

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

³⁹ [Figure 1 about here.]

⁴⁰ 6 Methods

⁴¹ 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)	

42 **6.1.1 Paleo food web inference model**

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

52 **6.1.1.1 Defining organism ecologies, feeding interactions and trophic guilds**

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

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

65 **6.1.2 Allometric diet breadth model**

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

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

70 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
 71 energy content of the resource and H_{ij} is the ratio handling time, with the relationship being dependent on
 72 the ratio of predator and prey body mass as follows:

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

73 or

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

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

75 6.1.3 Body size ratio model

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

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

80 where

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

81 The original latent-trait model developed by Rohr et al. (2010) also included an additional latent trait term
 82 $v_i \delta f_j$ however for simplicity we will use Equation 2 as per Yeakel et al. (2014) Based on Rohr et al. (2010) it
 83 is possible to estimate the parameters α , δ , and γ using a GLM but we will use the parameters from Yeakel
 84 et al. (2014), which was ‘trained’ on the Serengeti food web data and are as follows: $\alpha = 1.41$, $\delta = 3.75$, and
 85 $\gamma = 1.87$.

86 **6.1.4 L matrix**

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

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

92 where

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

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

95 **6.1.5 Niche model**

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

103 **6.2 Assessing model performance**

104 In terms of wanting to asses and compare across the different models it is beneficial to approach this task
105 by thinking about the different aspects of the network as well as interactions that are being predicted by the
106 different models. It is perhaps beneficial to think of these across different ‘scales’ of organisation within the
107 network, namely macro (the entire network), meso (smaller interacting units within the network), and micro
108 (species-level attributes). Although there are a myriad of possible ways to ‘measure’ and analyse ecological
109 networks (Delmas et al., 2018) we do still lack a clear set of guidelines for assessing how well models recover

110 network structure (Allesina et al., 2008) and it is beneficial to use a small subset of metrics that can clearly
111 be tied to broader aspects of network function or capturing a ecological process.

112 **6.2.1 Macro network properties**

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

121 **6.2.2 Meso network properties**

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

127 **6.2.3 Micro network properties**

128 The number of interactions established (**generality**) or received (**vulnerability**) by each species (Schoener,
129 1989), are (broadly) indicative of consumer-resource relationships and diet breadth of species [ref]. Although
130 this is usually determined at the species level the standard deviation of the generality and vulnerability of
131 species is often used when benchmarking predicted networks (Petchey et al., 2008; *e.g.*, Williams & Martinez,
132 2008).

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

135 **Shape:** to determine if the ‘shape’ of the network is correct we are looking at the ratio of
136 ‘top’:‘basal’ species (where ‘top’ species are those that have a vulnerability of 0 and ‘basal’ species
137 have a generality of 0) as well as the distance to base from one of the top species (this will
138 represent the shortest path but a large discrepancy between the real and predicted network would

139 be indicative that the model is not predicting a similar ‘shape’). This will allow us to see if the
140 models construct tall ‘pencil’ vs flat ‘pancake’ networks (Beckerman 2024, pers comms). A small
141 (< 1) number will thus be indicative of a ‘bottom-heavy’ network and the opposite for larger
142 numbers

143 **6.2.4 Interactions**

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

146 **7 Results**

147 **7.1 Comparing predicted networks**

148 [Figure 2 about here.]

149 **7.2 Comparing inference**

150 **7.3 Extinctions**

151 [Figure 3 about here.]

152 [Figure 4 about here.]

153 **References**

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

- ¹⁶⁴ Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).
¹⁶⁵ 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>
- ¹⁶⁶
- ¹⁶⁷ 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>
- ¹⁶⁸
- ¹⁶⁹
- ¹⁷⁰ 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>
- ¹⁷¹
- ¹⁷² Martinez, N. D. (1992). Constant connectance in community food webs. *The American Naturalist*, 139(6), 1208–1218. <http://www.jstor.org/stable/2462337>
- ¹⁷³
- ¹⁷⁴ 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>
- ¹⁷⁵
- ¹⁷⁶
- ¹⁷⁷ 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>
- ¹⁷⁸
- ¹⁷⁹
- ¹⁸⁰ 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>
- ¹⁸¹
- ¹⁸²
- ¹⁸³ 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>
- ¹⁸⁴
- ¹⁸⁵
- ¹⁸⁶ Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32(1), 1–19. <http://www.jstor.org/stable/4096814>
- ¹⁸⁷
- ¹⁸⁸ Roopnarine, P. D. (2017). *Ecological Modelling of Paleocommunity Food Webs* (pp. 201–226). University of Chicago Press.
- ¹⁸⁹
- ¹⁹⁰ 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>
- ¹⁹¹
- ¹⁹² 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>
- ¹⁹³
- ¹⁹⁴ 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>
- ¹⁹⁵
- 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: It would be very sexy if we could get a figure that looks something like this together...

