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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       This expectation has never, to our knowledge, been tested, nor has the effect size been  
12       quantified.

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- 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, though which 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, and this can be attributed to the higher connectance of the predicted food webs. On average, for every one unit of increase in connectance, we found the food webs to be robust by 0.52 units and 0.04 units for the most connected and the random species extinction scenarios respectively while no effect in the least connected species extinction scenario.
- 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, and so it would be interesting to compare the dynamical stability of observed and predicted food webs, as well as 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, for example due to habitat destruction and climate change (Pimm et al. 2006; J. A. Thomas et al. 2004; C. D. Thomas et al. 2004). An example of a secondary extinction is when a consumer goes extinction because its sole resource species goes extinct. Therefore, research focused on cascading secondary extinctions also known as ‘community viability analysis’ have been performed extensively in the past few decades to quantify how robust are food webs to species extinction (Jennifer A. Dunne, Williams, and Martinez 2002b; Jennifer A. Dunne and Williams 2009; Berg et al. 2011; Ebenman, Law, and Borrvall 2004; Ebenman and Jonsson 2005). This research revealed that the rate of collapse of a food web is dependent on its structure and complexity (Jennifer A. Dunne, Williams, and Martinez 2002b; Jennifer A. Dunne and 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 (Jennifer A. Dunne, Williams, and Martinez 2002b; Jennifer A. Dunne and Williams 2009). Primary species loss is considered to be extinction of a species due to causes external to the food web. In research with

models, the specific cause or causes are usually not specified. Overharvesting of a population which causes extinction could be considered a driver of a primary extinction. A secondary extinction is an extinction caused by a previous extinction (either primary or secondary). Numerous studies have used a topological criteria for assigning a secondary extinction to a species, i.e., if an extinction is of the last resource species of a consumer species, then the consumer species suffers secondary extinction because it has no resources.

When there are few primary extinctions, and these cause many secondary extinctions, a food web is said to be fragile or not robust. When there are few secondary extinctions, a food web is said to be robust. Several studies have shown that the robustness of the food webs increases with food web connectance. Also, the removal (primary extinction) of the most connected species cause considerably more secondary extinctions than the random removals of species (Jennifer A. Dunne, Williams, and Martinez 2002a; Sol'e and 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 (Jennifer A. Dunne and Williams 2009).

Along with quantifying food web robustness based on its topological structure, studies such as Williams (2008), Brose, Williams, and Martinez (2006) and Martinez, Williams, and Dunne (2006) have quantified robustness based on the abundance dynamics of a food web. The topological approach of quantifying a food web robustness only requires the food web structure whereas the dynamical approach not only requires the food web structure but also the temporal dynamics of abundance of species in that food web. For example: Williams (2008) combined models of network structure with models of bioenergetic dynamics 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 then do not represent all of the feeding links that can occur (Caron et al. 2022; Patonai and Jord'an 2017; Jordano 2016). Some rare trophic links require more sampling effort as compared to others, whereas some trophic links remain unobserved because of linkage constraints irrespective of sufficient sampling effort (Jordano 2016). Previous studies such as Caron et al. (2022) and Gupta, Furrer, and Petchey (2022) have shown that the predicted food webs from these models usually have greater connectance than the observed ones. Therefore, one solution to compensate for undersampling is to use a food web model such as the Allometric Diet Breadth Model (ADBM) to predict the missing links, and to 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 as compared to the observed food webs, and for the greater robustness to be related to the amount by which the ADBM overestimates connectance. We do this by simulating primary species loss in 12 food webs predicted from the ADBM to quantify the secondary loss of extinctions. 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 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 to 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 and Pianka 1966). We chose this model because we have already used it to predict missing links in the predicted food webs, whereby it consistently overestimated connectance Gupta, Furrer, and Petchey (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 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. These food webs contain primary producers, herbivores, carnivores, parasites, and parasitoids and also contain various types of feeding interactions, including predation, herbivory, bacterivory, parasitism and pathogenic. The observed connectance of these food webs varies from 0.03 to 0.24 and the number of species varies from 29 to 239 species.

The goodness of fit of the ADBM’s predictions depends on the interaction types in the food webs. Those with size-structured interactions, such as herbivory in aquatic ecosystems interactions being better predicted

when compared to less 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	95% prediction interval of predicted connectance (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
Capinteria (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

### 113 **2.3 Model parameterisation using approximate Bayesian computation**

114 The ADBM was parameterised using approximate Bayesian computation (ABC) where a set of  
 115 parameter values were sampled from the prior distributions. That set of parameter values was either  
 116 accepted or rejected based on how close the predicted food web is to the observed food web using an  
 117 accuracy metric – true skill statistic (TSS). The accepted parameter values then formed a posterior  
 118 distribution. Further, prediction intervals of the true skill statistic and connectance of the predicted  
 119 food webs were computed. In our study, we considered food webs where the predicted connectance  
 120 lay within the 95% prediction interval. A detailed explanation of the parameterisation method can  
 121 be found in Gupta, Furrer, and Petchey (2022).

