
MISSING LINKS AND THE TOPOLOGICAL ROBUSTNESS OF FOOD WEBS

A PREPRINT

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Abstract

- 1) Undersampling can lead to missing trophic interactions in recorded food webs, with potential consequences for the perceived functioning and stability of the food webs. Undersampling can be compensated for by using food web models such as the allometric diet breadth model (ADBM) to predict missing links. Simultaneously, models might predict links which cannot occur, i.e., real false positives.
- 2) Previous research shows that (i) food web robustness (the inverse of the number of secondary extinctions occurring due to primary extinctions) increases with connectance (the number of realised trophic links divided by the number of possible links), and (ii) that model predicted food webs usually have greater connectance than the observed ones. Thus, we expect that predicted food webs are more robust than the observed ones. 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. 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 or very little 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. Also, the differences in the structural properties of the model predicted food webs and the observed food webs suggest structural properties of a food web could be used as summary statistics to fit models such as the ADBM to the observed data.

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).

Structural properties other than food web connectance such as the proportion of basal species and the maximum trophic level of species in a food web can influence the robustness of a food web (Mendonça et al., 2022; Riede et al., 2011). For example, a food web with a higher proportion of basal species on average will be more robust as compared to otherwise (Mendonça et al., 2022) because extinctions of all the basal species will lead to collapse of the complete food web. A food web with a lower maximum trophic level of species on average will be more robust as compared to otherwise (Riede et al., 2011). This is because a food web with a lower maximum trophic level will have higher number of species per trophic level on average as compared to otherwise.

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 (sometimes referred to as forbidden 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) (Gupta et al., 2023; 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 achieved this by simulating primary species loss in 12 food webs predicted by the model to quantify secondary loss of extinctions and compare the robustness of food webs predicted by the model to the robustness of the observed food webs. We expect the model 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 model predicts greater connectance compared to that of the observed food webs. We also examined how different structural food web properties other than the connectance can influence this difference in the perceived robustness. In order to do that, we define our null hypothesis to be: (H1) The missing links that are filled in by the model increase robustness because they increase connectance; and our alternate hypothesis to be: (H2) Although the model fills in missing links, it also changes other structural properties and these outweigh the effects of connectance on robustness.

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 varies from 0.03 to 0.24 (Links/Species²), and the number of species varies from 29 to 239. The goodness of fit of the ADBM’s predictions depends on the interaction types in the food webs. For example, those with size-structured interactions, such as herbivory in aquatic ecosystems, are better predicted compared to less size-structured ones, such as parasitoids and terrestrial herbivory ones (Petchey et al., 2008).

All food webs with one exception (Broadstone Stream) was available only at the species level, i.e. with information about interactions between species and the body size of species. We use the term “species” in this study to indicate a “node” in a food web in which nodes are connected by trophic interactions, and nodes are a collection of individuals that share links. These species/nodes are not always taxonomic species, but can be broader taxonomic ranks.

In contrast, the Broadstone Stream food web data contained interactions between individuals and the individual body sizes. Thus, the Broadstone Stream food web can be constructed by aggregating by either taxonomy or size (Woodward et al., 2010).

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 ²)	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
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

2.3 Model parameterisation using approximate Bayesian computation

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

2.4 Extinction scenarios and robustness

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

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

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

2.5 Simulating species extinctions

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

2.6 Analysis

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

3 Results

We first compare the robustness of the model food webs against that of the observed food webs. We then quantify the effect of difference in their connectance on the difference in their robustness estimates.

The model food webs were more robust than the observed food webs on average in the most connected and random extinction scenarios (Fig. 1 (a, b)). However, there were large variations in the robustness within the model food webs in the most connected extinction scenario (Fig. 1 (a)). For example, the model food webs for the Caricaie Lakes food web was more robust than the observed food web on average but had a larger variation in the robustness within the model food webs compared to other food webs.

The food webs were more robust to the random extinction scenario than the most connected scenario (Fig. 1 (a, b)). Small Reef and Benguela Pelagic food webs had more variations in robustness within the model food webs as compared to the other food webs (Fig. 1 (b)). Skipwith Pond, Broadstone Stream (taxonomic aggregation) and Broadstone Stream (size aggregation) food webs were the most robust (Median $R_{50} = 0.5$) for both model and observed food webs (Fig. 1 (b)). Although there were few less robust model food webs in the Broadstone Stream (size aggregation) as shown by the outliers.

In the least connected extinction scenario, the food webs had a very high robustness (Median $R_{50} = 0.5$) for most of the food webs (Fig. 1 (c)), however there were some exceptions. The model food webs for Small Reef and Benguela Pelagic had very low median robustness. The model food webs for the Benguela Pelagic, Broom and Capinteria food webs had larger variations in robustness when compared to that of the others.