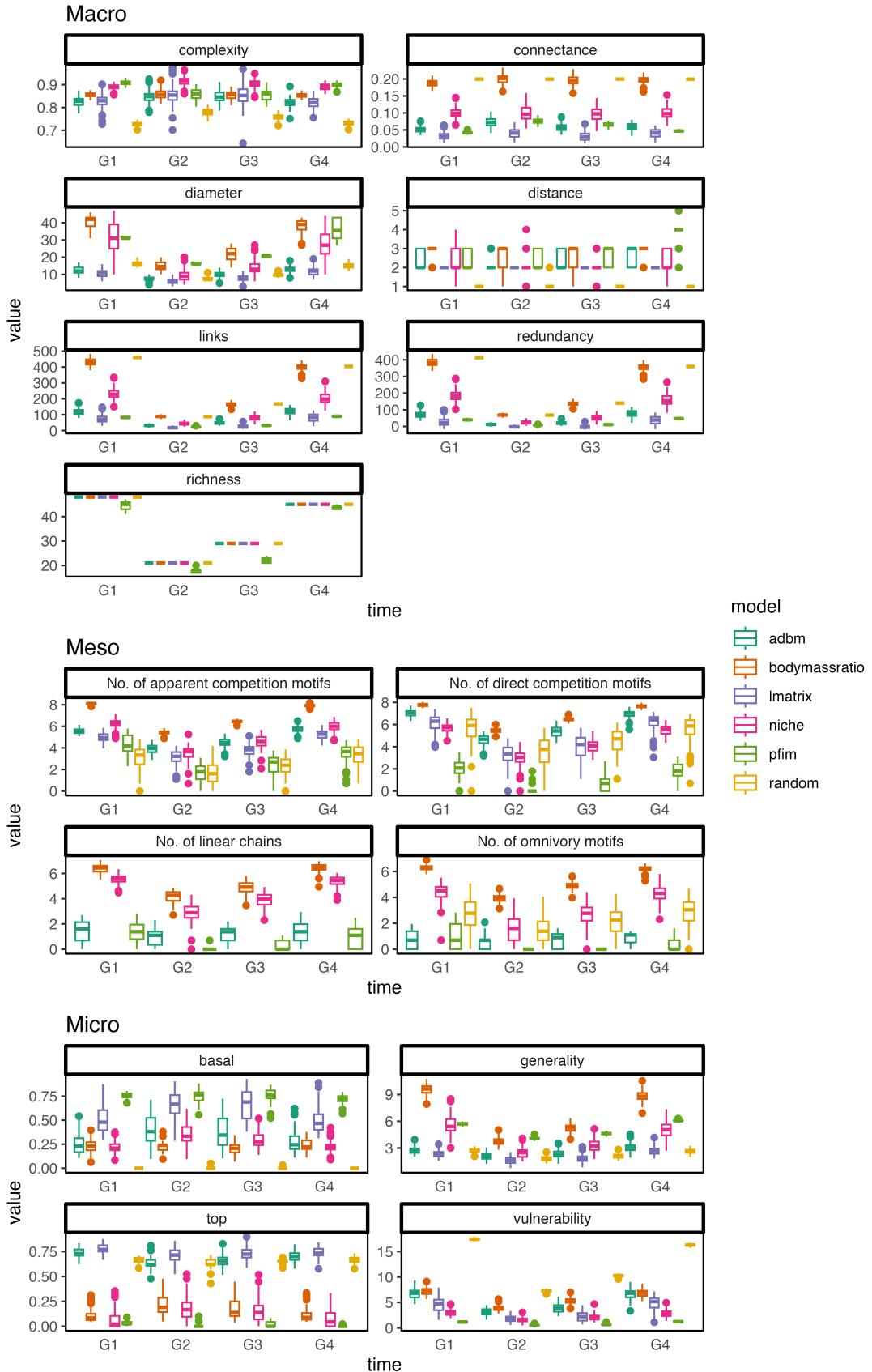


Figure 2: stuff... For display purposes the counts for the different motifs are log transformed

