

Response to Reviewer: Inferring food web structure from predator-prey body size relationships

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Reviewer 2:

Overall, I think this is an excellent manuscript, nicely written, well explained (despite some marginal points that might be clarified, see below) and addressing an important topic. The overall quality of the description of the approach is above average and addressing these points should be simple.

Main comments:

Comment: The method assumes a general relationship between the prey-size range and predator mass. While I think that this assumption holds when predator and prey are pooled across broad size classes, I think that many predator groups also have quite specific size ranges. For instance, we have carried out laboratory studies (Brose et al. 2008, Rall et al. 2011) with different predator groups on prey that vary in their sizes. Our general finding were: (1) specific size ranges of prey are attacked, (2) the lower and upper ends of these size ranges can be mechanistically explained by processes that constrain attack rates, and (3) these size ranges (centre and width) vary across predator groups. The first two points strongly support the approach presented here by Gravel et al., but the third indicates how phylogenetic differences between predator groups could cause imprecise predictions. Although I am a huge fan of this type of allometric scaling work, I am sure (and I have experienced this quite often) that many other ecologists would be very interested in an extended discussion where and how phylogenetic differences among predators could be added to the model.

Response: *We do agree that using phylogenetic information should help improve the technique much beyond what we actually do. This is why we made a mention of this opportunity toward the end of the discussion. But it's right we only mentionned it and did not developped our ideas any further. We added the following lines (LXXX) to the discussion:*

Bayesian inference appears a good candidate to achieve goal. It offers the possibility to constrain the prior distribution of the likelihood of any pairwise interaction, based on trait matching, using alternative source of data. The method we employed here was based on the match between predator and prey traits. This method could be generalized by looking at the match between all potential traits. Eklof et al. (2013) indeed found that the match between only three traits is enough to encompass a vast majority of interactions. But when such data is not always available, then it might be possible to use phylogeny as a proxy for a high dimensional trait species, provided that traits are conserved along the phylogeny (Mouquet

et al. 2012). A bayesian addition to the model would be to weight the likelihood that species j is a predator of species i , considering that the closest relative of this predator is also a predator of i . It could account for part of the unexplained variation we found in our analysis, for instance by constraining the range of the diet for some large predators or by creating holes within the feeding range (Rall et al. 2011).

Comment: The three regression lines in Fig. 2 demonstrate the mean, maximum and minimum prey size of a predator. I found this quite intriguing that for a given meta-community, this would predict how the number of links to resources (the generality of the predator) and the number of links to consumers (the vulnerability of a resource) depend on the body-mass on the x-axis of the figure. We have analyzed these relationship for a variety of food webs (Digel et al. 2011), but I could imagine that the methods introduced here would allow a more thorough investigation of this relationship. If possible, a general graph showing the relationship between generality and predator body mass would be very interesting to see.

Response: *This is certainly an intriguing result coming out from our analysis. We also find this result interesting because it links to some of our previous work on persistence in metacommunities and our current work on the biogeography of body size. We also had a discussion with Neo Martinez at a previous workshop about this relationship, he was curious to see if his assumption of a linear relationship between the niche and the range of the diet was confirmed (Williams and Martinez, 2000). There are already a large number of figures in the paper (6) so we prefer not to add a new one, that could already be guessed from the Fig. 2. We however added the following discussion (at PXLX):*

It appears at Fig. 2 that the feeding range increases with the body size of the predator. This result was quite general across datasets with a good fit of the predator-prey body size relationship, although with considerable variation in the slope of the relationship. It offers the possibility to compare empirical based estimates of the parameters to the original niche model of Williams (2011). For this specific dataset that the model for the centroid is $c_i = -1.34 + 0.66n_i$ and the average range ($\bar{r}_i = (r_{high,i} - r_{low,i})/2$) is $\bar{r}_i = 0.63 + 0.78n_i$. The original niche models assumed that r_i scales linearly with connectance C and the niche position, such that $r_i = 2Cn_i$. Even though the parameterization suggests a linear increase of generality with body size, the final number of preys in the diet for a given size will depend on the frequency distribution of body size. A large predator for instance could have a large feeding range, but only few species to find on and effectively appears as a specialist. This relationship will have to be investigated further, among several food webs (e.g. Digel et al. 2011), because the scaling of generality with trophic rank has several consequences on persistence (Gravel et al. 2011) and food web dynamics (e.g. Brose et al. 2006, Berlow et al. 2009).

Comment: The decrease of the fraction of potential links that are realized from local to

landscape scales was the central topic of one of our prior projects (Brose et al. 2004). You might find this useful to support your assumption that meta-communities should include links that are not realized at local scales – and meta food webs should thus contain more links than the sum of the local food webs. This is exactly the pattern that we documented for different types of ecosystems.

