

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 **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 5.1 Species occurrence

37 Here we use the fossil occurrence data over an interval extends from the upper Pliensbachian (~185 Ma) to
38 the upper Toarcian (~175 Ma) of the Cleveland Basin (see Dunhill et al., 2024 for a more comprehensive
39 overview). The data set consists of a subset of four broad time periods, or assemblages, which are treated as
40 communities of interacting organisms; pre-extinction, post-extinction, early recovery, and late recovery.

41 5.2 Defining modes of life (traits)

42 We used the modes of life (traits) as identified in Dunhill et al. (2024), who defined the motility (fast, slow,
43 facultative, non-motile), tiering (pelagic, erect, surficial, semi-infaunal, shallow infaunal, deep infaunal),
44 feeding (predator, suspension feeder, deposit feeder, mining, grazer), and size: gigantic (>500 mm), very
45 large (>300–500 mm), large (>100–300 mm), medium (>50–100 mm), small (>10–50 mm), tiny (10 mm),
46 for each fossil species based on the ecological traits defined in the Bambach ecospace model (Bambach et al.,
47 2007). It would be very sexy if we could get a figure that looks something like this together...

48 6 Methods

49 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)	

50 6.1.1 Paleo food web inference model

51 The Paleo food web inference model (PFIM; Shaw et al. (2024)) uses a series of rules for a set of trait
 52 categories (such as habitat and body size) to determine if an interaction can feasibly occur between a species
 53 pair. If all conditions are met for the different rule classes then an interaction is deemed to be feasible. The
 54 original work put forward in Shaw et al. (2024) also includes a ‘downsampling’ step developed by Roopnarine
 55 (2006) that uses a power law, defined by the link distribution, to ‘prune’ down some of the links. It is worth
 56 mentioning that this approach is similar to that developed by Roopnarine (2017) with the exception that
 57 Shaw does not specifically bin species into guilds, and so we choose to use the method developed by Shaw
 58 since both methods should produce extremely similar networks as they are built on the same underlying
 59 philosophy.

60 6.1.2 Allometric diet breadth model

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

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

65 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
 66 energy content of the resource and H_{ij} is the ratio handling time, with the relationship being dependent on

⁶⁷ the ratio of predator and prey body mass as follows:

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

⁶⁸ or

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

⁶⁹ Refer to Petchey et al. (2008) for more details as to how these different terms are parametrised.

⁷⁰ 6.1.3 Body size ratio model

⁷¹ The body size ratio model (Rohr et al., 2010) determines feeding interactions using the ratio between consumer
⁷² (M_i) and resource (M_j) body sizes - which supposedly stems from niche theory (still trying to reconcile that).
⁷³ The probability of a link existing between a consumer and resource (in its most basic form) is defined as
⁷⁴ follows:

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

⁷⁵ where

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

⁷⁶ The original latent-trait model developed by Rohr et al. (2010) also included an additional latent trait term
⁷⁷ $v_i \delta f_j$ however for simplicity we will use Equation 2 as per Yeakel et al. (2014) Based on Rohr et al. (2010) it
⁷⁸ is possible to estimate the parameters α , δ , and γ using a GLM but we will use the parameters from Yeakel
⁷⁹ et al. (2014), which was ‘trained’ on the Serengeti food web data and are as follows: $\alpha = 1.41$, $\delta = 3.75$, and
⁸⁰ $\gamma = 1.87$.