### 122 **2.4 Extinction scenarios and robustness**

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

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

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

## 150 2.5 Simulating species extinctions

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

## 158 2.6 Analysis

159 In the random extinction scenario, we computed robustness  $R_{50}$  for all 1000 independent random  
 160 extinction sequences and calculated the median as a summary statistics to quantify the average  
 161 robustness of a single food web to random extinction. To quantify the effect of undersampling,  
 162 i.e. overestimation of connectance, we compute the ratio of the difference in normalised robustness  
 163 between the ADBM predicted food webs and observed food webs to the difference in their normalised  
 164 connectance, where normalisation was performed by dividing the variables by their maximum  
 165 possible values (I.e 0.5 for  $R_{50}$  and 1 for connectance). However, we did not perform any statistical  
 166 significance test because we work with simulated food webs and therefore the p-values of these tests  
 167 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 overestimation of 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 at a lower number of primary species removal in the observed food webs 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 were 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 as compared to that of the observed food webs i.e. primary removal of some species in an extinction sequence can lead to 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

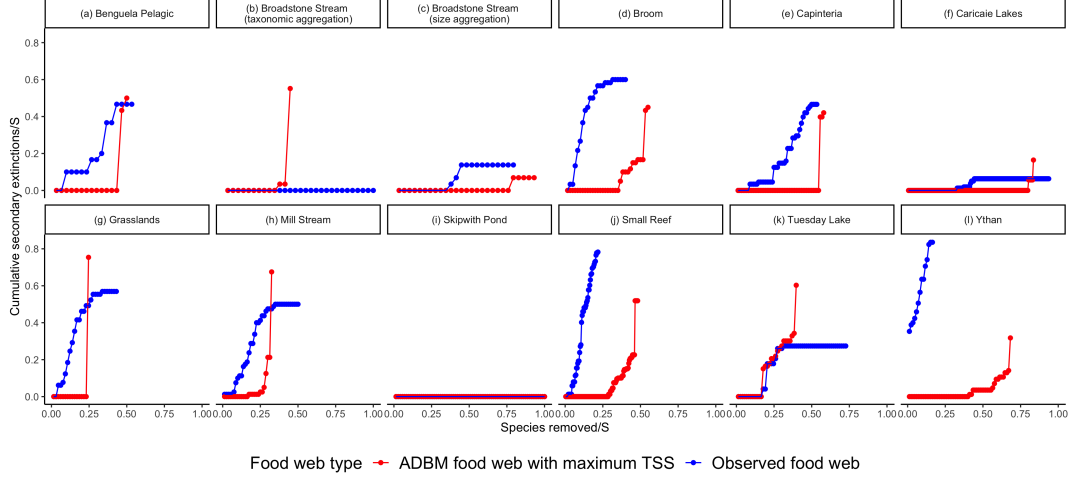


Figure 1: Cumulative secondary extinctions of species resulting from the primary removals of the **most connected species** in the ADBM predicted food webs corresponding to the maximum TSS and observed food webs.  $S$  denotes the number of species in a food web. The cumulative secondary extinctions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

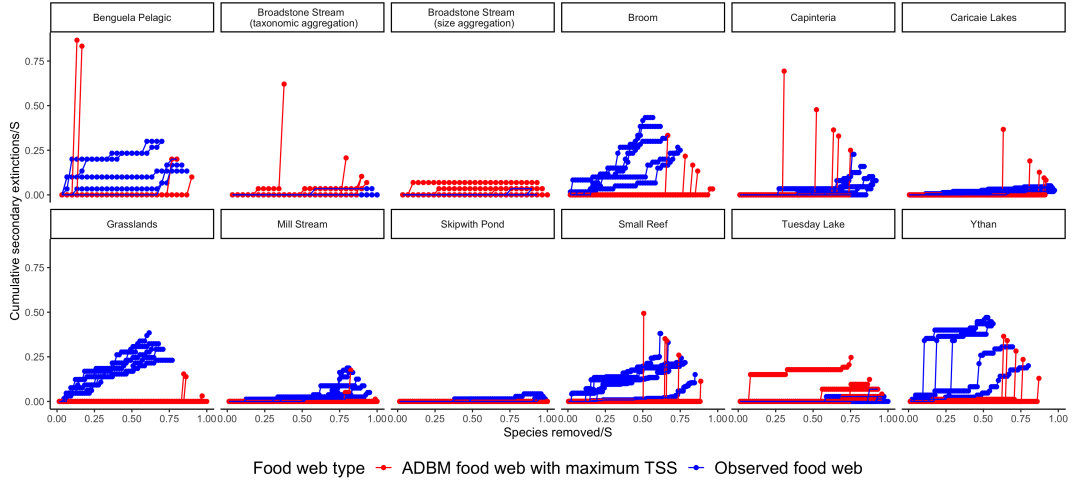


Figure 2: Cumulative secondary extinctions of species resulting from the primary removals of **random species** in the ADBM predicted food webs corresponding to the maximum TSS and observed food webs for five independent random extinction sequences.  $S$  denotes the number of species in a food web.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

