

Methods for Reconstructing Paleo Food Webs

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Abstract: TODO.

Keywords: food web, network construction

₁ **1 Why build paleo food webs?**

- ₂ • Because its interesting?
- ₃ • Value in using hindcasting to aid in forecasting. *e.g.*, the Toarcian ms (Dunhill et al., 2024) shows how
- ₄ we can use these paleo communities to understand trophic-level responses to extinctions.

₅ **2 How do we do it?**

- ₆ • There is an evolving body of work that focuses on developing tools specifically for the task of predicting
- ₇ food webs.
- ₈ • There are a handful that have been developed specifically in the context of paleo settings *e.g.*, TODO
- ₉ but we can also talk about those that might have been developed/tested in contemporary settings but
- ₁₀ still have applicability in paleo ones.
- ₁₁ • Different underlying theory though
- ₁₂ – Focus here on the idea of different ‘currencies’ but also aggregations - energy vs compatibility.
- ₁₃ • Insert brief overview of the different methods as they pertain to approach (so the T4T triangle)
- ₁₄ • Challenges we face (even in contemporary settings)?
- ₁₅ – keep high level - I think the argument here should fall more in the data trade offs...

₁₆ **3 Understanding how networks are different**

₁₇ It is important to be aware that networks can be configured in different ways depending on how the inter-

₁₈ actions are defined (Strydom, in prep). Basically we have metawebs, which represent *potential* interactions,

₁₉ and realised networks, which represent the subset of potential that are realised as a result of community and

₂₀ environmental context.

₂₁ **4 Challenges specific to paleo communities/networks**

₂₂ Although there are a suite of tools and methods that have been developed to predict species interactions and

₂₃ networks they will not all be suitable for the prediction of paleo communities. Some of these include the fact

₂₄ that the fossil record is incomplete/preservation is biased [REF] which means that we have an incomplete

₂₅ picture of the entire community. Fossils are 2D and only represent specific ‘parts’ of an individual (hard and

²⁶ bone-y bits), this means we don't have a complete picture of the physical traits of species *e.g.*, no body mass
²⁷ (but yes size), behaviours, or ability to construct well resolved phylogenetic trees the deeper we go back in
²⁸ time. Also owing to the patchy nature of fossils one often has to aggregate over large spatial scales, and also
²⁹ fossils are preserved in 2D so no *real* idea of spatial arrangements, compounded that fossils aren't necessarily
³⁰ conserved/found 'in situ' but can be moved (*e.g.*, alluvial deposits). Methodologically speaking some tools
³¹ that 'learn' from contemporary communities (*e.g.*, Strydom et al. (2023), Caron et al. (2022)) will become
³² 'worse' the further one goes back in time since species then look very different from now but can still be
³³ useful for 'recent' communities (*e.g.*, Fricke et al. (2022)). Something about the intersectionality of the data
³⁴ we don't have for paleo communities and the data we need for some of the different modelling approaches.

³⁵ 5 Dataset Overview

- ³⁶ • Species
³⁷ • Time/space
³⁸ • And probably some other paleo things that will be relevant...

³⁹ 6 Methods

⁴⁰ 6.1 Models

Table 1: A summary of the different families of tools that can be used to generate paleo food webs.

Model	Predicts	Notes
Allometric diet breadth model	Realised network	
Body size ratio model	Metaweb (?)	
Niche model	Structural network	Is not species specific - cannot apply species metadata
Paleo food web inference model	Realised network (if downsampling)	

41 **6.1.1 Paleo food web inference model**

42 The Paleo food web inference model (PFIM; Shaw et al. (2024)) uses a series of rules for a set of trait
43 categories (such as habitat and body size) to determine if an interaction can feasibly occur between a species
44 pair. If all conditions are met for the different rule classes then an interaction is deemed to be feasible. The
45 original work put forward in Shaw et al. (2024) also includes a ‘downsampling’ step developed by Roopnarine
46 (2006) that uses a power law, defined by the link distribution, to ‘prune’ down some of the links. It is worth
47 mentioning that this approach is similar to that developed by Roopnarine (2017) with the exception that
48 Shaw does not specifically bin species into guilds, and so we choose to use the method developed by Shaw
49 since both methods should produce extremely similar networks as they are built on the same underlying
50 philosophy.

