 proxies. *Trends in Ecology & Evolution*, 30(6), 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- 377 Perez-Lamarque, B., Andréoletti, J., Morillon, B., Pion-Piola, O., Lambert, A., & Morlon, H. (2026). Darwin's
378 entangled bank through deep time: Structural stability of mutualistic networks over large geographic and
379 temporal scales. *EcoEvoRxiv*. <https://doi.org/10.1101/2025.10.08.681159>
- 380 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure.
381 *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 382 Pichler, M., & Hartig, F. (2023). Machine learning and deep learning—a review for ecologists. *Methods in
383 Ecology and Evolution*, 14(4), 994–1016. <https://doi.org/10.1111/2041-210X.14061>
- 384 Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature
385 Ecology & Evolution*, 1(4), 101. <https://doi.org/10.1038/s41559-017-0101>
- 386 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., &
387 Vissault, S. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*,
388 48(1), 1–12. <https://doi.org/10.1111/jbi.13530>
- 389

- 391 jbi.14127. <https://doi.org/10.1111/jbi.14127>
- 392 Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of species interaction
393 networks. *Ecology Letters*, 15(12), 1353–1361. <https://doi.org/10.1111/ele.12002>
- 394 Poisot, T., Cirtwill, A., Cazelles, K., Gravel, D., Fortin, M.-J., & Stouffer, D. (2016). The structure of
395 probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303312. <https://doi.org/10>
- 396 Poisot, T., & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree
397 distribution and emerging network properties. *PeerJ*, 2, e251. <https://doi.org/10.7717/peerj.251>
- 398 Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
399 through space and time. *Oikos*, 124(3), 243–251. <https://doi.org/10.1111/oik.01719>
- 400 Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring
401 unexplained structure using latent traits. *The American Naturalist*, 176(2), 170–177. <https://doi.org/10.1086/653667>
- 402 Roopnarine, P. D. (2017). *Ecological modelling of paleocommunity food webs* (pp. 201–226). University of
403 Chicago Press.
- 404 Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32(1),
405 1–19. <https://www.jstor.org/stable/4096814>
- 406 Roopnarine, P. D., & Dineen, A. A. (2018). *Coral reefs in crisis: The reliability of deep-time food web
407 reconstructions as analogs for the present* (C. L. Tyler & C. L. Schneider, Eds.; pp. 105–141). Springer
408 International Publishing. https://doi.org/10.1007/978-3-319-73795-9_6
- 409 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for
410 reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. [//doi.org/10.1101/2024.01.30.578036](https://doi.org/10.1101/2024.01.30.578036)
- 411 Solé, R. V., & Montoya, M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal
412 Society of London. Series B: Biological Sciences*, 268(1480), 2039–2045. <https://doi.org/10.1098/rspb.2001.1767>
- 413 Stouffer, D. B., Camacho, J., Guimerà, R., Ng, C. A., & Nunes Amaral, L. A. (2005). Quantitative patterns
414 in the structure of model and empirical food webs. *Ecology*, 86(5), 1301–1311. <https://doi.org/10.1890/04-0957>
- 415 Stouffer, D. B. (2019). All ecological models are wrong, but some are useful. *Journal of Animal Ecology*,
416 88(2), 192–195. <https://doi.org/10.1111/1365-2656.12949>
- 417 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust
418 pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621),
419 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>

- 424 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
425 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap
426 towards predicting species interaction networks (across space and time). *Philosophical Transactions of the*
427 *Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 428 Strydom, T., Dunhill, A. M., Dunne, J. A., Poisot, T., & Beckerman, A. P. (2026). Scaling from metawebs
429 to realised webs: A hierarchical approach to network ecology. *EcoEvoRxiv*. <https://doi.org/10.32942/X2JW8K>
- 431 Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of*
432 *Ecology, Evolution, and Systematics*, 48(1), 25–48. <https://doi.org/10.1146/annurev-ecolsys-110316-022821>
- 433 Vullo, R. (2011). Direct evidence of hybodont shark predation on late jurassic ammonites. *Naturwissenschaften*,
434 98(6), 545–549. <https://doi.org/10.1007/s00114-011-0789-9>
- 435 Williams, R. J., & Martinez, N. D. (2004). Stabilization of chaotic and non-permanent food-web dynamics.
436 *The European Physical Journal B - Condensed Matter*, 38(2), 297–303. <https://doi.org/10.1140/epjb/e2004-00122-1>
- 438 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
439 <https://doi.org/10.1038/35004572>
- 440 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food
441 webs. *The Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 442 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T.
443 (2014). Collapse of an ecological network in ancient egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>

