Methods for Reconstructing Paleo Food Webs

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Abstract

Food webs represent the feeding relationships between species and can help infer ecosystem-level processes. Alongside the development of food web theory, methods for constructing food webs have been developed to infer species interactions when empirical data is lacking. Food web construction methods are diverse, each utilising different approaches to infer species interactions —such as the use of traits to infer mechanistic relationships vs using gut content as a proxy for species diets. These methods have distinct theories, mechanisms, and data requirements. In paleoecology, where direct evidence of feeding interactions are rare, food web construction methods are especially valuable and affords us the opportunity to make inferences about paleo communities beyond simply a record of species composition. However, the limitations of paleontological data (e.g., information of species traits is limited to that which can be preserved) restrict which methods can reliably be used. By considering both ecological theory and the constraints of what can be derived from the fossil record, we identify the methods best suited for the construction of paleo food webs. Specifically, we focus on how these methods differ in the networks they produce and what these networks can reveal about species interactions. In doing so we hope to clarify the ecological nuances of network prediction and help prevent the accidental misuse or misinterpretation of paleo food webs.

There has been a growing interest in looking at community responses to environmental changes across events in deep time as a means to help understand current and future biodiversity changes [1,2]. The use of species interactions and networks to help us understand aspects of community composition has gained an interest in contemporary settings (eg [3] and ??) and so it is perhaps unsurprising that there has been a growing interest in using paleo food webs in a similar manner [\*e.g.,\* 4 looked at…,5 looked at…,6 looked at…]. However, one of the core challenges and limitations of being able to *use* food webs to answer ecological questions is the challenge of *creating* them [7], a challenge which is compounded when using paleo data as we are limited by that which has been preserved in the fossil record. The challenges with recording species interaction networks has driven the development of a large number of models and tools that can be used to infer either species interactions [see *e.g.,* 8,9,10 for broader reviews] or networks [see *e.g.,* 11 (it is one of the more complete review of methods IMO)], each with their own set of nuances and considerations [modify this to organically link to T4T, probably something along the lines of how different network construction approaches are encoding different processes]. Although the paleo food web space has seen its own development of tools that are more tailored to paleo date [\*e.g.,\* 12,13,14] these tools typically only predict the *feasibility* of pairwise interactions and thus the canonical paleo food web models are only occupying a subset of the ‘network construction’ space. Specifically within the paleo space there is a need for models that are able to generate networks that are structurally correct and do not simply represent a collation of pairwise interactions. It is thus useful to identify a broader suite of methods within the contemporary toolbox that can be appropriately scaled/tailored for the constraints of paleo communities (should we include [6] here as an *e.g.,* of how this is ‘possible’).

Here we: want to identify the differences between models that predict interactions, and models that predict network structure. Specifically we want to look at 1) the structural difference between all models (*i.e.,* do we see a difference in the distribution of links between networks that have the same number of nodes?) and 2) the identity of pairwise links between species pairs (*i.e.,* do different models differ in which links are present (or absent) between species pairs?) Additionally we want to establish if using networks that are constructed using different models will change the the downstream inferences that are made for this we use the work from [4] as a case study.

# 1. Contextualising the prediction of paleo webs within the contemporary toolbox

There is an evolving body of work that focuses on developing tools specifically for the task of predicting food webs. However as highlighted in Strydom (T4T in prep) it is important that we understand what assumptions are being embedded within the network as a result of the underlying philosophy which a model was built on. Broadly we can think about models that are nested within two different schools of thought (and thus methodological approaches, [Figure 1](#fig-concept)), models that focus on assessing the *mechanistic* feasibility of an interaction being able to occur between two species or models that are more closely married to specific bodies of ecological *theory* - such as niche theory or foraging ecology. Broadly speaking the difference between these two modelling approaches is that mechanistic models typically asses interactions at a pairwise level buy determining if an interaction is feasible between a species *pair* (extended *e.g.,* here about trait-based assumptions), whereas theoretical models typically use some set of assumptions to constrain the distribution of links at the *community* scale (extended *e.g.,* here probably niche model or DBM).

