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 deep time events as a means to help understand current and future biodiversity changes [1,2]. Species interactions and and the resulting networks hav gained an interest in contemporary settings as a means to help us to understand aspects of community composition and biodiversity (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 effectively *use* food webs is the challenge of *creating* them [7], although this is a challenge within contemporary settings it is compounded in paleo contexts as we are dependant on the fossil record (and the inherent limitation it imposes) to infer interactions from. As a way to address the challenges with recording species interactions there has been 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]. Although there has been the development of models and tools that are specific for inferring paelo food webs [*e.g.,* 12,13,14], it should be noted that these models only occupy a subset of the broader family of approaches that are used to predict networks as they typically use only one mechanism for determining interactions (the feasibility of the interaction being able to occur). Being able to only construct one ‘type’ of network means that we are limited in the scope of questions that we can appropriately answer with those networks [see Strydom in prep; [15]]. However there is scope that models and tools that have been developed in contemporary settings have the potential to be used for paleo settings [*e.g.,* 6], which opens the door for researchers to ask a broader and more complete range of questions about community responses to environmental change.

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 paleo web prediction within the contemporary toolbox

Although there is an evolving body of work focused on the development of food web prediction tools it is important that we understand how the underlying philosophy on which a model was built will result in different assumptions being embedded within the network [Strydom in prep]. 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.

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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.* [16]) 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. Along with constructing different 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.

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.,* [17]) 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.

# 2. 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 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], which part of a species is preserved (part vs whole), the ambiguity of the ‘true’ community composition [were communities conserved *in situ* or were they there owing to geological processes?; REF], as well as the availability/accessibility of different rock layers (and thus the completeness of data we might have for a specific era in time). Additionally there is an increasing degree of ‘fuzziness’ around the ecology and life histories of species the further one moves back in geological time [REF]. This is not to say that because we have imperfect data we should not be attempting to construct paleo food webs but rather that we need to be aware of what the uncertainties are and how these might impact the assumptions that we need to make when constructing a network (as well as how this will intersect with the intended end use of the network). This will allow us to best identify an approach that minimises the assumption and potential uncertainties within the data while still constructing a suitable network. 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.

## 2.1 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 | [18] | | niche | Networks are interval, species can be ordered on a ‘niche axis’ | richness, connectance | parameter assumptions, species agnostic | structural network | [19] | | 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 | [20] | | 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 | [21] | | 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 | [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 | theoretical network | [22] | |

# 3. Case study: Toarcian mass extinction event

## 3.1 Dataset overview

### 3.1.1 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.

### 3.1.2 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 [23].

### 3.1.3 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 kept consistent for both models. For each network we calculated the properties listed in [Table 2](#tbl-properties)

## 3.2 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.

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| Table 2: Network properties used fo 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 | [24] | | Diameter | Diameter can also be measured as the average of the distances between each pair of nodes in the network | Macro | [25] | | Complexity | SVD complexity of a network, defined as the Pielou entropy of its singular values | Macro | [10] | | 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 | [26]; [27] | | S2 | Number of omnivory motifs, normalised | Meso | [26]; [27] | | S4 | Number of apparent competition motifs, normalised | Meso | [26]; [27] | | S5 | Number of direct competition motifs, normalised | Meso | [26]; [27] | | Generality | Normalized standard deviation of generality of a species standardized by | Micro | [28] | | Vulnerability | Normalized standard deviation of vulnerability of a species standardized by | Micro | [28] | |

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 [25] 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) to assess the differences between networks generated by different models based on the combined information of the multiple structural network measures. Model defined as network structure values ~ model + time period additionally we used a Linear Discriminant Analysis (LDA) to determine if different models produced networks with differing structure. In order to do the MANOVA and LDA we had to create within model variation for the different networks, with the exception of the PFIM model all models have some inherent variation. In order to generate variation within the PFIM metawebs we applied a *minimal* degree of downsampling following the protocol described in [ROOPNARINE]. This downsampling approach uses a power law distribution to essentially ‘prune’ links from the most generalist species (See SUPP MATT for a more detailed overview).

**Need to report the relevant effect of time in driving observed differences???**

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| Figure 2: Linear Discriminant Analysis using thirteen different metrics of network structure. The colours represent the different models. The black points represent the predicted metaweb co-ordinates for the four different time periods. |

should I report some more ‘quantitative results’ i.e. a summary table…

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 there 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 required data are not available. Although it is still important that an effort is made to match the ‘best’ model/network to the question being asked.

It would be remiss to not think about the fact that niche models are supposed to work with trophic species not taxonomic species - I wonder if we should run the niche (and possibly random) models with trophic species as the starting richness and not the taxo richness…

**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.

## 3.3 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 [29] 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) + paramterisiation of links by ecological theory) is very different from the PFIM model that makes assumptions on a trait-based, mechanistic 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 and on a consceptual basis it means that we cannot use something like the ADBM to ask questions about diet breadth (note here this makes the assumption that something like the PFIM is truly aligning with dieat breadth, which I am inclined to say it is).

## 3.4 Model choice changes the narrative

#### 3.4.0.1 Simulating Extinctions

Extinctions were simulated using different plausible mechanisms based on 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 mechanism. 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 [30] and reassess the vulnerability/generality of each species after each extinction event to ‘redetermine’ the extinction order based on their position in the newly generated network.

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 [31] 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 [32]

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| Figure 4: stuff… Recreation of the figure from Dunhill 2024. I think it makes sense to split and divide into the below sections (depending on potential figure limitations of target journal) |

### 3.4.1 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.

### 3.4.2 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?

# 4. 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?? Something like [Figure 5](#fig-guidelines)
* 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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| Figure 5: TODO. |

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