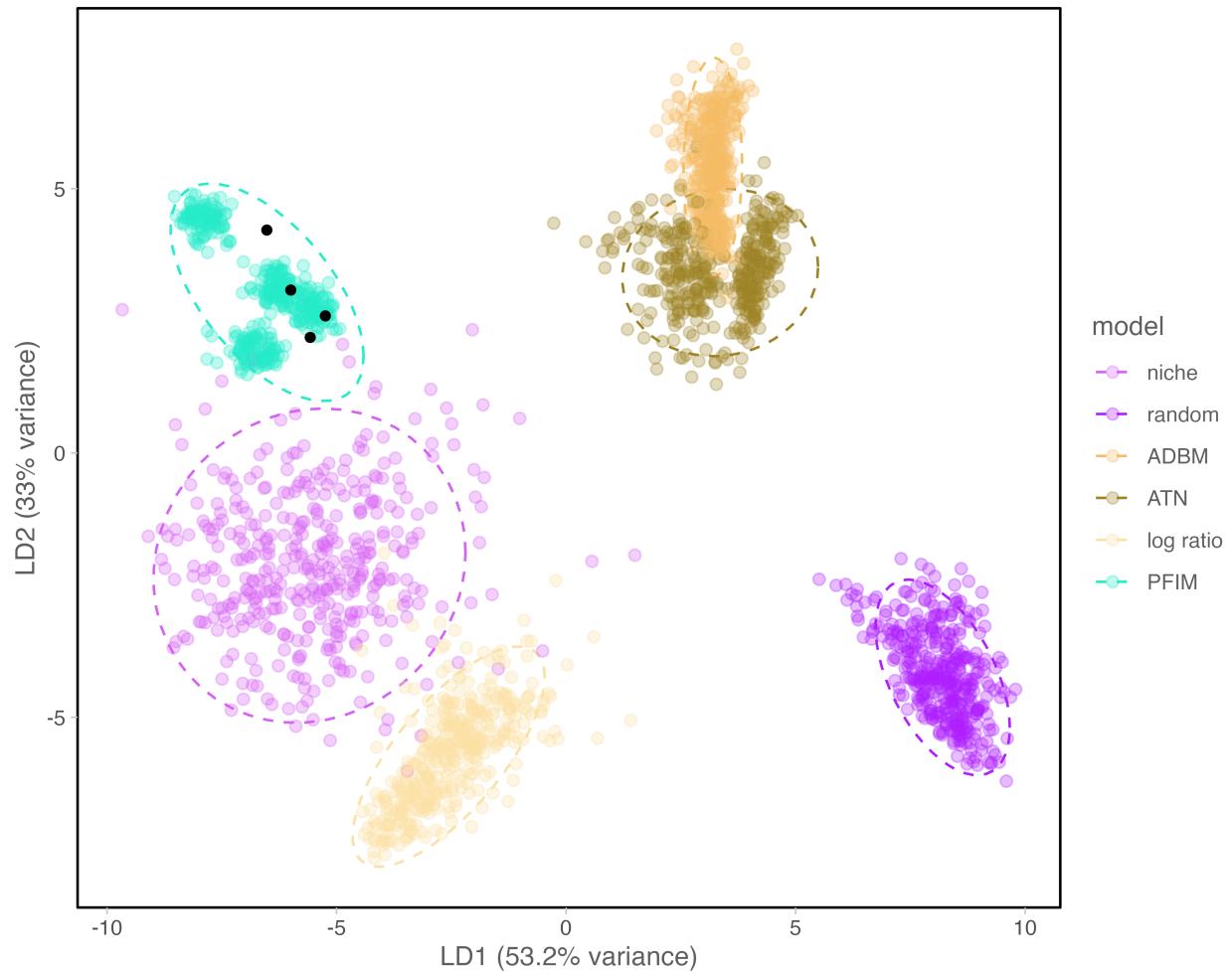


Figure 1: Linear discriminant analysis (LDA) of ecological network metrics for six model types. Each point represents a replicate, and ellipses indicate 95% confidence regions for each model. The second column represents the correlation of the various network metrics with the respective LDA axes.

