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.

1 Why build paleo food webs?

- Because its interesting? Point to works that showcase how we can learn form the past and inform on the current but possibly also the future

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

- Close out with the inherit challenge that we cannot observe paleo feeding interactions (barring rare instances, and often only for a limited subset of species) and so we are often using expert knowledge/mechanistic assumptions to infer links between species (*e.g.,* Dunne et al., 2014; Roopnarine, 2006).

2 How do we build paleo food webs?

- There is an evolving body of work that focuses on developing tools specifically for the task of predicting food webs.

- There are a handful that have been developed specifically in the context of paleo settings (Fricke et al., 2022; Roopnarine, 2006; *e.g.,* Shaw et al., 2024) but we can also talk about those that might have been developed/tested in contemporary settings but still have applicability in paleo ones.

- Different underlying theory though

  - Focus here on the idea of different 'currencies' but also aggregations - energy vs compatibility.

- Insert brief overview of the different methods as they pertain to approach (so the T4T triangle)

- Challenges we face (even in contemporary settings)?

  - keep high level - I think the argument here should fall more in the data trade offs...

3 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.

27 Speciifcally link this to models - *i.e.,* different models have been developed to construct a *specific* network

28 representation.

29 Think about the axes - trait-based/mechanistic model (metawebs) and then we have the statistical/theoretical

30 models (which have their own mini axis of regression vs full theory models...

31 Need to link to Gauzens et al. (2025) here.

4 Challenges specific to building paleo communities/networks

33 Although there has been a push for the development of tools and methods that allow us to predict species

34 interactions and networks [see *e.g.,* XXX for some reviews] they will not all be suitable for the prediction of

35 paleo communities. This is primarily due to limitations that we are faced with in terms of the information

36 that can be inferred from the fossil record (such as species traits abundances, and assemblages), which is

37 needed as input data for the different models. The limited information available from the fossil record is

38 compounded by the incomplete and biased preservation of species [REF], the spatial ambiguity of fossils

39 found in a location [were species conserved *in situ* or were they there owing to geological processes; REF],

40 and an increasing degree of 'fuzziness' the further one moves back in geological time [our understanding

41 of both phylogenetic and functional trait space, REF]. Methodologically speaking some tools that 'learn'

42 from contemporary communities (*e.g.,* Strydom et al. (2023), Caron et al. (2022)) will become 'worse' the

43 further one goes back in time since species then look very different from now but can still be useful for 'recent'

44 communities (*e.g.,* Fricke et al. (2022)). This is not to say that it is impossible to construct paleo networks

45 but rather identify that there are a subset of models that are probably not at all suitable for constructing

46 paleo networks (*e.g.,* Null models, since there are fully driven by abundance), other methods will be better

47 suited depending on the community of interest *e.g.,* for more contemporary communities that have modern

48 analogs we can use methods rooted in phylogeny (*e.g.,* Fricke et al. (2022), Strydom et al. (2023)) or traits

49 (*e.g.,* Caron et al. (2022)), and then there is the third axis which is to think about which are the assumptions

50 that are made and there trade off of that. This includes thinking about both assumptions you are making

51 about the actual data *e.g.,* trying to extrapolate body size from fossil data but also assumptions across time

52 *e.g.,* assuming modern trait-feeding modes are the same OR that assumptions about network structure will

53 hold across deep time.

5 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) 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'.

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	Erdős & Rényi (1959)
niche	Networks are interval, species can be ordered on a 'niche axis'	richness, connectance	parameter assumptions, species agnostic	structural network	Williams & Martinez (2008)
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	Petchey et al. (2008)

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Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference
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	Schneider et al. (2016)
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	Shaw et al. (2024)

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference
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??	Rohr et al. (2010)

5.1 Structural models

5.1.1 Random model

The Erdős–Rényi random graph model (Erdős & Rényi, 1959) uniformly at random assigns an L number of links to an S 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 *(S)* and connectance (L/S^2)

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.

