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# MISSING LINKS AND THE TOPOLOGICAL ROBUSTNESS OF FOOD WEBS

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A PREPRINT

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## Abstract

- 1        1) Undersampling can lead to missing trophic interactions in recorded food webs, with  
2            potential consequences for the perceived functioning and stability of the food webs.  
3            Undersampling can be compensated for by using food web models such as the allometric  
4            diet breadth model (ADBM) to predict missing links. Simultaneously, models might  
5            predict links which cannot occur, i.e., false positives.
- 6        2) Previous research shows that (i) food web robustness (the inverse of the number of  
7            secondary extinctions occurring due to primary extinctions) increases with connectance  
8            (the number of realised trophic links divided by the number of possible links), and  
9            (ii) that model predicted food webs usually have greater connectance than observed  
10          ones. Thus, we expect that predicted food webs are more robust than observed ones.  
11          However, this expectation has never, to our knowledge, been tested, nor has the effect

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size, i.e. the difference in robustness of predicted and observed food web with respect to the difference in their connectance, been quantified.

- 3) We fill this research gap by comparing the robustness of observed food webs to the robustness of food webs predicted by a model (the ADBM) that can account for missing links but does not predict all links correctly. We did this for 12 different food webs from a wide variety of ecosystems. We used three extinction scenarios: random, most connected, and least connected.
- 4) We found, as expected, that the predicted food webs were more robust than the observed food webs, which can be attributed to the higher connectance of the predicted food webs. On average, for every one unit of increase in connectance, we found that the food webs robustness increased by 0.52 units for the most connected species extinction scenario and by 0.04 units for the random species extinction scenarios. On the other hand, we saw no effect, on average, of increased connectance for the least connected species extinction scenario for all except two of the 12 food webs.
- 5) These results show that undersampling can lead to large underestimates of food web robustness that can be compensated for by filling in missing links with food web models. Nevertheless, increased connectance may contribute to lower dynamical stability, so it would be interesting to compare the dynamical stability of observed and predicted food webs and the topological stability that we have focused on.

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

## 1 Introduction

Anthropogenic changes such as climate change and habitat destruction are a threat to biodiversity and can lead to food web collapse (Ullah et al., 2018). This food web collapse is due to the cascades of secondary extinctions in a food web because of the primary loss of species due to environmental change (Pimm et al., 2006; C. D. Thomas et al., 2004; J. A. Thomas et al., 2004). An example of a secondary extinction is when a consumer goes extinct because its sole resource species goes extinct. Therefore, research focused on cascading secondary extinctions, also known as ‘community viability analysis’, has been performed extensively in the past few decades to quantify how robust food webs are to species extinction (Berg et al., 2011; Dunne et al., 2002a; Dunne & Williams, 2009; Ebenman et al., 2004; Ebenman & Jonsson, 2005). This research revealed that the rate of collapse of a food web depends on its structure and complexity (Dunne et al., 2002a; Dunne & Williams, 2009).

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 (Dunne

et al., 2002a; Dunne & Williams, 2009). Primary species loss is considered to be extinction of a species due to causes external to the food web, e.g. overharvesting (Koning & McIntyre, 2021), introduction of invasive species (David et al., 2017). A secondary extinction is an extinction caused by a previous extinction (either primary or secondary). Numerous studies have used topological criterion for assigning a secondary extinction to a species, i.e., if extinction is of the last resource species of a consumer species, then the consumer species suffers secondary extinction (Dunne et al., 2002a; Dunne & Williams, 2009; Sol'e & Montoya, 2001).

When there are few primary extinctions, and these cause many secondary extinctions, a food web is said to be fragile or not robust. In contrast, a food web is said to be robust when there are only a few secondary extinctions. Several studies have shown that the robustness of the food webs increases with food web connectance (Dunne et al., 2002b; Dunne & Williams, 2009). Additionally, these studies have demonstrated that the removal (primary extinction) of the most connected species causes considerably more secondary extinctions than the random removals of species (Dunne et al., 2002b; Sol'e & Montoya, 2001). Simulation studies like these, which investigate the impact of primary extinctions in a food web to quantify robustness based on its topological structure, provide an alternate solution to canonical experiments in natural ecosystems, which are not possible or very difficult to conduct (Dunne & Williams, 2009).

Along with quantifying food web robustness based on its topological structure, studies such as Williams (2008), Brose et al. (2006), and Martinez et al. (2006) have quantified robustness based on the abundance dynamics of a food web. However, the topological approach of quantifying a food web's robustness only requires the food web structure, whereas the dynamical approach requires the food web structure and the temporal dynamics of the abundance of species in that food web. For example, Williams (2008) combined network structure models with bioenergetic dynamics models to study the role of food web topology and nonlinear dynamics on species coexistence in complex ecological networks.

A key assumption of the observed food webs is that they are very well sampled, i.e. all the links that in reality can occur are represented. However, it is known that not all food webs are very well sampled and do not represent all of the feeding links that can occur (Caron et al., 2022; Jordano, 2016; Patonai & Jord'an, 2017). Some rare trophic links require more sampling effort than others, whereas some trophic links remain unobserved because of biological constraints such as spatio-temporal uncoupling, size or reward mismatching, foraging constraints and physiological-biochemical constraints, which are irrespective of sufficient sampling effort (Jordano, 2016). Previous studies such as Caron et al. (2022) and Gupta et al. (2022) have shown that the predicted food webs from these models usually have greater connectance than the observed ones. One solution to compensate for undersampling is using a food web model such as the Allometric Diet Breadth Model (ADBM) (Petchey et al., 2008) to predict the missing links and then measure the robustness of the predicted food web. The ADBM is a mechanistic model constructed using foraging rules based on the body sizes of prey and predator, where trophic interactions satisfying those rules would be predicted by the model, which are perhaps not observed because those interactions are rare. However, this solution is not infallible, as

it is likely that the food web model might still miss some links and also may predict some links that could not, in fact occur.