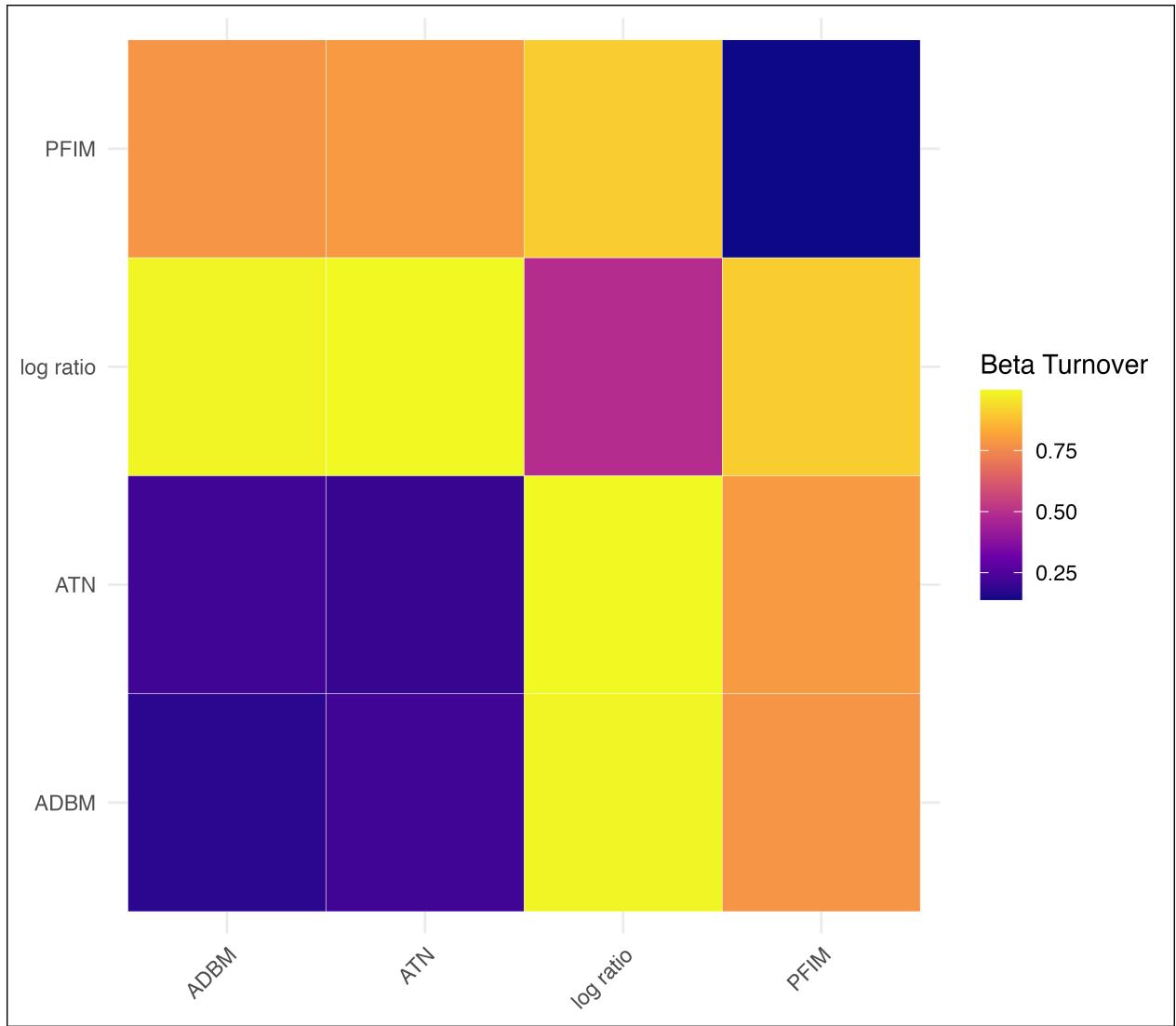


Figure 2: Pairwise beta turnover in species interactions among four ecological network models (ADBM, lmatrix, body-size ratio, and pfim). Each cell represents the mean turnover value between a pair of models, with warmer colors indicating greater dissimilarity in inferred interactions. The diagonal is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

