Reconstructing deep-time food webs: model assumptions drive paleoecological inference

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Abstract

Food webs provide a powerful lens for understanding ecosystem structure and function, but reconstructing them in paleoecological contexts remains challenging because direct evidence of feeding interactions is rarely preserved. A wide range of models now exist for predicting interactions and inferring network structure, yet these models differ substantially in their assumptions, mechanisms, and data requirements. Here, we evaluate which network construction approaches are most suitable for paleo food webs given the constraints of the fossil record, and we assess how model choice influences the networks we infer. Using the Toarcian Oceanic Anoxic Event as a case study, we compare six modelling approaches encompassing mechanistic, structural, and theory-based methods. We show that the models produce strikingly different network structures and pairwise interactions, and that these differences propagate into ecological inference—including conclusions about extinction dynamics. Our results highlight the importance of aligning model choice with research questions and underscore the interpretative risks of treating all food-web reconstruction methods as interchangeable.

There has been growing interest in using deep-time fossil data to understand how ecological communities respond to environmental change [1,2]. In modern systems, species interactions and the networks that they form have become central to studying biodiversity, energy flow, and community stability (*e.g.,* [3]). Consequently, paleoecologists have increasingly sought to reconstruct ancient food webs to gain similar insights across major environmental transitions (*e.g.,* [4]; [5]; [6]). However, we are faced by the limitation that interactions cannot be directly observed in the fossil record (with the exception of rare instances) and as a result, the construction of paleo food webs depends on models that allow us to infer feeding relationships from preserved traits, analogies to modern taxa, or ecological theory. While numerous models exist for predicting interactions (see [7]; [8]; [9]; [10] for broader reviews), only a subset can reliably be applied in paleo contexts, where data on traits, abundances, and community composition are inherently incomplete and biased.

The growing interest in paleo food webs has outpaced a clear discussion of *which* construction methods are suitable for which purposes. Different models generate different kinds of networks (feasible, realised, or purely structural) and these differences can fundamentally alter ecological interpretations. In this study, we evaluate a suite of methods that can be feasibly applied to paleo communities and explore how their underlying assumptions shape both network structure and ecological inference. Specifically we focus on identifying a suite of models that are appropriate for use with paleo data that can feasibly be constructed within the limitations that are imposed by fossil data while still spanning the larger network space. Here we use the data from [4] as a case study to understand how different models recover different networks, both in terms of structure as well as pairwise interactions and establish if there are consequences for using networks that are constructed using different models in terms of making inferences about the behaviour of the system by looking at how the model type influences what we infer to be the dominant driver of extinctions across a mass extinction event.

# 1. Constructing paleo webs

## 1.1 Challenges specific to building paleo networks

Reconstructing paleo food webs presents challenges that differ from those encountered in modern systems. First, the fossil record provides an incomplete and selectively preserved subset of the original community. Preservation biases (driven by habitat, skeletal composition, and sedimentary environment) mean that some trophic groups are over-represented (*e.g.,* hard-shelled organisms), while others (*e.g.,* soft-bodied taxa, plankton) are systematically under-sampled. This directly constrains the kinds of models that can be applied, because models requiring complete assemblages or accurate guild representation will perform poorly when preservation is uneven. Second, there is inherent uncertainty about the true community boundaries. Fossil assemblages may represent time-averaged accumulations, transported material, or mixed habitats. As a result, any species list is best interpreted as a set of taxa that could have interacted, rather than a snapshot of a specific subset of interaction species. Third, many extinct taxa have ambiguous trait states, especially regarding diet and behaviour. Even when functional morphology is preserved, ecological behaviour is seldom directly evident. Such uncertainty propagates differently across model families: mechanistic models tend to accommodate broad trait assignments, whereas theory-driven models are more sensitive to uncertainty in body size, foraging mode, or feeding constraints. These limitations do not render reconstruction impossible but highlight the importance of choosing a model whose assumptions match the type of ecological inference being attempted.