In our study, we investigate the topological robustness of the ADBM predicted food webs and compare it to that of the observed food webs. We expect the ADBM predicted food webs to be more robust than the observed food webs, and for the greater robustness to be related to the amount by which the ADBM predicts greater connectance compared to that of the observed food webs. We do this by simulating primary species loss in 12 food webs predicted by the ADBM to quantify the secondary loss of extinctions and compare the robustness of food webs predicted by the ADBM to the robustness of the observed food webs. We use three different approaches of primary species removal: (i) most connected species, (ii) random species and (iii) least connected species to understand if the outcome varies among these approaches.

## 2 Materials and methods

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

### 2.1 Allometric Diet Breadth Model (ADBM)

The allometric diet breadth model (ADBM) is based on optimal foraging theory, specifically the contingency model (MacArthur & Pianka, 1966). We chose this model because it is known to predict greater connectance in the predicted food webs compared to the observed food webs (Gupta et al., 2022). 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 used in the model are the energy content of prey, handling times of the predator on prey, space clearance rate, i.e. how fast a predator searches space, and prey densities. Each of these variables is derived from the allometric scaling relationship using the body sizes of species. More details on the foraging rules defined in the ADBM and ADBM’s predictive power across different food webs can be found in open access Petchey et al. (2008).

### 2.2 Food web data

The observed food webs that we fit the ADBM to belong to marine, freshwater and terrestrial ecosystems (Table 1). We considered these food webs because they belong to diverse ecosystems and follow FAIR (Findable Accessible Interoperable Reusable) principles (Wilkinson et al., 2016). These food webs contain primary producers, herbivores, carnivores, parasites, and parasitoids and various feeding interactions, including predation, herbivory, bacterivory, parasitism and pathogenic. The observed connectance of these food webs

111 varies from 0.03 to 0.24 (Links/Species<sup>2</sup>), and the number of species varies from 29 to 239. The goodness of  
112 fit of the ADBM's predictions depends on the interaction types in the food webs. For example, those with  
113 size-structured interactions, such as herbivory in aquatic ecosystems, are better predicted compared to less  
114 size-structured ones, such as parasitoids and terrestrial herbivory ones (Petchey et al., 2008).

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	Observed connectance (Links/Species <sup>2</sup> )	95% prediction interval of predicted connectance of the ADBM (Gupta et al. 2022)
Benguela Pelagic (Yodzis 1998)	Brose et al. (2005)	Marine	30	0.21	0.26 - 0.59
Broadstone Stream (taxonomic aggregation) (Woodward and Hildrew 2001; Woodward et al. 2005)	Brose et al. (2005)	Freshwater	29	0.19	0.18 - 0.72
Broom (Mommott et al. 2000)	Brose et al. (2005)	Terrestrial	60	0.03	0.12 - 0.89
Capintaria (Lafferty et al. 2006)	Hechinger et al. (2011)	Marine (Salt Marsh)	88	0.08	0.11 - 0.80
Caricaie Lakes (Cattin et al. 2004)	Brose et al. (2005)	Freshwater	158	0.05	0.11 - 0.81
Grasslands (Dawah et al. 1995)	Brose et al. (2005)	Terrestrial	65	0.03	0.03 - 0.44
Mill Stream (Ledger, Edwards, Woodward unpublished)	Brose et al. (2005)	Freshwater	80	0.06	0.08 - 0.60
Skipwith Pond (Warren 1989)	Brose et al. (2005)	Freshwater	71	0.07	0.17 - 0.90
Small Reef (Opitz 1996 Table 8.6.2)	Alyssa R. Cirtwill and Anna Eklöf (2018)	Marine (Reef)	239	0.06	0.07 - 0.66
Tuesday Lake (Jonsson et al. 2005)	Brose et al. (2005)	Freshwater	73	0.08	0.09 - 0.57
Ythan (Emmerson and Raffaelli 2004)	Alyssa R. Cirtwill and Anna Eklöf (2018)	Marine (Estuarine)	85	0.04	0.13 - 0.84
Broadstone Stream (size aggregation) (Woodward et al. 2010)	Guy Woodward (2021)	Freshwater	29	0.24	0.25 - 0.47

### 115 **2.3 Model parameterisation using approximate Bayesian computation**

116 The ADBM was parameterised using approximate Bayesian computation (ABC), where a set of  
 117 parameter values were sampled from a prior distribution. Then, that set of parameter values was  
 118 either accepted or rejected based on how close the predicted food web was to the observed food  
 119 web using an accuracy metric – true skill statistic (TSS). The accepted parameter values formed a  
 120 posterior distribution (Fig. 4 and S14-S25 in Gupta et al. (2022)). Further, prediction intervals of  
 121 the true skill statistic and connectance of the predicted food webs were computed (Fig. 5 (a, b) in  
 122 Gupta et al. (2022)). In our study, we considered model predicted food webs where the predicted  
 123 connectance lay within the 95% prediction interval of all model predicted food webs. A detailed  
 124 explanation of the parameterisation method can be found in Gupta et al. (2022).