⁸¹ 6.1.4 L matrix

⁸² For now we can link to thATNr package (Gauzens et al., 2023) until I can find a more suitable manuscript
⁸³ that breaks down this construction method. Schneider et al. (2016) Interactions are determined by allometric
⁸⁴ rules (ratio of consumer (M_i) and resource (M_j) body sizes) and a Ricker function as defined by R_{opt} and

85 γ and returns The probability of a link (P_{ij}) existing between a consumer and resource, and is defined as
86 follows:

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

87 where

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

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

90 **6.1.5 Niche model**

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

98 **6.2 Assessing model performance**

99 In terms of wanting to asses and compare across the different models it is beneficial to approach this task
100 by thinking about the different aspects of the network as well as interactions that are being predicted by the
101 different models. It is perhaps beneficial to think of these across different ‘scales’ of organisation within the
102 network, namely macro (the entire network), meso (smaller interacting units within the network), and micro
103 (species-level attributes). Although there are a myriad of possible ways to ‘measure’ and analyse ecological
104 networks (Delmas et al., 2018) we do still lack a clear set of guidelines for assessing how well models recover
105 network structure (Allesina et al., 2008) and it is beneficial to use a small subset of metrics that can clearly
106 be tied to broader aspects of network function or capturing a ecological process.

107 **6.2.1 Macro network properties**

108 **Connectance** (Martinez, 1992) has been shown to be the feature of networks that underpin a series of other
109 properties and function (Strydom, Catchen, et al., 2021) and so it is perhaps the most important structural
110 attribute for a model to be able to retrieve correctly. Additionally we consider the **complexity** of networks by
111 calculating their SVD entropy (this gives us an estimate of the physical as opposed to behavioural complexity
112 of networks; Strydom, Dalla Riva, et al. (2021)), we could also look at the rank/rank deficiency of networks
113 which (theoretically) represents the number fo unique interaction strategies in the network (Strydom, Dalla
114 Riva, et al., 2021), which may be specifically interesting in terms of looking at pre and post extinction but
115 also as a way to unpack ‘functional redundancy’ that some models may introduce.

116 **6.2.2 Meso network properties**

117 Motifs represent smaller subset of interactions between three species, and are argued to capture dynamics
118 that are likely to be ecologically relevant (Milo et al., 2002; Stouffer et al., 2007). Here we specifically look
119 at the number of **linear chains**, **omnivory**, **apparent competition**, and **direct competition** motifs. In
120 the broader context the ability of a model in being able to capture these smaller motifs will inform as to its
121 suitability of use understanding the more dynamic component of network ecology.

122 **6.2.3 Micro network properties**

123 The number of interactions established (**generality**) or received (**vulnerability**) by each species (Schoener,
124 1989), are (broadly) indicative of consumer-resource relationships and diet breadth of species [ref]. Although
125 this is usually determined at the species level the standard deviation of the generality and vulnerability of
126 species is often used when benchmarking predicted networks (Petchey et al., 2008; *e.g.*, Williams & Martinez,
127 2008).

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

130 **Shape:** to determine if the ‘shape’ of the network is correct we are looking at the ratio of
131 ‘top’:‘basal’ species (where ‘top’ species are those that have a vulnerability of 0 and ‘basal’ species
132 have a generality of 0) as well as the distance to base from one of the top species (this will
133 represent the shortest path but a large discrepancy between the real and predicted network would
134 be indicative that the model is not predicting a similar ‘shape’). This will allow is to see if the
135 models construct tall ‘pencil’ vs flat ‘pancake’ networks (Beckerman 2024, pers comms). A small
136 (< 1) number will thus be indicative of a ‘bottom-heavy’ network and the opposite for larger

137 numbers

138 **6.2.4 Interactions**

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

141 **6.2.5 Robustness**

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

143 **7 Results**

144 **7.1 Comparing predicted networks**

145 [Figure 1 about here.]

146 **7.2 Comparing inference**

147 **7.3 Extinctions**

148 [Figure 2 about here.]

149 [Figure 3 about here.]