## 1.2 Understanding the approaches to network construction

Network construction approaches can be broadly grouped into three methodological and conceptual approaches [Figure 1](#fig-concept). The first are mechanistic models evaluate whether an interaction is *feasibly possible*. These models typically use trait-based rules (*e.g.,* feeding mode, body size, or functional morphology) or evolutionary relationships to determine whether a species *could* consume another. Mechanistic approaches tend to produce metawebs - the full set of all plausible interactions given biological constraints. Theory-driven models, embed assumptions from ecological theory (such as niche theory or foraging ecology) to generate realised interactions and networks. Structural models are similar to theory-driven models, with the exception that these models are species agnostic and as such can only be used to make inferences about network structure. Both theory-driven and structural models aim to reproduce characteristic patterns observed in modern food webs, such as intervality, trophic hierarchies, or body-size-scaled feeding ranges. They do not necessarily require detailed trait information and instead rely on ecological rules or statistical distributions consistent with empirical food webs.

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| Figure 1: This obviously needs work but a variation on this to try and articulate the different approaches and broadly how they may differ. |

Most existing paleo-specific approaches fall within the mechanistic tradition (e.g., [11]; [12]; [13]). While these are well-suited for reconstructing feasible interactions, they represent only a subset of the broader space of network construction methods. Incorporating theory-driven models allows paleoecologists to explore realised interaction structures and address a wider suite of ecological questions—provided their assumptions are compatible with the limitations of fossil data. Here we present a range of models [Table 1](#tbl-models) that carry specific assumptions and data requirements. For instance, allometric models depend on quantitative body-size estimates, which must be inferred from size classes or functional morphology in the fossil record. Structural models such as the niche model require only richness and connectance, but their species-agnostic nature limits their usefulness for trait-based or diet-specific questions. Mechanistic models rely on accurate assignment of feeding traits, which may be uncertain for extinct taxa but are often more tractable than estimating abundances or interaction strengths. Understanding how these limitations intersect with what fossil data can reliably provide is essential for selecting an appropriate modelling approach.

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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 | | --- | --- | --- | --- | --- | --- | | random | Links are randomly distributed within a network | richness, number of links | parameter assumptions, species agnostic | structural network | [14] | | niche | Networks are interval, species can be ordered on a ‘niche axis’ | richness, connectance | parameter assumptions, species agnostic | structural network | [15] | | 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 | theoretical network | [16] | | l-matrix | 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 | theoretical network | [17] | | 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) | mechanistic web | [11] | | 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 | theoretical network | [18] | |

# 2. Case study: Toarcian mass extinction event

## 2.1 Dataset overview

### 2.1.1 Species occurrence

We used fossil occurrence data spanning the upper Pliensbachian (~185 Ma) to the upper Toarcian (~175 Ma) of the Cleveland Basin, following [4] . The dataset comprises four paleo-communities representing the pre-extinction, post-extinction, early recovery, and late recovery intervals of the Toarcian Oceanic Anoxic Event. Each assemblage was treated as a community of potentially interacting taxa. ***([Insert here]: total number of taxa; numbers per time bin; brief note on sampling completeness?)*** Although the Toarcian occurs within “deep time,” the depositional environment of the Cleveland Basin provides an unusually well-resolved record of community change, making it a suitable system for comparing network reconstruction methods.

### 2.1.2 Defining modes of life (traits)

We used the modes of life (traits) as identified in [4], who defined four traits: motility (fast, slow, facultative, non-motile), tiering (pelagic, erect, surficial, semi-infaunal, shallow infaunal, deep infaunal), feeding (predator, suspension feeder, deposit feeder, mining, grazer), and size: gigantic (>500 mm), very large (>300–500 mm), large (>100–300 mm), medium (>50–100 mm), small (>10–50 mm), tiny (≤10 mm), for each fossil species based on the ecological traits defined in the Bambach ecospace model [19].