### 125 **2.4 Extinction scenarios and robustness**

126 We implemented the primary species removal method from Dunne & Williams (2009) by sequentially  
 127 removing species using one of the three criteria: removal of (i) the most connected species, (ii) the  
 128 least connected species and (iii) randomly chosen species. The most connected and least connected  
 129 criteria are based on species’ degree (i.e. the total number of links to resources and from consumers).  
 130 We considered these three criteria because the random extinction scenario takes into account all  
 131 the theoretically possible extinction sequences of species that can occur in a food web, while the  
 132 extinction of the most connected species and least connected species takes into account the two  
 133 opposite extreme scenarios. These extinction scenarios have been widely used in studying species  
 134 extinctions and the collapse of food webs and other networks (Albert & Barab’asi, 2002; J. Dunne  
 135 et al., 2004; Dunne et al., 2002a; Dunne & Williams, 2009; Sol’e & Montoya, 2001).

136 Given a primary removal of species in a food web, if any remaining species lost all of their  
 137 resource species, or any cannibalistic species lost all of their resource species except the cannibalistic  
 138 links, they are removed from the web, and a secondary extinction was recorded. Secondary extinctions  
 139 may cause further secondary extinctions, which were also checked for and recorded. Once no more  
 140 secondary extinctions occurred, then another primary extinction was made of the next appropriate  
 141 species depending on the extinction scenario. This process was carried out until all the species were  
 142 extinct from the food web.

143 The robustness ( $R$ ) of a food web was defined as the proportion of species subjected to primary  
 144 removals resulting in extinction (primary and secondary extinctions) of some specified proportion  
 145 of the species. In our study, we use  $R_{50}$ , the number of primary extinctions divided by the total  
 146 number of species, which results in at least 50% of total species loss (J. Dunne et al., 2004; Dunne  
 147 et al., 2002a; Dunne & Williams, 2009; Jonsson et al., 2015). Therefore, if primary extinctions never  
 148 cause any secondary extinctions, the food web is maximally robust and ( $R_{50} = 0.50$ ). Whereas in  
 149 a minimally robust community ( $R_{50} = 1/S$ , where  $S$  is the number of species), the first primary  
 150 extinction causes a cascade of secondary extinctions of at least nearly half of the species in the food  
 151 web (i.e. at least  $S/2 - 1$ ).

## 152 2.5 Simulating species extinctions

153 First, we simulated primary species loss in food webs predicted by the ADBM which had the  
 154 maximum true skill statistics and compared it to primary species loss in observed food webs. Second,  
 155 to take into account the uncertainty in robustness in the ADBM predicted food webs, we simulated  
 156 primary species loss and thereby computed robustness for all the ADBM predicted food webs  
 157 corresponding to the 95% prediction interval of the predicted connectance. Furthermore, in the  
 158 case of the random extinction scenario, we simulated 1000 random extinction sequences in a single  
 159 ADBM predicted food web.

## 160 2.6 Analysis

161 In the random extinction scenario, we computed robustness  $R_{50}$  for all 1000 independent random  
 162 extinction sequences and calculated the median as a summary statistics to quantify the average  
 163 robustness of a single food web to random extinction. To quantify the effect of undersampling,  
 164 i.e. greater connectance of connectance, we compute the ratio of the difference in normalised  
 165 robustness between the ADBM predicted food webs and observed food webs to the difference in  
 166 their normalised connectance, where normalisation was performed by dividing the variables by their  
 167 maximum possible values (i.e. 0.5 for  $R_{50}$  and 1 for connectance). However, we did not perform any  
 168 statistical significance test because we work with simulated food webs and therefore, the p-values of  
 169 these tests are influenced by the number of model simulations (White et al., 2014).



### 3 Results

We first present the secondary extinction curves of the ADBM predicted food webs which had the maximum true skill statistics and of the observed food webs for 12 food webs under three different extinction scenarios. We then compare the robustness of all the ADBM predicted food webs within the 95% prediction interval against that of the observed food webs to take into account uncertainty in the robustness across food webs predictions. Finally, we quantify the effect of the difference in their connectance on the difference in their robustness estimates.

#### 3.1 Secondary extinctions

In the most connected extinction scenario, the cumulative secondary extinction curves started to rise steeply in the observed food webs at a lower number of primary species removal as compared to the ADBM predicted food webs for nine food webs (Fig. 1 (a, c, d, e, f, g, h, j, l)). However, there was a higher number of cumulative secondary extinctions occurring in the ADBM predicted food webs when compared to that of the observed food webs at a high number of primary species removal in five food webs (Fig. 1 (a, f, g, h, k)). In the Skipwith Pond food web, there were no secondary extinctions for any number of primary removal of species (Fig. 1 (i)), whereas in the Broadstone Stream (taxonomic aggregation) food web the same was true only for the observed food web but in the ADBM predicted food web there was a steep rise in the cumulative secondary extinctions (Fig. 1 (b)).

In Fig. 2, we present the cumulative secondary extinctions in the ADBM predicted and the observed food webs for five (out of 1000) independent random extinction sequences to show example variation caused by different random primary extinction orders. The secondary extinction curves of the ADBM predicted food webs were steeper than that of the observed food webs, i.e. primary removal of some species in an extinction sequence can lead to the complete collapse of the remaining food web in the ADBM predicted food webs.

