
MISSING LINKS, FALSE POSITIVES, AND THE TOPOLOGICAL ROBUSTNESS OF PREDICTED FOOD WEBS

A PREPRINT

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February 27, 2022

Abstract

- 1 1) Undersampling of species in a food web can lead to missing trophic interactions in the
2 food web. This can be compensated by using food web models such as allometric diet
3 breadth model (ADBM) to predict those missing links. At the same time, these models
4 might predict links which are probably not true i.e. false positives. So, it is crucial to
5 understand how this affects the stability of predicted food webs when compared with
6 the observed food webs.
- 7 2) In our study, we compare the number of secondary extinctions when there is a primary
8 extinction of species in food webs predicted by the ADBM to that in the observed food
9 webs, and compute the robustness across 12 different food webs from a wide variety of
10 ecosystems.

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3) We found that the ADBM predicted food webs were more robust than the observed food webs, and this can be attributed to connectance of the ADBM predicted food webs being higher than that of the observed food webs.

4) These results suggest that real food webs might be more robust as compared to the food webs constructed using observed data.

Keywords connectance · ABC · ADBM · food web · extinction · uncertainty

1 Alternate titles

- Robustness of ADBM predicted food webs

2 Introduction

2.1 Background on anthropogenic changes and its impact on food web

Anthropogenic changes such as climate change and habitat destruction is a threat to biodiversity, and can lead to food web collapse (Ullah et al. 2018). Primary extinctions in a food web can give rise to further secondary extinctions in a food web which can result in collapse of the food web (reference). The rate at which a primary extinctions can lead to secondary extinctions is dependent on the structure and complexity of that food web (reference). Understanding this can help to implement conservation efforts tailored to a given food web structure (reference).

2.2 Briefly explain work done by Jennifer Dunne on food web [OP] robustness to primary extinctions, and also what has been done since, particularly concerning the importance of connectance

Simulation of primary species loss has been conducted in observed food webs and model food webs from terrestrial and aquatic ecosystems where robustness was measured in terms of secondary extinctions (Jennifer A. Dunne, Williams, and Martinez 2002b; Jennifer A. Dunne and Williams 2009). These studies showed that the robustness of the food webs increases with food web connectance. Also, the removal of the most connected species cause considerably more secondary extinctions than random removals of species (Jennifer A. Dunne, Williams, and Martinez 2002a; Sol'e and Montoya 2001). These studies provide an alternate solution to investigate the impact of primary extinctions in a food web when canonical experiments in natural ecosystems are not possible.

Along with robustness based on topological structure of a food web, robustness based on the food web dynamics has been studied as well (reference). Topological approaches only require the food web structure whereas dynamical approaches also require the temporal dynamics of the food web along with the food web

structure. For example: Williams (2008) combined models of network structure with models of bionergetic dynamics to study the role of food web topology and nonlinear dynamics on species coexistence in complex ecological networks.

[OP] Explain (either here or in the methods) difference between topological and abundance (given by dynamics) based criteria for a secondary extinction occurring.

2.3 [OP] State what is the problem...

A key assumption of this work is that food webs are very well sampled, so that all links that in reality can occur are represented. Yet it is known that not all food webs are very well sampled, and then do not represent all of the feeding links that occur (reference). One solution to this problem is to use a food web model to predict which are the missing links, and to then measure the robustness of the predicted food web. This solution is not fool proof, however, as it is likely that the food web model is not perfect, and so may still miss some links, and also may predict some links that could not, in fact occur.