### 2.1.3 Constructing networks

For each paleo community, we constructed 100 networks using each of the modles listed in [Table 1](#tbl-models) (6 models × 4 time intervals × 100 replicates = 2,400 networks). Networks were then simplified by removing disconnected species, ensuring that all nodes participated in at least one interaction. Models requiring body-size inputs (ADBM, l-matrix, and body-size ratio models) were parameterised by drawing body masses from uniform distributions bounded by the size-class limits assigned in [4]. This approach propagates uncertainty inherent in fossil size estimates while preserving consistent relative sizes among species within a replicate. For each replicate, the same set of body masses was used across models that depend on size. For structural models (random and niche), connectance was drawn uniformly from 0.07–0.34 to ensure networks spanned a realistic range of empirical food-web connectances, while holding richness constant. The same connectance value was used for both models within a replicate to facilitate direct comparison. For each network, we calculated the metrics listed in [Table 2](#tbl-properties), capturing macro-, meso-, and micro-scale structural properties.

## 2.2 Models capture different network structure but in unexpected ways

When quantifying network structure, we are essentially asking how interactions are distributed across species and how these patterns scale from individual nodes to the whole community. Structural metrics are informative because they reflect underlying ecological processes: how energy flows through trophic levels, how disturbances propagate, where redundancy or fragility exists, and how species specialise or generalise in their diets. To capture these different facets, we evaluated a suite of macro-, meso-, and micro-scale metrics [Table 2](#tbl-properties), ranging from global properties like connectance and complexity to motifs and species-level generality and vulnerability.

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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 | [20] | | Diameter | Diameter can also be measured as the average of the distances between each pair of nodes in the network | Macro | [21] | | Complexity | SVD complexity of a network, defined as the Pielou entropy of its singular values | Macro | [9] | | Redundancy | , where is the number of species and the number of links. Indicates the number of edges beyond what is needed for a minimum-connected tree | Macro |  | | S1 | Number of linear chains, normalised | Meso | [22]; [23] | | S2 | Number of omnivory motifs, normalised | Meso | [22]; [23] | | S4 | Number of apparent competition motifs, normalised | Meso | [22]; [23] | | S5 | Number of direct competition motifs, normalised | Meso | [22]; [23] | | Generality | Normalized standard deviation of generality of a species standardized by | Micro | [24] | | Vulnerability | Normalized standard deviation of vulnerability of a species standardized by | Micro | [24] | |

Despite being supplied with the same species pools, the different models generated networks with systematically different structural signatures. A MANOVA revealed a strong multivariate effect of model type on network structure (Pillai’s Trace = 3.89, p < 0.001), indicating that each modelling approach produces a distinct ‘structural fingerprint’. Follow-up ANOVAs confirmed that model choice had substantial effects on every metric we examined, with effect sizes typically exceeding 0.80. The only exception was maximum trophic level (η² = 0.19), suggesting some convergence in vertical structure even when structure differs widely.

Post-hoc comparisons [Figure 2](#fig-marginal) revealed three broad clusters. PFIM consistently yielded the most connected, dense networks, reflecting its mechanistic emphasis on trait-based feasibility. Niche, random, and body-size ratio models formed an intermediate group, producing networks with moderate connectance and motif frequencies. ADBM and l-matrix formed a tight cluster characterised by constrained feeding ranges, reflecting their shared basis in energetic and allometric theory. Although these groupings broadly align with *a priori* expectations about model families, several patterns emerged that were less intuitive. Most notably, the body-size ratio model which is theoretically grounded but aligned more closely with structural models than with the fully allometric ones. This suggests that even slight differences in how body-size constraints are implemented can shift a model’s position within the network-structure landscape. A Linear Discriminant Analysis further illustrated the distinctiveness of the model families [Figure 3](#fig-structure). Classification accuracy of the LDA was 85%, demonstrating that the combination of dependent variables effectively discriminates among model types, indicating the strong imprint that model assumptions leave on inferred ecological patterns. The PFIM model is strongly separated, while ADBM and l-matrix networks cluster closely together. The niche and random models occupy intermediate positions. Importantly these results indicate that model choice is the dominant driver of inferred network structure, often overwhelming the ecological signal embedded within the species pool itself. Models designed to reproduce feasible interactions and those designed to generate realised niche structure occupy fundamentally different portions of ‘network space’, even when operating on identical taxa. Such structural divergences could have direct implications for ecological inference, particularly when comparing networks across time or when using network metrics to infer processes such as community stability, trophic organisation, or susceptibility to cascading extinctions.