Compared to the most connected and random extinction scenarios, there were fewer secondary extinctions in the least connected extinction scenario, and therefore the secondary extinction curves were flat for many of the food webs (Fig. 3). In some of the food webs, the extinction curves of the ADBM predicted food webs overlapped with the observed food webs (Fig. 3 (b, c, g, h, i, k, l)). In

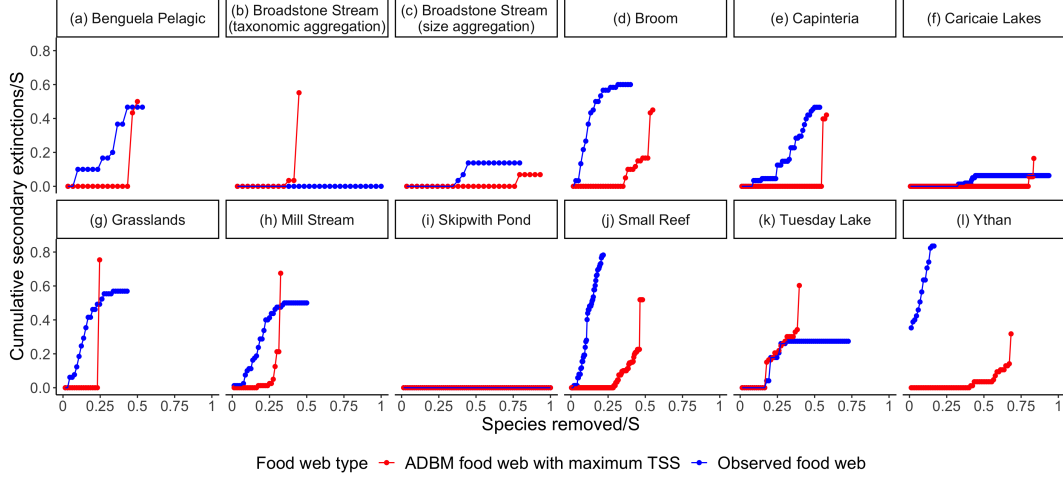


Figure 1: Cumulative secondary extinctions of species resulting from the primary removals of the **most connected species** in the ADBM predicted food webs corresponding to the maximum TSS and observed food webs.  $S$  denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number of species.

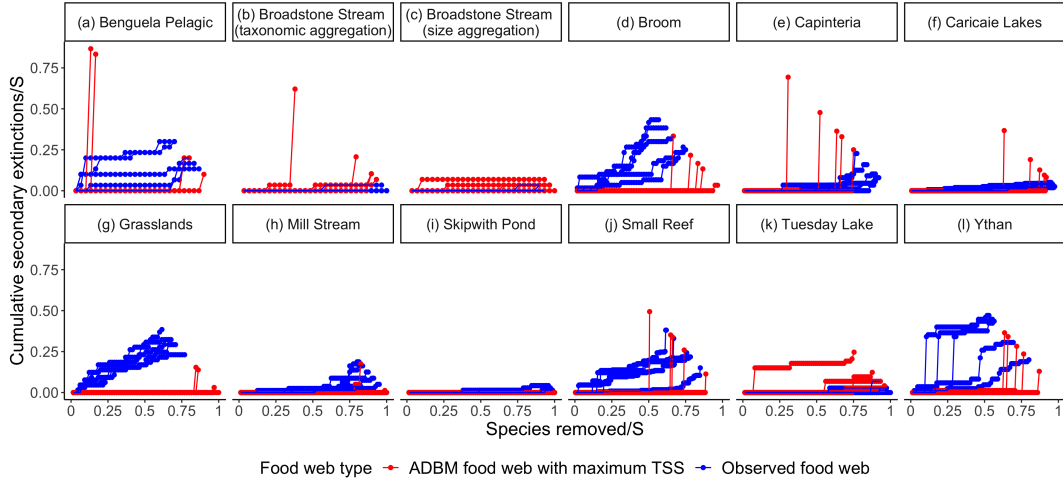


Figure 2: Cumulative secondary extinctions of species resulting from the primary removals of **random species** in the ADBM predicted food webs corresponding to the maximum TSS and observed food webs for five (out of 1000) independent random extinction sequences.  $S$  denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number of species.

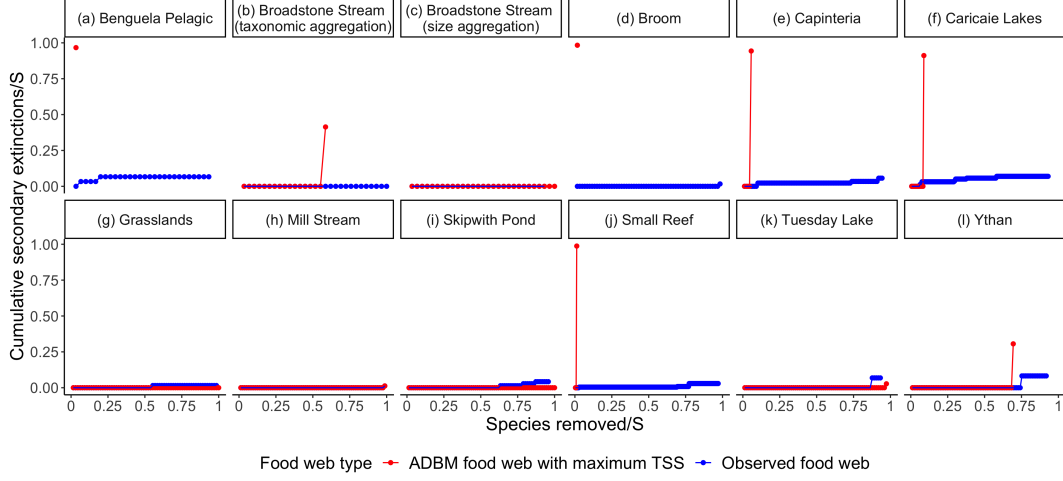


Figure 3: Cumulative secondary extinctions of species resulting from the primary removals of the **least connected species** in the ADBM predicted food webs corresponding to the maximum TSS and observed food webs.  $S$  denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number of species.