2.4 In previous work...

In Gupta et al. (2022) we made predictions of food web structure using the allometric diet breadth model (ADBM, (Beckerman, Petchey, and Warren 2006; Petchey et al. 2008)) by fitting it to empirical data using approximate Bayesian computation, and the goodness of fit of the ADBM was measured using the true skill statistics which takes into account the presence of links as well as the absence of links. (ADBM uses foraging theory specifically the contingency model (MacArthur and Pianka 1966) to predict the diet of each potential consumer and thereby the food web structure.) A key finding of Gupta et al. (2022) was that the predicted food web connectance was consistently higher as compared to the observed connectance. This means that there were some trophic links (false positives) predicted by the ADBM which are not observed in the empirical food web data. Simultaneously there were some trophic links (false negatives) that were not predicted by the ADBM but were observed in the empirical food web. In that work there was no attempt to estimate the importance of these findings on computing the robustness of these food webs to species extinctions.

2.5 What we do in this study

It is crucial to investigate the implication of this consistent overestimation of connectance in the robustness of predicted food webs. We expect that the ADBM predicted food webs would be more robust as compared to the observed food webs, and for the greater robustness to be related to the amount by which the ADBM overestimates connectance. In this study, we simulate primary species loss in 12 food webs predicted from the ADBM to quantify the secondary loss of extinctions. We use three different approaches of species removal: (i) most connected species, (ii) random species and (iii) least connected species to understand if the outcome varies among these approaches.

3 Materials and methods

[OP] ## Provide overview of the methods

In the upcoming sections, we present a detailed account of the implementation of simulation of primary extinctions for three different scenarios on 12 food webs predicted by the ADBM from wide variety of ecosystems, and compute the resultant secondary extinctions. We then compute a robustness metric to quantify the robustness of those predicted food webs.

3.1 Allometric Diet Breadth Model (ADBM)

The allometric diet breadth model (ADBM) is based on optimal foraging theory, specifically the contingency foraging model (MacArthur and Pianka 1966). The ADBM predicts the set of prey species a consumer should feed upon to maximise its rate of energy intake (Petchey et al. 2008). The foraging variables in the model: energy content of the resources, handling times of the prey, space clearance rate and prey densities are allometrically scaled to the body sizes of the species.

3.2 Food web data

The observed food webs that we fit the ADBM to belong to marine, freshwater and terrestrial ecosystems (Table 1). The observed connectance of these food webs is from 0.03 to 0.24 and there are 29 to 239 species. The food webs contain primary producers, herbivores, carnivores, parasites, and parasitoids. They also contain various types of feeding interactions, including predation, herbivory, bacterivory, parasitism, pathogenic, and parasitoid.

Table 1: Information about the food webs predicted using the ADBM.

Common food web name (Original Publication)	Predation matrix source	General ecosystem	Number of species	Connectance	Type of interactions
Benguela Pelagic (Yodzis 1998)	Brose et al. (2005)	Marine	30	0.21	Predation
Broadstone Stream (taxonomic aggregation) (Woodward and Hildrew 2001; Woodward et al. 2005)	Brose et al. (2005)	Freshwater	29	0.19	Predation
Broom (Mommott et al. 2000)	Brose et al. (2005)	Terrestrial	60	0.03	Herbivory, Parasitism, Predation, Pathogenic
Capinteria (Lafferty et al. 2006)	Hechinger et al. (2011)	Marine (Salt Marsh)	88	0.08	Predator-parasite, Parasite-parasite
Caricaie Lakes (Cattin et al. 2004)	Brose et al. (2005)	Freshwater	158	0.05	Predation, Parasitism
Grasslands (Dawah et al. 1995)	Brose et al. (2005)	Terrestrial	65	0.03	Herbivory, Parasitism
Mill Stream (Ledger, Edwards, Woodward unpublished)	Brose et al. (2005)	Freshwater	80	0.06	Herbivory, Predation
Skipwith Pond (Warren 1989)	Brose et al. (2005)	Freshwater	71	0.07	Predation
Small Reef (Opitz 1996 Table 8.6.2)	Alyssa R. Cirtwill and Anna Eklöf (2018)	Marine (Reef)	239	0.06	Predation, Herbivory
Tuesday Lake (Jonsson et al. 2005)	Brose et al. (2005)	Freshwater	73	0.08	Predation
Ythan (Emmerson and Raffaelli 2004)	Alyssa R. Cirtwill and Anna Eklöf (2018)	Marine (Estuarine)	85	0.04	Predation
Broadstone Stream (size aggregation) (Woodward et al. 2010)	Guy Woodward. (2021)	Freshwater	29	0.24	Predation

