

Methods for Reconstructing Paleo Food Webs

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Abstract: TODO.

Keywords: food web, network construction

₁ **1 Why build paleo food webs?**

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

₅ **2 How do we do it?**

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

₁₆ **3 Understanding how networks are different**

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

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

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

₂₀ environmental context.

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

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

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

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

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

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

³⁵ 5 Dataset Overview

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

³⁹ 6 Methods

⁴⁰ 6.1 Models

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

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

41 **6.1.1 Paleo food web inference model**

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

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

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

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

64 **6.1.2 Allometric diet breadth model**

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

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

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

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

72 or

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

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

74 6.1.3 Body size ratio model

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

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

79 where

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

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

85 **6.1.4 Niche model**

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

93 **6.2 Assessing model performance**

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

102 **6.2.1 Meta network properties**

103 **Connectance** (Martinez, 1992) has been shown to be the feature of networks that underpin a series of other
104 properties and function (Strydom, Catchen, et al., 2021) and so it is perhaps the most important structural
105 attribute for a model to be able to retrieve correctly. Additionally we consider the **complexity** of networks by
106 calculating their SVD entropy (this gives us an estimate of the physical as opposed to behavioural complexity
107 of networks; Strydom, Dalla Riva, et al. (2021)).

108 **6.2.2 Meso network properties**

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

¹¹⁴ **6.2.3 Micro network properties**

¹¹⁵ The number of interactions established (**generality**) or received (**vulnerability**) by each species (Schoener,
¹¹⁶ 1989), are (broadly) indicative of consumer-resource relationships and diet breadth of species [ref]. Although
¹¹⁷ this is usually determined at the species level the standard deviation of the generality and vulnerability of
¹¹⁸ species is often used when benchmarking predicted networks (Petchey et al., 2008; *e.g.*, Williams & Martinez,
¹¹⁹ 2008).

¹²⁰ The **specificity** of species in a network is measured as a function of the proportion of resources they effectively
¹²¹ use (Poisot et al., 2012)

¹²² **Shape:** to determine if the ‘shape’ of the network is correct we are looking at the ratio of
¹²³ ‘top’:‘basal’ species (where ‘top’ species are those that have a vulnerability of 0 and ‘basal’ species
¹²⁴ have a generality of 0) as well as the distance to base from one of the top species (this will
¹²⁵ represent the shortest path but a large discrepancy between the real and predicted network would
¹²⁶ be indicative that the model is not predicting a similar ‘shape’). This will allow us to see if the
¹²⁷ models construct tall ‘pencil’ vs flat ‘pancake’ networks (Beckerman 2024, pers comms). A small
¹²⁸ (< 1) number will thus be indicative of a ‘bottom-heavy’ network and the opposite for larger
¹²⁹ numbers

¹³⁰ **7 Results**

¹³¹ **7.1 Comparing predicted networks**

¹³² [Figure 1 about here.]

¹³³ **7.2 Comparing inference**

¹³⁴ **7.3 Extinctions**

¹³⁵ [Figure 2 about here.]

¹³⁶ [Figure 3 about here.]

¹³⁷ **References**

- ¹³⁸ Allesina, S., Alonso, D., & Pascual, M. (2008). A general model for food web structure. *Science*, *320*(5876),
¹³⁹ 658–661. <https://doi.org/10.1126/science.1156269>