51 **6.1.1.1 Defining organism ecologies, feeding interactions and trophic guilds**

52 This is currently verbatim from the Dunhill ms...

53 Modes of life were defined for each fossil species based on the ecological traits defined in the Bambach
54 ecospace model (Bambach et al., 2007). Ecological traits were assigned based on interpretations from the
55 published literature which are largely based on functional morphology and information from extant relatives.
56 Information on the body size of each species was also recorded by summarising mean specimen sizes from the
57 section into a categorical classification. The following ecological characteristics were recorded for each fossil
58 species; motility (fast, slow, facultative, non-motile), tiering (pelagic, erect, surficial, semi-infaunal, shallow
59 infaunal, deep infaunal), feeding (predator, suspension feeder, deposit feeder, mining, grazer), and size:
60 gigantic (>500 mm), very large (>300–500 mm), large (>100–300 mm), medium (>50–100 mm), small (>10–
61 50 mm), tiny (10 mm). Size categories are defined by the longest axis of the fossil, estimates of tracemaker
62 size from trace fossils based on literature accounts, or by extrapolating the total length for belemnites from
63 the preserved guard using established approaches^{78,79}.

64 **6.1.2 Allometric diet breadth model**

65 The Allometric diet breadth model (ADBM; Petchey et al. (2008)) is rooted in feeding theory and allocates
66 the links between species based on energetics, which predicts the diet of a consumer based on energy intake.
67 This means that the model is focused on predicting not only the number of links in a network but also the
68 arrangement of these links based on the diet breadth of a species, where the diet (K) is defined as follows:

$$K = \frac{\sum_{i=1}^k \lambda_{ij} E_i}{1 + \sum_{i=1}^k \lambda_{ij} H_{ij}} \quad (1)$$

69 where λ_{ij} is the handling time, which is the product of the attack rate A_i and resource density N_i , E_i is the
 70 energy content of the resource and H_{ij} is the ratio handling time, with the relationship being dependent on
 71 the ratio of predator and prey body mass as follows:

$$H_{ij} = \frac{h}{b - \frac{M_i}{M_j}} \text{ if } \frac{M_i}{M_j} < b$$

72 or

$$H_{ij} = \infty \geq b$$

73 Refer to Petchey et al. (2008) for more details as to how these different terms are parametrised.

74 6.1.3 Body size ratio model

75 The body size ratio model (Rohr et al., 2010) determines feeding interactions using the ratio between consumer
 76 and resource body sizes - which supposedly stems from niche theory (still trying to reconcile that myself).
 77 The probability of a link existing between a consumer and resource (in its most basic form) is defined as
 78 follows:

$$P_{ij} = \frac{p}{1 + p}$$

79 where

$$p = \exp[\alpha + \beta \log(\frac{M_i}{M_j}) + \gamma \log^2(\frac{M_i}{M_j})] \quad (2)$$

80 The original latent-trait model developed by Rohr et al. (2010) also included an additional latent trait term
 81 $v_i \delta f_j$ however for simplicity we will use Equation 2 as per Yeakel et al. (2014) Based on Rohr et al. (2010) it
 82 is possible to estimate the parameters α , δ , and γ using a GLM but we will use the parameters from Yeakel
 83 et al. (2014), which was ‘trained’ on the Serengeti food web data and are as follows: $\alpha = 1.41$, $\delta = 3.75$, and
 84 $\gamma = 1.87$.

85 **6.1.4 Niche model**

86 The niche model (Williams & Martinez, 2000) introduces the idea that species interactions are based on the
87 ‘feeding niche’ of a species. Broadly, all species are randomly assigned a ‘feeding niche’ range and all species
88 that fall in this range can be consumed by that species (thereby allowing for cannibalism). The niche of each
89 species is randomly assigned and the range of each species’ niche is (in part) constrained by the specified
90 connectance of the network. The niche model has also been modified, although it appears that adding to
91 the ‘complexity’ of the niche model does not improve on its ability to generate a more ecologically ‘correct’
92 network (Williams & Martinez, 2008).

93 **6.2 Assessing model performance**

- 94 • **Links:** to determine if the number of links are ‘correct’ we use *connectance*
- 95 • *Shape:* to determine if the ‘shape’ of the network is correct we are looking at the ratio of ‘top’:‘basal’
96 species (where ‘top’ species are those that have a vulnerability of 0 and ‘basal’ species have a generality
97 of 0) as well as the distance to base from one of the top species (this will represent the shortest path
98 but a large discrepancy between the real and predicted network would be indicative that the model is
99 not predicting a similar ‘shape’). This will allow us to see if the models construct tall ‘pencil’ vs flat
100 ‘pancake’ networks (Beckerman 2024, pers comms).
- 101 – A small (< 1) number will thus be indicative of a ‘bottom-heavy’ network and the opposite for
102 larger numbers
- 103 • **Structure:** to determine if we are capturing some higher level of ‘structure’ we are using SVD entropy
104 (Strydom et al., 2021)
- 105 • **Motifs:** We can extract the motifs (Milo et al., 2002; Stouffer et al., 2007), namely:
- 106 – S1: Number of linear chains
- 107 – S2: Number of omnivory motifs
- 108 – S4: Number of apparent competition motifs
- 109 – S5: Number of direct competition motifs