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| Figure 2: Estimated marginal means (EMMs) of ecological network metrics across six model types with 95% confidence intervals. Bars represent the predicted values for each model, and error bars indicate the 95% confidence limits. Letters above each bar denote Tukey-adjusted pairwise significance: models sharing the same letter are not significantly different, while models with different letters are significantly different (p < 0.05). The plot reveals three tiers of model performance, with pfim consistently higher, log ratio, niche, and random at intermediate levels, and adbm and lmatrix lower, consistent with the MANOVA and post-hoc analyses. |

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| Figure 3: 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. |

## 2.3 Some networks don’t share any interactions and some share a lot

Beyond differences in global structure, researchers are often interested in specific ecological relationships, *e.g.,* who eats who, which species share predators, and how trophic roles change across communities or time. For these types of questions, it is essential to understand how models differ at the level of pairwise interactions. To quantify this, we measured interaction turnover between networks to allow us to assess the degree to which two models predict the same or different links for the same set of species. This is analogous to β-diversity but applied to links rather than species [25]. Specifically we only looked at the dissimilarity of interaction between shared species. Even when supplied with identical species pools, models varied dramatically in the interactions they inferred [Figure 4](#fig-beta_div). Some pairs of models showed substantial agreement, whereas others shared almost no interactions at all. Note here that we did not include the Random or Niche models as these networks are species agnostic and as such are not designed for inferring species-specific pairwise links.

The body-size ratio model had consistently high turnover relative to all others, indicating that it inferred diets that were largely distinct. This reflects the strong constraints imposed by its logit-based linking rule, which sharply restricts prey to a narrow ‘optimal’ size range. Small differences in body-size estimates or functional groupings therefore lead to disproportionately large changes in inferred interactions. In contrast, the ADBM and L-matrix showed low turnover between each other, reflecting their shared theoretical foundations (operationalising foraging decisions and energetic constraints using similar allometric principles). As a result, they tend to produce similar pairwise interactions even when implemented independently. The PFIM exhibited intermediate turnover, sharing more interactions with size-based theoretical models than with the body-size ratio model. This makes sense: although PFIM uses categorical traits and hierarchical feeding rules rather than quantitative foraging theory, these constraints will still produce broadly similar trophic groupings.

Taken together, these patterns show that pairwise interactions differ far more across models than global metrics alone might suggest. Two models with superficially similar connectance or trophic structure may nonetheless infer completely different diets for individual taxa. This has large implications for any question focused on species-level ecology, including predator–prey specialisation, trophic niche breadth, or the identity of keystone consumers. These findings reinforce the importance of selecting a model whose assumptions align with the intended inference. If the goal is to explore the full set of *possible* interactions a species could have had, a mechanistic model such as PFIM is appropriate. If instead the goal is to infer the likely *realised* interactions or energy pathways, models grounded in allometric foraging theory (ADBM, L-matrix) will provide more ecologically coherent results. Conversely, models like the body-size ratio may be too restrictive or idiosyncratic for diet-based questions because they force interactions into narrow, trait-determined windows.

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| Figure 4: Pairwise beta turnover in species interactions among four ecological network models (adbm, lmatrix, log-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. |

## 2.4 Model choice changes the narrative

The structural and interaction-level differences documented above raise a central question: do different models also lead to different interpretations of ecological dynamics? In other words, does model choice merely affect the architecture of the reconstructed networks, or does it shape the actual stories we tell about how communities collapsed and recovered during the Toarcian extinction event? Using the pre-extinction networks as starting points, we simulated species losses under a suite of ecologically plausible extinction scenarios, including trait-based removals (e.g., body size, motility), network-position removals (e.g., vulnerability, generality), and random extinctions. In each case, we allowed for cascading secondary extinctions. For each model and scenario, we then measured how closely the simulated post-extinction network resembled the real fossil community.

