Missing links, forbidden 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 web. Undersampling can be compensated for by using food web models such as allometric diet breadth model (ADBM) to predict missing links. Simultaneously, models might predict links which cannot occur, i.e., false positives.

2) Previous research shows that (i) food web robustness (the inverse of the number of secondary extinctions occuring due to primary extinctions) increases with connectance (the number of trophic links divided by the number of possible links), and (ii) that predicted food webs usually have greater connectance than observed ones. Thus we expect that predicted food webs are more robust than observed ones. This expectation has never, to our knowledge, been tested, nor has the effect size been 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 can also make false positives. We did this for 12 different food webs from a wide variety of ecosystems.
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 X unit of increase in connectance, we found the food webs to be robust by YY units for random extinction scenario.**OP: Here something about the effect size.**
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

1.1 Background on anthropogenic changes and its impact on food web

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 collapse in the food web is due to cascades of secondary extinctions in a food web because of primary loss of species, for example due to habitat destruction. The rate of collapse of these predicted food webs is dependent on the structure and complexity of those food webs (Jennifer A. Dunne, Williams, and Martinez 2002b; Jennifer A. Dunne and Williams 2009). Therefore, research focused on cascading secondary extinctions also known as 'community viability analysis' have been performed extensively in the past few decades (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).

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

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

Along with robustness based on topological structure of a food web, robustness based on the food web dynamics has been studied as well (reference). Topological approaches only require the food web structure whereas dynamical approaches also require the temporal dynamics of the food web along with the food web structure. For example: Williams (2008) combined models of network structure with models of bionergetic dynamics to study the role of food web topology and nonlinear dynamics on species coexistence in complex ecological networks.

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

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

A key assumption of the observed food webs is that the food webs 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 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). One solution to this problem is to use a food web model such as Allometric Diet Breadth Model (ADBM) to predict which are the missing links, and to then measure the robustness of the predicted food web. ADBM is a mechanistic model constructed using rules based on body sizes of prey and predator where trophic interactions satisfying those rules would be predicted by the model which at the same time 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.

1.4 What we do in this study

In our study, we investigate the robustness of the ADBM predicted food webs as compared to the observed food webs and quantify the effect of overestimation of connectance on the robustness of these predicted food webs. 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 species removal: (i) most connected species, (ii) random species and (iii) least connected species to understand if the outcome varies among these approaches.

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

2 Materials and methods

[OP] ## Provide overview of the methods

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

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). The ADBM predicts the set of prey species a consumer should feed upon to maximise its rate of energy intake (Petchey et al. 2008). The foraging variables in the model are: energy content of prey, handling times of the predator on prey, space clearance rate of predator on prey, and prey densities. All are derived from the body sizes of the species via allometries.

2.2 Food web data

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

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

Common food web name (Original Publication)	Predation matrix source	General ecosystem	Number of species	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 (Memmott 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 **OP: need a section on how the food web model was fit to the data. Also should state how we deal with / use the uncertainty contained in the posterior joint distribution.

2.4 Primary and secondary extinctions

We implemented the primary species removal method from Jennifer A. Dunne and Williams (2009) by sequentially removing species using one of 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 the degree (i.e. total number of links to resources and from consumers) of species. Given a primary removal 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. One no more secondary extinctions occured, then another primary extinctions was made, of the next appropriate species. This process was carried out until all species were extinct from the web.

2.5 Calculating robustness

Robustness (R) of food web was quantified as the proportion of species subjected to primary removals that resulted in a loss (i.e. primary removals plus 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, that result in at least 50 per cent of total species loss (Jennifer A. Dunne, Williams, and Martinez 2002b; J. Dunne, Williams, and Martinez 2004; Jennifer A. Dunne and Williams 2009). 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 ($R_{50} = 1/S$), since the first primary extinction causes as cascade of secondary extinctions of at least nearly half of the species in the food web (i.e. at least $S/2 - 1$).

3 Results

3.1 Show and describe the secondary extinction curves

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

In general, irrespective of the extinction scenarios, we found that the cumulative secondary extinction was higher for the ADBM predicted food webs as compared to the observed food webs for most of the food webs **OP: this is not so clear to me. State how many cases? It seems there are many cases where secondary extinctions are more numerous in the observed food web: blue line above the red.**.