Response: *We fully agree with this result, it was also the central motivation for our investigations in a recent paper by Gravel et al. (2011, Ecology Letters). We hypothesized that this difference was the result of extinction-colonization dynamics, promoting the persistence of the most generalist species in local communities. It is however hard to figure out where to put this result in the current manuscript. We are currently working on a theory for metawebs, trying to develop a framework to improve inference of local web structure given the probability of the interactions in the metaweb. This approach considers the likelihood of an interaction between a pair of species given their co-occurrence and favorable environmental conditions. This topic is however beyond the topic of the current paper. In fact, it goes the other way around. We need information on trait-matching to predict potential interactions in the metaweb (the topic of the current ms), and then a theory for sampling the metaweb.*

Comment: My apologies if these points rely heavily on our own prior work. I found this manuscript very inspiring and also highly related to our studies. Overall, I would recommend publication of this manuscript, the minor points listed below should be no obstacle.

Line 152: using the abbreviation B (often used for biomass) for individual mass may be confusing – could be replaced by M.

Response: *We corrected accordingly by replacing the abbreviation B by M*

Fig. 2: preys should be prey

Response: *We corrected accordingly*

Line 214: shouldn't it be up to eight dimensions?

Response: *We do not find the corresponding point to correct. The lines following L214 refer to the paper by Eklöf et al., and after a double checking of the paper it was found that most webs had between 3 and 6 dimensions, up to 9. We corrected accordingly.*

Some references are incomplete (Eklöf, Mouquet, Thuiller).

Response: *We corrected accordingly*

Reviewer 3:

This paper presents a simple method to infer trophic interactions in food-webs from information on the body size of the species. While the topic is important and such a method potentially very useful, I believe that the present work suffers from many problems.

Main comments:

Comment 1: It is not clear if the method is useful to infer a particular food-web (as indicated in the title), or a "metaweb". I was much confused about the scope of the method, which should be more clearly stated. From the example with the Mediterranean fishes, it appears that the proposed approach is useful to build a metaweb. It is not clear to me if it could be of any use for the description of a "local" food-web. Also, even at the metaweb level, it is apparent that additional information (spatial co-occurrence) is needed to obtain a "sensible" metaweb. Ultimately, this questions the usefulness of the method.

Response: *As stated in the abstract, our method allows to “infer the matrix of potential interactions among a pool of species”, and does so regardless of whether one is working at the local or regional scale. In the text, we give examples at both these scales (locally in figures 2 and 3, regionally in figure 5). We do agree with the fact that additional information will make the predictions better; this is described at length in the text, and an example of this (including co-occurrence along the depth gradient) is pictured in Fig. 5b. This is also explicitly written in the discussion (L. XXX-XXX). We corrected the abstract and the last paragraph of the introduction to make clear that our methodology applies at both the local and metaweb scales.*

Comment 2: The authors illustrate the approach with the use of a food-web based on fishes. It is known that body-size is important to understand trophic interactions for fishes and for aquatic systems in general. It is questionable that the approach would be useful for 1) terrestrial food-webs, and 2) for "complete" food-webs encompassing a larger array of taxa (this could be circumvented by applying different regressions for different taxonomic groups; see the paper of Naisbit et al. 2011 in Ecology).

Response: *We agree that the fit of the model is only as strong as the relationship between prey and predator body-size. This is the purpose of Fig. 3; this relationship is also described in section 3.1 “Predictive performance”. We made this point clear in the opening paragraph of the Discussion: ‘However, because this allometric relationship is characteristic of predatory interactions, our method will likely not hold for other types of non-body-size structured interactions such as herbivory and parasitism’. We added also some cautionary remarks in the last paragraph of the introduction: ‘The method is best suited for strongly size-structured food webs and will likely not hold for other types of non-body-size structured interactions. We therefore conclude on the future issues to generalize this approach to other types of trait matching models’.*

Comment 3: Important contributions are not discussed in the manuscript. To my knowledge, the first approach that was able to predict trophic interactions was given by Ives and Godfray (Am. Nat. 2006), but based on phylogenetic information (their method is admittedly

much more complex). The authors cite the paper of Petchey et al. (PNAS 2008), but it true that the aim of their model was surely not to forecast possible interactions. However, a quite similar approach was proposed by Rohr et al. (Am. Nat. 2010), which can be easily used to predict interactions. Their first model (Body-size model) is also very simple, based on the ratio of prey/predator body sizes, and assumes an optimal ratio (if I am correct, it would be similar to the approach of the authors with a slope fixed at a value of 1). Because of the simplicity of the approach, a comparison of both methods could be useful (however, Rohr et al. approach predicts a total number of interactions that is very close to the number of interactions used in the "training" food-web; this could be simply adjusted by decreasing the threshold (see their fig. 1) to a level corresponding to the 5 and 95% quantiles used by the authors).