### 2.4.1 Inferred extinction drivers

To assess how consistently different modelling approaches evaluate extinction scenarios, we quantified the agreement in scenario rankings produced by multiple models across several network metrics. For each model, each extinction scenario, and each network metric we calculated the mean absolute difference (MAD) between the observed metric value and the value predicted following the simulated extinction sequence. Lower MAD values indicate a closer match to the empirical network structure and therefore a better-performing extinction scenario for that model and metric. Additionally, we used a derivative of [26] true skill statistic (TSS, see [Equation 1](#eq-1)), where a score below zero indicates that the simulated extinction performs no better than random, and a score of one indicates a perfect match between real and simulated. Here we calculated both a node-level TSS as well as link-level TSS, by parsing out the TSS into two components we are able to assess if differences between real and simulated networks are due to node-level (the wrong species being removed) or link-level (the wrong links be recovered) mismatches. Because the extinction simulations do not allow for the origination of species, when calculating the TSS we only retained species that were present in both the pre and post extinction community and so any node-level mismatches between real and simulated networks was due to the wrong species being removed and not because new species were not.

For each network metric, we treated each model as an independent evaluator of scenario performance. MAD and TSS values were converted to within-model rankings, with rank 1 assigned to the scenario with the smallest MAD (*i.e.,* the closest match to the empirical value) or highest TSS score. Ranking was performed independently for each combination of model and network metric to avoid assumptions about comparability across metrics. To evaluate whether different models produced consistent rankings of extinction scenarios, we quantified rank correlation among models separately for each network metric. Agreement among model rankings was assessed using Kendall’s rank correlation coefficient (τ), which measures the degree of agreement between two ordinal rankings. Kendall’s τ was selected because it is robust for small sample sizes, handles tied ranks appropriately, and provides a direct measure of the probability that model pairs agree or disagree on the relative ordering of scenarios. Kendall’s τ ranges from –1 to +1, where +1 indicates perfect agreement between rankings, 0 reflects no relationship, and –1 represents complete disagreement such that one ranking is the exact reverse of the other.

When we look at Kendall’s τ for the MAD across network structure and models [Figure 5](#fig-mad) we see that generally there is a positive correlation between the different different models. This implies that different models are often recovering a similar ranking of extinction mechanisms (as in the ‘signal’ as to which extinction mechanisms may be the most plausible are the same). Although there is not a strong agreement between models as values tend to be low it is positive to observe that it is not often that we have a completely different ranking of extinction mechanisms, with the exception of complexity and the number of direct competition motifs. When looking at the macro-level network properties the random model often showcases a disagreement in terms of the MAD. This is unsurprising as we expect random networks to produce networks that are not ecologically sound and thus will not behave as one may expect [27]. Interestingly we once again see the strong similarity between the L-matrix and the ADBM (have a high Kendall’s τ). meaning that they recover a similar ranking of extinction mechanisms, this is unsurprising given that we know these networks tend to recover a similar structure [Figure 2](#fig-marginal). Broadly when we look at the behaviour of the different model families (with the exception of the Random model) we see that they recover similar structural signals with regards to the mechanisms potentially driving extinctions.

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| Figure 5: 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 illustrate how consistently different modelling approaches evaluate the relative realism of extinction scenarios across multiple network properties. |

When looking at the node-level TSS scores ([Figure 5](#fig-mad), TSS, panel 2) we see that in general the signal of the extinction mechanism is maintained across the different models. However as many of the extinction mechanisms are determine by the *traits* of the node it is not surprising that we see a similar signal as the species are being removed in the exact same order. Link-level TSS scores ([Figure 5](#fig-mad), TSS, panel 1) do not show the same within extinction mechanism ranking/signal. We see that the Random and PFIM models have high TSS scores (*i.e.,* have a ‘good fit’), however in the case of the PFIM this is to be expected as the links are deterministic and so if you have the same two species pools you will recover the same links. The ‘stochastic’ element of the theoretical models (ADBM, l-matrix, and log-ratio) means that they create a degree of noise at the link-level and thus they are probably inappropriate to use for the type of extinction mechanism question we are asking here - specifically does the real and the simulated network look the same. Link-level TSS is perhaps also not an appropriate approach to determine the ‘best fit’ extinction mechanism if used in isolation and we advocate that the node-level TSS score (or alternatively some measure of diversity is used). Finally, if we were to focus only on node level TSS we do not observe any strong differences between the models and it suggests that node-level driven (topological) extinction processes are insensitive to model type.