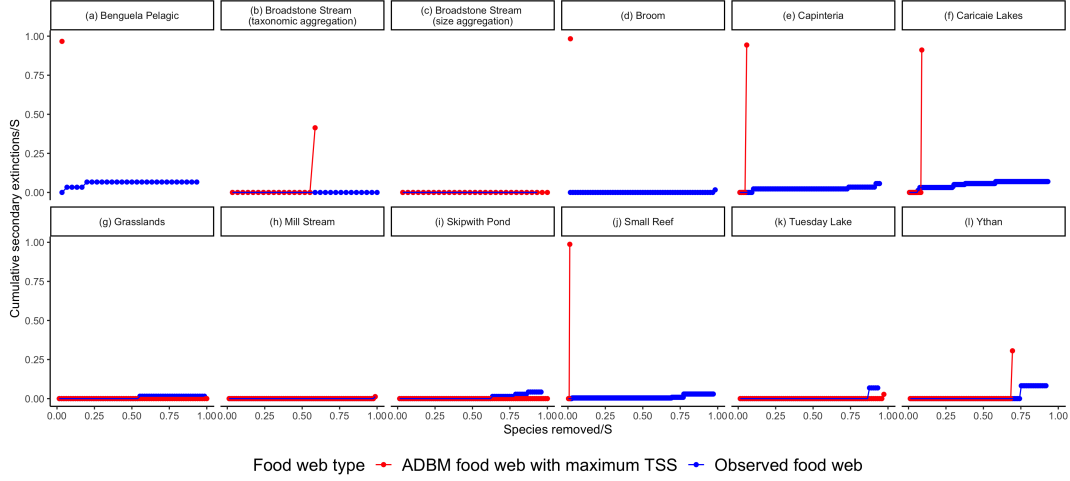


Figure 3: Cumulative secondary extinctions of species resulting from the primary removals of the **least connected species** in the ADBM predicted food webs corresponding to the maximum TSS and observed food webs.  $S$  denotes the number of species in a food web. The cumulative secondary extinctions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

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

### 198 3.2 Robustness

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

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

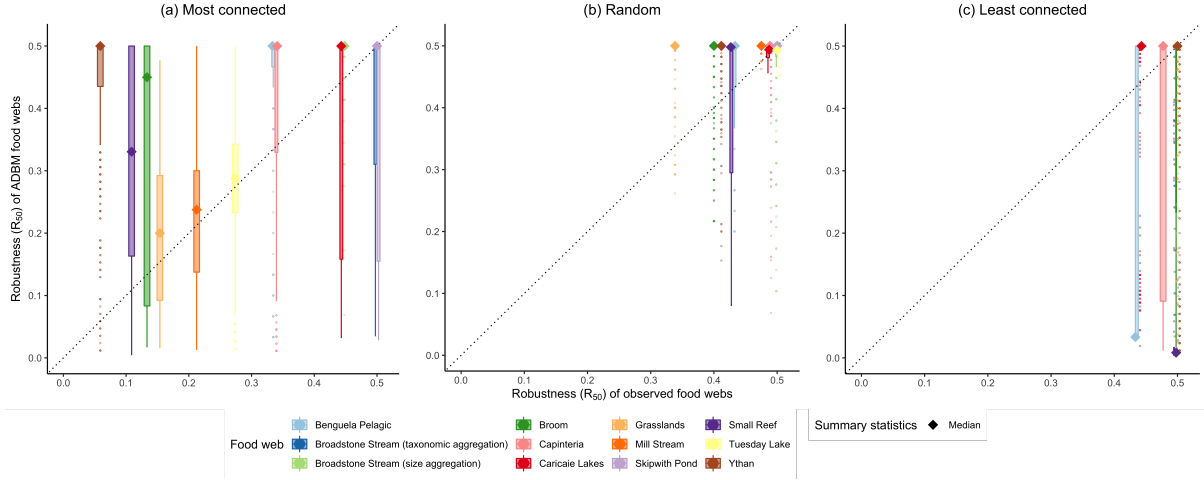


Figure 4: Robustness comparison between the ADBM predicted food webs and the observed food webs for 12 food webs across different ecosystems. Here,  $R_{50}$  is the proportion of species that have to be removed to achieve a total loss of at least 50% of total species (primary removals and secondary extinctions). Box represent 25th and 75th percentile; solid diamond represent median; whisker represent 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.

210 Although there were few less robust ADBM predicted food webs in the Broadstone Stream (size  
211 aggregation) as shown by the outliers.

