

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

Dominique Gravel, Timothée Poisot, Camille Albouy, Laure Velez, David Mouillot

Reviewer(s)' Comments to Author:

Knowledge of how large-scale changes in species abundance distributions will alter food web interactions and community structure and dynamics is a major challenge for community ecology. This paper combines the use of the niche model with predator-prey body mass relationships to predict existing food webs (from body size information of the species only). Not surprisingly, the model predicts food webs that have stronger underlying prey-prey mass relationships better than those that do not. The approach is then used to infer food web interactions based on species lists and their respective body sizes and is then combined with spatial distributional data. Reductions of sizes and removal of larger species are subsequently examined in a simulation, showing very different consequences for degree distributions.

Main comments:

Comment: I found this paper really interesting (with very nice figures), but I did wonder whether the method is actually new or whether it is a new application of an existing method (the niche model)?

Response: *The niche model is not new in itself, it has been developed in 2000 by Williams and Martinez and later generalized by Stouffer et al. (2005). While the most obvious candidate axis underlying the niche model is body size, it was never made explicit. In addition, despite the fact that this model is useful to predict network structure, we lack a simple yet robust way to parameterize it. Results presented by Williams and Martinez are stochastic simulations with species richness and connectance as input parameters. They also implicitly assumed a linear relationship of slope 1 between the niche position and the range. Their approach does not allow to infer the niche position of a given species entering a food web. The novelty of our approach is to provide a methodology to infer, for each species of a given species pool, the three species specific parameters of the niche model. Previous attempts have been done to evaluate the niche position of a species and these are mentioned in the introduction (LXX). As we discuss in the introduction, these methods do not however allow to evaluate the parameters of a new species entering the community. It is therefore not possible to infer the potential links an immigrating species will have with the resident species. These methods also require a complete knowledge of the interactions in the community, which is difficult to achieve in nature, and unattainable for species entering the community. As we discuss in the paper (PXLX), we have much greater confidence in documenting an interaction than its absence. 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 is novel enough and will be useful to study the interactions in emerging communities following global changes.

Comment: Since this paper is a methods paper, I feel that the method should be much clearer. For example, what are the steps involved more explicitly

Step 1: get food web data and parameterise a predator-prey relationship (which is used for evaluating the model against the Brose dataset) used in the application to the Mediterranean? It wasn't clear how the local food web data were used - was it to parameterise the niche model only?

Step 2: compute metaweb from a species list and mean or maximum body sizes

Step 3: predict metaweb species interactions based on the regional (subset) parameterization of the niche model (eg. fitting Figure 1 to subset of data)?

Maybe these steps could be more clearly drawn out, since the paper is supposed to convey a methodology. For example, it is not clear to me which parameters are fixed in the niche model and which ones are being estimated.

Response: *We do agree the methods should be made clear enough to be easily reproducible. We did improve the manuscript in two ways to address this comment:*

i) We clearly listed with in a bullet-point enumeration the steps of the analysis at the beginning of the Methods section. We also added a paragraph describing how to interpret linear model coefficients and compute the metaweb. See PXLX.

ii) We agree with the referee that adding R code to the paper would help others using the method. We consequently produced a clean version of the code with simulated data. Instructions are made clear throughout the code and we indicated where the user has to supply his own data. The following steps are provided in the code: loading of the dataset, useful functions used, calculation of the parameters for the simulated data, reconstruction of the metaweb, illustration of a local iteration of the metaweb. We provide the fish dataset used in the example (with removal of species names to respect data ownership).

Comment.: Also, is this approach flexible enough to consider ontogenetic changes in food webs, since these have been widely shown to be important for fish. Could ontogenetic changes within fish species also be used here? Or alternatives to the niche model for example? If so perhaps it could be worth pointing out that the alternative "rules" could be tested to constrain the interactions in Step 2 (it would have been interesting to examine this more).