Broad inferred extinction mechanisms were relatively robust across models. This is probably in part because species are removed in the same order, node-level outcomes (which species survive) tended to agree. However, at the link level, where secondary cascades depend sensitively on inferred interactions, models often showed limited agreement. PFIM produced consistent link-level outcomes due to its deterministic rules, whereas theory-driven models (ADBM, L-matrix, body-size ratio) generated more variable trajectories due to stochastic link assignment. As a result, different models sometimes reconstructed different pathways of collapse, inferred different trophic groups as being the most affected, or ranked extinction scenarios differently. In other words, while the high-level narrative (e.g., traits matter) is stable, the fine-grained story of ecosystem disruption (who lost interactions first, how cascades unfolded, which species acted as bottlenecks) changes depending on the chosen model. Thus, the Toarcian mass extinction looks subtly but meaningfully different through the lens of each modelling framework. Model choice therefore must be treated as a core component of ecological inference, not a neutral preprocessing step. Some broad signals are robust—especially those driven by species traits—but many of the finer details that paleoecologists care about, such as trophic cascading pathways, keystone taxa, or the ordering of collapse, depend strongly on the chosen model. Researchers must therefore treat model choice not as a technical detail but as a central component of ecological inference.

# 3. Model Choice as an Ecological Inference Decision

Reconstructing food webs from fossil data is an exercise in inference under uncertainty, and our results demonstrate that the choice of network construction model is itself a major ecological decision. Despite using the same species pools, different models produced networks with profoundly different structural properties, interaction patterns, and inferred extinction dynamics. These differences emerge not from the fossil data themselves but from the assumptions embedded within each modelling approach. As a consequence, network reconstruction cannot be treated as a neutral methodological step: model choice fundamentally shapes the ecological narratives we extract from the fossil record.

## 3.1 What our results demonstrate about model families

Across every structural metric we measured, model identity explained the majority of variation. PFIM-produced networks were consistently the most connected, while the ADBM and l-matrix produced sparser networks with tighter energetic constraints. Structural models (niche and random) fell between these extremes. These clusters reflect the conceptual differences between feasible, realised, and structural network representations. Importantly, these differences were not superficial. Pairwise interaction turnover revealed that models often disagreed not just on the number of links but on who interacts with whom. Such discrepancies directly affect diet-based ecological questions and interpretations of trophic roles.

## 3.2 Consequences for interpreting paleoecological dynamics

The downstream effects of model choice were most evident when evaluating extinction dynamics. Models often recovered comparable high-level patterns (e.g., trait-driven extinction signals remained robust across models), but the specific ranking of extinction mechanisms varied. Node-level patterns were relatively stable because extinction scenarios based on intrinsic traits remove species in the same order regardless of network structure. However, link-level outcomes—particularly those concerning secondary extinctions, network collapse, and recovery trajectories—were highly model-dependent.

This means that conclusions about *how* an extinction unfolded, *which* interactions disappeared first, or *what* drove cascading losses are not simply properties of the fossil data but emerge from the assumptions embedded in the chosen model. Researchers therefore need to be explicit about the type of ecological signal they are trying to recover and select models accordingly.

## 3.3 Aligning ecological questions with model choice

Our findings support a simple but crucial principle: different ecological questions require different types of network representations. The assumption that all food-web models are interchangeable is not supported by our results.