₁₁₀ **7 Results**

₁₁₁ **7.1 Comparing predicted networks**

₁₁₂ [Figure 1 about here.]

₁₁₃ **7.2 Comparing inference**

₁₁₄ **7.3 Extinctions**

₁₁₅ [Figure 2 about here.]

₁₁₆ [Figure 3 about here.]

₁₁₇ **References**

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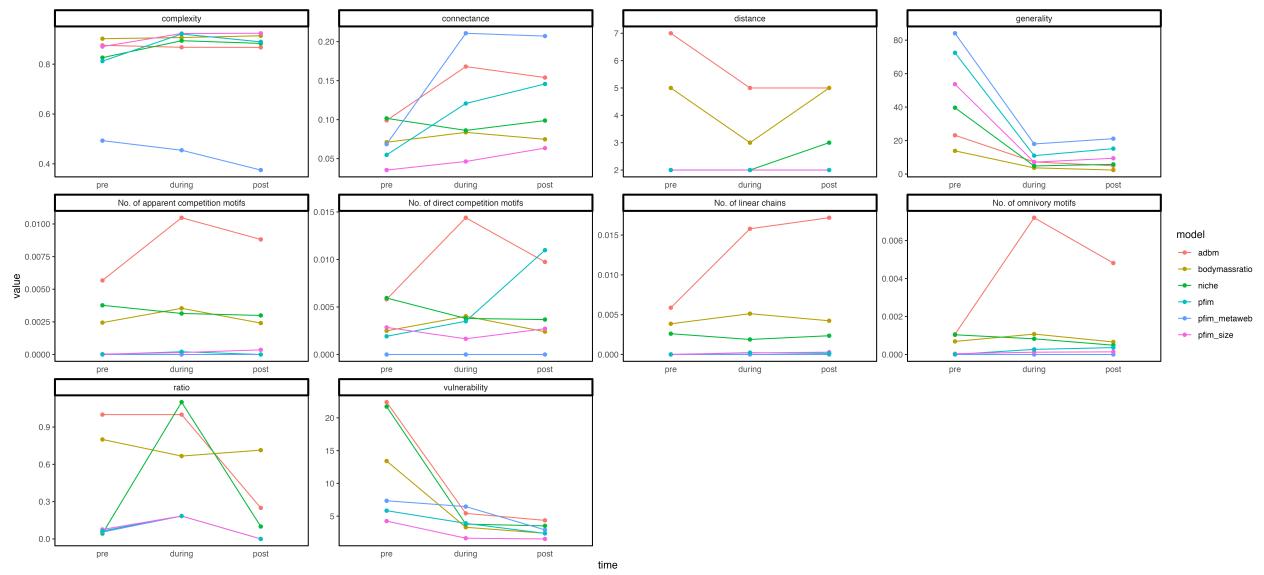