150 **References**

- 151 Allesina, S., Alonso, D., & Pascual, M. (2008). A general model for food web structure. *Science*, 320(5876),
152 658–661. <https://doi.org/10.1126/science.1156269>
- 153 Bambach, R. K., Bush, A. M., & Erwin, D. H. (2007). Autecology and the Filling of Ecospace: Key Metazoan
154 Radiations. *Palaeontology*, 50(1), 1–22. <https://doi.org/10.1111/j.1475-4983.2006.00611.x>
- 155 Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with
156 trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>
- 157 Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Dalla Riva, G. V., Fortin, M.-J., Gravel, D., Guimarães,
158 P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2018).
159 Analysing ecological networks of species interactions. *Biological Reviews*, 112540. <https://doi.org/10.1111/brv.12433>

- 161 Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).
162 Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event. *Nature*
163 *Communications*, 15(1), 8599. <https://doi.org/10.1038/s41467-024-53000-2>
- 164 Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,
165 J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.
166 *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- 167 Gauzens, B., Brose, U., Delmas, E., & Berti, E. (2023). ATNr: Allometric Trophic Network models in R.
168 *Methods in Ecology and Evolution*, 14(11), 2766–2773. <https://doi.org/10.1111/2041-210X.14212>
- 169 Jonsson, T., Berg, S., Pimenov, A., Palmer, C., & Emmerson, M. (2015). The reliability of R50 as a
170 measure of vulnerability of food webs to sequential species deletions. *Oikos*, 124(4), 446–457. <https://doi.org/10.1111/oik.01588>
- 171 Martinez, N. D. (1992). Constant connectance in community food webs. *The American Naturalist*, 139(6),
172 1208–1218. <http://www.jstor.org/stable/2462337>
- 173 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple
174 building blocks of complex networks. *Science*, 298(5594), 824–827. <https://doi.org/10.1126/science.298.5594.824>
- 175 Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web
176 structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- 177 Poisot, T., Canard, E., Mouquet, N., & Hochberg, M. E. (2012). A comparative study of ecological spe-
178 cialization estimators. *Methods in Ecology and Evolution*, 3(3), 537–544. <https://doi.org/10.1111/j.2041-210x.2011.00174.x>
- 179 Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring
180 unexplained structure using latent traits. *The American Naturalist*, 176(2), 170–177. <https://doi.org/10.1086/653667>
- 181 Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32(1),
182 1–19. <http://www.jstor.org/stable/4096814>
- 183 Roopnarine, P. D. (2017). *Ecological Modelling of Paleocommunity Food Webs* (pp. 201–226). University of
184 Chicago Press.
- 185 Schneider, F. D., Brose, U., Rall, B. C., & Guill, C. (2016). Animal diversity and ecosystem functioning in
186 dynamic food webs. *Nature Communications*, 7(1), 12718. <https://doi.org/10.1038/ncomms12718>
- 187 Schoener, T. W. (1989). Food Webs From the Small to the Large: The Robert H. MacArthur Award Lecture.
188 *Ecology*, 70(6), 1559–1589. <https://doi.org/10.2307/1938088>

- 194 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*
195 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 196
- 197 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a
198 robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*,
199 274(1621), 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>
- 200 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,
201 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer
202 learning can help predict potential species interaction networks despite data limitations. *Methods in*
203 *Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 204 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
205 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap
206 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*
207 *the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 208 Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD entropy reveals the high complexity of ecological
209 networks. *Frontiers in Ecology and Evolution*, 9. <https://doi.org/10.3389/fevo.2021.623141>
- 210 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
211 <https://doi.org/10.1038/35004572>
- 212 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food
213 webs. *The Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 214 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).
215 Collapse of an ecological network in ancient egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>
- 216