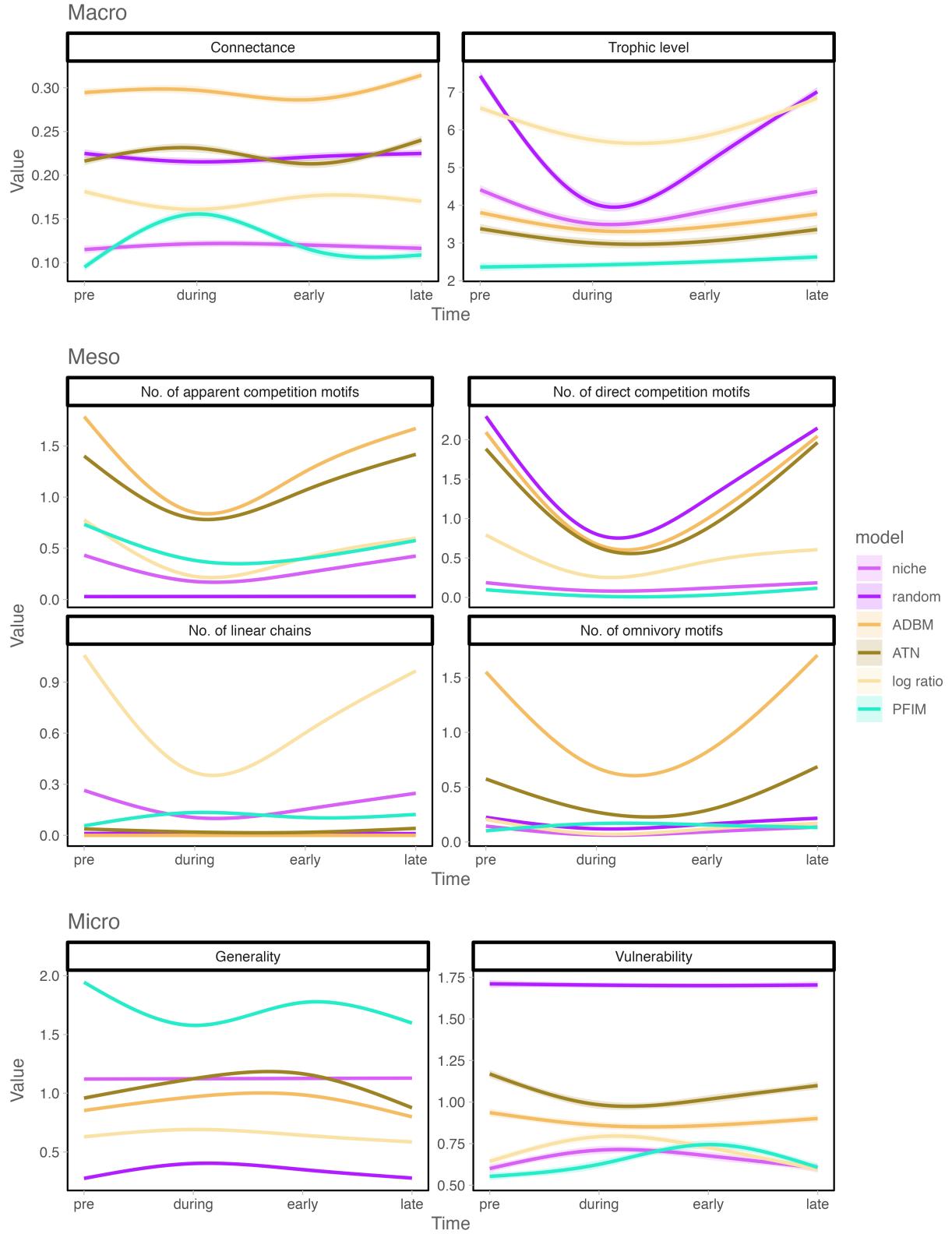
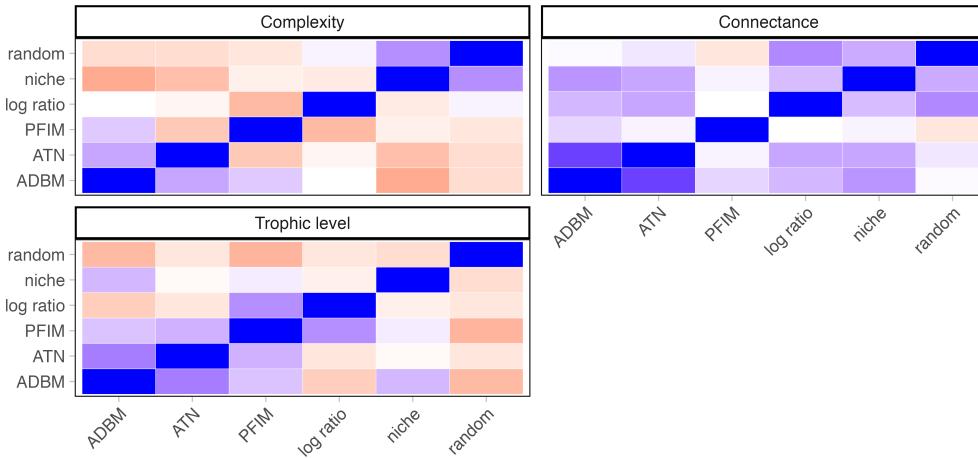
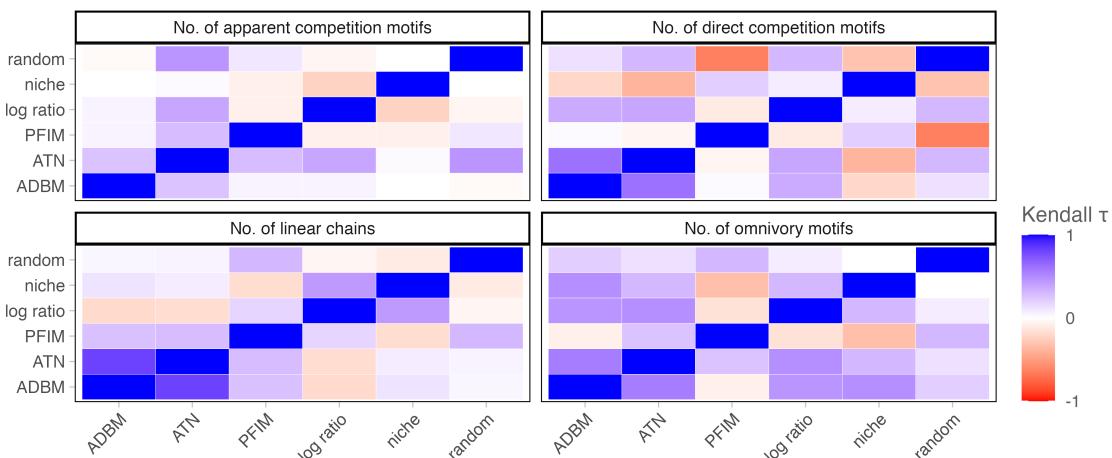