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

217 In all of the food webs except Small Reef and Broadstone Stream (taxonomic aggregation), the  
218 effect size of connectance on robustness was positive on average in the most-connected extinction  
219 scenario (Fig. 5 (a)) i.e. overestimation of connectance had a positive effect on the robustness. In  
220 the random extinction scenario, there was a positive effect of overestimation of connectance on  
221 the robustness for Ythan, Small Reef, Mill Stream, Grasslands, Caricaie Lakes, Capinteria, Broom  
222 and Benguela Pelagic (Fig. 5 (b)). However, the effect size varied across the food webs. In the  
223 least-connected extinction scenario, the median effect sizes were zero or very close to zero for all the

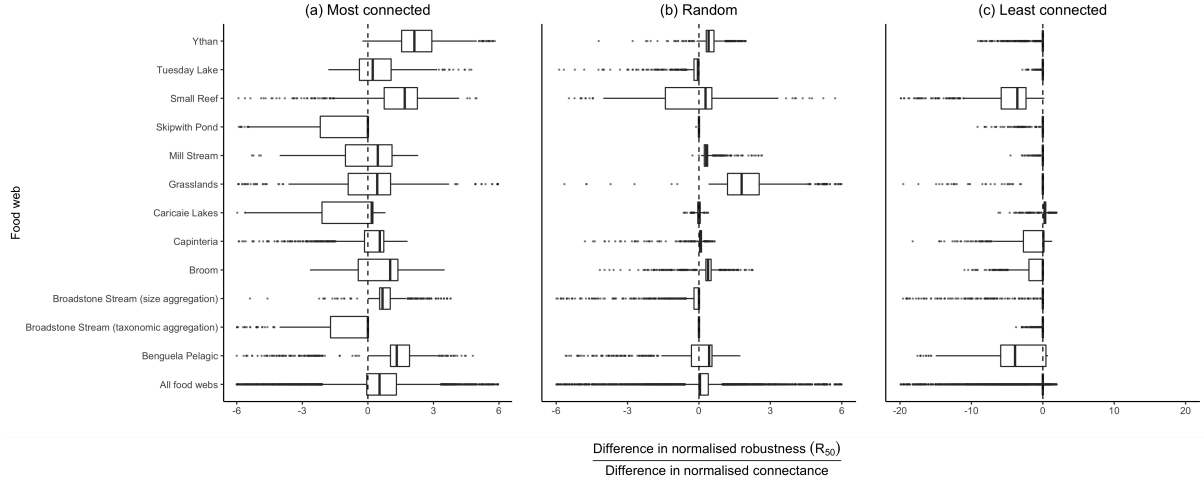


Figure 5: Effect size (i.e ratio of difference in normalised robustness between ADBM predicted food webs and observed food webs to difference in their normalised connectance) shown for the 12 food webs. Box represent 25th and 75th percentile; black bold midline represent median; whisker represent outlier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

224 food webs except Benguela Pelagic and Small Reef food webs where the median effect sizes were  
 225 negative (Fig. 5 (c)). However, there were lots of outlier effect sizes less than zero.

## 226 4 Discussion

227 As expected, the ADBM predicted food webs were more robust than the observed food webs on  
 228 average. The considerable variation of the robustness of the ADBM predicted food webs suggests,  
 229 however, that undersampling in food webs can lead to considerable uncertainty in the estimates of  
 230 food web robustness, even when a model is used to compensate for undersampling. As was previously  
 231 found, the food webs are least robust to primary extinction of the most connected species compared  
 232 to that of least connected and random extinction scenarios on average. A future development would  
 233 be to understand how undersampling, i.e. overestimation of connectance, influences the stability  
 234 of the dynamics of the ADBM predicted food webs against that of the observed food webs, and  
 235 compare it with the patterns in our study in which extinction occur only by topological criteria.  
 236 However one would expect a decrease in food web stability with overestimation of connectance  
 237 (Martinez, Williams, and Dunne 2006; May 1972).

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

245 The findings from our study are similar to what had been documented for other food web  
 246 models (Jennifer A. Dunne and Williams 2009), in terms of an increase in the robustness when  
 247 the connectance of a food web is increased. However, contrary to general expectations (Jennifer  
 248 A. Dunne, Williams, and Martinez 2002a), food web robustness did not always increase with the  
 249 connectance (Fig. 5). For example: the Benguela Pelagic and Small Reef food webs were surprisingly  
 250 less robust to primary extinctions on average in the least-connected extinction scenario (Fig. 4  
 251 (c) and 5 (c)). In these two food webs, extinction of the least connected species could cause an  
 252 almost complete, or complete collapse of the food web. We suspect this is because the ADBM is  
 253 underestimating the proportion of basal species in the predicted food webs when compared to that  
 254 of the observed food webs (Fig: 6 (a) in Gupta, Furrer, and Petchey (2022)). As a result, these low  
 255 degree basal species are the ones to be removed at an early stage in the deletion sequence thereby  
 256 resulting in an earlier food web collapse in the ADBM predicted food web as compared to that of  
 257 the observed food web (Fig: 3 (a) and (j)). This suggests that the overestimation of connectance by  
 258 the ADBM resulted in a more robust food web on average but differences in the predicted food web  
 259 properties such as underestimation of the proportion of basal species, and overestimation of the  
 260 maximum trophic level (Fig: 6) counteracted that effect and led to reduced robustness because a  
 261 consumer in a food web with a higher maximum trophic level on average would have more resources  
 262 and be less susceptible to extinctions as compared to consumer in a food web with lower maximum  
 263 trophic level. This suggests that food web properties other than connectance play an important role  
 264 in determining the robustness of a food web and therefore should be also taken into account (Binzer  
 265 et al. 2011; Mendonça et al. 2022; Riede et al. 2011).