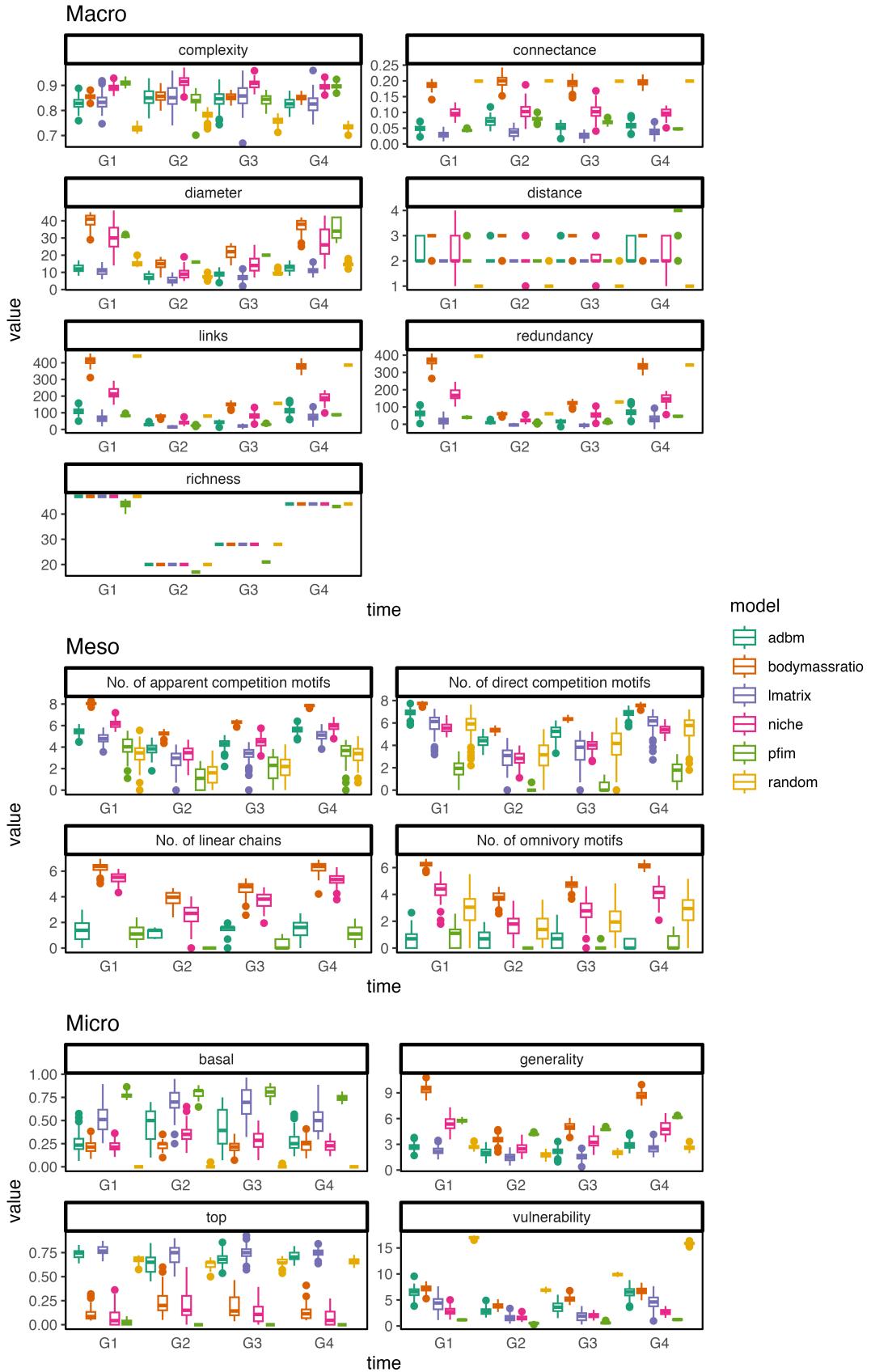


Figure 1: stuff... For display purposes the counts for the different motifs are log transformed