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

Except Broadstone Stream (taxonomic aggregation), Broadstone Stream (size aggregation) and Tuesday Lake food webs (Fig. 2 (b, c and k)), the **mean cumulative secondary extinction curves OP: must be explained somewhere how/why this is a mean** for all the other food webs predicted by the ADBM were always lower than that of the observed food webs in the random extinction scenario. The shape of the cumulative secondary extinctions curves varied across the food webs.

Compared to the most connected and random extinction scenarios, the cumulative extinction curves in the least connected extinction scenario had very low values and were flat for most of the

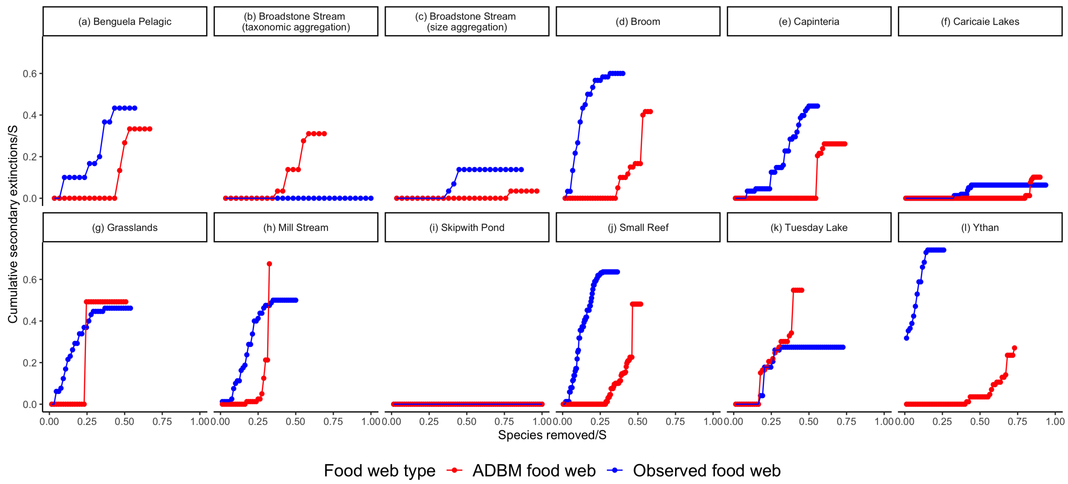

Figure 1: Cumulative secondary extinctions of species resulting from the primary **removals of the most connected species** for 12 food webs. S denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number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

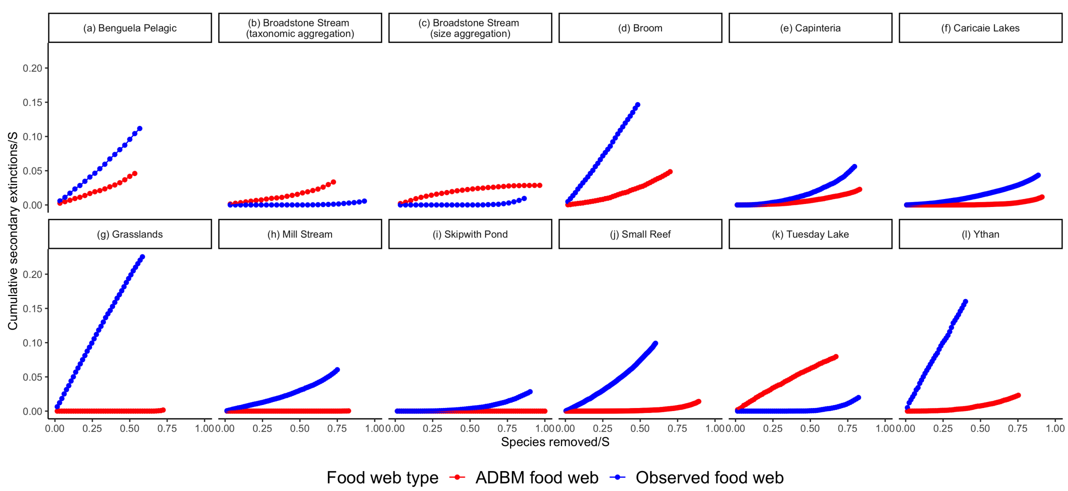

Figure 2: Mean cumulative secondary extinctions of species resulting from the primary **removals of random species** for 12 food webs. S denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number of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