5.1.2 Niche model

The niche model (Williams & Martinez, 2000) 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 (Co) 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 (Williams & Martinez, 2008).

Each of S species assigned a 'niche value' parameter n_i drawn uniformly from the interval [0,1]. Species i consumes all species falling in a range (r_i) that is placed by uniformly drawing the center of the range (c_i) from $[\frac{r_i}{2}, n_i]$ The size of r_i is assigned by using a beta function to randomly draw values from [0,1] whose expected value is $2 \times Co$ and then multiplying that value by n_i to obtain the desired Co.

5.1.3 Allometric diet breadth model

The Allometric diet breadth model (ADBM; Petchey et al. (2008)) 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 (K) is defined as follows:

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

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 energy content of the resource and H_{ij} is the ratio handling time, with the relationship being dependent on the ratio of predator and prey bodymass as follows:

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

or

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

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

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5.1.4 L matrix

For now we can link to the ATNr package (Gauzens et al., 2023) until I can find a more suitable manuscript that breaks down this construction method. Schneider et al. (2016) Interactions are determined by allometric rules (ratio of consumer (M_i) and resource (M_j) body sizes) and a Ricker function as defined by R_{opt} and γ and returns The probability of a link (P_{ij}) existing between a consumer and resource, and is defined as follows:

$$P_{ij} = (L \times \exp(1 - L))^{\gamma}$$

where

$$L = \frac{M_i}{M_j \times R_{opt}}$$

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

5.2 Interaction predictions

5.2.1 Paleo food web inference model

The Paleo food web inference model (PFIM; Shaw et al. (2024)) 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 Shaw et al. (2024) also includes a 'downsampling' step developed by Roopnarine (2006) 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 Roopnarine (2017) with the exception that Shaw et al. (2024) does not specifically bin species into guilds, and so we choose to use the method developed by Shaw et al. (2024) since both approaches should produce extremely similar networks as they are built on the same underlying philosophy.

5.2.2 Body size ratio model

The body size ratio model (Rohr et al., 2010) determines the probability of feeding interactions occurring between species by using the ratio between the consumer (M_i) and resource (M_j) body sizes. In order to represent the predator-prey bodymass ratio as a 'feeding niche' the ratio is also modified by both a β and γ

distribution. The probability of a link existing between a consumer and resource (in its most basic form) is defined as follows:

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

where

$$p = exp[\alpha + \beta log(\frac{M_i}{M_j}) + \gamma log^2(\frac{M_i}{M_j})] \tag{1}$$

The original latent-trait model developed by Rohr et al. (2010) also included an additional latent trait term $v_i \delta f_j$ however for simplicity we will use Equation 1 as per Yeakel et al. (2014) . Based on Rohr et al. (2010) it is possible to estimate the parameters α, δ, and γ using a GLM but we will use the parameters from Yeakel et al. (2014), which was 'trained' on the Serengeti food web data and are as follows: $\alpha = 1.41$, $\delta = 3.75$, and $\gamma = 1.87$.

6   Aims...

Here we do this because it lets us unpack the nuances of what the different network representation. Firstly we want ot identify the differences between models that predict interactions (and thus metawebs), 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 by repeating the work done by Dunhill et al. (2024).

7   Methods

7.1   Dataset Overview

7.1.1   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 Dunhill et al., 2024 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.

7.1.2 Defining modes of life (traits)

We used the modes of life (traits) as identified in Dunhill et al. (2024), 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 (Bambach et al., 2007).

7.2 Assessing structural differences

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 (Delmas et al., 2018) we do still lack a clear set of guidelines for assessing how well models recover network structure (Allesina et al., 2008) 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.