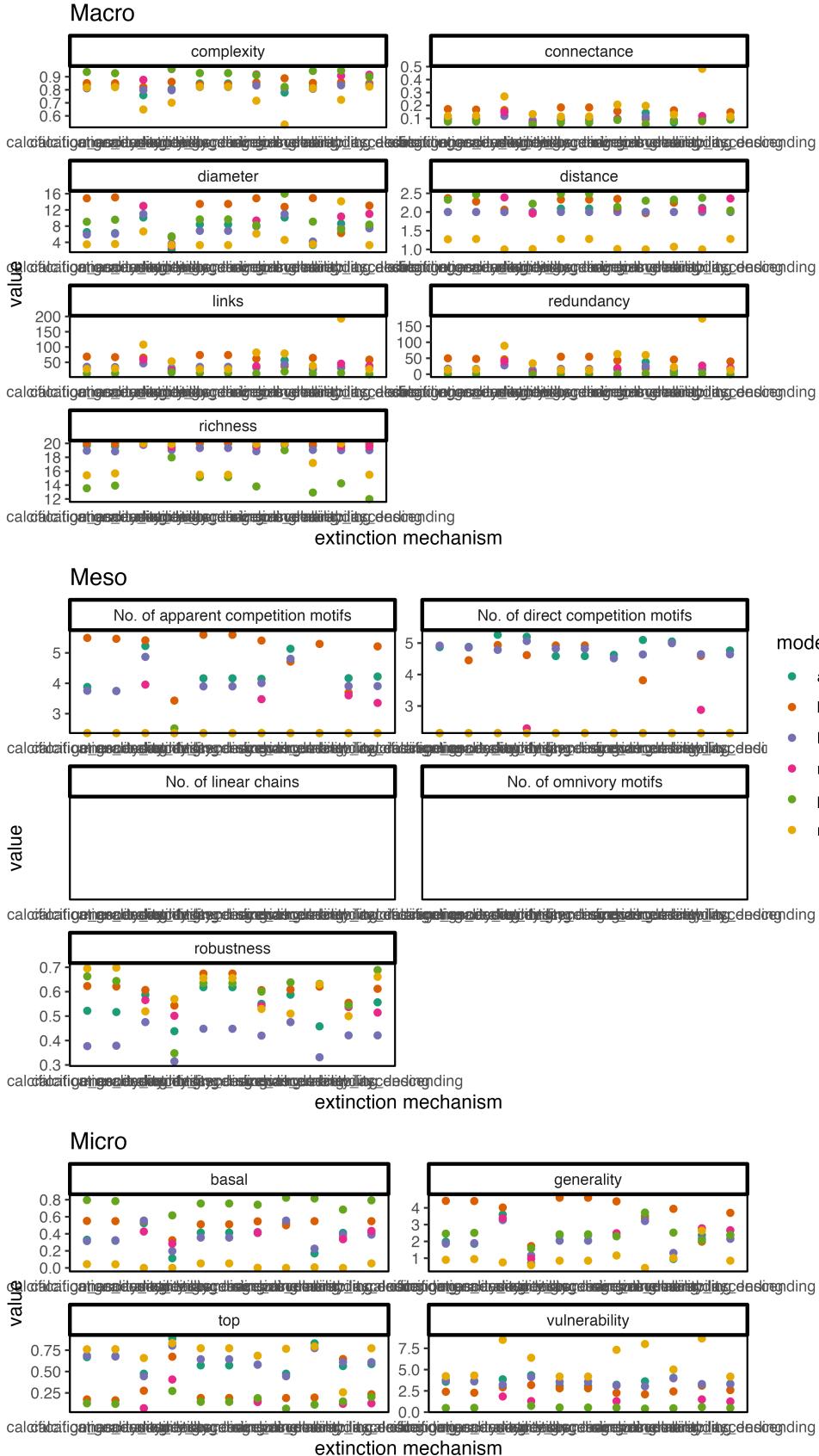


Figure 2: Dashed line indicates the (mean) extinction simulation results (post value, start values are those estimated by the relevant model). For display purposes the counts for the different motifs are log transformed