Below is a conceptual summary (corresponding to a possible [Figure 6](#fig-guidelines)):

| **Ecological question** | **Recommended model type** | **Rationale** |
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| What *could* have eaten what? (feasible interactions; trophic potential) | Mechanistic (PFIM, trait-based, evolutionary-signal models) | Captures all trait-feasible links; appropriate for reconstructing dietary breadth or assessing potential niches. |
| What interactions were *likely realised*? | Theory-driven (ADBM, l-matrix) | Encodes foraging ecology and energetic constraints; provides ecologically plausible realised networks. |
| How do global structural properties vary? | Structural models (niche, random as baseline) | Useful for understanding generic patterns (connectance, trophic depth) without trait reliance. |
| How do traits influence dynamics (e.g., cascade sensitivity)? | Theory-driven models | Capture body-size scaling, energetic constraints, and trophic dependencies. |
| How robust are inferences to uncertainty? | Ensembles across multiple model families | Allows quantifying how conclusions depend on assumptions. |

## 3.4 Implications for the use of food webs in paleoecology

Our analysis underscores three important implications for the broader field:

1. **Interpretations of ancient food webs must explicitly acknowledge model assumptions:** Without this, differences in reconstructed networks may be mistakenly attributed to biological change rather than methodological artifacts.
2. **Comparisons across studies must be standardised by model family:** Comparing a metaweb from one study to a realised network from another risks generating misleading conclusions about ecological differences across space or time.
3. **Mechanistic paleo-specific models alone cannot capture the full spectrum of possible network archetypes:** Incorporating theory-driven models allows paleoecology to leverage decades of research on modern food-web structure and dynamics, broadening the range of ecological questions that can be asked.

## 3.5 Recommendations and best practices

To support consistent, transparent use of network reconstruction methods in paleoecology, we propose the following guidelines (which could be highlighted as a boxed summary):

1. **Start with the ecological question:**, then identify the network representation (feasible, realised, structural) best aligned with it.
2. **Use multiple models whenever possible:** to evaluate whether key conclusions are model-dependent.
3. **Report all assumptions explicitly:**, including body-size estimation methods, trait inference procedures, and parameter choices.
4. **Perform sensitivity analyses:**, particularly for size-based models and connectance assumptions.
5. **Avoid comparing networks built with different model families** unless explicitly testing model effects.
6. **Distinguish between node-level and link-level inference**, as they respond differently to model choice.

## 3.6 Concluding remarks

Our results reveal that network construction models differ far more than is commonly appreciated in paleoecology. Because food webs are increasingly used to infer ecological resilience, collapse dynamics, and responses to environmental change, it is crucial to recognise that these inferences are shaped as much by modelling decisions as by fossil data. By mapping model families to ecological questions and demonstrating how model assumptions influence inferred patterns, our study provides a framework for more transparent, robust, and question-driven reconstruction of paleo food webs.

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| Figure 6: TODO. |

# References

1. Kiessling, W. *et al.* (2019) [Addressing priority questions of conservation science with palaeontological data](https://doi.org/10.1098/rstb.2019.0222). *Philosophical Transactions of the Royal Society B: Biological Sciences* 374, 20190222

2. Dillon, E.M. *et al.* (2022) [What is conservation paleobiology? Tracking 20 years of research and development](https://doi.org/10.3389/fevo.2022.1031483). *Frontiers in Ecology and Evolution* 10

3. Thuiller, W. *et al.* (2024) [Navigating the integration of biotic interactions in biogeography](https://doi.org/10.1111/jbi.14734). *Journal of Biogeography* 51, 550–559

4. Dunhill, A.M. *et al.* (2024) [Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event](https://doi.org/10.1038/s41467-024-53000-2). *Nature Communications* 15, 8599

5. Hao, X. *et al.* (2025) [Global Projection of Terrestrial Vertebrate Food Webs Under Future Climate and Land-Use Changes](https://doi.org/10.1111/gcb.70061). *Global Change Biology* 31, e70061

6. Yeakel, J.D. *et al.* (2014) [Collapse of an ecological network in ancient egypt](https://doi.org/10.1073/pnas.1408471111). *PNAS* 111, 14472–14477

7. Morales-Castilla, I. *et al.* (2015) [Inferring biotic interactions from proxies](https://doi.org/10.1016/j.tree.2015.03.014). *Trends in Ecology & Evolution* 30, 347–356