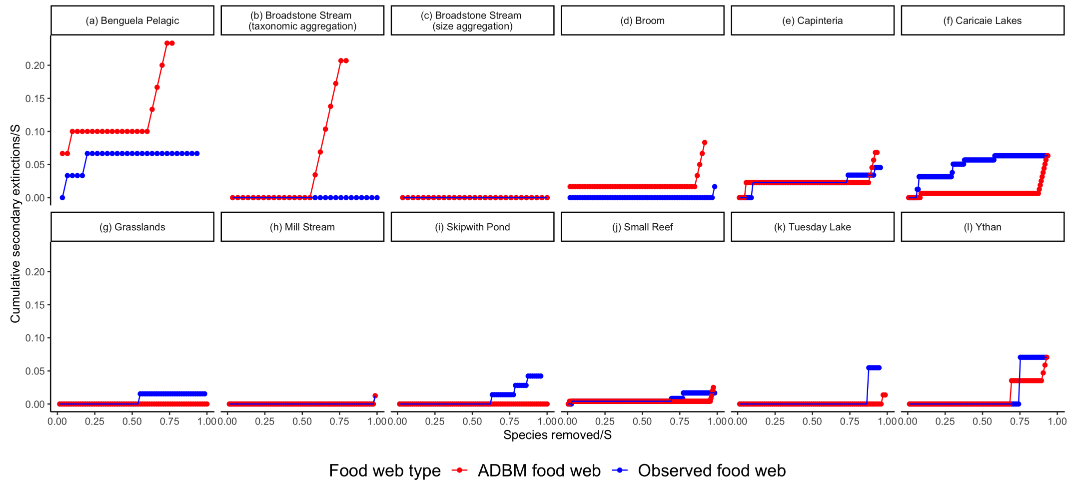

Figure 3: Cumulative secondary extinctions of species resulting from the primary **removals of the least connected species** for 12 food webs. S denotes the number of species in a food web. The cumulative secondary extinctions of species and the number of species removed have been normalised by the number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

food webs (Fig. 3) compared to the most connected extinction and random extinction scenarios. In most of the food webs, there was a lot of overlap between the extinction curves of the ADBM predicted food webs and the observed food webs.

OP: write text describing the effect sizes, e.g. how big is the difference between observed and ADBM webs.

3.2 Show and describe the following:

I suggest to focus on the relationship between (difference in robustness between observed and predicted connectance) and (difference in robustness between the observed and predicted food web). **OP: I miss text describing this relationship. OP: Allow the panels in the figure to have different y-axis scales.**

OP: This paragraph should go in the previous section. The ADBM predicted food webs were more robust than the observed food web with some exceptions (Fig. 4). The food webs were more robust to least connected and random extinction scenarios than the primary deletion of the most connected species. The difference in the robustness values between the ADBM predicted