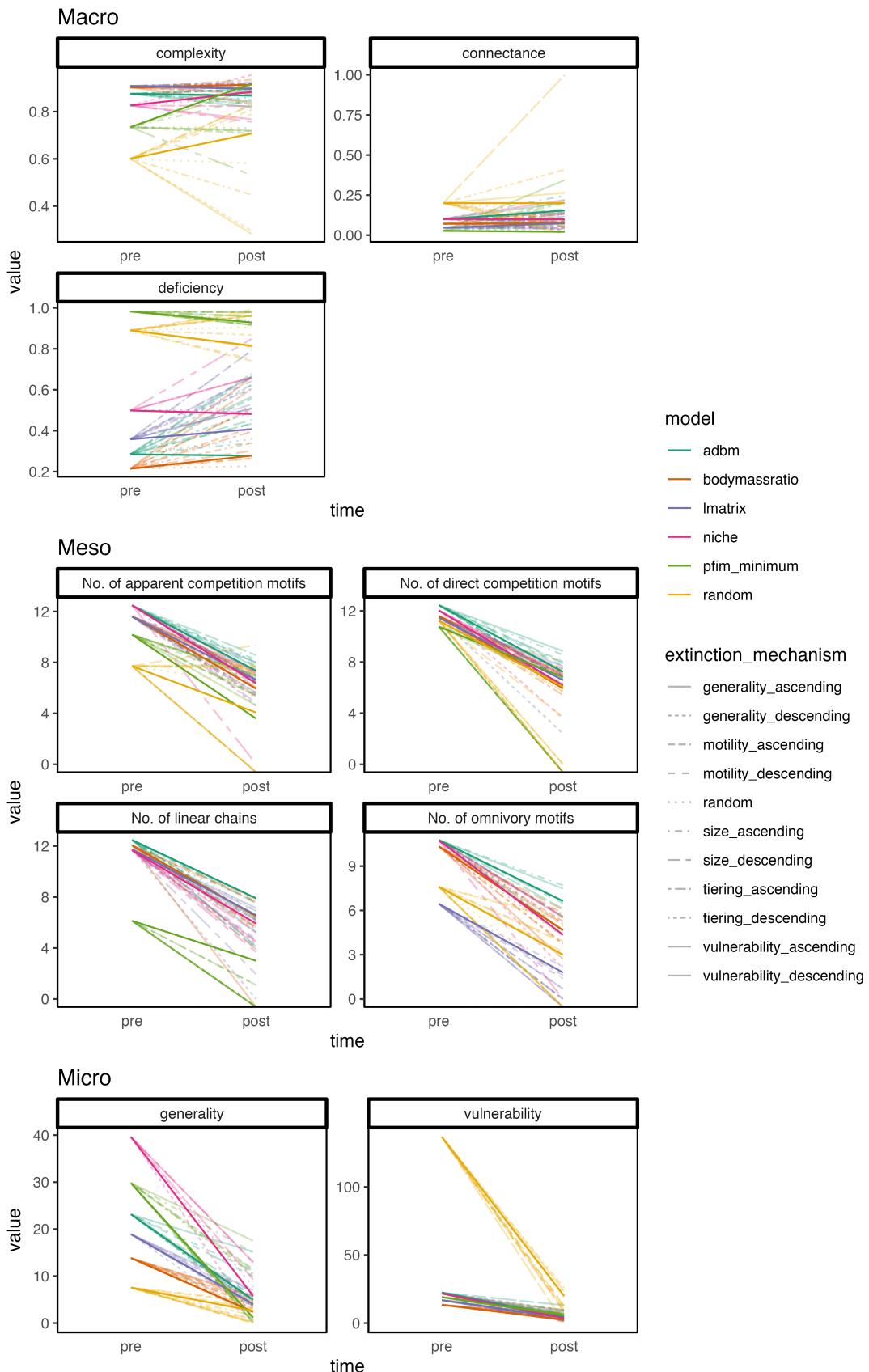


Figure 3: Dark line indicates ‘real’ extinction simulation results the lighter lines show each model individually, which is also denoted by the linetype. For display purposes the counts for the different motifs are log transformed