Figure 3: GAM-predicted trajectories of network structure during extinction simulations reveal pronounced differences in the timing and magnitude of change across reconstruction models. Lines show model-specific smooths and shaded areas indicate 95% confidence intervals. Deterministic approaches produce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

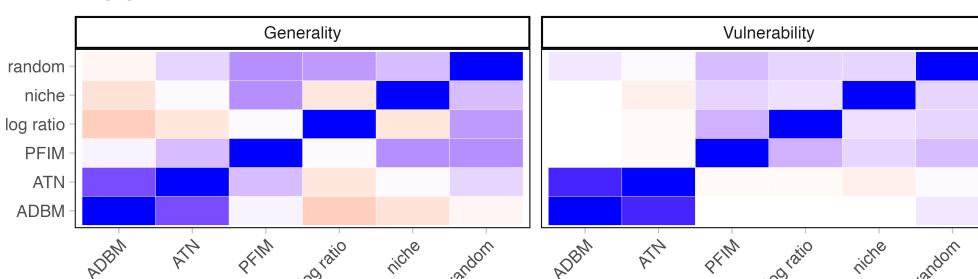
Macro



Meso



Micro



TSS

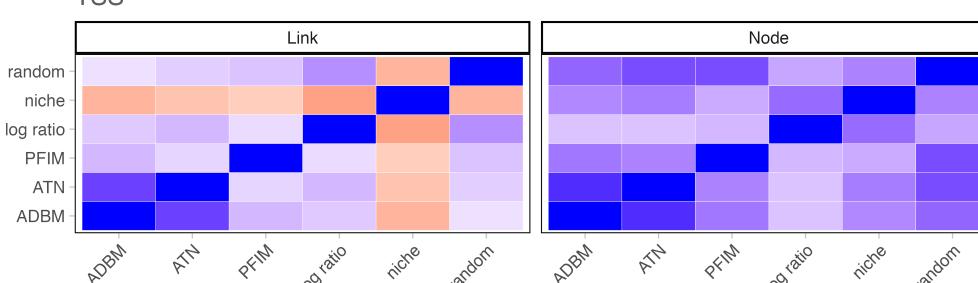


Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients (τ) between models for each network metric. Each panel corresponds to a different metric and displays the degree of agreement in extinction-scenario rankings across models based on mean absolute differences (MAD) between observed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