198 five of the food webs, a very high number of secondary extinctions occurred at a very low number of  
 199 primary species removal (Fig. 3 (a, d, e, f, j)).

### 200 3.2 Robustness

201 The ADBM predicted food webs were more robust than the observed food webs on average in the  
 202 most connected and random extinction scenarios (Fig. 4 (a, b)). However, there were large variations  
 203 in the robustness within the ADBM predicted food webs in the most connected extinction scenario  
 204 (Fig. 4 (a)). For example, the ADBM predicted Caricaie Lakes food web was more robust than  
 205 the observed food web on average but had a larger variation in the robustness within the ADBM  
 206 predicted food webs compared to other food webs.

207 The food webs were more robust to the random extinction scenario than the most connected  
 208 scenario (Fig. 4 (a, b)). Small Reef and Benguela Pelagic food webs had more variations in robustness  
 209 within the ADBM predicted food webs as compared to the other food webs (Fig. 4 (b)). Skipwith  
 210 Pond, Broadstone Stream (taxonomic aggregation) and Broadstone Stream (size aggregation) food  
 211 webs were the most robust (Median  $R_{50} = 0.5$ ) for both ADBM predicted and observed food webs.

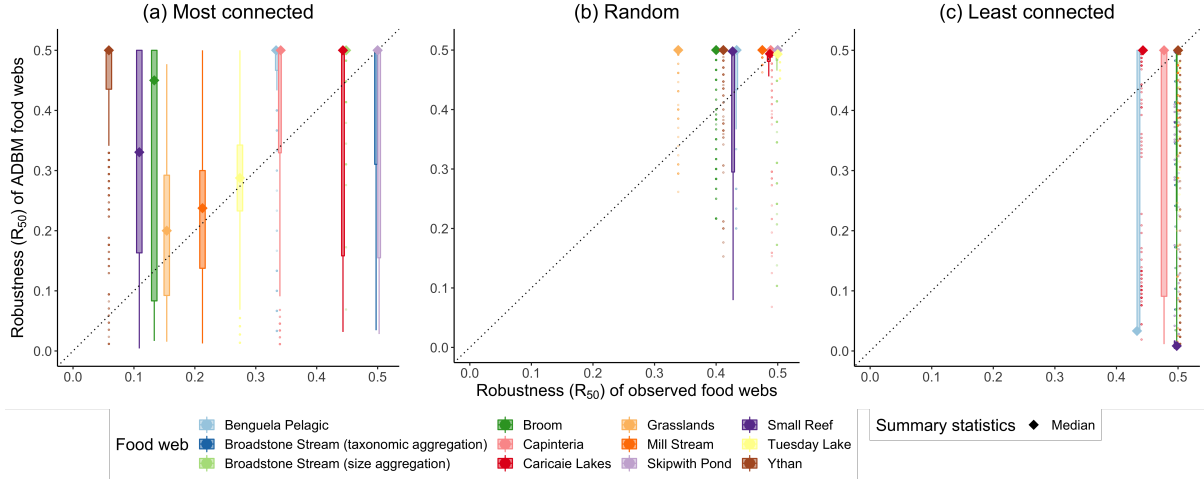


Figure 4: Robustness comparison between the ADBM predicted food webs and the observed food webs for 12 food webs across different ecosystems. Here,  $R_{50}$  is the proportion of species that have to be removed to achieve a total loss of at least 50% of total species (primary removals and secondary extinctions). Box represent the 25th and 75th percentile; solid diamond represents the median; whisker represents outlier limits; the outlier coefficient used was 1.5. Some points are not visible due to perfect overlap in b and c. Refer to Fig. 7 in the Supplementary Information for a faceted visualisation. The dashed black lines are the 1:1 relationships for reference.

212 Although there were few less robust ADBM predicted food webs in the Broadstone Stream (size  
 213 aggregation) as shown by the outliers. The food webs were more robust to the random extinction  
 214 scenario than the most connected scenario (Fig. 4 (a, b)). Small Reef and Benguela Pelagic food  
 215 webs had more variations in robustness within the ADBM predicted food webs as compared to the  
 216 other food webs (Fig. 4 (b)). Skipwith Pond, Broadstone Stream (taxonomic aggregation) and  
 217 Broadstone Stream (size aggregation) food webs were the most robust (Median  $R_{50} = 0.5$ ) for both  
 218 ADBM predicted and observed food webs. Although there were few less robust ADBM predicted  
 219 food webs in the Broadstone Stream (size aggregation) as shown by the outliers.

220 In the least connected extinction scenario, the food webs had a very high robustness (Median  
 221  $R_{50} = 0.5$ ) for most of the food webs (Fig. 4 (c)), however there were some exceptions. The ADBM  
 222 predicted food webs for Small Reef and Benguela Pelagic had very low median robustness. Benguela  
 223 Pelagic, Broom and Capinteria food webs from the ADBM had larger variations in robustness when  
 224 compared to that of the others.