91 3.3 Primary and secondary extinctions

92 We implemented the primary species removal method from Jennifer A. Dunne and Williams (2009)
 93 by sequentially removing species using one of three criteria: removal of (i) the most-connected
 94 species, (ii) the least-connected species and (iii) randomly chosen species. The most-connected and
 95 least-connected criteria are based on the degree (i.e. total number of links to resource and links
 96 from consumer for each species) of species. Given a primary removal if any remaining species lost
 97 all of their resource species, or any cannibalistic species lost all of their resource species except the
 98 cannibalistic links, they are dropped from the web and were recorded as a secondary extinction.
 99 Then the next appropriate species are removed determining the most- and least-connected species
 100 based on the web remaining after all prior primary removals and secondary extinctions had occurred.
 101 This process was carried out until all species were extinct from the web.

102 3.4 Calculating robustness

103 Robustness (R) of food web was quantified as the proportion of species subjected to primary removals
 104 that resulted in a total loss (i.e. primary removals plus secondary extinctions) of some specified
 105 proportion of the species. In our study, we use R_{50} , the number of primary extinctions divided
 106 by the total number of species, that result in at least 50 per cent of total species loss (Jennifer A.
 107 Dunne, Williams, and Martinez 2002b; J. Dunne, Williams, and Martinez 2004; Jennifer A. Dunne
 108 and Williams 2009). Therefore, there is no secondary extinction in a maximally robust community
 109 ($R_{50} = 0.50$), whereas in a minimally robust community ($R_{50} = 1/S$) there is extensive secondary
 110 extinctions (i.e. at least $S/2 - 1$).

111 4 Results

112 We first present the cumulative secondary extinctions in the food webs for three different extinction
 113 scenarios. We also computed the robustness metric for the food webs where the robustness metric
 114 quantifies the number of species extinctions required to have at least 50% of total number of species
 115 extinctions in a food web.

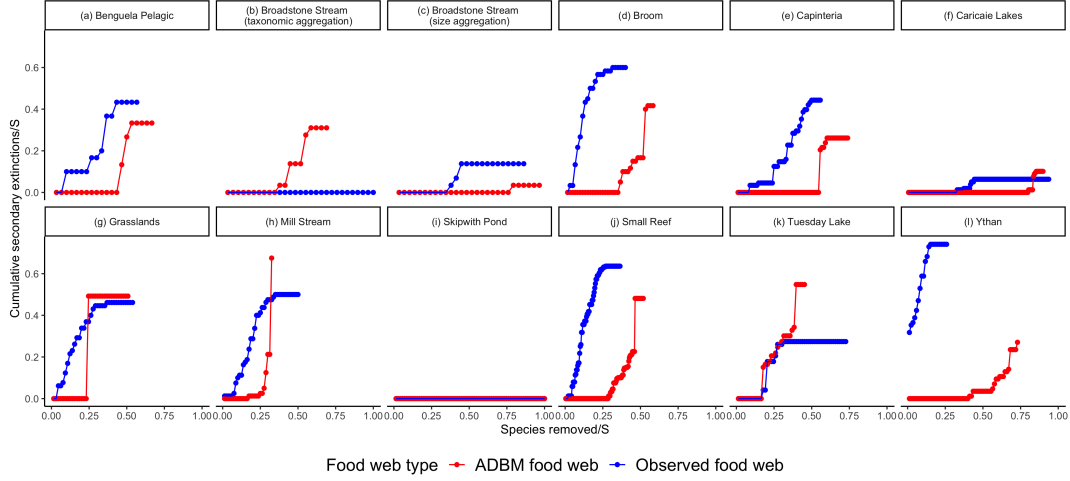


Figure 1: Cumulative secondary extinctions of species resulting from the primary removals of the most connected species for 12 food webs. S denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number of species.