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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. |

Models that have specifically been developed in the paleo space tend to be mechanistic models that focus on using a trait-based approach to formalise feeding interactions (*e.g.,* [12]; [13]), are assembled by expert opinion (*e.g.* [15]) or make assumptions based on the evolutionary signals of interactions (*e.g.,* [14]). However, there is an argument that the theoretical models that have been developed in contemporary settings should hold even for paleo communities as we expect the fundamental ‘currencies of life’ to have remained constant - *e.g.,* the energetic constraints of foraging or foraging niches (is that the right way to phrase it, also I wonder is we can link to some other paleo work that showcases *e.g.,* niche/competition is something present among some of the earliest animals). Somehow close this out by going from we should be able to use contemporary models we need to think about the constraints that are typically placed on us by paleo data as well as the assumptions that some of these models might require us to make (*e.g.* the niche model makes some heavy assumptions by constraining the connectance - which itself is often used as a metric to understand changes or differences in network structure).

Additionally there are models that allow one to construct structurally sound networks that require very little input data. These are methods that are amenable to the data constraints that are prevalent in paleo communities in terms of both the completeness of fossil records as well as how the deeper in time we move the further away we might be moving from contemporary analogs. Secondly it should also be noted that different network construction approaches are encoding different processes (T4T, in prep) and there is value in showcasing how the networks construct models may differ.

Introduce here that it is thus important to understand that not all contemporary models may actually be suitable for paleo contexts as the assumptions that they make (or the data that they require) may actually introduce uncertainty/errors into the resulting network rendering them of little use. SImilarly not all paleo methods will be suitable for all paleo communities. As a simple example the framework developed by [14] uses phylogenetic relatedness as a way to infer interactions of Pleistocene mammals by looking at how their extant relatives interact. Although this approach is ecologically sound (phylogenetic relatedness is also used in other approaches *e.g.,* [16]) there is also an argument that the further back in evolutionary time we go (and the greater the phylogenetic distance between extant and extinct communities become) there is more uncertainty introduced by the phylogenetic tree than what is introduced by assuming that interactions will be phylogenetically conserved. On the other side of the coin it can be very challenging to determine traits from the fossil record and so it may be instead by more pragmatic to use models that that are completely agnostic to the identity of the species and are instead concerned with the network structure (*e.g.,* the niche model developed by [17]). Fundamentally this means that there is a trade off between the data that is available and the type of network one is interested in creating.

this section should be a box we can link to in the intro I think. We can also include some key ‘definitions’

# 2. Understanding how networks are different

It is important to be aware that networks can be configured in different ways depending on how the interactions are defined (Strydom, in prep) and that the configuration of the desired network should be informed by the research question [18].

Think about the axes - trait-based/mechanistic model (metawebs) and then we have the statistical/theoretical models (which have their own mini axis of regression vs full theory models… - see also [Figure 1](#fig-concept)). Basically we have metawebs (which represent *potential* interactions, mechanistic networks), realised networks (which represent the subset of potential that are realised as a result of community and environmental context, theory networks), and structural networks (species agnostic networks that are structurally informative, theory networks). Here also talk about the implications of these different networks types - different uses and capturing different processes. Specifically link this to models - *i.e.,* different models have been developed to construct a *specific* network representation.

#### 2.0.0.1 Key Definitions

* Metaweb:
* Realised Network:
* Structural Network:
* Feasible Interactions:
* Realised interactions:

# 3. Challenges specific to building paleo networks

Although there has been a push for the development of tools and methods that allow us to predict species interactions and networks [see *e.g.,* XXX for some reviews] they will not all be suitable for the prediction of paleo communities. This is primarily due to limitations that we are faced with in terms of the information that can be inferred from the fossil record (such as species traits abundances, and assemblages), which is needed as input data for the different models. The limited information available from the fossil record is compounded by the incomplete and biased preservation of species [REF], the spatial ambiguity of fossils found in a location [were species conserved *in situ* or were they there owing to geological processes; REF], and an increasing degree of ‘fuzziness’ the further one moves back in geological time [our understanding of both phylogenetic and functional trait space, REF]. Methodologically speaking some tools that ‘learn’ from contemporary communities (*e.g.,* [19], [20]) will become ‘worse’ the further one goes back in time since species then look very different from now but can still be useful for ‘recent’ communities (*e.g.,* [14]). This is not to say that it is impossible to construct paleo networks but rather identify that there are a subset of models that are probably not at all suitable for constructing paleo networks (*e.g.,* Null models, since there are fully driven by abundance), other methods will be better suited depending on the community of interest *e.g.,* for more contemporary communities that have modern analogs we can use methods rooted in phylogeny (*e.g.,* [14], [19]) or traits (*e.g.,* [20]), and then there is the third axis which is to think about which are the assumptions that are made and there trade off of that. This includes thinking about both assumptions you are making about the actual data *e.g.,* trying to extrapolate body size from fossil data but also assumptions across time *e.g.,* assuming modern trait-feeding modes are the same OR that assumptions about network structure will hold across deep time.