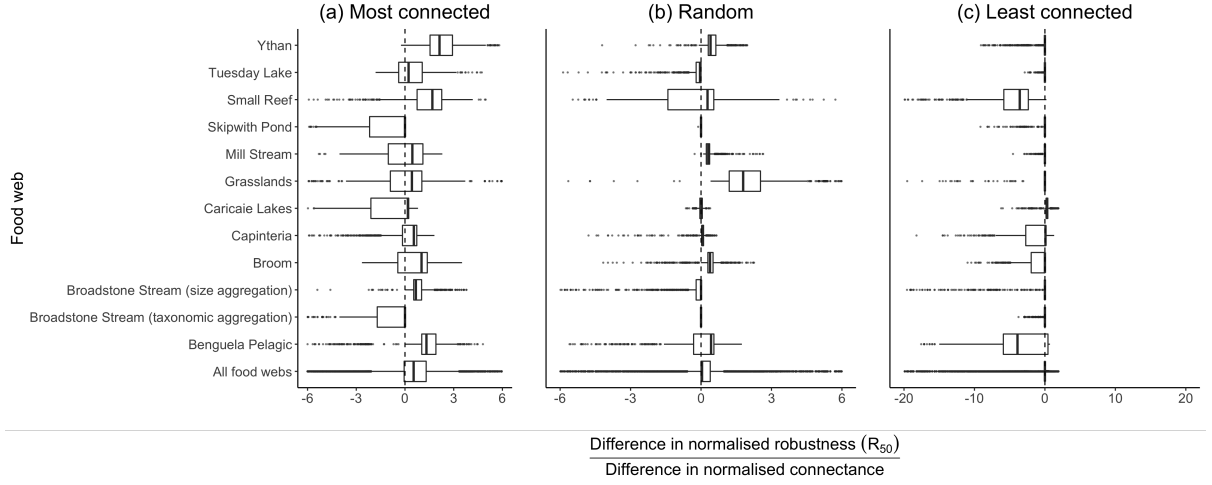


Figure 5: Effect size (i.e. ratio of the difference in normalised robustness between ADBM predicted food webs and observed food webs to the difference in their normalised connectance) shown for the 12 food webs. Box represent the 25th and 75th percentile; bold black midline represents the median; whisker represents outlier limits; the outlier coefficient used was 1.5.

In all of the food webs except Small Reef and Broadstone Stream (taxonomic aggregation), the effect size of connectance on robustness was positive on average in the most connected extinction scenario (Fig. 5 (a)), i.e. greater connectance had a positive effect on the robustness. In the random extinction scenario, there was a positive effect of greater connectance on the robustness for Ythan, Small Reef, Mill Stream, Grasslands, Caricaie Lakes, Capinteria, Broom and Benguela Pelagic (Fig. 5 (b)). However, the effect size varied across the food webs. In the least connected extinction scenario, the median effect sizes were zero or very close to zero for all the food webs except Benguela Pelagic and Small Reef food webs where the median effect sizes were negative (Fig. 5 (c)). However, there were lots of outlier effect sizes less than zero.

## 4 Discussion

As expected, the ADBM predicted food webs were more robust than the observed food webs on average. The considerable variation of the robustness of the ADBM predicted food webs suggests, however, that undersampling in food webs can lead to considerable uncertainty in the estimates of food web robustness, even when a model is used to compensate for undersampling. Furthermore, as was previously found, the food webs are least robust to primary extinction of the

most connected species compared to that of least connected and random extinction scenarios on average. Future development would be to understand how undersampling, i.e. predicted greater connectance, influences the stability of the dynamics of the ADBM predicted food webs against that of the observed food webs and compare it with the patterns in our study in which extinction occur only by topological criteria. However, one would expect a decrease in food web stability with greater connectance (Martinez et al., 2006; May, 1972).

As mentioned, the robustness of the ADBM predicted food webs was higher than that of the observed food webs on average (Fig. 4) for all of the 12 food web ecosystems (with some exceptions). This is likely due to the greater connectance of the ADBM predicted food webs as compared to that of the observed food webs because a species in a food web with a higher connectance has, on average, more trophic links as compared to a food web with a lower connectance (Fig. 5). Our study suggests that it is important to consider undersampling in observed food webs when computing their robustness.

Contrary to general expectations (Dunne et al., 2002b), food web robustness did not always increase with the connectance (Fig. 5). For example, the Benguela Pelagic and Small Reef ADBM predicted food webs were surprisingly less robust to primary extinctions on average in the least connected extinction scenario compared to the observed food webs (Fig. 4 (c) and 5 (c)). In these two food webs, the extinction of the least connected species could cause an almost complete, or complete collapse of the food web. We suspect this is because the ADBM predicted food webs have a lower proportion of basal species when compared to that of the observed food webs (Fig: 6 (a) in Gupta et al. (2022)). As a result, these low-degree basal species are the ones to be removed at an early stage in the deletion sequence, thereby resulting in an earlier food web collapse in the ADBM predicted food web as compared to that of the observed food web (Fig: 3 (a) and (j)). This suggests that the greater connectance predicted by the ADBM resulted in a more robust food web on average. However, differences in the predicted food web properties, such as a lower proportion of basal species and higher maximum trophic level (Fig: 6) when compared to that of the predicted food webs counteracted that effect and led to reduced robustness. On average, a consumer in a food web with a higher maximum trophic level would have fewer resources and be more susceptible to extinction than a consumer in a food web with a lower maximum trophic level (Binzer et al., 2011). This suggests that food web properties other than connectance play an important role in

determining a food web’s robustness and, therefore, should also be taken into account (Binzer et al., 2011; Mendonça et al., 2022; Riede et al., 2011).