- ¹⁴⁰ Bambach, R. K., Bush, A. M., & Erwin, D. H. (2007). Autecology and the Filling of Ecospace: Key Metazoan
¹⁴¹ Radiations. *Palaeontology*, 50(1), 1–22. <https://doi.org/10.1111/j.1475-4983.2006.00611.x>
- ¹⁴² Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with
¹⁴³ trait-based interaction models. *Ecology Letters*, 25(4), 889–899. <https://doi.org/10.1111/ele.13966>
- ¹⁴⁴ Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Dalla Riva, G. V., Fortin, M.-J., Gravel, D., Guimarães,
¹⁴⁵ P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2018).
¹⁴⁶ Analysing ecological networks of species interactions. *Biological Reviews*, 112540. <https://doi.org/10.1111/brv.12433>
- ¹⁴⁸ Dunhill, A. M., Zarzyczny, K., Shaw, J. O., Atkinson, J. W., Little, C. T. S., & Beckerman, A. P. (2024).
¹⁴⁹ 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>
- ¹⁵¹ Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan, J., Svenning,
¹⁵² J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs since the Late Pleistocene.
¹⁵³ *Science*, 377(6609), 1008–1011. <https://doi.org/10.1126/science.abn4012>
- ¹⁵⁴ Martinez, N. D. (1992). Constant connectance in community food webs. *The American Naturalist*, 139(6),
¹⁵⁵ 1208–1218. <http://www.jstor.org/stable/2462337>
- ¹⁵⁶ Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple
¹⁵⁷ building blocks of complex networks. *Science*, 298(5594), 824–827. <https://doi.org/10.1126/science.298.5594.824>
- ¹⁵⁹ Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web
¹⁶⁰ structure. *Proceedings of the National Academy of Sciences*, 105(11), 4191–4196. <https://doi.org/10.1073/pnas.0710672105>
- ¹⁶² Poisot, T., Canard, E., Mouquet, N., & Hochberg, M. E. (2012). A comparative study of ecological spe-
¹⁶³ cialization estimators. *Methods in Ecology and Evolution*, 3(3), 537–544. <https://doi.org/10.1111/j.2041-210x.2011.00174.x>
- ¹⁶⁵ Rohr, R., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring
¹⁶⁶ unexplained structure using latent traits. *The American Naturalist*, 176(2), 170–177. <https://doi.org/10.1086/653667>
- ¹⁶⁸ Roopnarine, P. D. (2006). Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, 32(1),
¹⁶⁹ 1–19. <http://www.jstor.org/stable/4096814>
- ¹⁷⁰ Roopnarine, P. D. (2017). *Ecological Modelling of Paleocommunity Food Webs* (pp. 201–226). University of
¹⁷¹ Chicago Press.
- ¹⁷² Schoener, T. W. (1989). Food Webs From the Small to the Large: The Robert H. MacArthur Award Lecture.

- 173 *Ecology*, 70(6), 1559–1589. <https://doi.org/10.2307/1938088>
- 174 Shaw, J. O., Dunhill, A. M., Beckerman, A. P., Dunne, J. A., & Hull, P. M. (2024). *A framework for*
175 *reconstructing ancient food webs using functional trait data* (p. 2024.01.30.578036). bioRxiv. <https://doi.org/10.1101/2024.01.30.578036>
- 176
- 177 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a
178 robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*,
179 274(1621), 1931–1940. <https://doi.org/10.1098/rspb.2007.0571>
- 180 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J., Mercier, B.,
181 Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T. (2023). Graph embedding and transfer
182 learning can help predict potential species interaction networks despite data limitations. *Methods in*
183 *Ecology and Evolution*, 14(12), 2917–2930. <https://doi.org/10.1111/2041-210X.14228>
- 184 Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., Forero-Muñoz,
185 N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., & Poisot, T. (2021). A roadmap
186 towards predicting species interaction networks (across space and time). *Philosophical Transactions of*
187 *the Royal Society B: Biological Sciences*, 376(1837), 20210063. <https://doi.org/10.1098/rstb.2021.0063>
- 188 Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD entropy reveals the high complexity of ecological
189 networks. *Frontiers in Ecology and Evolution*, 9. <https://doi.org/10.3389/fevo.2021.623141>
- 190 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.
191 <https://doi.org/10.1038/35004572>
- 192 Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food
193 webs. *The Journal of Animal Ecology*, 77(3), 512–519. <https://doi.org/10.1111/j.1365-2656.2008.01362.x>
- 194 Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., & Gross, T. (2014).
195 Collapse of an ecological network in ancient egypt. *PNAS*, 111(40), 14472–14477. <https://doi.org/10.1073/pnas.1408471111>
- 196