Table 2: An informative caption about the different network properties

Label	Definition	Scale	Reference (for maths), can make footnotes probs
Connectance	L/S^2, where S is the number of species and L the number of links	Macro	

Label	Definition	Scale	Reference (for maths), can make footnotes probs
GenSD	Normalized standard deviation of generality of a species standardized by L/S	Micro	Williams & Martinez (2000)
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	Williams & Martinez (2004)
VulSD	Normalized standard deviation of vulnerability of a species standardized by L/S	Micro	Williams & Martinez (2000)
Diameter	Diameter can also be measured as the average of the distances between each pair of nodes in the network	Macro	Delmas et al. (2018)

Label	Definition	Scale	Reference (for maths), can make footnotes probs
ρ	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	Staniczenko et al. (2013)
Complexity	SVD complexity of a network, defined as the Pielou entropy of its singular values	Macro	Strydom, Dalla Riva, et al. (2021)
S1	Number of linear chains	Meso	Milo et al. (2002); Stouffer et al. (2007)
S2	Number of omnivory motifs	Meso	Milo et al. (2002); Stouffer et al. (2007)
S4	Number of apparent competition motifs	Meso	Milo et al. (2002); Stouffer et al. (2007)
S5	Number of direct competition motifs	Meso	Milo et al. (2002); Stouffer et al. (2007)

7.2.1 Macro network properties

Connectance (Martinez, 1992) has been shown to be the feature of networks that underpin a series of other properties and function (Strydom, Catchen, et al., 2021) 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; Strydom, Dalla Riva, et al. (2021)), we could also look at the rank/rank deficiency of networks

which (theoretically) represents the number fo unique interaction strategies in the network (Strydom, Dalla Riva, et al., 2021), 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.

7.2.2 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 (Milo et al., 2002; Stouffer et al., 2007). 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.

7.2.3 Micro network properties

The number of interactions established (**generality**) or received (**vulnerability**) by each species (Schoener, 1989), 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 (Petchey et al., 2008; *e.g.,* Williams & Martinez, 2008).

The **specificity** of species in a network is measured as a function of the proportion of resources they effectively use (Poisot et al., 2012)

7.3 Assessing pairwise interaction differences

Interaction turnover (Poisot et al., 2012) tells us which interactions are 'conserved' (shared) across the networks from the same period but constructed using different models.

7.4 Assessing network inference

Here we will look at extinctions of the different paleo TSS Gupta et al. (2022)

7.4.1 Robustness

R_{50} see Jonsson et al. (2015)

7.5 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 $U(300, 500)$. 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

7.5.1 Simulating Extinctions

8 Results

8.1 Comparing predicted networks

8.1.1 Structure

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.

[Figure 1 about here.]

8.1.2 Interaction/species turnover

[Figure 2 about here.]

8.2 Comparing inference

[Figure 3 about here.]

References

Allesina, S., Alonso, D., & Pascual, M. (2008). A general model for food web structure. *Science*, *320*(5876), 658–661. https://doi.org/10.1126/science.1156269

Bambach, R. K., Bush, A. M., & Erwin, D. H. (2007). Autecology and the Filling of Ecospace: Key Metazoan Radiations. *Palaeontology*, *50*(1), 1–22. https://doi.org/10.1111/j.1475-4983.2006.00611.x

Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with trait-based interaction models. *Ecology Letters*, *25*(4), 889–899. https://doi.org/10.1111/ele.13966

Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Dalla Riva, G. V., Fortin, M.-J., Gravel, D., Guimarães, P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2018). Analysing ecological networks of species interactions. *Biological Reviews*, 112540. https://doi.org/10.1111/brv.12433

Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024). Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event. *Nature Communications*, *15*(1), 8599. https://doi.org/10.1038/s41467-024-53000-2

Dunne, J. A., Labandeira, C. C., & Williams, R. J. (2014). Highly resolved early eocene food webs show development of modern trophic structure after the end-cretaceous extinction. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782), 20133280. https://doi.org/10.1098/rspb.2013.3280

Erdős, P., & Rényi, A. (1959). On random graphs. i. *Publicationes Mathematicae Debrecen*, *6*(3-4), 290–297. https://doi.org/10.5486/pmd.1959.6.3-4.12

Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning, J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene. *Science*, *377*(6609), 1008–1011. https://doi.org/10.1126/science.abn4012