266 As with any food web model, we expect that there are real false positives in the food webs  
 267 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 when it could have been observed. 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, Furrer, and Petchey 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 similar result in a size-based deterministic model but a different result i.e. underestimation of robustness in a size-based stochastic model because the latter can take into account non contiguity in predator diets (Williams, Anandanadesan, and Purves 2010). It would also be interesting to use food web models which are not based on body size such as Cattin et al. (2004) and Allesina, Alonso, and Pascual (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 bioenergetic food web model by Brose, Williams, and Martinez (2006)) to model the temporal dynamics of the ADBM predicted food webs. We expect that the overestimation of connectance will lead to reduced dynamical stability in the ADBM predicted food web as compared to that of the predicted food web and the difference in stability will be linearly related to the difference in connectance because Martinez, Williams, and Dunne (2006) have shown that food web stability linearly decreases with connectance.

Since the ADBM underestimates the proportion of basal species and overestimates the maximum trophic level in the predicted food webs compared to that of the observed food webs (Fig: 6 (a) in Gupta, Furrer, and Petchey (2022) and Fig. 6 in Supplementary Information), it would be interesting to use these properties as summary statistics to parameterise the ADBM and investigate

298 how that influences the difference in the robustness between the ADBM predicted and the observed  
 299 food webs. We would explain more highly constrained predicted food web structure, lower variation  
 300 in robustness, and a greater apparent influence of connectance on robustness.

301 We have used a food web model to compensate for undersampling in recorded food webs  
 302 and thereby quantified the influence of missing links i.e. overestimation of connectance on the  
 303 topological robustness of 12 food webs from various ecosystems. We found that the overestimation  
 304 of connectance can have large impacts on the robustness of the food webs, while at the same  
 305 time producing large variation in robustness among the predicted food webs. Differences in other  
 306 structural food web properties between the ADBM predicted food webs and the observed food webs  
 307 are responsible.

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## 311 6 Conflict of interest

312 None declared

## 313 7 Author contributions

314 **Anubhav Gupta:** Conceptualisation; Data curation; Formal analysis; Investigation; Methodology;  
 315 Project administration; Software; Validation; Writing – original draft; Writing – review and editing.

316 **Owen L. Petchey:** Conceptualization; Funding acquisition; Resources; Supervision; Writing –  
 317 review & editing.

## 318 8 Data Accessibility Statement

319 All the data used in this study was collected in other studies and is openly available. We list those  
 320 studies and the open access source in Table 1. The complete code used in the analysis is available in  
 321 the repository **to be added** .