As with any food web model, we expect that there are real false positives in the food webs predicted by the ADBM. Real false positive means that the food web model predicts a link between two species that can never interact. (The other type of false positive is when the model predicts a link that was not observed but could have been observed if the food web was sampled enough. In this case, further sampling should result in the link being observed and a change from false positive to true positive.) Firstly, this may be because the ADBM uses only body size as a trait. A trait uncorrelated with the body size may be influential in determining the interaction between two species (Gupta et al., 2022). Secondly, the ADBM can only predict diets that are contiguous with respect to the size of the prey. I.e. it cannot predict that the consumer will consume prey of size 1 and 3, and not consume prey of size 2. However, it is important to note that observed diets are not always contiguous when prey are ordered by their size due to some ecological differences in how predator species choose their prey (Caron et al., 2022). Hence, it would be intriguing to extend our study to use other food web models based on size-based rules, such as Gravel et al. (2013) and Vagnon et al. (2021), to understand if the results are dependent on the decision of model selection. We expect to get a similar result in a size-based deterministic model but a different result, i.e. lower robustness in a size-based stochastic model as compared to the ADBM because the latter can take into account non-contiguity in predator diets (Williams et al., 2010). It would also be interesting to use food web models not based on body size, such as Cattin et al. (2004) and Allesina et al. (2008). We expect to have a difference in results based on whether the trophic interactions in the food webs are governed by size-structured rules or not.

It would be intriguing to know if this difference in connectance has a similar influence on the dynamical stability of the food webs as well. Hence, a prospect could be to use a dynamical model (for example, the bioenergetic food web model by Brose et al. (2006)) to model the temporal dynamics of the ADBM predicted food webs. We expect that the greater connectance will lead to reduced dynamical stability in the ADBM predicted food web compared to that of the predicted food web. The difference in stability will be linearly related to the difference in connectance because Martinez et al. (2006) has shown that food web stability linearly decreases with connectance.

Since the ADBM predicted food webs have a lower proportion of basal species and a higher maximum trophic level as compared to that of the observed food webs (Fig: 6 (a) in Gupta et al. (2022) and Fig. 6 in Supplementary Information), it would be interesting to use these properties as summary statistics to parameterise the ADBM and investigate how that influences the difference in the robustness between the ADBM predicted and the observed food webs. We would expect a more highly constrained predicted food web structure, lower variation in robustness, and a greater apparent influence of connectance on robustness.

We have used a food web model to compensate for undersampling in recorded food webs and thereby quantified the influence of missing links, i.e. greater connectance on the topological robustness of 12 food webs from various ecosystems. We found that the greater connectance can have a large impact on the robustness of the food webs while at the same time producing large variations in robustness among the predicted food webs. Furthermore, differences in other structural food web properties between the ADBM predicted food webs and the observed food webs are also responsible.

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## 6 Conflict of interest

None declared

## 7 Author contributions

**Anubhav Gupta:** Conceptualisation; Data curation; Formal analysis; Investigation; Methodology; Project administration; Software; Validation; Writing – original draft; Writing – review and editing.  
**Owen L. Petchey:** Conceptualization; Funding acquisition; Resources; Supervision; Writing – review & editing.



## 324 8 Data Accessibility Statement

325 All the data used in this study was collected in other studies and is openly available. We list those  
 326 studies and the open access source in Table 1. The complete code used in the analysis is available in  
 327 the repository <https://doi.org/10.5281/zenodo.7180835>.