4.1 Show and describe the secondary extinction curves

In Fig. 1, 2 and 3, we show the secondary extinction curves of ADBM predicted food webs and observed food webs for 12 different food webs under three different extinction scenarios. In general, irrespective of the extinction scenarios, we found that the cumulative secondary extinction was higher for the ADBM predicted food webs as compared to the observed food webs for most of the food webs.

In the most connected extinction scenario, the cumulative secondary extinction curve for the observed food webs rose quickly as compared to the ADBM predicted food webs, and then reach saturation after a certain number of primary removal of species. In some of the food webs (Fig. 1 (f, g, h, i, j, k)), there were intersection between the cumulative secondary extinction curves of ADBM predicted food webs and that of the observed food webs. In case of the Broadstone Stream (taxonomic aggregation) food web and the Tuesday Lake food web (Fig. 1 (b and k)), the secondary extinction curves for the ADBM food webs were higher than the observed food webs, whereas in case of the Skipwith Pond food web (Fig. 1 (i)), there were no secondary extinctions for any given number of primary removal of species.

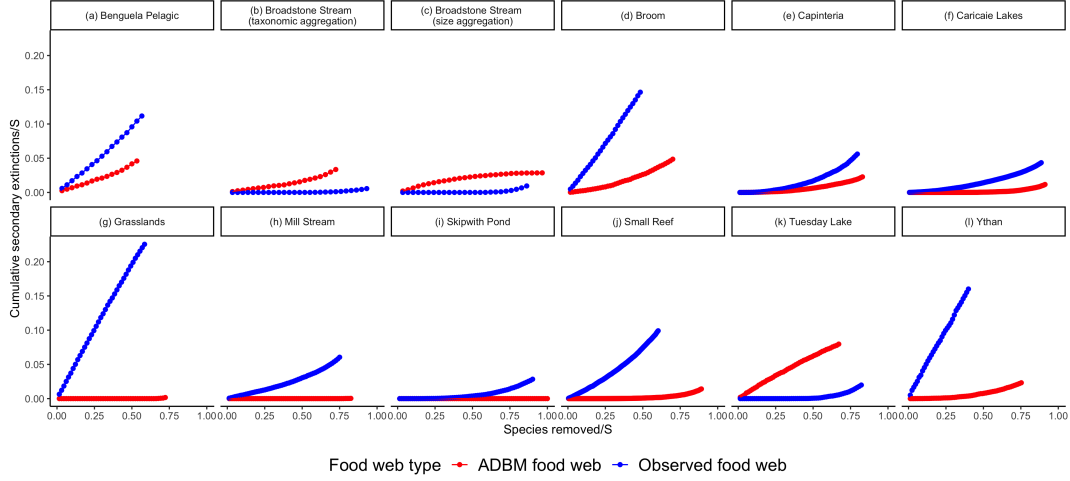


Figure 2: Mean cumulative secondary extinctions of species resulting from the primary removals of random species for 12 food webs. S denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number of species.

131 Except Broadstone Stream (taxonomic aggregation), Broadstone Stream (size aggregation)
 132 and Tuesday Lake food webs (Fig. 2 (b, c and k)), the mean cumulative secondary extinction curves
 133 for all the other food webs predicted by the ADBM were always lower than that of the observed
 134 food webs in the random extinction scenario. The shape of the cumulative secondary extinctions
 135 curves varied across the food webs.

136 Compared to the most connected and random extinction scenarios, the cumulative extinction
 137 curves in the least connected extinction scenario had very low values and were flat for most of the
 138 food webs (Fig. 3) compared to the most connected extinction and random extinction scenarios.
 139 In most of the food webs, there was a lot of overlap between the extinction curves of the ADBM
 140 predicted food webs and the observed food webs.

141 4.2 Show and describe the following:

142 I suggest to focus on the relationship between (difference in robustness between observed and
 143 predicted connectance) and (difference in robustness between the observed and predicted food web).