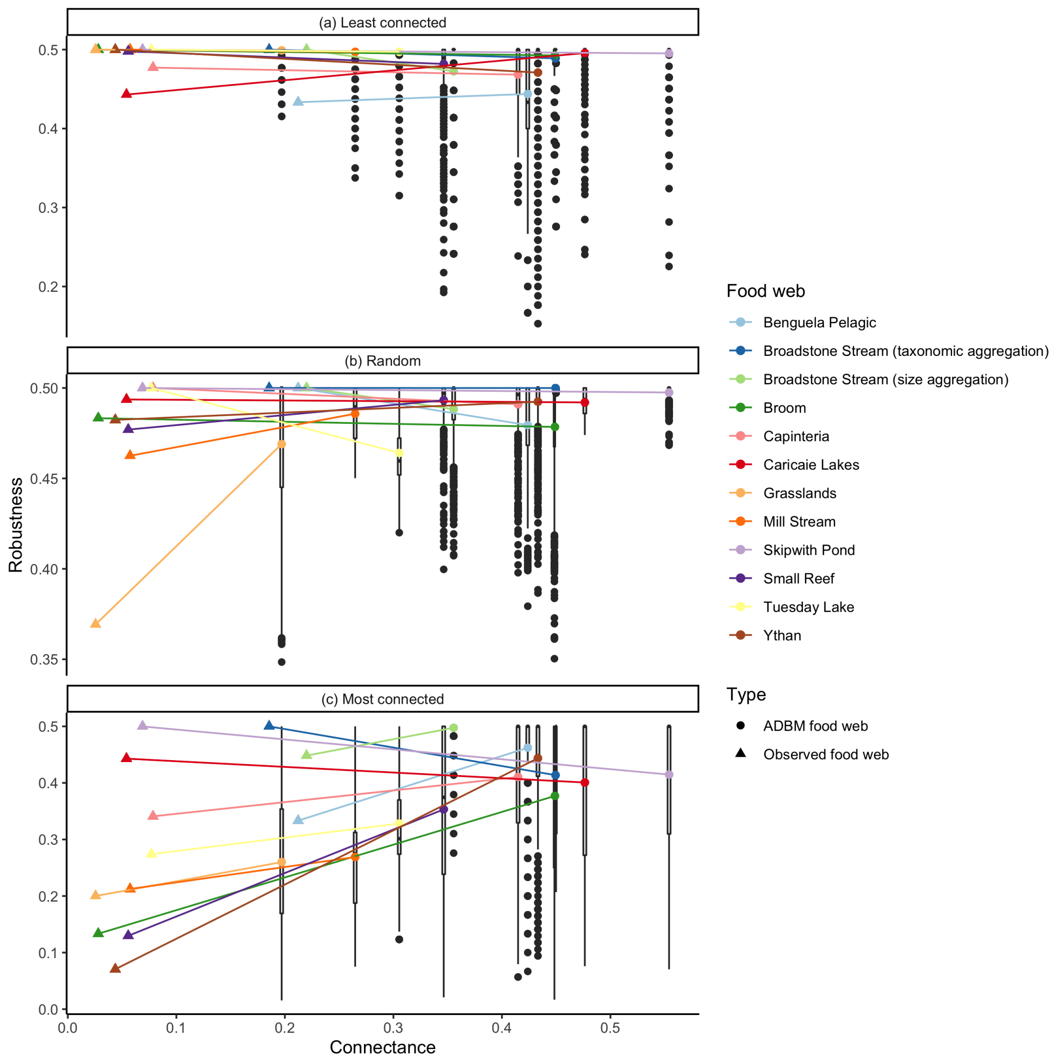

Figure 4: Robustness plots for 12 food webs across different ecosystems. Here, R_{50} is the proportion of species that have to be removed to achieve a total loss of at least 50% of total species (primary removals and secondary extinctions).

food webs and observed food webs was higher in the most connected extinction scenario as compared to the least connected extinction and random extinction scenarios.

AG: I will also update the robustness plot for random extinction (Fig. 4 (b)) once the simulation is completed. The one shown here is only for few simulations and as a placeholder. It takes more time to compute.

4 Discussion

The primary removal of species revealed that the ADBM predicted food webs are more robust than the observed food webs, and the shape of the robustness extinction curves varies between food webs.

The food webs are least robust to primary extinction of the most connected species scenario compared to that of least connected and random extinction scenarios. A future development would be to understand the stability of the dynamics of the ADBM predicted food webs and compare it with our study.

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4.1 What does overestimation of connectance imply in terms of stability?

For most of the food webs, the primary removals of species resulted in a higher secondary extinction in the ADBM predicted food webs than that of the observed food webs (Fig. 1, 2 and 3). This can be attributed to the higher 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 high connectance has on average more number of trophic links as compared to the food webs with low connectance. **OP: should here cite figure 4.**

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

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

4.2 Explain that the ADBM can only predicts contiguous diets [OP] and the implications of this

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

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

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

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

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

The findings from our study is similar to what had been documented for other food web models (Jennifer A. Dunne and Williams 2009), in terms of increase in the robustness when the connectance of the food web is increased. A future study could be to understand the robustness of other food web models (Gravel et al. 2013) and compare it with our study. We expect similar results.

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

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