## 328 9 Supplementary Information

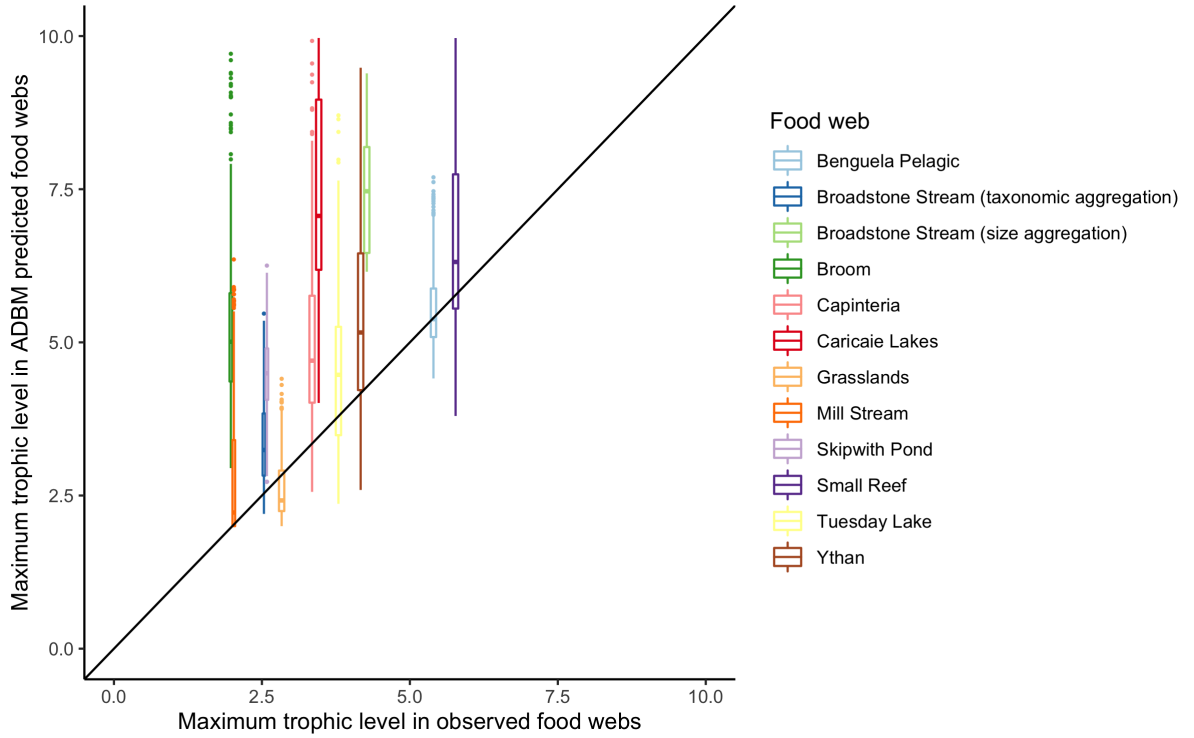


Figure 6: The maximum trophic level of ADBM predicted food webs plotted against that of the observed food webs. Box represent the 25th and 75th percentile; bold midline represents the median; whisker represents outlier limits; the outlier coefficient used was 1.5. The dashed black lines are the 1:1 relationships for reference.

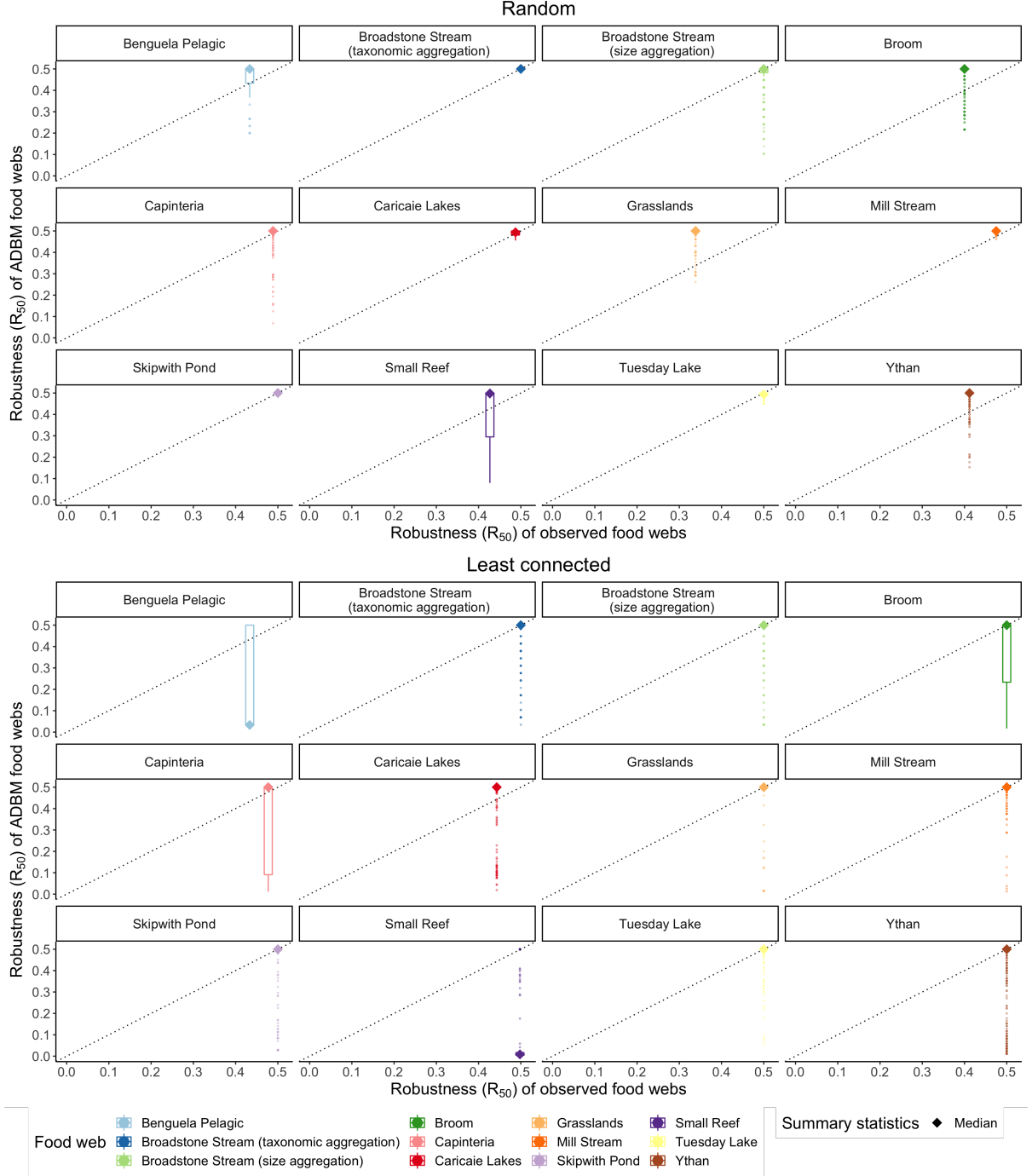


Figure 7: Robustness comparison between the ADBM predicted food webs and the observed food webs for 12 food webs across different ecosystems for random and least connected extinction scenarios. Here,  $R_{50}$  is the proportion of species that have to be removed to achieve a total loss of at least 50% of total species (primary removals and secondary extinctions). Box represent the 25th and 75th percentile; solid diamond represents the median; whisker represents outlier limits; the outlier coefficient used was 1.5. The dashed black lines are the 1:1 relationships for reference.

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