Gauzens, B., Brose, U., Delmas, E., & Berti, E. (2023). ATNr: Allometric Trophic Network models in R. *Methods in Ecology and Evolution*, *14*(11), 2766–2773. https://doi.org/10.1111/2041-210X.14212

Gauzens, B., Thouvenot, L., Srivastava, D. S., Kratina, P., Romero, G. Q., Berti, E., O'Gorman, E. J., González, A. L., Dézerald, O., Eisenhauer, N., Pires, M., Ryser, R., Farjalla, V. F., Rogy, P., Brose, U., Petermann, J. S., Geslin, B., & Hines, J. (2025). Tailoring interaction network types to answer different ecological questions. *Nature Reviews Biodiversity*, 1–10. https://doi.org/10.1038/s44358-025-00056-7

Gupta, A., Furrer, R., & Petchey, O. L. (2022). Simultaneously estimating food web connectance and structure with uncertainty. *Ecology and Evolution*, *12*(3), e8643. https://doi.org/10.1002/ece3.8643

Jonsson, T., Berg, S., Pimenov, A., Palmer, C., & Emmerson, M. (2015). The reliability of R50 as a measure of vulnerability of food webs to sequential species deletions. *Oikos*, *124*(4), 446–457. https://doi.org/10.1111/oik.01588

Martinez, N. D. (1992). Constant connectance in community food webs. *The American Naturalist*, *139*(6), 1208–1218. http://www.jstor.org/stable/2462337

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple building blocks of complex networks. *Science*, *298*(5594), 824–827. https://doi.org/10.1126/science.298.5594.824

Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences*, *105*(11), 4191–4196. https://doi.org/10.1073/pnas.0710672105

Poisot, T., Canard, E., Mouquet, N., & Hochberg, M. E. (2012). A comparative study of ecological specialization estimators. *Methods in Ecology and Evolution*, *3*(3), 537–544. https://doi.org/10.1111/j.2041-210x.2011.00174.x

Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring unexplained structure using latent traits. *The American Naturalist*, *176*(2), 170–177. https://doi.org/10.1086/653667

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

Roopnarine, P. D. (2017). *Ecological Modelling of Paleocommunity Food Webs* (pp. 201–226). University of Chicago Press.

Schneider, F. D., Brose, U., Rall, B. C., & Guill, C. (2016). Animal diversity and ecosystem functioning in dynamic food webs. *Nature Communications*, *7*(1), 12718. https://doi.org/10.1038/ncomms12718

Schoener, T. W. (1989). Food Webs From the Small to the Large: The Robert H. MacArthur Award Lecture. *Ecology*, *70*(6), 1559–1589. https://doi.org/10.2307/1938088

Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. https://doi.org/10.1101/2024.01.30.578036

Staniczenko, P. P. A., Kopp, J. C., & Allesina, S. (2013). The ghost of nestedness in ecological networks. *Nature Communications*, *4*(1), 1391. https://doi.org/10.1038/ncomms2422

Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1621), 1931–1940. https://doi.org/10.1098/rspb.2007.0571

Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer learning can help predict potential species interaction networks despite data limitations. *Methods in*

Ecology and Evolution, *14*(12), 2917–2930. https://doi.org/10.1111/2041-210X.14228

Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz, N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap towards predicting species interaction networks (across space and time). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1837), 20210063. https://doi.org/10.1098/rstb.2021.0063

Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD entropy reveals the high complexity of ecological networks. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.623141

Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, *404*(6774), 180–183. https://doi.org/10.1038/35004572

Williams, R. J., & Martinez, N. D. (2004). Stabilization of chaotic and non-permanent food-web dynamics. *The European Physical Journal B - Condensed Matter*, *38*(2), 297–303. https://doi.org/10.1140/epjb/e2004-00122-1

Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food webs. *The Journal of Animal Ecology*, *77*(3), 512–519. https://doi.org/10.1111/j.1365-2656.2008.01362.x

Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014). Collapse of an ecological network in ancient egypt. *PNAS*, *111*(40), 14472–14477. https://doi.org/10.1073/pnas.1408471111
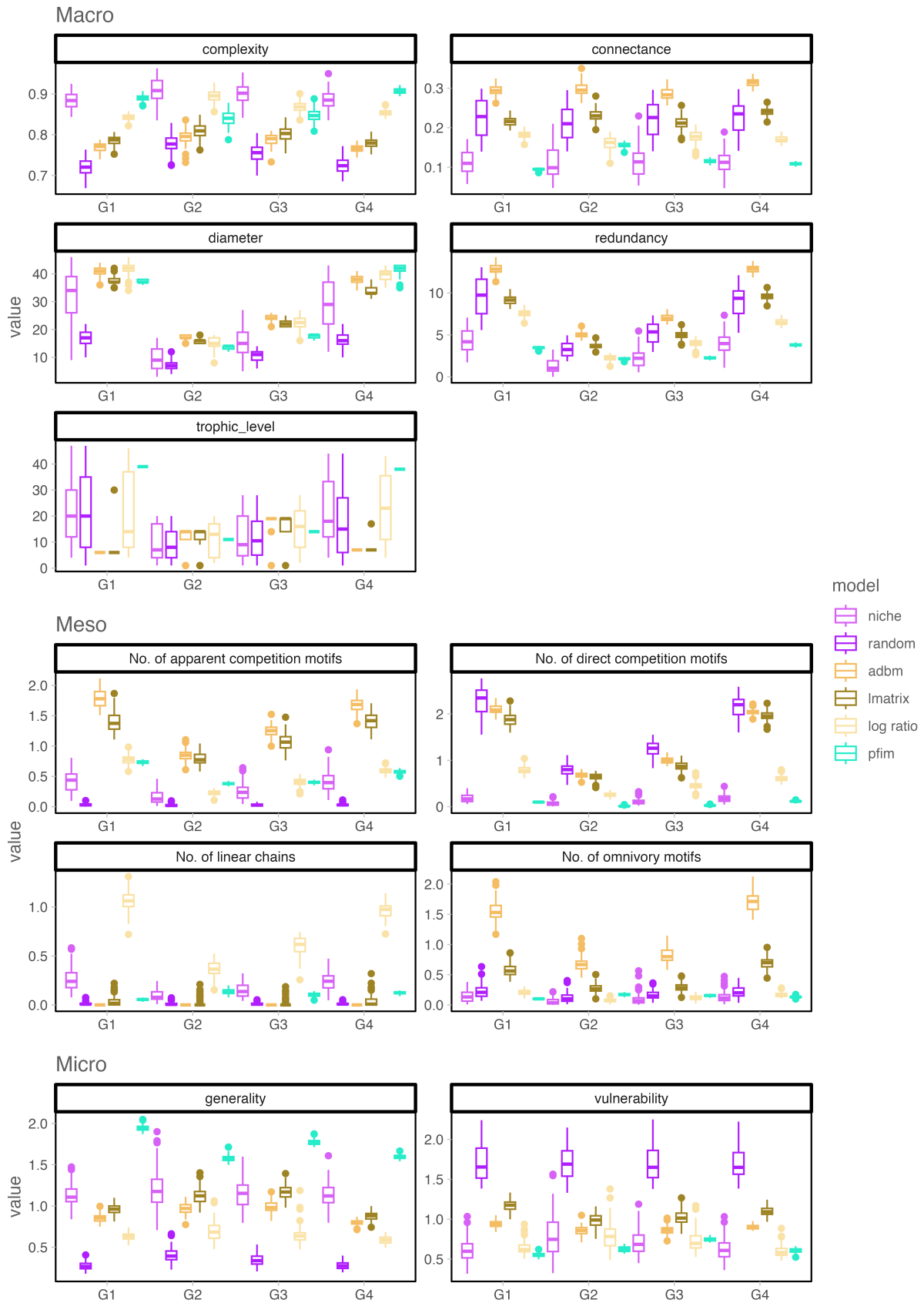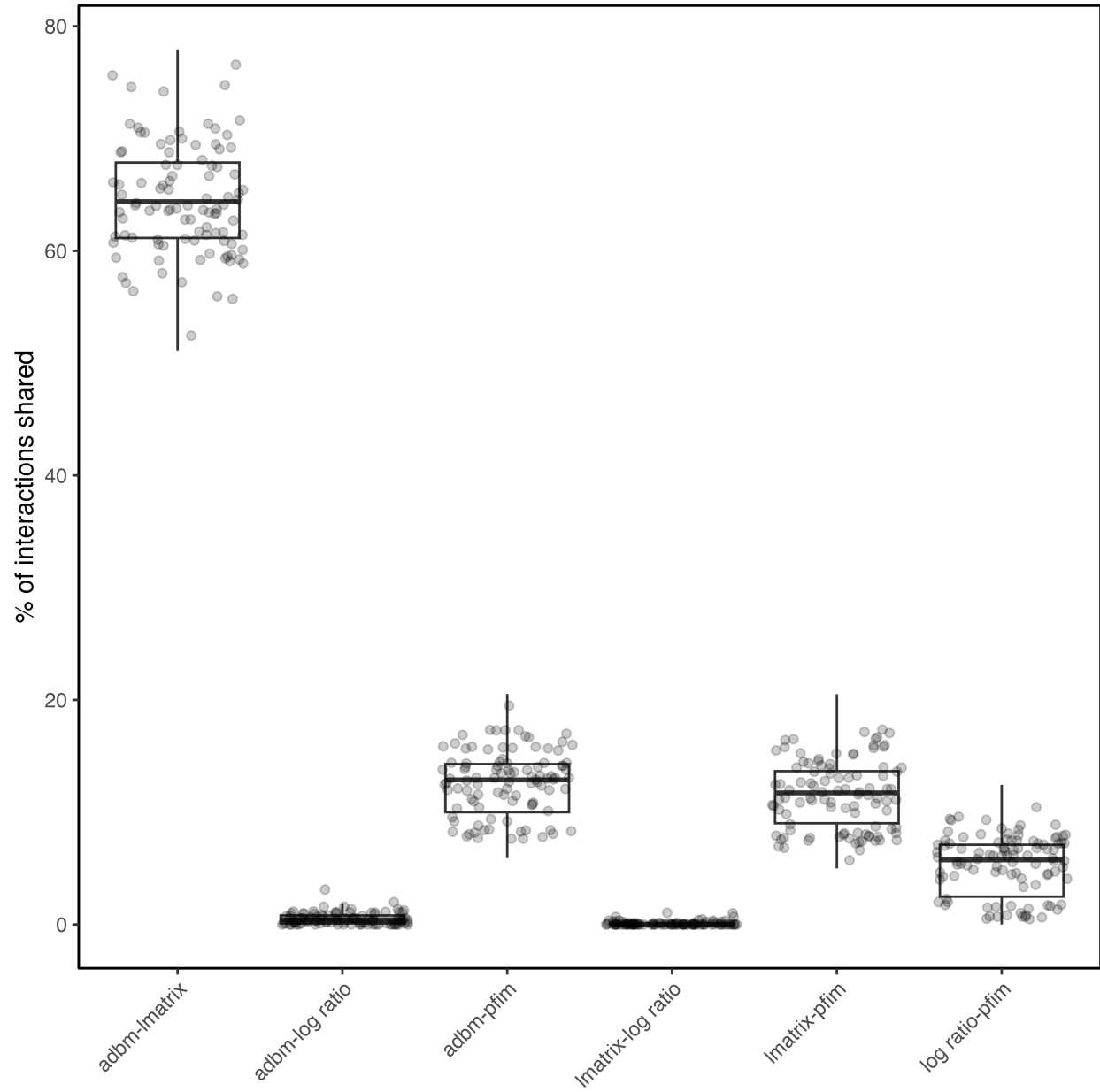
Figure 1: stuff...