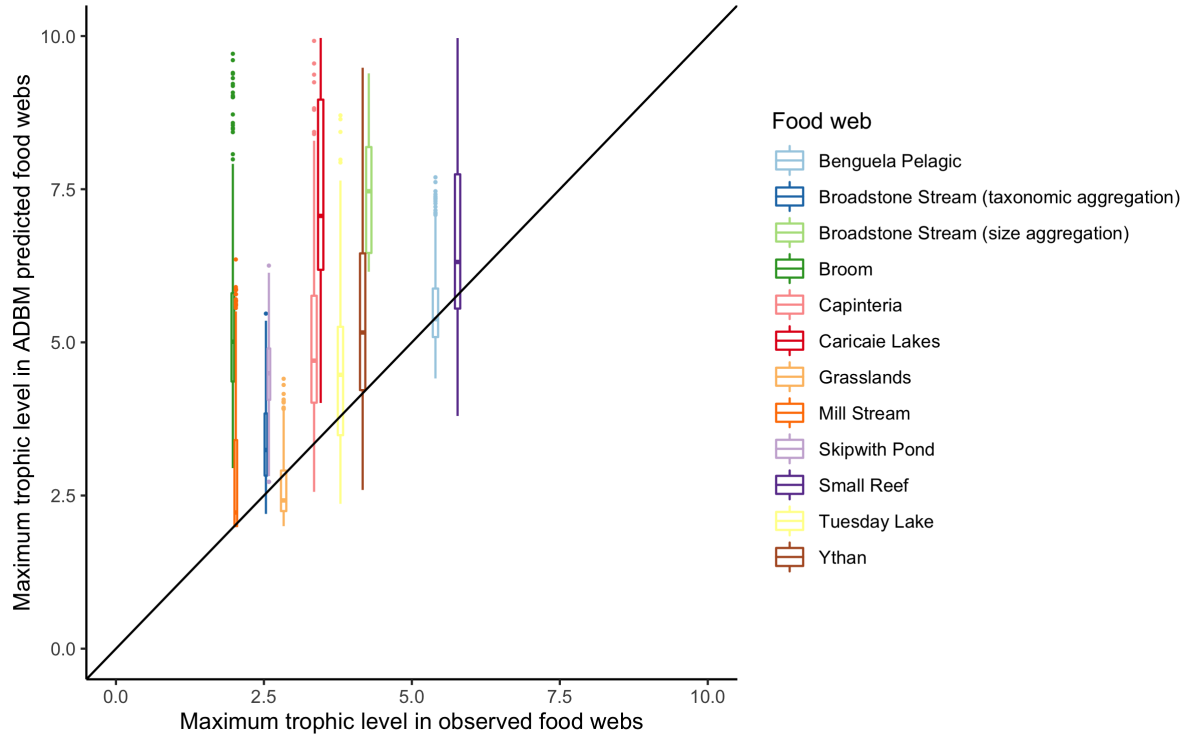


Figure 6: Maximum trophic level of ADBM predicted food webs plotted against that of the observed food webs. Box represent 25th and 75th percentile; bold midline represent median; whisker represent outlier limits; the outlier coefficient used was 1.5. The dashed black lines are the 1:1 relationships for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

## 9 Supplementary Information

## References

- Albert, R'eka, and Albert-L'aszl'o Barab'asi. 2002. "Statistical Mechanics of Complex Networks." *Reviews of Modern Physics* 74 (1): 47–97. <https://doi.org/10.1103/RevModPhys.74.47>.
- Allesina, Stefano, David Alonso, and Mercedes Pascual. 2008. "A General Model for Food Web Structure." *Science* 320 (5876): 658–61. <https://doi.org/10.1126/science.1156269>.
- Berg, Sofia, Maria Christianou, Tomas Jonsson, and Bo Ebenman. 2011. "Using Sensitivity Analysis to Identify Keystone Species and Keystone Links in Size-Based Food Webs." *Oikos* 120 (4): 510–19. <https://doi.org/10.1111/j.1600-0706.2010.18864.x>.

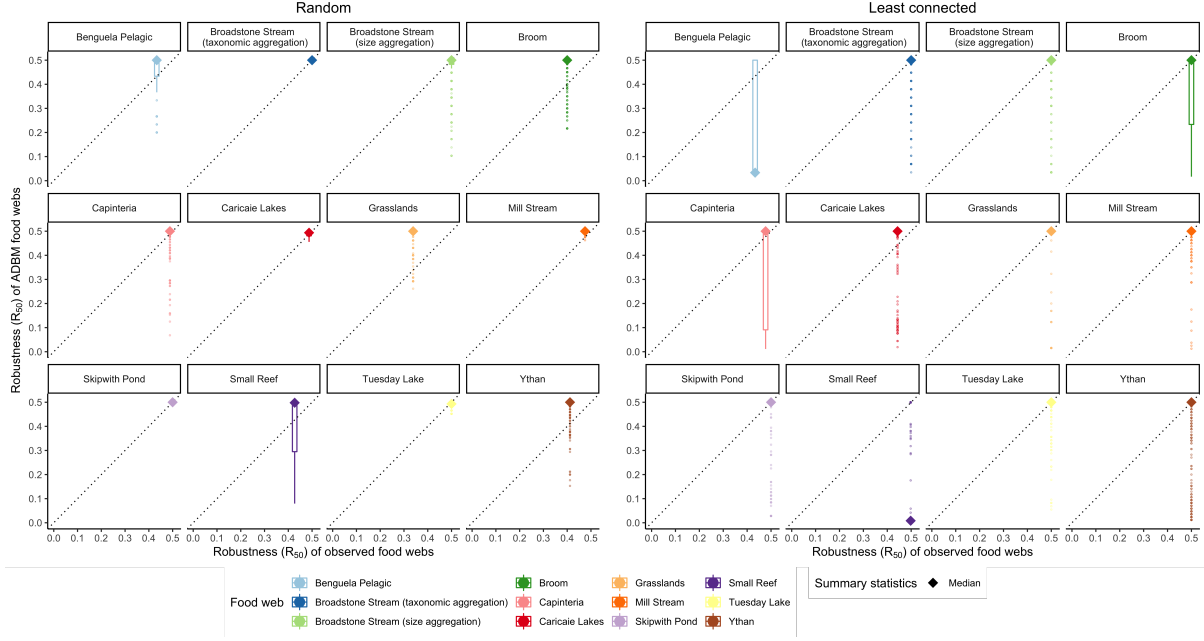


Figure 7: Robustness comparison between the ADBM predicted food webs and the observed food webs for 12 food webs across different ecosystems for random and least connected extinction scenarios. Here,  $R_{50}$  is the proportion of species that have to be removed to achieve a total loss of at least 50%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