Figure 1: stuff

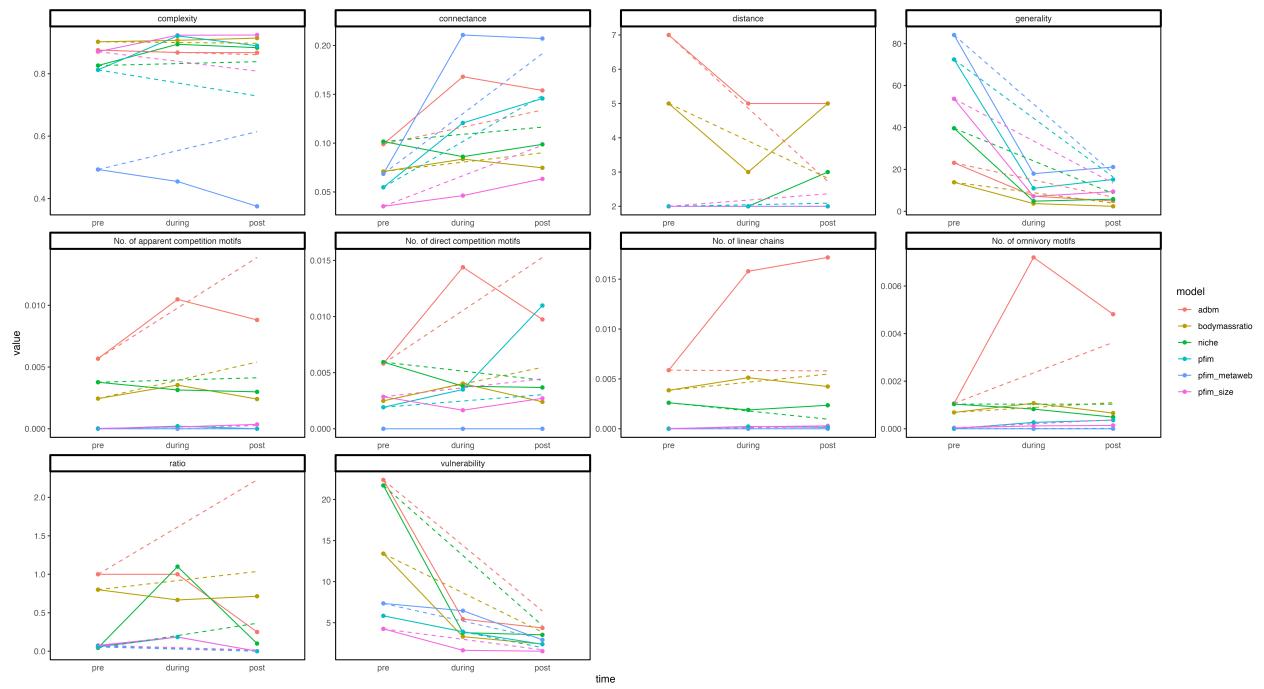


Figure 2: Dashed line indicates the (mean) extinction simulation results (post value, start values are those estimated by the relevant model)

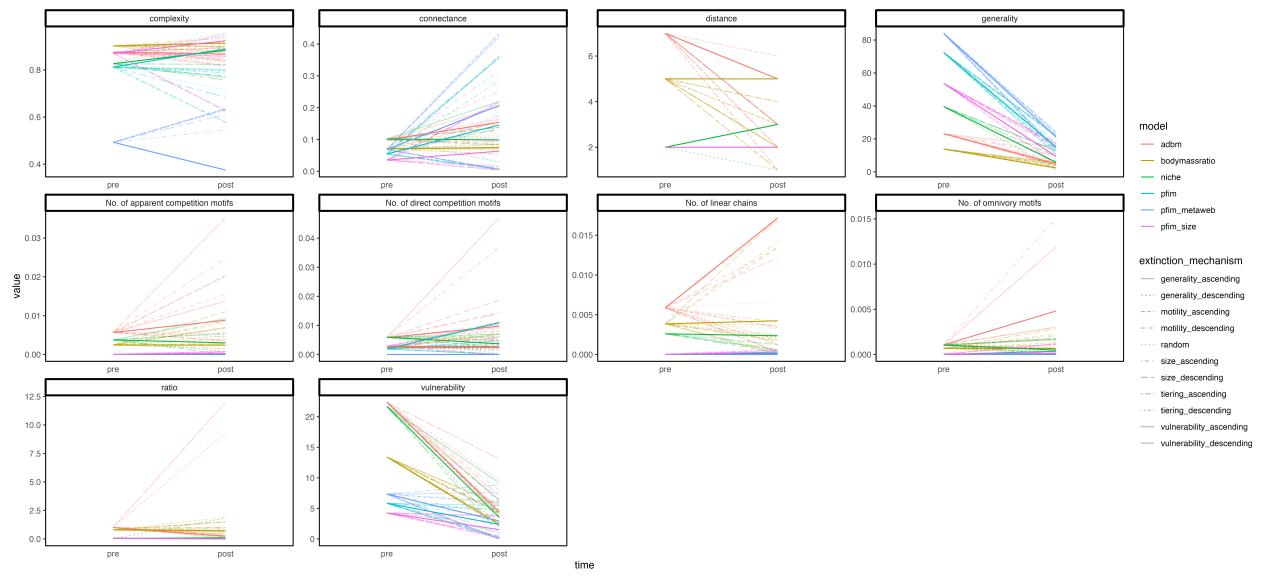


Figure 3: Dark line indicates ‘real’ extinction simulation results the lighter lines show each model individually, which is also denoted by the linetype