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.

# 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). Basically we have metawebs (which represent *potential* interactions), realised networks (which represent the subset of potential that are realised as a result of community and environmental context), and structural networks (species agnostic networks that are structurally informative). Here also talk about the implications of these different networks types - different uses and capturing different processes. Speciifcally link this to models - *i.e.,* different models have been developed to construct a *specific* network representation.

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…

Need to link to [18] here.

# 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 should take the time to go in and just articulate that there are nuance and differences in terms of predicting interactions vs predicting networks. Once it is finally on a preprint server we can obviously link to the T4T stuff…

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] | |

## 3.2 Structural models

### 3.2.1 Random model

The Erdős–Rényi random graph model [21] uniformly at random assigns an number of links to an number of nodes (species richness). From an ecological perspective this model assumes that the interactions between species occurs regardless of the identity of the species (*i.e.,* species have no agency) and links are randomly distributed throughout the network. This creates a food web that is as free as possible from biological structuring while maintaining the expected richness *(*) and connectance ()

We could theoretically use the other ‘null models’ BUT I feel like in the context of constructing a network for a given community the Erdős–Rényi is the better choice than the other models that (IMO) are more suited to hypothesis testing e.g. do observed networks differ from the null network… Whereas Erdős–Rényi really is just a case of here is a truly random network with the specified number of links and nodes and anyway one of the Null models is a derivative of Erdős–Rényi if I remember correctly.

### 3.2.2 Niche model

The niche model [25] introduces the idea that species interactions are based on the ‘feeding niche’ of a species. Broadly, all species are randomly assigned a ‘feeding niche’ range and all species that fall in this range can be consumed by that species (thereby allowing for cannibalism). The niche of each species is randomly assigned and the range of each species’ niche is (in part) constrained by the specified connectance () of the network. The niche model has also been modified, although it appears that adding to the ‘complexity’ of the niche model does not improve on its ability to generate a more ecologically ‘correct’ network [17].

Each of species assigned a ‘niche value’ parameter drawn uniformly from the interval [0,1]. Species consumes all species falling in a range () that is placed by uniformly drawing the center of the range () from The size of is assigned by using a beta function to randomly draw values from [0,1] whose expected value is and then multiplying that value by to obtain the desired .

### 3.2.3 Allometric diet breadth model

The Allometric diet breadth model (ADBM; [22]) is rooted in feeding theory and allocates the links between species based on energetics, which predicts the diet of a consumer based on energy intake. This means that the model is focused on predicting not only the number of links in a network but also the arrangement of these links based on the diet breadth of a species, where the diet () is defined as follows:

where is the handling time, which is the product of the attack rate and resource density , is the energy content of the resource and is the ratio handling time, with the relationship being dependent on the ratio of predator and prey bodymass as follows:

or

Refer to [22] for more details as to how these different terms are parametrised.

### 3.2.4 L matrix

For now we can link to the ATNr package [26] until I can find a more suitable manuscript that breaks down this construction method. [23] Interactions are determined by allometric rules (ratio of consumer () and resource () body sizes) and a Ricker function as defined by and and returns The probability of a link () existing between a consumer and resource, and is defined as follows:

where

It is also possible to apply a threshold value to , whereby any probabilities below that threshold are set to zero.

## 3.3 Interaction predictions

### 3.3.1 Paleo food web inference model

The Paleo food web inference model (PFIM; [12]) uses a series of rules for a set of trait categories (such as habitat and body size) to determine if an interaction can feasibly occur between a species pair. If all conditions are met for the different rule classes then an interaction is deemed to be feasible. The original work put forward in [12] also includes a ‘downsampling’ step developed by [13] that uses a power law, defined by the link distribution, to ‘prune’ down some of the links. It is worth mentioning that this approach is similar to that developed by [27] with the exception that [12] does not specifically bin species into guilds, and so we choose to use the method developed by [12] since both approaches should produce extremely similar networks as they are built on the same underlying philosophy.

### 3.3.2 Body size ratio model

The body size ratio model [24] determines the probability of feeding interactions occurring between species by using the ratio between the consumer () and resource () body sizes. In order to represent the predator-prey bodymass ratio as a ‘feeding niche’ the ratio is also modified by both a and distribution. The probability of a link existing between a consumer and resource (in its most basic form) is defined as follows:

where

The original latent-trait model developed by [24] also included an additional latent trait term however for simplicity we will use [Equation 1](#eq-bodymass) as per [6] . Based on [24] it is possible to estimate the parameters , , and using a GLM but we will use the parameters from [6], which was ‘trained’ on the Serengeti food web data and are as follows: = 1.41, = 3.75, and = 1.87.

# 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 [28].

### 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). 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)

### 4.1.4 Simulating Extinctions

## 4.2 Do different models recover different network structures?

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 [29] 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 ANOVA or 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.

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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 | [25] | | 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 | [30] | | VulSD | Normalized standard deviation of vulnerability of a species standardized by | Micro | [25] | | Diameter | Diameter can also be measured as the average of the distances between each pair of nodes in the network | Macro | [29] | |  | 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 | [31] | | Complexity | SVD complexity of a network, defined as the Pielou entropy of its singular values | Macro | [10] | | S1 | Number of linear chains | Meso | [32]; [33] | | S2 | Number of omnivory motifs | Meso | [32]; [33] | | S4 | Number of apparent competition motifs | Meso | [32]; [33] | | S5 | Number of direct competition motifs | Meso | [32]; [33] | |

### 4.2.1 Macro network properties

**Connectance** [34] has been shown to be the feature of networks that underpin a series of other properties and function [35] 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 [32,33]. 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 [36], 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 [37]

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| Figure 2: stuff… |

And we can discuss the results and implications here…

## 4.3 Assessing pairwise interaction differences

**Interaction turnover** [37] tells us which interactions are ‘conserved’ (shared) across the networks from the same period but constructed using different models.

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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 |

## 4.4 Assessing network inference

Here we will look at extinctions of the different paleo TSS [38]

### 4.4.1 Robustness

see [39]

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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… |

# Discussion

Blah blah blah

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