- 331 Binzer, Amrei, Ulrich Brose, Alva Curtsdotter, Anna Eklöf, Björn C. Rall, Jens O. Riede, and  
 332 Francisco de Castro. 2011. “The Susceptibility of Species to Extinctions in Model Communities.”  
 333 *Basic and Applied Ecology* 12 (7): 590–99. <https://doi.org/10.1016/j.baae.2011.09.002>.  
 334 Brose, Ulrich, Richard J. Williams, and Neo D. Martinez. 2006. “Allometric Scaling Enhances  
 335 Stability in Complex Food Webs.” *Ecology Letters* 9 (11): 1228–36. <https://doi.org/10.1111/j.1461-0248.2006.00978.x>.  
 336  
 337 Caron, Dominique, Luigi Maiorano, Wilfried Thuiller, and Laura J. Pollock. 2022. “Addressing  
 338 the Eltonian Shortfall with Trait-Based Interaction Models.” *Ecology Letters* n/a (n/a). <https://doi.org/10.1111/ele.13966>.  
 339  
 340 Cattin, Marie-France, Louis-F’elix Bersier, Carolin Banašek-Richter, Richard Baltensperger, and  
 341 Jean-Pierre Gabriel. 2004. “Phylogenetic Constraints and Adaptation Explain Food-Web  
 342 Structure.” *Nature* 427 (6977, 6977): 835–39. <https://doi.org/10.1038/nature02327>.

- 343 Dunne, Ja, Rj Williams, and Nd Martinez. 2004. “Network Structure and Robustness of Marine Food  
344 Webs.” *Marine Ecology Progress Series* 273: 291–302. <https://doi.org/10.3354/meps273291>.
- 345 Dunne, Jennifer A., and Richard J. Williams. 2009. “Cascading Extinctions and Community  
346 Collapse in Model Food Webs.” *Philosophical Transactions of the Royal Society B: Biological  
347 Sciences* 364 (1524): 1711–23. <https://doi.org/10.1098/rstb.2008.0219>.
- 348 Dunne, Jennifer A., Richard J. Williams, and Neo D. Martinez. 2002a. “Network Structure and  
349 Biodiversity Loss in Food Webs: Robustness Increases with Connectance.” *Ecology Letters* 5 (4):  
350 558–67. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>.
- 351 Dunne, Jennifer A, Richard J Williams, and Neo D Martinez. 2002b. “Network Structure and  
352 Biodiversity Loss in Food Webs: Robustness Increases with Connectance.” *Ecology Letters* 5 (4):  
353 558–67.
- 354 Ebenman, Bo, and Tomas Jonsson. 2005. “Using Community Viability Analysis to Identify  
355 Fragile Systems and Keystone Species.” *Trends in Ecology & Evolution* 20 (10): 568–75.  
356 <https://doi.org/10.1016/j.tree.2005.06.011>.
- 357 Ebenman, Bo, Richard Law, and Charlotte Borrvall. 2004. “COMMUNITY VIABILITY ANALYSIS:  
358 THE RESPONSE OF ECOLOGICAL COMMUNITIES TO SPECIES LOSS.” *Ecology* 85 (9):  
359 2591–2600. <https://doi.org/10.1890/03-8018>.
- 360 Gravel, Dominique, Timoth’ee Poisot, Camille Albouy, Laure Velez, and David Mouillot. 2013.  
361 “Inferring Food Web Structure from Predator–Prey Body Size Relationships.” *Methods in Ecology  
362 and Evolution* 4 (11): 1083–90. <https://doi.org/10.1111/2041-210X.12103>.
- 363 Gupta, Anubhav, Reinhard Furrer, and Owen L. Petchey. 2022. “Simultaneously Estimating  
364 Food Web Connectance and Structure with Uncertainty.” *Ecology and Evolution* 12 (3): e8643.  
365 <https://doi.org/10.1002/ece3.8643>.
- 366 Jonsson, Tomas, Sofia Berg, Alexander Pimenov, Catherine Palmer, and Mark Emmerson. 2015.  
367 “The Reliability of R50 as a Measure of Vulnerability of Food Webs to Sequential Species  
368 Deletions.” *Oikos* 124 (4): 446–57. <https://doi.org/10.1111/oik.01588>.
- 369 Jordano, Pedro. 2016. “Sampling Networks of Ecological Interactions.” *Functional Ecology* 30 (12):  
370 1883–93. <https://doi.org/10.1111/1365-2435.12763>.
- 371 MacArthur, Robert H., and Eric R. Pianka. 1966. “On Optimal Use of a Patchy Environment.” *The  
372 American Naturalist* 100 (916): 603–9. <https://www.jstor.org/stable/2459298>.