144 The ADBM predicted food webs were more robust than the observed food web with some
 145 exceptions (Fig. 4). The food webs were more robust to least connected and random extinction

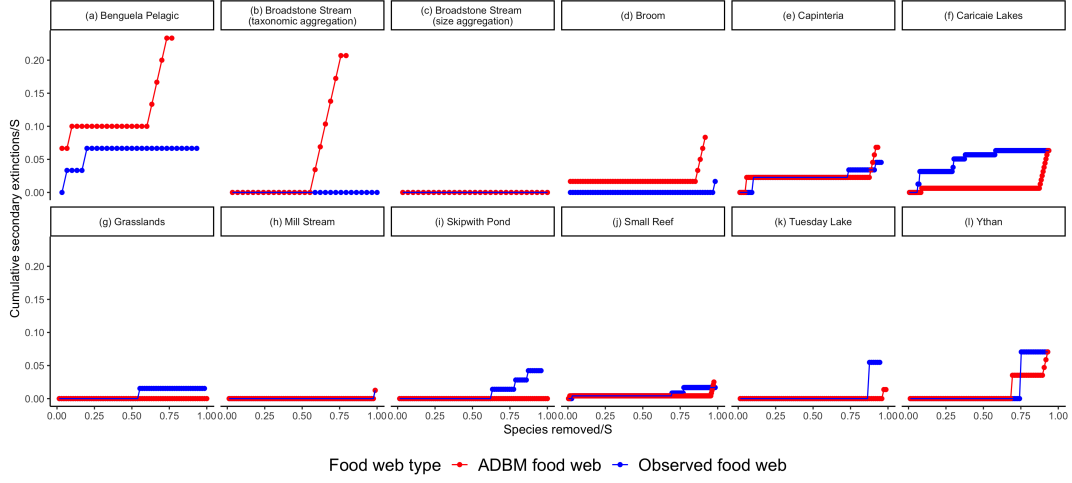


Figure 3: Cumulative secondary extinctions of species resulting from the primary removals of the least connected species for 12 food webs. S denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number of species.

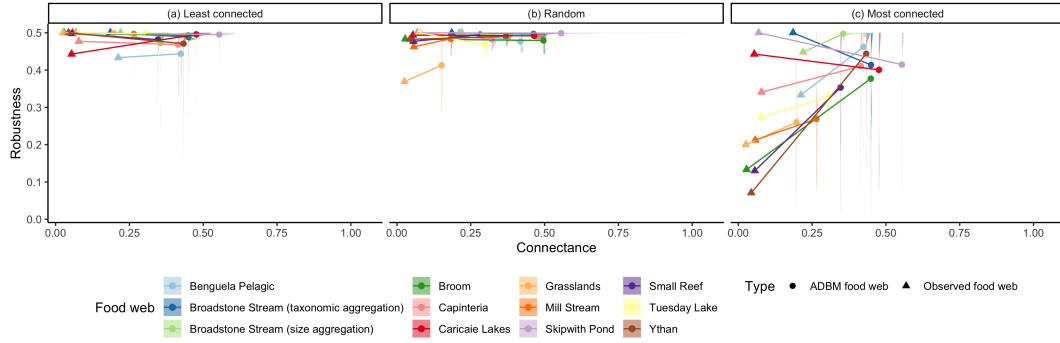


Figure 4: Robustness plots for 12 food webs across different ecosystems. Here, R_{50} is the proportion of species that have to be removed to achieve a total loss of at least 50% of total species (primary removals and secondary extinctions).

146 scenarios than the primary deletion of the most connected species. The difference in the robustness
 147 values between the ADBM predicted food webs and observed food webs was higher in the most
 148 connected extinction scenario as compared to the least connected extinction and random extinction
 149 scenarios.