## 3.1 Approaches to food web prediction

Here we present six different models ([Table 1](#tbl-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 are ‘paleo friendly’.

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| Table 1: A summary of the different families of tools that can be used to generate paleo food webs.   | 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 | [21] | | niche | Networks are interval, species can be ordered on a ‘niche axis’ | richness, connectance | parameter assumptions, species agnostic | structural network | [17] | | 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 | [22] | | 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 | realised network | [23] | | 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) | metaweb | [12] | | body size ratio model | Interactions inferred using allometric rules (ratio of body sizes between predator and prey). :ogit 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 | metaweb?? | [24] | |

# 4. Case study: Toarcian mass extinction event

## 4.1 Dataset overview

### 4.1.1 Species occurrence

Here we use the fossil occurrence data over an interval extends from the upper Pliensbachian (~185 Ma) to the upper Toarcian (~175 Ma) of the Cleveland Basin [see 4 for a more comprehensive overview]. The data set consists of a subset of four broad time periods (pre-extinction, post-extinction, early recovery, and late recovery). The assemblages are treated as communities of interacting organisms. Something about the total number of taxa as well as numbers per a time period? Probbaly also make a comment that this is a ‘deep time’ community we are looking at.

### 4.1.2 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 [25].

### 4.1.3 Constructing networks

For each paleo community (time bin) we constructed **100** networks for each model (so 6 \* 100) networks. These networks were ‘simplified’ to removed any disconnected species. In total 2400 networks were constructed. When a quantitative measure of body size is needed (ADBM, bodymassratio, lmatrix) we drew a body mass for each species from a uniform distribution. The ranges were defined by the different size classes as discussed in insert cross ref to correct subsection here *e.g.,* a species classed as ‘very large’ would have a body mass drawn from . This was repeated for each run in order to add variation to the networks constructed, however the same body sizes were kept consistent for the relevant models (adbm, bodymassratio, l-matrix) *i.e.,* an ADBM and bodymassratio network from the same rep number would have used the same bodysizes. The PFIM networks were downsampled (see relevant section is S1). For both the random and niche model the desired connectance was randomly selected between the range 0.07 - 0.15 for each repetition but kep consistent for both models. For each network we calculated the properties listed in [Table 2](#tbl-properties)

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

Why is structure important and what can it tell us? Broadly when we talk about quantifying the structure of a network we are interesting in capturing some aspect of how the links are distributed between nodes, or alternatively about properties of the nodes (specifically in terms of the number of links coming in to (prey) or out of (predators) the node). What are some things we can learn/infer from network structure: energy flows and fluxes [REF], propagation of stress [REF], roles of species in the community [REF, think trophic levels]. Some closing statement about how thus there are different facets of network structure and the value of understanding generally how different models differ in terms of the structure that they recover - link to [Table 2](#tbl-properties) maybe.

In terms of wanting to asses and compare across the different models it is beneficial to approach this task by thinking about the different aspects of the network as well as interactions that are being predicted by the different models. It is perhaps beneficial to think of these across different ‘scales’ of organisation within the network, namely macro (the entire network), meso (smaller interacting units within the network), and micro (species-level attributes). Although there are a myriad of possible ways to ‘measure’ and analyse ecological networks [26] we do still lack a clear set of guidelines for assessing how well models recover network structure [11] and it is beneficial to use a small subset of metrics that can clearly be tied to broader aspects of network function or capturing a ecological process.