In all of the food webs except Broadstone Stream (taxonomic aggregation) and Skipwith Pond, the effect size of connectance on robustness was positive on average in the most connected extinction scenario (Fig. 2 (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. 2 (b)). However, the effect size varied across the food webs. In the least connected extinction scenario, the median effect sizes were zero for all the food webs except for Caricaie Lakes

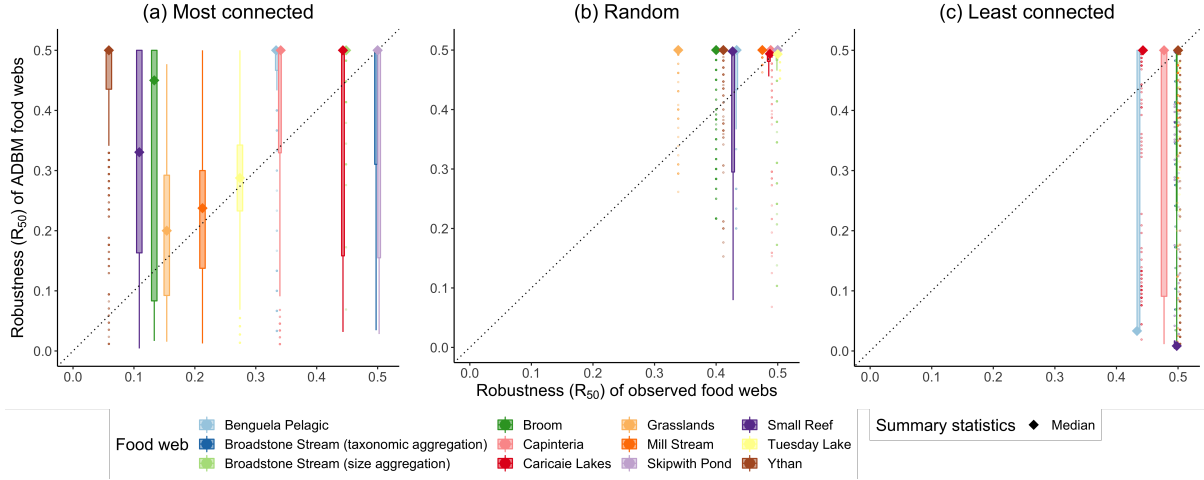


Figure 1: Robustness comparison between the ADBM predicted food webs and the observed food webs for 12 food webs across different ecosystems. Here, R_{50} is the proportion of species that have to be removed to achieve a total loss of at least 50% of total species (primary removals and secondary extinctions). 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. S3 in the Supplementary Information for a faceted visualisation. The dashed black lines are the 1:1 relationships for reference.

and Capinteria food webs where the effect sizes were very close to zero and for Benguela Pelagic and Small Reef food webs where the median effect sizes were negative (Fig. 2 (c)). However, there were lots of outlier with effect sizes negative.

4 Discussion

As expected, the model food webs were more robust than the observed food webs on average. The considerable variation of the robustness of the model 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 model food webs against that of the observed food webs and compare it with the

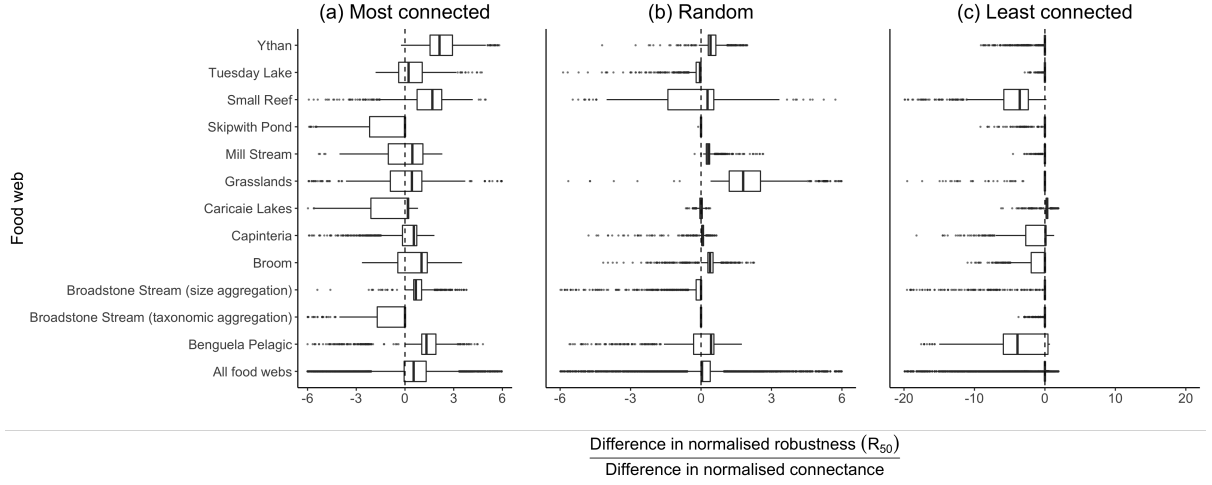


Figure 2: Effect size (i.e. ratio of the difference in normalised robustness between ADBM predicted food webs and observed food webs to the difference in their normalised connectance) shown for the 12 food webs. Box represent the 25th and 75th percentile; bold black midline represents the median; whisker represents outlier limits; the outlier coefficient used was 1.5.

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. 1) 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. 2). Our study suggests that it is important to consider undersampling in observed food webs when computing their robustness.

Our study also depicts that the uncertainty in the model predictions can have a strong influence on the perceived robustness of the observed food webs. The large variations in the robustness of the model predicted food webs suggest why it is crucial to incorporate uncertainty in the food web predictions. At the same time, our study also quantifies the impact of undersampling on the perceived robustness of the observed food webs which then influences the perceived functioning and stability of the food webs (Dunne et al., 2002a; Thompson et al., 2012). This strongly suggest why it is crucial to incorporate the influence of undersampling.

Contrary to general expectations (Dunne et al., 2002b), food web robustness did not always increase with the connectance (Fig. 2). 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. 1 (c) and 2 (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. S1 (a) and (j) in the Supplementary Information). 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 (Fig. 6 (a) in Gupta et al. (2022)) and higher maximum trophic level (Fig. S2 in the Supplementary Information) 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. S2 in the 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.

8 Data Accessibility Statement

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

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