Response: *The study of Rohr et al. (2010), does not allow to evaluate the parameters of a new species entering a local community, neither the metaweb (which is the object of the current study). It is therefore not possible to infer the potential links an immigrating species will do with the resident species. These methods also require a complete knowledge of the interactions in the community. Our method is consequently much more robust than previous methods to infer the parameters of the niche model. Based on these arguments, we believe that the method will be used for instance to study the interactions in emerging communities following global changes.*

Comment 4: The authors use Model 1 regression in their analysis. To me, this is problematic as measurement error on body mass is similar for prey and predators. I recommend the use of Model 2 regression.

Response: *We do agree that the best statistical model for this analysis should be a type 2 regression. We however deliberately used a type 1 regression for two reasons: i) we needed the R^2 of the model to perform the analysis of predictive performance (Fig. 3). ii) we are not aware of any quantile regression that could account for uncertainty in the independent variable. We added a mention to this issue at LXXX.*

1.50: The use of "emergent" sounds strange here. Please clarify.

Response: *We replaced the word "emergent" by "novel".*

2nd paragraph: the metaweb concept is introduced here, but it is not clear why. If the aim of the authors is to infer a metaweb, this should be clearly stated here.

Response: *We modified the sentence to avoid amiguities. The metaweb gives interactions among a given set of species, wether at local or regional scales.*

1.128: Here, it is apparent that the authors aim is to infer a metaweb. Again, this should be clearly stated earlier (and even in the title?)

Response: *See the above responses to previous comments.*

l.139-140: How can you state this here without performing an analysis? This is unclear to me (at least, this is not intuitive).

Response: *This is a basic postulate of the niche model. We have added a reference to the original paper to eliminate ambiguity.*

l.155: grey or dotted lines?

Response: *The dotted lines. We corrected accordingly and apologize for the mistake.*

l.157: what are these betas?

Response: *These are the parameters of the linear quantile regressions. The sentence was corrected accordingly.*

l.167: should the α_1 rather be a β_1 (see my former comment)? Please clarify.

Response: *No. The centroid is a function of the two body sizes (hence α), while the range limits are a function of the predator body size and its range.*

l.199-201: if I understand correctly Fig. 3, the increase in TSS is due mostly to the correct prediction of the fraction d (predicted absences), and not to correctly predicted presences (fraction a), which is likely the most interesting fraction for any practical reason. This should be stated.

Response: *Whether the correct prediction of absence or presence of an interaction is the most interesting part of a model is ultimately a matter of personal taste, and adequation to the study objectives. Given that (especially when no other traits than body size are included), this method tends to over-estimate the number of links, we argue that correctly predicting absences of links is an extremely important feature.*

l.304: expected, not expect

Response: *We corrected accordingly.*

l.511: I would not discuss the problem of ontogenic shift in the figure legend.

Response: *We argue it is an important piece of information, which was required by a previous reviewer. We made no changes.*

l.515: Is there any justification behind the use of 5 and 95% quantiles? Why not the usual 2.5 and 97.5%, or 0 and 100%?

Response: *The choice of quantiles are left free to the user in the R code providing with this article, by default, we chose the most commonly used threshold of 5% and 95%. A threshold of 100% would include all interactions, but would tend to overpredict the link density.*

l.522: black and open dots: I guess it is the contrary.

Response: *We corrected accordingly and apologize for the mistake*

1. 526: "with not pbervation" ?

Response: *We corrected accordingly.*

Figure 2: An important difference between the original and the parameterized niche model is apparent in this figure: here, the c_i and r_i are constrained by the allometric regression, which is not the case in the original model. From the distribution of the open dots, this appears quite problematic in this figure (many open dots are outside the predicted range; many predicted interactions are not existing), and this questions the usefulness of the whole approach. Other traits may be needed; perhaps performing several regressions for different broad taxonomic groups may also improve the approach, and widen its applicability.

Response: *The c is constrained by n in the original niche model: it is drawn uniformly between $r/2$ and n , with the expected value of r being $2Cn$.*

The fact that our model over-predict the number of interactions is discussed in the manuscript (along with why, and how to overcome it). However, the purposes of the two models are not the same. The niche model allows to generate a distribution of network properties based only on connectance and richness. We add allometric informations so as to be able to estimate species-level interactions in addition to network properties. The allometric relationships on which we rely are well documented. As for the fact that other traits can be added, this is discussed in the manuscript at several places, including a figure.