Here we used a Multivariate Analysis Of Variance (MANOVA) as it is able to capture model differences based on the combined information of the multiple structural network measures. Model defined as network structure values ~ model + time period and Linear Discriminant Analysis (LDA) to determine if different models produced networks with differing structure. **Need to report the relevant effect of time in driving observed differences**

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| Table 2: An informative caption about the different network properties   | Label | Definition | Scale | Reference (for maths), can make footnotes probs | | --- | --- | --- | --- | | Connectance | , where is the number of species and the number of links | Macro |  | | GenSD | Normalized standard deviation of generality of a species standardized by | Micro | [27] | | LinkSD | Normalized standard deviation of links (number of consumers plus resources per taxon) | Micro |  | | Richness | Number of nodes in the network | Macro |  | | TL | Prey-weighted trophic level averaged across taxa | Macro | [28] | | VulSD | Normalized standard deviation of vulnerability of a species standardized by | Micro | [27] | | Diameter | Diameter can also be measured as the average of the distances between each pair of nodes in the network | Macro | [26] | |  | Spectral radius is a a conceptual analog to nestedness (and more appropriate for unipartite networks). It is defined as the absolute value of the largest real part of the eigenvalues of the *undirected* adjacency matrix | Macro | [29] | | Complexity | SVD complexity of a network, defined as the Pielou entropy of its singular values | Macro | [10] | | S1 | Number of linear chains | Meso | [30]; [31] | | S2 | Number of omnivory motifs | Meso | [30]; [31] | | S4 | Number of apparent competition motifs | Meso | [30]; [31] | | S5 | Number of direct competition motifs | Meso | [30]; [31] | |

### 4.2.1 Macro network properties

**Connectance** [32] has been shown to be the feature of networks that underpin a series of other properties and function [33] and so it is perhaps the most important structural attribute for a model to be able to retrieve correctly. Additionally we consider the **complexity** of networks by calculating their SVD entropy (this gives us an estimate of the physical as opposed to behavioural complexity of networks; [10]), we could also look at the rank/rank deficiency of networks which (theoretically) represents the number fo unique interaction strategies in the network [10], which may be specifically interesting in terms of looking at pre and post extinction but also as a way to unpack ‘functional redundancy’ that some models may introduce.

### 4.2.2 Meso network properties

Motifs represent smaller subset of interactions between three species, and are argued to capture dynamics that are likely to be ecologically relevant [30,31]. Here we specifically look at the number of **linear chains**, **omnivory**, **apparent competition**, and **direct competition** motifs. In the broader context the ability of a model in being able to capture these smaller motifs will inform as to its suitability of use understanding the more dynamic component of network ecology.

### 4.2.3 Micro network properties

The number of interactions established (**generality**) or received (**vulnerability**) by each species [34], are (broadly) indicative of consumer-resource relationships and diet breadth of species [ref]. Although this is usually determined at the species level the standard deviation of the generality and vulnerability of species is often used when benchmarking predicted networks [*e.g.,* 17,22].

The **specificity** of species in a network is measured as a function of the proportion of resources they effectively use [35]

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| Figure 2: stuff… |

What is perhaps the most striking result in [Figure 2](#fig-structure) is that although there are clear structural differences between the different models the differences are not distinct between the broader model families but rather that there is a degree of overlap between them (specifically the log ratio, PFIM, and niche models). Although the log ratio and niche models are classified as different families they are built on similar ecological background and theory and so it is perhaps not surprising that these networks capture a similar structure (the same holds for the ADBM and l-matrix models). The fact that the random model occupies a completely different space is unsurprising as it has clearly been shown that networks are non-random in nature [REF] and so we expect random models to be constructing ecologically illogical networks. What is perhaps the most interesting result is that the PFIM model constructs networks that are very similar to those that are rooted in niche-based processes despite the model being more mechanistic in nature. Not sure how to articulate but this is cool because the is *something* in network structure constraints that is straddling the trait-niche space of ecology - but also see my next point about it being ‘correct’ is still up for debate

Although it is not possible to confidently identify the models that are predicting the *‘correct’* network structure the fact that a models from different families are able to recover similar structures is reassuring as it suggests that it might be possible to substitute one model for another if the input data is insufficient.

**TODO** Is it sound to try and unpack the ‘pairwise differences’ between the different structural metrics as well (or some) as this will allow us to say e.g. Niche and PFIM might recover the same connectance but differ in vulnerability.

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

In addition to wanting to measure network structure researchers may also be interested in understanding aspects about the diets and predators of *specific* species in a community. In this instance the interest should be in understanding how the pairwise links predicted between species pairs differ between models. Here we look ath the interaction turnover [35] both within and between the different models. This can be thought of as the equivalent of species turnover and tells us which interactions are ‘conserved’ (shared) across the networks but only between species pairs that are shared - *i.e.,* this turnover is only driven by interaction and not species turnover. Here we only compared networks that we constructed for the same period (as our interest is only in between model differences) and excluded the random and niche networks from consideration as these two models are essentially species agnostic.