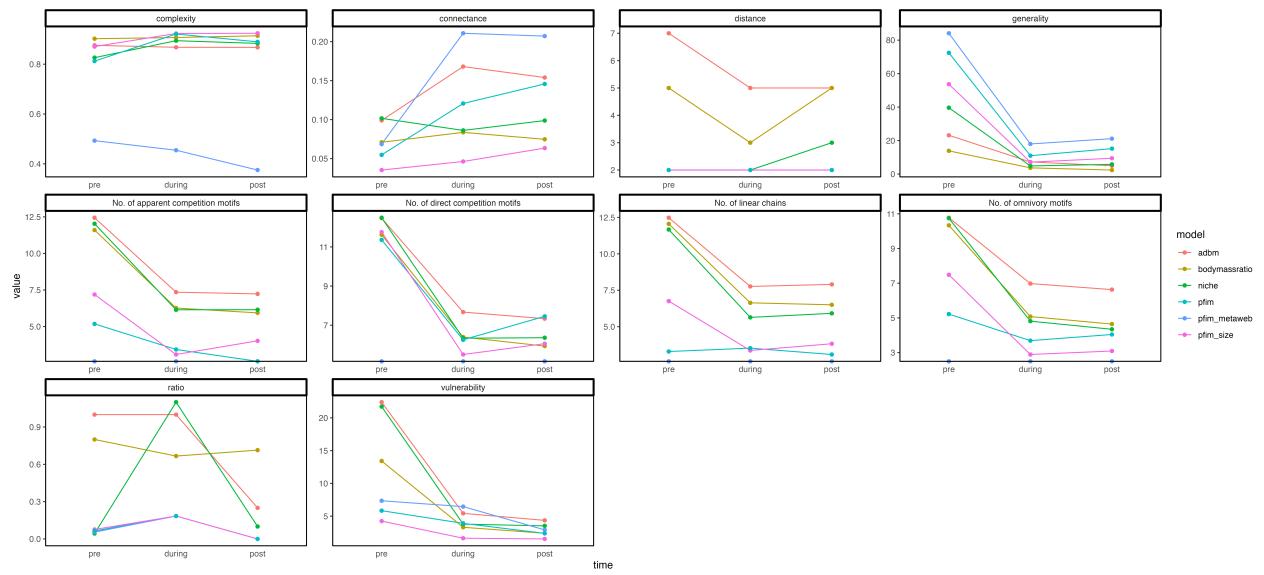


Figure 1: stuff... For display purposes the counts for the different motifs are log transformed

