Methods for Reconstructing Paleo Food Webs

Tanya Strydom ¹; Andrew P. Beckerman ¹

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.

Keywords: food web, network construction

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.

6 2 How do we do it?

- 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 e.g., TODO 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

- 18 It is important to be aware that networks can be configured in different ways depending on how the interactions
- ¹⁹ are defined (Strydom, in prep). Basically we have metawebs (which represent *potential* interactions), realised
- 20 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.
- 23 Speciifcally link this to models i.e., different models have been developed to construct a specific network
- 24 representation.

12

16

25 4 Challenges specific to paleo communities/networks

Although there are a suite of tools and methods that have been developed to predict species interactions and networks they will not all be suitable for the prediction of paleo communities. Some of these include the fact that the fossil record is incomplete/preservation is biased [REF] which means that we have an incomplete picture of the entire community. Fossils are 2D and only represent specific 'parts' of an individual (hard and bone-y bits), this means we don't have a complete picture of the physical traits of species e.g., no body mass (but yes size), behaviours, or ability to construct well resolved phylogenetic trees the deeper we go back in time. Also owing to the patchy nature of fossils one often has to aggregate over large spatial scales, and also fossils are preserved in 2D so no real idea of spatial arrangements, compounded that fossils aren't necessarily conserved/found 'in situ' but can be moved (e.g., alluvial deposits). Methodologically speaking some tools that 'learn' from contemporary communities (e.g., Strydom et al. (2023), Caron et al. (2022)) 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., Fricke et al. (2022)). Something about the intersectionality of the data we don't have for paleo communities and the data we need for some of the different modelling approaches.

5 Interaction/food web prediction models/tools

- $_{40}$ Here we should take the time to go in and just articulate that there are nuance and differences in terms of
- 41 predicting interactions vs predicting networks. Once it is finally on a preprint server we can obviously link to
- the T4T stuff...
- 43 Here we present six different models (Table 1) that can be used to construct food webs for both this specific
- 44 community but are also broadly suited to paleo network prediction. These models span all facets of the
- 45 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	richness,	parameter	structural	Erdős & Rényi
	randomly	number of links	assumptions,	network	(1959)
	distributed		species agnostic		
	within a				
	network				

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference
niche	Networks are	richness,	parameter	structural	Williams &
	interval, species	connectance	assumptions,	network	Martinez (2008)
	can be ordered		species agnostic		
	on a 'niche axis'				
allometric diet	Interactions are	body mass,	does not	realised	Petchey et al.
breadth model	determined by	biomass	account for	network	(2008)
(ADBM)	energetic costs	(abundance)	forbidden links		
			in terms of trait		
			compatibility,		
			assumptions on		
			body size and		
			biomass		
			(abundance)		
			from fossil data		
l-matrix	Interactions	body mass,	does not	realised	Schneider et al.
	inferred using	number of	account for	network	(2016)
	allometric rules	producer	forbidden links		
	(ratio of body	species	in terms of trait		
	sizes between		compatibility,		
	predator and		assumptions on		
	prey)		body size from		
			fossil data,		
			assumptions as		
			to the number		
			of producer		
			species		

Model family	Assumptions	Data needs	'Limitation'	Network type	Key reference
paleo food web	Interactions can	feeding traits	Assumption	metaweb	Shaw et al.
inference model	be inferred by a	for taxa,	made as to the		(2024)
(PFIM)	mechanistic	mechanistic	feeding		
	framework/rela-	feeding rules	mechanisms,		
	tionships		need to		
			elucidate traits		
			from models		
			(although this		
			is a way smaller		
			issue)		
body size ratio	Interactions	body mass	does not	metaweb??	Rohr et al.
model	inferred using		account for		(2010)
	allometric rules		forbidden links		
	(ratio of body		in terms of		
	sizes between		evolutionary		
	predator and		compatibility,		
	prey)		assumptions on		
			body size from		
			fossil data		

5.1 Structural models

48 5.1.1 Random model

- $_{\rm 49}$ The Erdős–Rényi random graph model (Erdős & Rényi, 1959) uniformly at random assigns an L number of
- 50 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

59 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:

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

79 O1

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

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

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:

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

87 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.

₉₀ 5.2 Interaction predictions

91 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 does not specifically bin species into guilds, and so we choose to use the method developed by Shaw since both methods 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 feeding interactions using the ratio between consumer (M_i) and resource (M_j) body sizes - which supposedly stems from niche theory (still trying to reconcile that).

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

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

106 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 $\gamma = 1.87$.

112 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).

$_{\scriptscriptstyle 21}$ 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).It would be very sexy if we could get a figure that looks something like this together...

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

			Reference (for maths),	
			can make footnotes	
Label	Definition	Scale	probs	
Connectance	L/S^2 , where S is the number	Macro		
	of species and L the number			
	of links			
GenSD	Normalized standard	Micro	Williams & Martinez	
	deviation of generality of a		(2000)	
	species standardized by L/S			
LinkSD	Normalized standard	Micro		
	deviation of links (number of			
	consumers plus resources per			
	taxon)			
Richness	Number of nodes in the	Macro		
	network			
TL	Prey-weighted trophic level	Macro	Williams & Martinez	
	averaged across taxa		(2004)	
VulSD	Normalized standard	Micro	Williams & Martinez	
	deviation of vulnerability of a		(2000)	
	species standardized by L/S			
Diameter	Diameter can also be	Macro	Delmas et al. (2018)	
	measured as the average of			
	the distances between each			
	pair of nodes in the network			

Label	Definition	Scale	Reference (for maths), can make footnotes probs
$\overline{ ho}$	Spectral radius is a a	Macro	Staniczenko et al.
	conceptual analog to		(2013)
	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		
Complexity	SVD complexity of a network,	Macro	Strydom, Dalla Riva, et
	defined as the Pielou entropy		al. (2021)
	of its singular values		
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	Meso	Milo et al. (2002);
	competition motifs		Stouffer et al. (2007)
S5	Number of direct	Meso	Milo et al. (2002);
	competition motifs		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.