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| Figure 3: stuff… % interaction shared is calculated as number shared interactions / ((number interactions left - shared interactions) + (number interactions right - shared interactions) + shared interactions). Additionally niche and random models are excluded as it is illogical since both of these models are fundamentally species agnostic |

In [Figure 3](#fig-beta_div) it is clear that some models share a large percentage of interactions *e.g.,* between ADBM and l-matrix networks and others share nothing *e.g.,* ADBM and PFIM networks. This result is unsurprising as the mechanisms that determine interactions in ADBM and l-matrix (a single trait (bodysize) + some ecological theory) is very different from the PFIM model that makes assumptions on a trait-based hierarchy.

The key takeaway that this needs to lead into is thinking about diet related questions and the model that is best suited to get you there. It makes sense to contextualise this in the feasible vs realised interaction spectrum - specifically that from a ‘philosophical’ basis if you are asking questions about possible diets of species then it makes sense to use models that fall firmly in the ‘feasible’ space *e.g.,* PFIM model or even something like the [14] model. How these results support that is that we can see the ADBM and PFIM are recovering (almost) totally different pairwise links.

## 4.4 Model choice changes the narrative

#### 4.4.0.1 Simulating Extinctions

Extinctions were simulated using different plausible mechanisms based on both species traits (size, motility), their position within the network (generality, vulnerability), as well as randomly. Each network was subjected to **50** extinction runs for each extinction mechanisms. The extinctions themselves were cascading in nature meaning that after the target species was removed all species that no longer had any prey were also deemed as extinct (secondary extinction), checking for secondary extinctions was then repeated until there were no longer any species without prey. This represents one extinction event and only then would the proceeding target species be removed from the network and cascading extinctions assessed again. Note that for extinction simulations which use the network position of a species to determine extinction order we follow the protocol from [36] and reassess the vulnerability/generality of each species after each extinction event to ‘redetermine’ the extinction order.

As we are using [4] as a case study we followed their appraoch when simulating extinctions as well as assessing which extinction mechanism results in a simulated network that most closely matches the real post extinciton network. Extinction simulations were only run on the pre extinction networks whereby species were removed until they reached the ‘target richness’, which is the richness of the post extinction community. In order to determine which extinction mechnism creates a network most similar to the post extinction network we used the (get full name of score) TSS [37] to assess how different the pairwise interactions are between ‘simulated’ and ‘real’ post extinction communities as well as looking at the absolute differences in network structure metrics.

**TODO** not sure if we also want to unpack/showcase robustness [38]

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| Figure 4: stuff… Recreation of the figure from Dunhill 2024. Note not 100% sold on the TSS and absolute mean calculations… |

### 4.4.1 Trends over time

**TODO** Not sure statistically speaking what the best way to unpack this is… 2-way ANOVA/ANCOVA explanation is valuable? There are intercept differences (*e.g.,* baseline average values are different; are the rankings among all three response variables the same?) and there are shape differences/similarities (*e.g.,* motifs are all the same shape but Co and Gen show some among model differences in pattern.)

Visual take-away seems to suggest that we see that the values (intercepts) of the different summary statistics are different but (broadly) they are capturing the same trends. This might suggest that although we observe differences in structure ([Figure 2](#fig-structure)) the general patterns still remain the same. This is good news because it means that at least the models that we have used here tend to tell us the same general story - which is worth contextualising in the space of ‘right’ vs ‘wrong’ and as long as we are not fixated on the point value but rather on understanding the trends.

### 4.4.2 Inferred extinction drivers

Points of discussion one will be to point to the mean absolute distance and how generally the ADBM/l-matrix do really badly - high mean absolute value. And this maybe makes sense though because of how we specify extinction mechanisms (trait-based) and so it sets the body-size models are not ‘talking’ the same language. In terms of the TSS scores - not sure how we should unpack it. Individually by model family to see which model agrees with which appraoch and see if different mechanisms come out stronger? **TODO** still need to sanity check the TSS anyway…

# 5. Discussion (need a catchier heading)

I want this section to be more about contextualising model choice within the bigger research question discussion - i.e. mapping question and model choice more tightly…

Points to discuss:

* Guidlines - as a box? Can we give something concrete??
* How to we synthesise these results? As in should we give clear directives ot is it enough to do a bit more handwaving and have the bigger message be that model choice matters?

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