- 373 Martinez, Neo D, Richard J Williams, and Jennifer A Dunne. 2006. “Diversity, Complexity, and  
374 Persistence in Large Model Ecosystems,” 24.
- 375 May, Robert M. 1972. “Will a Large Complex System Be Stable?” *Nature* 238 (5364): 413.  
376 <https://doi.org/10.1038/238413a0>.
- 377 Mendonça, V, C Madeira, M Dias, Aav Flores, and C Vinagre. 2022. “Robustness of Temperate  
378 Versus Tropical Food Webs: Comparing Species Trait-Based Sequential Deletions.” *Marine*  
379 *Ecology Progress Series* 691 (June): 19–28. <https://doi.org/10.3354/meps14062>.
- 380 Patonai, Katalin, and Ferenc Jord’an. 2017. “Aggregation of Incomplete Food Web Data May Help  
381 to Suggest Sampling Strategies.” *Ecological Modelling* 352 (May): 77–89. [https://doi.org/10.](https://doi.org/10.1016/j.ecolmodel.2017.02.024)  
382 [1016/j.ecolmodel.2017.02.024](https://doi.org/10.1016/j.ecolmodel.2017.02.024).
- 383 Petchey, Owen L., A. P. Beckerman, J. O. Riede, and P. H. Warren. 2008. “Size, Foraging, and  
384 Food Web Structure.” *Proceedings of the National Academy of Sciences* 105 (11): 4191–96.  
385 <https://doi.org/10.1073/pnas.0710672105>.
- 386 Pimm, Stuart, Peter Raven, Alan Peterson, Çağan H. Şekercioglu, and Paul R. Ehrlich. 2006.  
387 “Human Impacts on the Rates of Recent, Present, and Future Bird Extinctions.” *Proceedings*  
388 *of the National Academy of Sciences* 103 (29): 10941–46. [https://doi.org/10.1073/pnas.](https://doi.org/10.1073/pnas.0604181103)  
389 [0604181103](https://doi.org/10.1073/pnas.0604181103).
- 390 Riede, Jens O., Amrei Binzer, Ulrich Brose, Francisco de Castro, Alva Curtsdotter, Björn C. Rall,  
391 and Anna Eklöf. 2011. “Size-Based Food Web Characteristics Govern the Response to Species  
392 Extinctions.” *Basic and Applied Ecology* 12 (7): 581–89. [https://doi.org/10.1016/j.baae.](https://doi.org/10.1016/j.baae.2011.09.006)  
393 [2011.09.006](https://doi.org/10.1016/j.baae.2011.09.006).
- 394 Sol’e, Ricard V., and M. Montoya. 2001. “Complexity and Fragility in Ecological Networks.”  
395 *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268 (1480): 2039–45.  
396 <https://doi.org/10.1098/rspb.2001.1767>.
- 397 Thomas, Chris D., Alison Cameron, Rhys E. Green, Michel Bakkenes, Linda J. Beaumont, Yvonne  
398 C. Collingham, Barend F. N. Erasmus, et al. 2004. “Extinction Risk from Climate Change.”  
399 *Nature* 427 (6970, 6970): 145–48. <https://doi.org/10.1038/nature02121>.
- 400 Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher, R. Fox, R. T.  
401 Clarke, and J. H. Lawton. 2004. “Comparative Losses of British Butterflies, Birds, and Plants

- 402 and the Global Extinction Crisis.” *Science* 303 (5665): 1879–81. [https://doi.org/10.1126/](https://doi.org/10.1126/science.1095046)  
403 [science.1095046](https://doi.org/10.1126/science.1095046).
- 404 Ullah, Hadayet, Ivan Nagelkerken, Silvan U. Goldenberg, and Damien A. Fordham. 2018. “Cli-  
405 mate Change Could Drive Marine Food Web Collapse Through Altered Trophic Flows and  
406 Cyanobacterial Proliferation.” Edited by Michel Loreau. *PLOS Biology* 16 (1): e2003446.  
407 <https://doi.org/10.1371/journal.pbio.2003446>.
- 408 Vagnon, Chlo’e, Franck Cattaneo, Chlo’e Goulon, David Grimardias, Jean Guillard, and Victor  
409 Frossard. 2021. “An Allometric Niche Model for Species Interactions in Temperate Freshwater  
410 Ecosystems.” *Ecosphere* 12 (3): e03420. <https://doi.org/10.1002/ecs2.3420>.
- 411 White, J. Wilson, Andrew Rassweiler, Jameal F. Samhouri, Adrian C. Stier, and Crow White. 2014.  
412 “Ecologists Should Not Use Statistical Significance Tests to Interpret Simulation Model Results.”  
413 *Oikos* 123 (4): 385–88. <https://doi.org/10.1111/j.1600-0706.2013.01073.x>.
- 414 Williams, Richard J. 2008. “Effects of Network and Dynamical Model Structure on Species Persistence  
415 in Large Model Food Webs.” *Theoretical Ecology* 1 (3): 141–51. [https://doi.org/10.1007/](https://doi.org/10.1007/s12080-008-0013-5)  
416 [s12080-008-0013-5](https://doi.org/10.1007/s12080-008-0013-5).
- 417 Williams, Richard J., Ananthi Anandanadesan, and Drew Purves. 2010. “The Probabilistic Niche  
418 Model Reveals the Niche Structure and Role of Body Size in a Complex Food Web.” Edited  
419 by Louis-Felix Bersier. *PLoS ONE* 5 (8): e12092. [https://doi.org/10.1371/journal.pone.](https://doi.org/10.1371/journal.pone.0012092)  
420 [0012092](https://doi.org/10.1371/journal.pone.0012092).