Response: *Ontogenic shifts in diet could be accounted for in two ways with this methodology. First, they will enter the model parameterization by simply including a link from species A (the largest) to species B (the smallest), and the opposite. This would result in a data point for species B above the 1:1 relationship. Such a data point will obviously influence the model evaluation and enlarge the regime of all species. It is not obvious however that ontogenic shifts will be found back in the metaweb as it would require an upper limit of the range above the 1:1 relationship. The alternative approach would be to distinguish "sub-species" by size categories in the model calibration and then in the reconstruction of the metaweb. This approach would force ontogenic shifts and perhaps more precisely represent the interaction matrix where the within-population size structure is important. We understand this is a particular concern for some systems, such as freshwater and marine food webs, and consequently added a paragraph describing these two options in the discussion (LXX).*

Comment.: The text needs cleaning up throughout and would benefit from some more explanatory text in places, to ensure the methodology being described and tested is clear enough for people to repeat. For example, is there a piece of example R code that could accompany the paper with some data, to show how each step in the analysis should be carried out, if someone wanted to apply this method to a new region or species list? Doing that might also enhance interest and clarity of the method.

Response: *As mentioned above, we added extra text to the methods and added supplementary R code to the paper.*

Minor comments.

Line 37: word webs misspelled

We corrected accordingly

Line 44: word illustrate misspelled

We corrected accordingly

Line 56: "stomacal" -> stomach

We corrected accordingly

Line 67: hands->hand

We corrected accordingly

Line 79: functioning misspelled

We corrected accordingly

Line 88: derived from these rules instead of somehow derived from these rules

We corrected accordingly

Line 91: Sentence structure

We replaced the sentence "The major recent breakthrough in food-web theory have been the attempts to parameterize the niche model and other food-web models from field data

and to compare their fit through likelihood methods" by the following sentence "The recent breakthrough in food-web theory have permitted to parameterize the niche model and food-web models from field data, then to compare their adequation to real data through likelihood methods."

Lines 96-104: I agree with what is being said here, but the text in this part could do with some reworking: check clarity, tense and grammar

We corrected accordingly

Line 106: data on species co-occurrence or stomach contents? What is being established predicted interaction matrix given the presence of different species; eg. so as to infer how likely an interactions could be in the future between 2 new species? Eg. based only on their body sizes? Perhaps you could say this more directly.

We changed the sentence to: "In this paper, we present a method designed to infer the potential interactions between all pairs of species of a species pool (the metaweb) based on observations of body size of predators and their prey."

Figure 1 shows each species being a point, but a similar type of pattern is observed across individuals of the same species feeding on a range of prey, and is important in fish; how flexible is the approach; could a size-structured approach also have be used with these methods?

See the response above and the corresponding paragraph in the discussion.

Line 127: has this been tested, could they be combined?

The reference to line 127 is confusing. We provide a reference to a recent studies looking at body size relationship in different environments. And it is obvious that the body size relationship we document do not apply to mutualistic or competition networks. The extension of this method to other traits is discussed at the end of the manuscript.

Line 153: it would be useful to know which datasets these were and why.

The corresponding references in Brose et al. (2005) are:

- Ledger, Edwards and Woodward, unpublished data*
- Memmott et al. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. Journal of Animal Ecology, 69: 1-15.*
- Ruess, unpublished data*
- Warren, unpublished data*

This information is however useless in this paper as it is not our aim to assess the generality of the predator-prey body size relationship.

Line 157: space after Brose

We corrected accordingly

I like the use of the true skill statistic

No correction needed

Lines 177-185: the model overestimates number of links, this has also been shown to be due to sampling artefacts in data (we are not sampling the food web perfectly... so we don't actually observe all of the links). What about the effect of aggregating to the species level when predators and prey (esp. in aquatic food webs) are more governed by individual size rather than mean size (eg. variation in size of species could matter for a larger species more so than for a small one). Maybe could be picked up in the Discussion?

See the response above and the corresponding paragraph in the discussion. We have also corrected the paragraph for clarity and introduce the question of sampling intensity (see comment below).

Line 184: Sentence clarity-not sure if this problem refers to the problem of over predicting links, or the continuous diet along a niche axis? Actually the whole paragraph could be tightened up with some minor edits... and because it leads on to the issue of sampling.