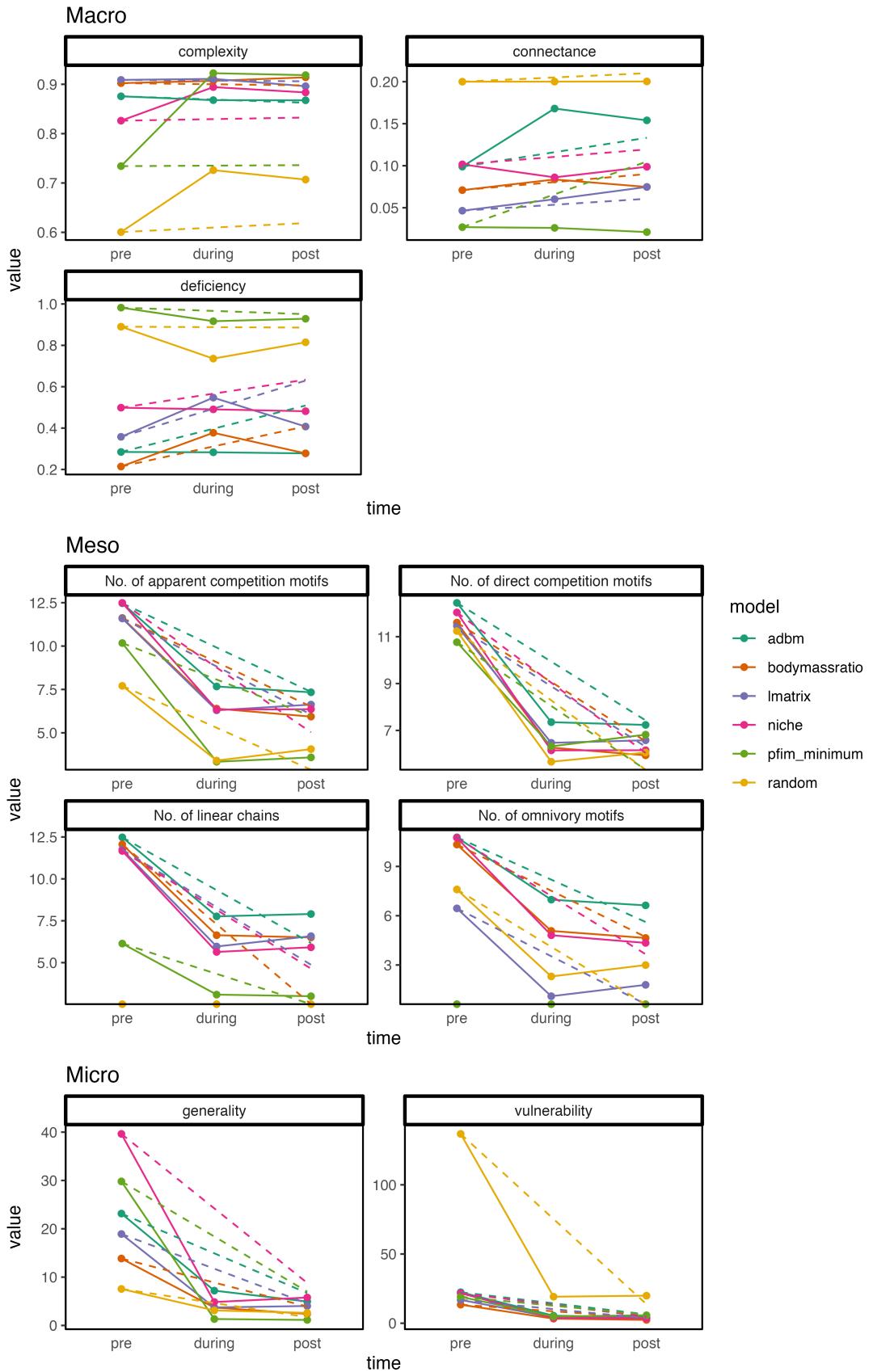


Figure 3: Dashed line indicates the (mean) extinction simulation results (post value, start values are those estimated by the relevant model). For display purposes the counts for the different motifs are log transformed