8. Pichler, M. and Hartig, F. (2023) [Machine learning and deep learningA review for ecologists](https://doi.org/10.1111/2041-210X.14061). *Methods in Ecology and Evolution* 14, 994–1016

9. Strydom, T. *et al.* (2021) [A roadmap towards predicting species interaction networks (across space and time)](https://doi.org/10.1098/rstb.2021.0063). *Philosophical Transactions of the Royal Society B: Biological Sciences* 376, 20210063

10. Allesina, S. *et al.* (2008) [A general model for food web structure](https://doi.org/10.1126/science.1156269). *Science* 320, 658–661

11. Shaw, J.O. *et al.* (2024) [A framework for reconstructing ancient food webs using functional trait data](https://doi.org/10.1101/2024.01.30.578036)bioRxiv, 2024.01.30.578036

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

13. Fricke, E.C. *et al.* (2022) [Collapse of terrestrial mammal food webs since the Late Pleistocene](https://doi.org/10.1126/science.abn4012). *Science* 377, 1008–1011

14. Erdős, P. and Rényi, A. (1959) [On random graphs. i.](https://doi.org/10.5486/pmd.1959.6.3-4.12) *Publicationes Mathematicae Debrecen* 6, 290–297

15. Williams, R.J. and Martinez, N.D. (2008) [Success and its limits among structural models of complex food webs](https://doi.org/10.1111/j.1365-2656.2008.01362.x). *The Journal of Animal Ecology* 77, 512–519

16. Petchey, O.L. *et al.* (2008) [Size, foraging, and food web structure](https://doi.org/10.1073/pnas.0710672105). *Proceedings of the National Academy of Sciences* 105, 4191–4196

17. Schneider, F.D. *et al.* (2016) [Animal diversity and ecosystem functioning in dynamic food webs](https://doi.org/10.1038/ncomms12718). *Nature Communications* 7, 12718

18. Rohr, R. *et al.* (2010) [Modeling food webs: Exploring unexplained structure using latent traits.](https://doi.org/10.1086/653667) *The American Naturalist* 176, 170–177

19. Bambach, R.K. *et al.* (2007) [Autecology and the Filling of Ecospace: Key Metazoan Radiations](https://doi.org/10.1111/j.1475-4983.2006.00611.x). *Palaeontology* 50, 1–22

20. Williams, R.J. and Martinez, N.D. (2004) [Stabilization of chaotic and non-permanent food-web dynamics](https://doi.org/10.1140/epjb/e2004-00122-1). *The European Physical Journal B - Condensed Matter* 38, 297–303

21. Delmas, E. *et al.* (2018) Analysing ecological networks of species interactions. *Biological Reviews* DOI: [10.1111/brv.12433](https://doi.org/10.1111/brv.12433)

22. Milo, R. *et al.* (2002) [Network motifs: Simple building blocks of complex networks](https://doi.org/10.1126/science.298.5594.824). *Science* 298, 824–827

23. Stouffer, D.B. *et al.* (2007) [Evidence for the existence of a robust pattern of prey selection in food webs](https://doi.org/10.1098/rspb.2007.0571). *Proceedings of the Royal Society B: Biological Sciences* 274, 1931–1940

24. Williams, R.J. and Martinez, N.D. (2000) [Simple rules yield complex food webs](https://doi.org/10.1038/35004572). *Nature* 404, 180–183

25. Poisot, T. *et al.* (2012) [A comparative study of ecological specialization estimators](https://doi.org/10.1111/j.2041-210x.2011.00174.x). *Methods in Ecology and Evolution* 3, 537–544

26. Gupta, A. *et al.* (2022) [Simultaneously estimating food web connectance and structure with uncertainty](https://doi.org/10.1002/ece3.8643). *Ecology and Evolution* 12, e8643

27. Ings, T.C. *et al.* (2009) [Ecological networks–beyond food webs](https://doi.org/10.1111/j.1365-2656.2008.01460.x). *The Journal of Animal Ecology* 78, 253–269