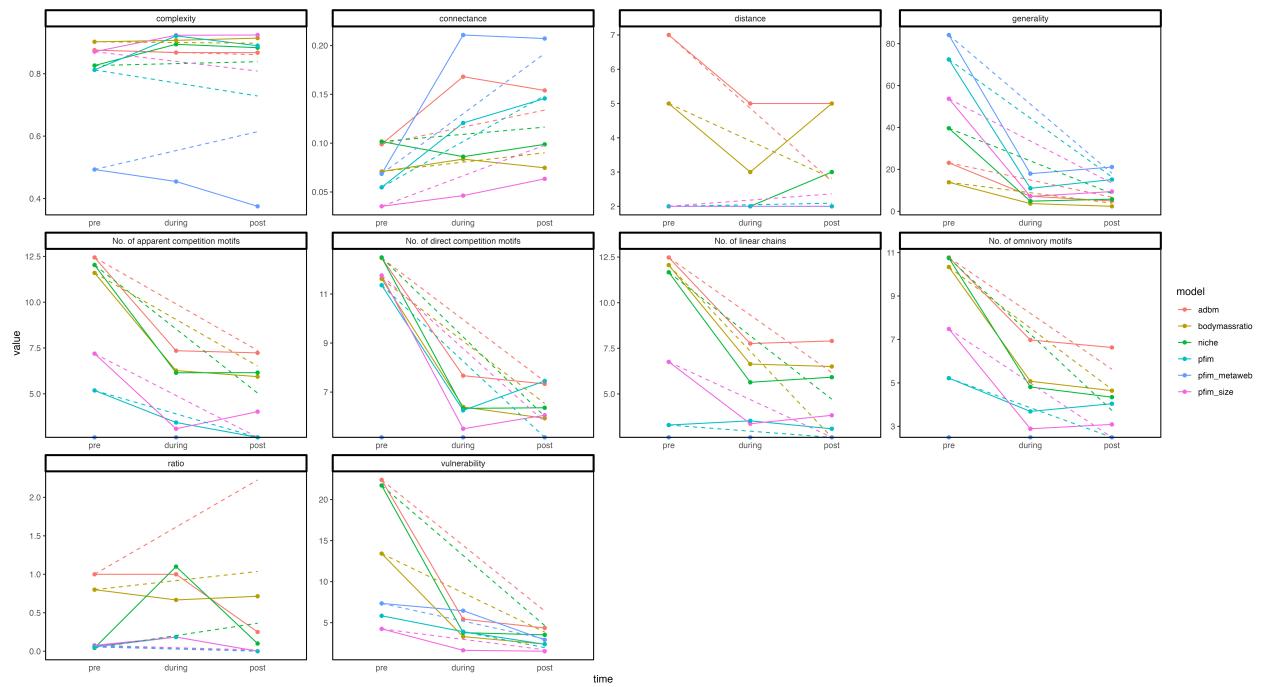


Figure 2: Dashed line indicates the (mean) extinction simulation results (post value, start values are those estimated by the relevant model). For display purposes the counts for the different motifs are log transformed

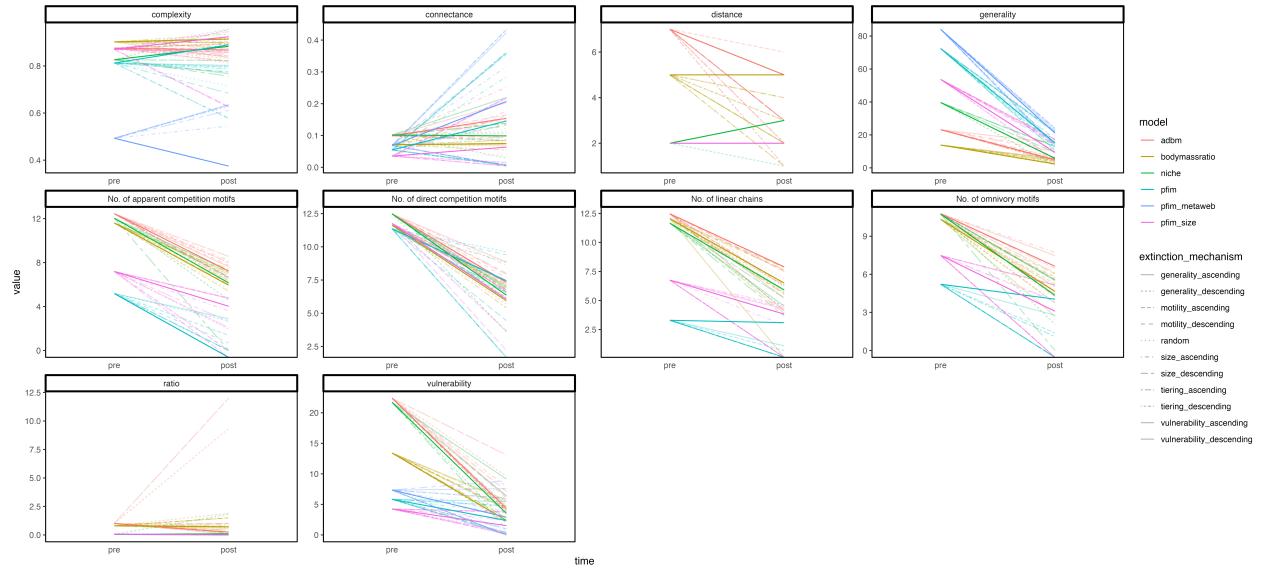


Figure 3: Dark line indicates ‘real’ extinction simulation results the lighter lines show each model individually, which is also denoted by the linetype. For display purposes the counts for the different motifs are log transformed