161 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)

169 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.

72 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)

5 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 to add variation to the networks constructed. For the PFIM networks were downsampled (see relevant section). For both the random and niche model the desired connectance was set to **0.1**. For each network we calculated the properties listed in Table 2

8 Results

8.1 Comparing predicted networks

8.1.1 Structure

188

191

[Figure 1 about here.]

9 8.1.2 Interaction/species turnover

190 8.2 Comparing inference

[Figure 2 about here.]

92 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.
- 200 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*
- 204 Communications, 15(1), 8599. https://doi.org/10.1038/s41467-024-53000-2
- 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.abn 4012
- Gauzens, B., Brose, U., Delmas, E., & Berti, E. (2023). ATNr: Allometric Trophic Network models in R.
- 211 Methods in Ecology and Evolution, 14(11), 2766–2773. https://doi.org/10.1111/2041-210X.14212
- ²¹² 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),
- 218 1208–1218. http://www.jstor.org/stable/2462337
- ²¹⁹ 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.
- 221 5594.824
- Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure.
- 223 Proceedings of the National Academy of Sciences, 105(11), 4191–4196. https://doi.org/10.1073/pnas.
- 224 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),
- 232 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
- 237 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
- 244 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),
- ²⁴⁶ 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
- 250 Ecology and Evolution, 14(12), 2917–2930. https://doi.org/10.1111/2041-210X.14228
- 251 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
- 254 Royal Society B: Biological Sciences, 376(1837), 20210063. https://doi.org/10.1098/rstb.2021.0063
- 255 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
- ²⁵⁷ 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-
- 261 00122-1
- ²⁶² 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

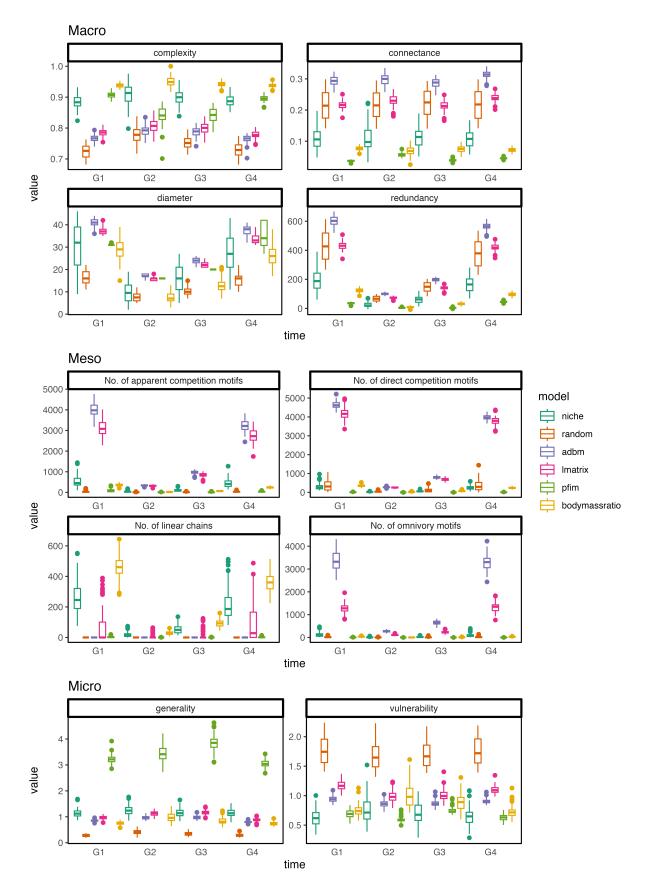


Figure 1: stuff... For display purposes the counts for the different motifs are \log transformed

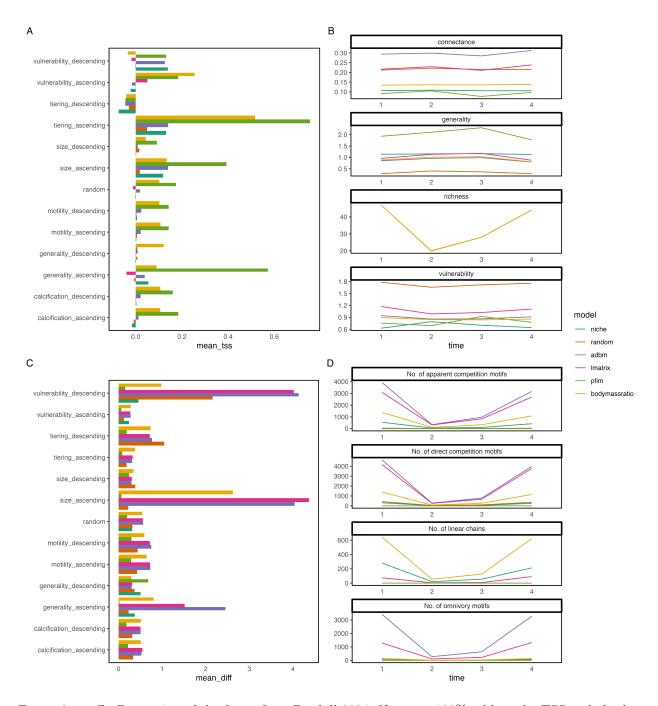


Figure 2: stuff... Recreation of the figure from Dunhill 2024. Note not 100% sold on the TSS and absolute mean calculations...