150 AG: I will also add robustness plot for random extinction. It takes more time to compute.

151 5 Discussion

152 The primary removal of species revealed that the ADBM predicted food webs are more robust than
 153 the observed food webs, and the shape of the robustness extinction curves varies between food
 154 webs. The food webs are least robust to primary extinction of the most connected species scenario
 155 compared to that of least connected and random extinction scenarios. A future development would
 156 be to understand the stability of the dynamics of the ADBM predicted food webs and compare it
 157 with our study.

158 ...

159 5.1 What does overestimation of connectance imply in terms of stability?

160 For most of the food webs, the primary removals of species resulted in a higher secondary extinction
 161 in the ADBM predicted food webs than that of the observed food webs (Fig. 1, 2 and 3). This can
 162 be attributed to the higher connectance of the ADBM predicted food webs as compared to that of
 163 the observed food webs because a species in a food web with a high connectance has on average
 164 more number of trophic links as compared to the food webs with low connectance.

165 It would be intriguing to know if this difference in connectance has a similar influence in the
 166 dynamical stability of the food webs as well. Hence, a future prospect could be to use a dynamical
 167 model (for example: bioenergetic food web model (Brose, Williams, and Martinez 2006)) to model
 168 the temporal dynamics of the ADBM predicted food webs. It would be interesting to know the
 169 temporal stability of these ADBM predicted food webs compared to the observed food webs because
 170 it has been known that food webs with increasing connectance stability diminishes (May 1972).

171 ...

172 Include here the possibility that the increased connectance would influence dynamical stability,
 173 and state if and why this may increase or decrease stability.

174 **5.2 Explain that the ADBM can only predicts contiguous diets [OP] and the** 175 **implications of this**

176 Using only body size as a trait, the ADBM can only predict diets that are contiguous with respect
 177 to the size of the prey. I.e. it cannot predict that a predator will consume prey of size 1 and 3, and
 178 not consume prey of size 2. Also, it is important to note that the observed diets were not contiguous
 179 when prey are ordered by their size, and this is due to some ecological differences in how predator
 180 group choose their prey (Caron et al. 2022). So, the parameterisation process lead to a greater
 181 number of predicted links than observed.

182 This higher connectance in the ADBM predicted food webs has lead to a higher robustness
 183 of the ADBM predicted food webs. An important question to ask here is how reliable are these
 184 results. We suspect that this is because the model and the observed data are wrong to some extent.
 185 We expect that some of the links that do in reality occur are not present in the observed datasets,
 186 which is quite possible because of low sampling effort or rare prey-predator interactions even when
 187 there is intensive sampling. This would mean that the false positives may actually be a correctly
 188 predicted link.

189 We suspect that the model is also predicting links which actually do not occur. This is because
 190 the current ADBM model only takes body size trait, and therefore only predicts contiguous diet.
 191 That would mean any interaction that is not possible because of some other traits not correlated
 192 with the body size would still be predicted by the model. For example, a species might have a
 193 defensive trait that could result in the predator species not predating on that species at all.

194 AG: (Caution) Some of the texts might be very similar to or same as in C1 MS. With multiple
 195 iterations of the current ms, the current text would be altered. Also, the current ms would be
 196 checked using a plagiarism software before submission.

197 ...

198 **5.3 Compare the results from our study with results from other food web models** 199 **(Jennifer A. Dunne and Williams (2009))**

200 The findings from our study is similar to what had been documented for other food web models
 201 (Jennifer A. Dunne and Williams 2009), in terms of increase in the robustness when the connectance

of the food web is increased. A future study could be to understand the robustness of other food web models (“Inferring Food Web Structure from Predator–Prey Body Size Relationships - Gravel - 2013 - Methods in Ecology and Evolution - Wiley Online Library” n.d.) and compare it with our study. We expect similar results.

[OP] Including if and why we expect our findings to be replicated with those other models. Include some of Gravel and Poissot’s models

...

Need to coordinate this content with what I proposed on line 141.

Line 141 is “Include here the possibility that the increased connectance would influence dynamical stability, and state if and why this may increase or decrease stability.”

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