Title: Inferring food web structure from predator-prey body size relationships

Authors: Dominique Gravel[1,2,*], Timothée Poisot[1,2], Camille Albouy[3,4], Laure Velez[3], David Mouillot[3,5]

1: Canada Research Chair on Terrestrial Ecosystems. Département de biologie, chimie et géographique, Université du Québec à Rimouski, 300 Allée des Ursulines, Québec, Canada. G5L 3A1.

2: Québec Centre for Biodiversity Sciences, Stewart Biological Sciences Building, 1205 Dr. Penfield Avenue, Montréal (QC), H3A 1B1, Canada

3: UMR CNRS-UM2-IRD-IFREMER 5119 ECOSYM, Université Montpellier 2, CC 093, 34095 Montpellier Cedex5, France.

4: Laboratoire Ecosystèmes Marins Exploités UMR 212, IRD, IFREMER, UMII, UMI, avenue Jean Monnet BP171, 34203 Sete Cedex, France.

5: ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld 4811, Australia

* Corresponding author. `dominique_gravel@uqar.ca`. Tel: 1-418-723-1986 #1752. Fax: 1-418-724-1849.

Keywords: Metaweb, Body size, Niche model, Food web

Words in the abstract: 179
Words in the main text: 2819
Words in the legends: 423
References: 45
Figures: 6
Table: 0

Abstract

Current global changes make it important to be able to predict which interactions will occur in emerging ecosystems. Most of the current methods to infer the existence of interactions between two species require a good knowledge of their behaviour or a direct observation of interactions. In this paper, we overcome these limitations by developing a method, inspired from the niche model of food web structure, using the statistical relationship between predator and prey body size to infer the matrix of potential interactions among a pool of species. The novelty of our approach is to infer, for any species of a given species pool, the three species specific parameters of the niche model. It allows one to evaluate the feeding interactions of a new species entering the community. We find that this method gives robust predictions of the structure of food webs, and that its efficiency is increased when the strength of the body- size relationship between predators and preys increases. We finally illustrate the potential of the method to infer the metaweb structure of pelagic fishes of the Meditarrannean sea under different global change scenarios.

1 Introduction

One of the current challenges in ecology is to predict the emergence and re-assembly of communities following species responses to global changes. Understanding this is made all the more important as these emergent ecosystems will be more common with increasing human pressure. We know that species invasions, biomass harvesting, ranges shifts, disturbances and changes in land use are important drivers of biodiversity turnover. How they affect species composition is now well described (Pereira et al. 2010), but forecasting their impact on community structure and functioning requires *a priori* knowledge of potential interactions among species. Predicting interactions among species that never co-occurred proves challenging, as traditional empirical methods of food web sampling such as stomacal content analysis cannot be applied. While for competitive communities this task could be achieved using predictive modeling based on functional traits (Albouy et al. 2010; McGill et al. 2006) or phylogeny (Cavender-Bares et al. 2009; Mouquet et al. 2012) , it is much more difficult to forecast trophic interactions in a food web (Ings et al. 2009; Montoya & Raffaelli 2010; Tylianakis et al. 2008).

Inferring potential interactions among species of an arbitrary defined pool is a major step to predict the structure of emergent communities and their functioning. We call these potential interactions among species from a regional pool the *metaweb* (Dunne 2006). A metaweb takes the form of an adjacency matrix $\mathbf{M}$, of size $s \times s$ for a pool of s species, and in which $\mathbf{M_{ij}} = 1$ if species i can consume species j, and 0 otherwise. This matrix aggregates the trophic interactions among all species from the pool that are susceptible to both co-occur and interact at the regional scale (Dunne 2006). With a metaweb in hands, one could analyze the impacts of global changes, such as range shifts or species invasions, on the potential community structure, by extracting the relevant species and examining the properties of the community they

3

define. While this concept is progressively finding its way through theoretical spatial food web ecology (Gravel et al. 2011a,b; Lafferty & Dunne 2010; Pillai et al. 2009), it is still limited by data availability and predictive accuracy. Published metaweb data rely on literature surveys (Baiser et al. 2012; Havens 1992; Piechnik et al. 2008), or a compilation of several local food webs (Poisot et al. 2012; "Mammal density and patterns of ectoparasite species richness and abundance"), making them resolved only for species that co-occurred a large enough number of times.