The paragraph has been edited. The problem of sampling intensity has been added. A reference to a recent study showing that most webs do have between 3 and 7 axis was also added.

Line 187: OK but what about biased sampling and aggregation effects? You looked at random removals. When were the data collected and does this match the sampling with the spatial distribution? Did you then evaluate how well these predictions replicated the Mediterranean food web data-or were these purely used for establishing predator-prey relationship. Can it be made more precise how these data entered into the analysis? Were the predictions then compared to the observed food webs (they seem to not have been).

Bias sampling and aggregation: we added precisions on this issue with an additional paragraph at LXX. The two questions related to the spatial distribution and the Mediterranean data are confusing. This analysis was conducted with the Brose et al. data and therefore such information is not available. We nonetheless precised how the predictions were compared to the observed food webs (they were).

Line 219: what do you mean was edited between 1984 and 1986, entries changed of the data were from these years?

The presence absence data came from an atlas and the data where collected between 1984 and 1986.

Line 226: Why is this different than what has been done before. Explain a bit more about assumptions being made about connectance with niche model (not everyone will be familiar with this approach)

We added the sentence (LXX): Connectance decreases because links are removed by incompatabilities in bathymetry but the total number of species stays constant.

Line 227: I like the observations that there are more modules occurring, but I am not entirely clear whether they are they meaningful modules, any idea whether these help ion predicting the observed webs (or realistic modules)?

They are meaningfull in the sense that they represent modularity in the coccurrence matrix. We added a sentence referring to the study of Araujo et al. 2011 on the structure of co-occurrence networks (LXX) and mention that the study of modularity is for future work.

Lines 230-236: OK how is it different-because you are inputting richness but estimating connectance, based on fitting the niche model to the realised food web? This is not very clear, but as you say it is crucial for applying the method under climate change. How was it done, much more detailed description of your methods, would benefit here or even in an earlier section above.

Additional details on the methodology were provided above (see Main comments). We also added details on the comparison with the original niche model (LXX).

Line 236: Change "This feature is particularly important when comes the time to understand global change impacts on community structure" to "This feature is particularly important for understanding global change impacts on community structure"

We corrected accordingly

Line 237: I guess by global change impact I was naively assuming you were going to discuss climate change...do you mean for each species or for the whole food web? Is this why you chose a scenario that was a reduction in size (shifts towards smaller species?)

We chose this particular scenario because climate warming is expected to reduce fish body size (we added a reference) just as increasing fisheries on larger bodied species.

Line 243: Average body size of each species or overall avg. body size? Better to be more precise about what was changed.

Reducing the average body size of each species or the average overall body size has the same consequence as long as the shape of the frequency distribution stays the same. We added precisions in the legend.

Line 244: I think a more detailed explanation of the consequences of the different scenarios on cumulative degrees distributions and a clearer description of what they mean is needed here.

The whole paragraph was edited accordingly.

Line 250: Is this really a new method or is it a new application of an existing method?

See the response to the first main comment.

Line 250: The discussion is written in a very casual way. Perhaps the text could be edited, also to be more concise and focused.

The text was edited and a paragraph was added according to some suggestions provided above.

Line 266: Please explain less interval, isn't this thought to be dependent on the number of species? It would be better to be clearer here as you link the idea with the inclusion of the additional environmental information. Also, the application is not very clear, how did you go from species pool, niche model and then the specific Mediterranean web data?

Intervality is strongly dependent on the presence of holes in each species diet and the successive alignments of diets along the main niche axis. It is independent of species richness. A clarification on intervality was added at LXX. Finally, we hope that the clarifications we added on the methodology helped solving the interrogations on the analysis of the Mediterranean data.

Line 272: comptability is not a word - a similar approach could incorporate?

We corrected accordingly

Line 278: Adding this method to the ecologist's toolbox is a timely issue. Maybe change to Addition of this method to the ecologist's toolbox is timely because... then go on to explain why...

We added a reference on the need to incorporate biotic interactions into biodiversity scenarios (LXX).