Figure 2: 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
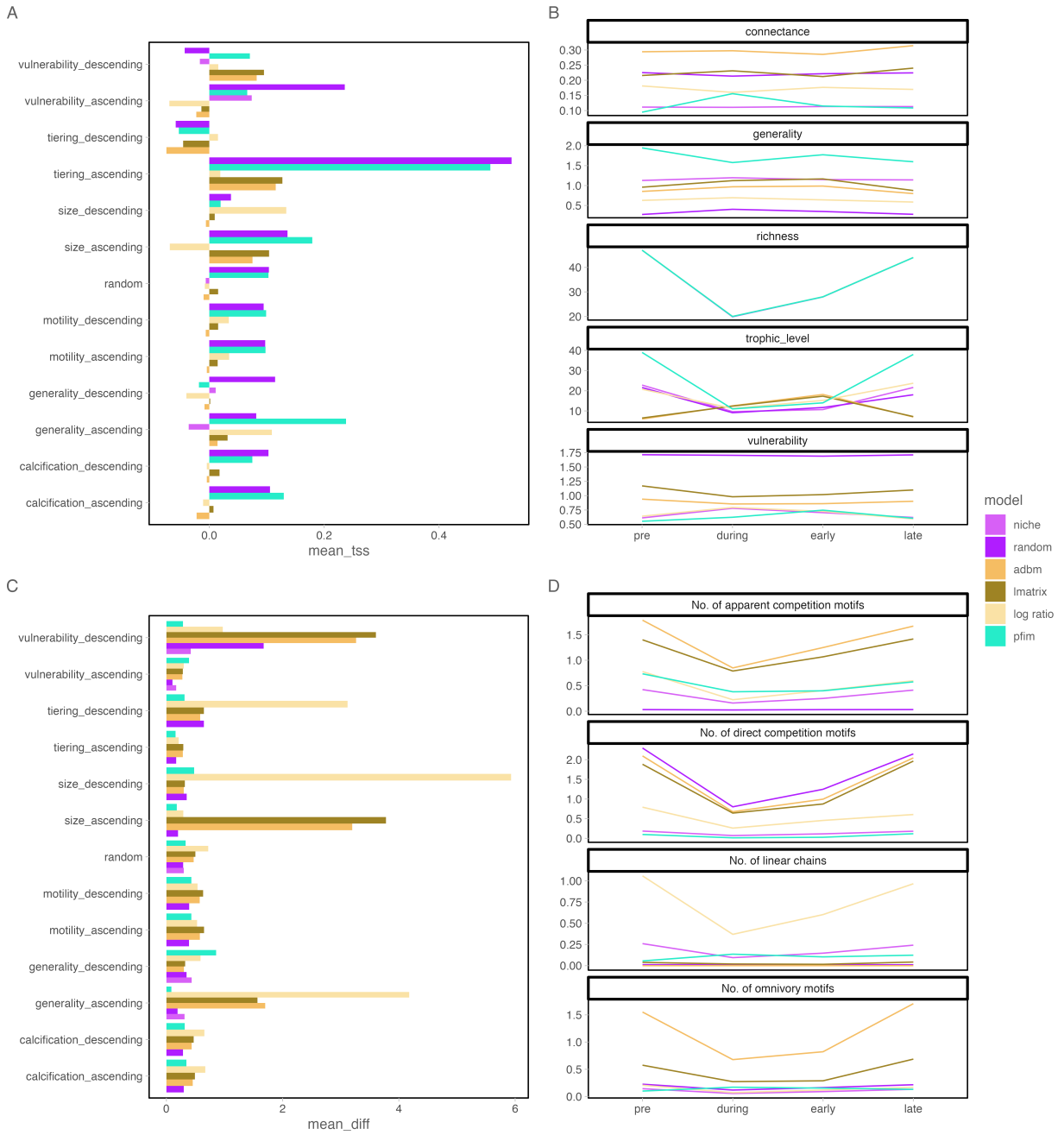
Figure 3: stuff... Recreation of the figure from Dunhill 2024. Note not 100% sold on the TSS and absolute mean calculations...