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

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Abstract

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

# 1. Introduction

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

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

Although numerous tools exist for inferring species interactions (see Morales-Castilla et al., 2015; Pichler & Hartig, 2023; Strydom et al., 2021; Allesina et al., 2008 for reviews), only a subset can be reliably applied in paleo contexts, where data on traits, abundances, and community composition are incomplete and systematically biased. This makes it essential to clearly articulate which reconstruction approaches are appropriate for which inferential purposes. Recent work has shown that reconstruction approaches (*e.g.,* models based on traits, abundances, or co-occurrence) can be categorised by the type of network that they predict (Strydom et al., 2026). These include feasible networks (derived from trait matching and phylogenetic inference that produce metawebs of plausible interactions), realised networks, (constrained by ecological rules and evidence of actual feeding relationships), and purely structural networks (which reproduce ecologically plausible topologies but lack species-level node identities). In this sense, food-web reconstructions are not empirical recoveries of a single past ecosystem, but rather represent alternative, model-based, hypotheses about interaction structure constrained by the fossil record.

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

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

# 2. Materials and Methods

## 2.1 Study system and fossil data

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

## 2.2 Network reconstruction approaches

### 2.2.1 Conceptual classification of network types

Most paleo-specific approaches currently operate within the feasibility space (*e.g.,* Shaw et al., 2024; Fricke et al., 2022; Roopnarine, 2006). Although well suited for reconstructing feasible interactions, these methods represent only a subset of the broader spectrum of network construction approaches. Here, we present a suite of models ([Table 1](#tbl-models)) that enable the construction of a wider range of ecological networks and the exploration of a broader set of ecological questions, provided that their underlying assumptions are compatible with the constraints of fossil data. For example, some tools require quantitative estimates of body size, which must often be inferred from size classes or functional morphology in the fossil record. Structural models, such as the niche model, rely only on species richness and estimates/specification of connectance, but their species-agnostic nature limits their applicability to trait-based or diet-specific questions, although they do still accurately recover network structure (Stouffer et al., 2005) . Mechanistic approaches, by contrast, depend on accurate assignment of feeding traits or robust phylogenetic support. Recognizing how these methodological requirements intersect with the limits of fossil evidence is essential for selecting an appropriate modelling framework.

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| Table 1: Six different models that can be used to construct food webs for both this specific community but are also broadly suited to paleo network prediction. These models span all facets of the network representation space (metaweb, realised, and structural network) and are suitable for an array of different paleo communities as the data requirements fall within the limitations set by the fossil record.   | Model family | Assumptions | Data needs | ‘Limitation’ | Network type | Key reference | Usage examples | | --- | --- | --- | --- | --- | --- | --- | | random | Links are randomly distributed within a network | richness, number of links | parameter assumptions, species agnostic | structural network | Erdős & Rényi (1959) |  | | niche | Networks are interval, species can be ordered on a ‘niche axis’ | richness, connectance | parameter assumptions, species agnostic | structural network | Williams & Martinez (2008) |  | | allometric diet breadth model (ADBM) | Interactions are determined by energetic costs (foraging ecology) | body mass, biomass (abundance) | does not account for forbidden links in terms of trait compatibility, assumptions on body size and biomass (abundance) from fossil data | realised network | Petchey et al. (2008) |  | | 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 framework/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) | | body size ratio model | Interactions inferred using allometric rules (ratio of body sizes between predator and prey). Logit of the linking probability used to further constrain links to an ‘optimal size range’ for prey. | body mass | does not account for forbidden links in terms of evolutionary compatibility, assumptions on body size from fossil data | realised network | Rohr et al. (2010) | Network collapse (Yeakel et al., 2014) | |

### 2.2.2 Network generation and replication

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

## 2.3 Network metrics and structural analyses

We quantified network structure using a suite of macro-, meso-, and micro-scale metrics [Table 2](#tbl-properties), capturing global properties, motif structure, and species-level variability. Differences among models were assessed using MANOVA, followed by univariate ANOVAs, post-hoc comparisons, and linear discriminant analysis. Pairwise interaction turnover was quantified using link-based beta diversity for models that infer species-specific interactions (Poisot et al., 2012)

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| 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 | , where is the number of species and the number of links | Macro |  | | Max trophic level | Prey-weighted trophic level averaged across taxa | Macro | Williams & Martinez (2004) | | S1 | Number of linear chains, normalised | Meso | Milo et al. (2002); Stouffer et al. (2007) | | S2 | Number of omnivory motifs, normalised | Meso | Milo et al. (2002); Stouffer et al. (2007) | | S4 | Number of apparent competition motifs, normalised | Meso | Milo et al. (2002); Stouffer et al. (2007) | | S5 | Number of direct competition motifs, normalised | Meso | Milo et al. (2002); Stouffer et al. (2007) | | Generality | Normalized standard deviation of generality of a species standardized by | Micro | Williams & Martinez (2000) | | Vulnerability | Normalized standard deviation of vulnerability of a species standardized by | Micro | Williams & Martinez (2000) | |