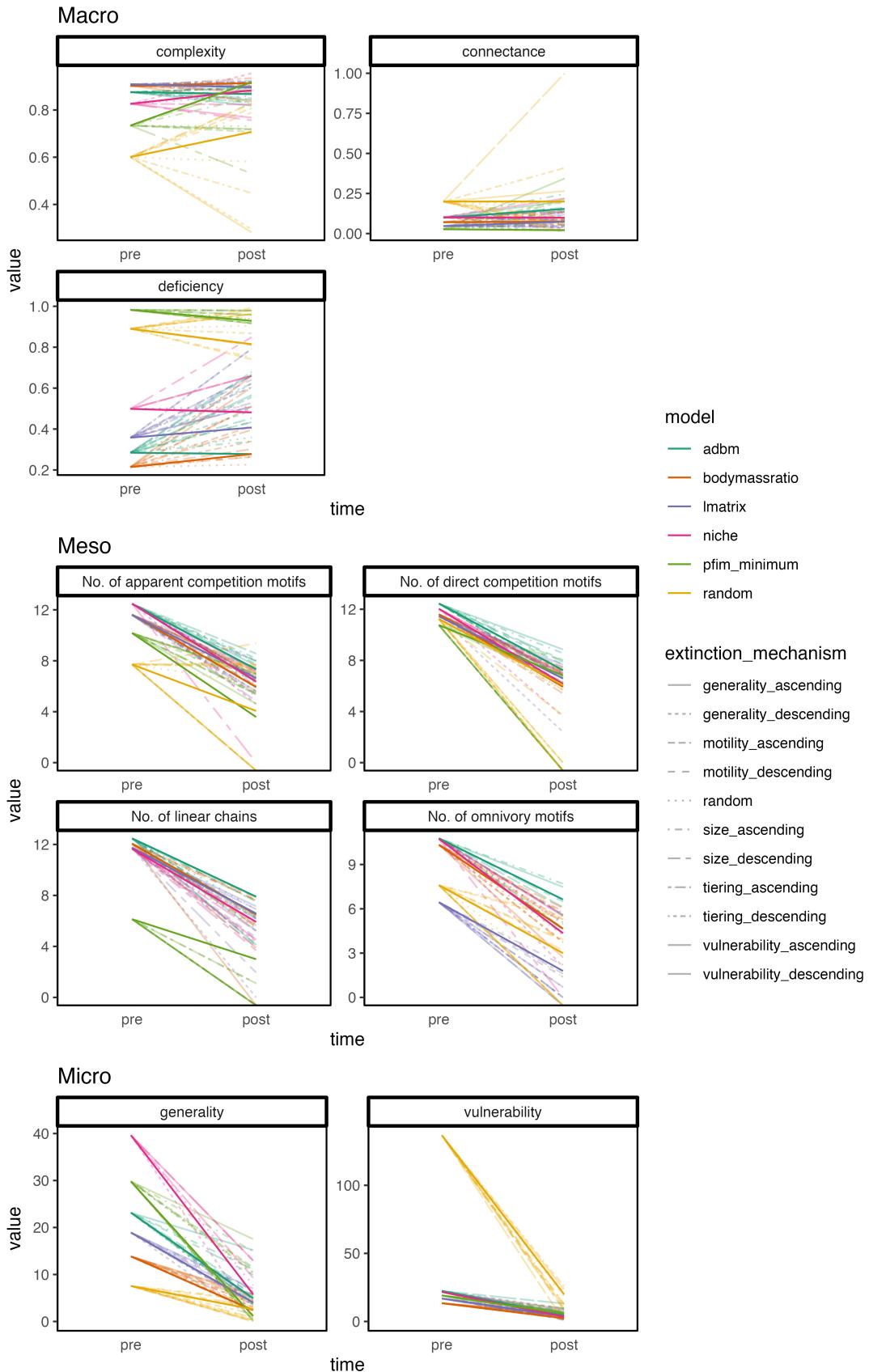


Figure 4: Dark line indicates ‘real’ extinction simulation results the lighter lines show each model individually, which is also denoted by the linetype. For display purposes the counts for the different motifs are log transformed