## 2.4 Extinction simulations and model evaluation

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

# 3. Results

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

## 3.1 Network structure differs among reconstruction approaches

To test whether network reconstruction approach influences inferred food-web structure, we compared multivariate patterns of network metrics across all six models using a MANOVA. Network structure differed strongly among reconstruction approaches (MANOVA, Pillai’s trace = 3.81, approximate = 962.12, p < 0.001). Univariate analyses showed that model choice explained a large proportion of variance in most network metrics, with high partial η² values for connectance, generality, vulnerability, and motif frequencies (η² = 0.66–0.92). In contrast, maximum trophic level exhibited a much smaller effect of model choice (η² = 0.04). Estimated marginal means and Tukey-adjusted comparisons indicated consistent differences among reconstruction approaches, with PFIM differing significantly from all other models (p ≤ 0.026), while ADBM and ATN did not differ from one another (p = 1.00). Linear discriminant analysis (LDA) further helped visualise distinctions among reconstruction approaches in multivariate network space [Figure 1](#fig-structure), with the first two axes explaining 86.5% of between-model variance (LD1 = 53.9%, LD2 = 32.6%). LD1 was most strongly correlated with vulnerability, connectance, and the number of direct competition motifs (S4), whereas LD2 was associated primarily with generality, number of omnivory motifs (S2), and number of apparent competition motifs (S5). Higher-order axes each explained less than 9% of the remaining variance. This demonstrates that the reconstruction approach leaves a strong multivariate signature independent of community composition.

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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. |

### 3.1.1 Inferred pairwise interactions vary widely among models

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

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

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| 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. |

## 3.2 Model choice influences inferred extinction dynamics

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

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| 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. |

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

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| Figure 4: Heatmaps showing pairwise Kendall rank correlation coefficients () 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 values (blue) indicate concordant rankings between models, whereas negative values (red) indicate opposing rankings. Warmer colours approaching zero represent little or no agreement. Panels illustrate how consistently different modelling approaches evaluate the relative realism of extinction scenarios across multiple network properties. |

# 4. Discussion

# 5. Model choice as a component of ecological inference

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

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

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

Pairwise β-turnover analysis underscores that disagreements among reconstruction approaches are not merely quantitative differences in metrics, but qualitative differences in the identity of inferred interactions. Models that may produce similar aggregate properties (*e.g.,* connectance) can still disagree strongly on species-level diets and trophic roles. This reinforces concerns raised in both paleoecological and modern studies that metrics alone can mask substantive differences in network structure and function (Fricke et al., 2022; Shaw et al., 2024).

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

Taken together, these results highlight that network reconstruction is not neutral. Rather, it is a hypothesis generation process where the chosen model encodes a set of ecological assumptions. Consequently, paleoecologists must carefully consider which ecological signals they aim to recover (potential interactions, realised 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. Recognising this is critical for advancing paleoecology beyond descriptive reconstruction toward rigorous comparative inference.

## 5.1 Aligning ecological questions with model choice

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

**Feasibility networks:** (*e.g.,* trait- and phylogeny-based metaweb approaches) are best suited for questions about potential trophic links and dietary breadth. These models aim to capture the range of interactions that are biologically plausible given species traits, even if not all are realised in any given context. Such an approach aligns with metaweb concepts in modern ecology, where large pools of potential interactions are used to understand regional species interaction potentials and local assembly processes (Tylianakis & Morris, 2017).

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

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

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

## 5.2 Implications for paleoecological network studies

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

1. **Explicitly acknowledge model assumptions:** Interpretations of ancient food webs must clearly articulate the assumptions underlying reconstruction models. Without this, differences in networks reconstructed from different datasets or by different research groups may be misattributed to ecological differences rather than methodological choices.
2. **Standardise comparative frameworks:** When comparing food webs across studies, researchers should ensure that networks are constructed and analysed using comparable model families. Without such standardisation, meta-analyses risk conflating methodological differences with ecological or temporal variation.
3. **Leverage modern theory to expand inference:** Integrating modern network ecology frameworks and methods with paleo-specific approaches enriches the inferential toolkit available to paleoecologists (Dunne et al., 2014; Solé & Montoya, 2001). Models developed for modern systems (*e.g.,* allometric or trait-based energy models) can be adapted to the constraints of fossil data (*e.g.,* Perez-Lamarque et al., 2026), enabling novel insights into deep-time dynamics.

## 5.3 Recommendations for network reconstruction in paleoecology

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

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

## 5.4 Future directions

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

# 6. Conclusions

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

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