Development of predictive models of trophic interactions could greatly improve our understanding of large scale food web structure and our capacity to anticipate major changes in ecosystem functionning. Theory should provide some guidance about the general rules underpinning interactions among a set of species and thus help us to infer the metaweb. The actual food web theory is largely derived from the niche model (Williams & Martinez 2000). This model simply and intuitively poses that each species in a food web has a niche position n_i, a feeding niche optimum c_i and a range r_i of suitable preys around that optimum (Fig. 1). These simples rules are sufficient to generate realistic food web structures that fit most of published food webs (Dunne 2006). The niche model was a substantial improvement of the previous cascade model (Cohen1990) and subsequent models (e.g. the nested hierachy model (Cattin et al. 2004), the minimum potential model (Allesina et al. 2008), the probabilistic niche model (Williams et al. 2010) are somehow derived from these rules (Stouffer et al. 2005). Although it is based on different assumptions, the adaptive foraging theory of food web structure (Petchey et al. 2008) provides comparable predictions (Williams et al. 2010). One 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 (Allesina et al. 2008; Williams 2011; Williams et al. 2010). These methods provide, for each species of the food web, the

4

optimal parameters to fit the empirical web structures, given the hypothesized underlying rules of the niche model.

Despite their theoretical interest, these methods however come with several drawbacks when comes the time to perform biodiversity scenarios. Firstly, they are difficult to apply at large scale because of the technical and logistical requirements of metaweb data collection. Secondly, once the model is parameterized, it could only be used to infer feeding interactions between species with already documented interactions (i.e. it is impossible to infer potential interactions among species that do never co-occurred). Finally, the model optimization is a serious challenge for large datasets with a large number of parameters to evaluate and rough likelihood surfaces. There is consequently an urgent need for a method that could rapidly and easily provide an estimate of potential interactions in a metaweb based on incomplete data.

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. We do so by a parameterization of the niche model, based on the well-documented allometric scaling relationship between predator and prey (Brose et al. 2006; Cohen et al. 2003; Riede et al. 2010). We first develop the method and apply it to food webs from various environments. We find the method accurately predicts the interactions (and lack thereof), and that the accuracy increases with the strength of the predator-prey body size relationship. We then analyze the sensitivity of the method to incomplete data (missing links) and find that it is robust to sampling effort. We finally illustrate the potential of the method to infer the metaweb structure of pelagic fishes of the Meditarrannean sea and the consequences of alteration of body size distribution by global changes or anthropic forcings.

2 Model description

The method aims to infer the potential interactions among a pool of species from a subset of observations of predator-prey interactions. The method follows the following steps, with details provided below:

Step 1: Log transformation of the body size data;

Step 2: Statistical analysis of the predator-prey body size relationship;

Step 3: Inferrence of the niche model parameters for all species from the species pool;

Step 4: Interpretation of the parameters and computation of the metaweb.

We also provide an example of R code (R Core Development Team) and data in the Supplementary Material, detailling the step by step procedure and the format of the input data.

2.1 Inferring parameters from the niche model and building the metaweb

The niche model predicts the food web structure from a set of three species-specific parameters: the niche position n_i, the feeding niche optimum c_i (called the centroid), and the feeding range r_i. A species i will predate all species j whose niche position n_j lies within the interval $[c_i - r_i/2, c_i + r_i/2]$ (Fig. 1). We evaluate all of these parameters from the predator-prey body size relationship, enabling us to parameterize the metaweb from *observed* interactions only. The parameterization is robust to the sampling effort, as it is much easier to document interactions than their absence (Martinez et al. 1999). Our approach is however mostly limited to predatory interactions since the body size relationship between herbivores and primary producers is not as general

6

(Riede et al. 2010), and obviously do not hold for parasitic, mutualistic, or competitive networks.

Assuming that body size is the main niche axis structuring trophic interactions, the parameter n_i corresponds simply to the log of body size (in mass or length) of species i. Though only the relative position of all species along the body size gradient needs to be respected, it is possible to standardize log body size values between 0 (minimum size in the regional species pool) and 1 (maximal size). We then consider a linear relationship between the decimal logarithm of body size and the centroid of the niche (the dark line at Fig. 1). This relationship is obtained by fitting the linear model $c = \log_{10}(B_{prey}) = \alpha_0 + \alpha_1 \times \log_{10}(B_{pred})$ to the data, where B_{prey} and B_{pred} are the prey and predator body size respectively. The lower and upper boundaries of the feeding range are easily obtained by fitting the 5% and 95% quantile regressions between $\log_{10}(B_{prey})$ and $\log_{10}(B_{pred})$ (the grey lines at Fig. 1, see the example at Fig. 2). We note them as $r_{low,i}$ and $r_{high,j}$ respectively, and the corresponding parameters $\beta_{0,low/high}$ and $\beta_{1,low/high}$. In sum, the parameter n_i for any species of the metaweb is given by the standardized value of the log body size B_i, c_i is estimated from the linear regression between predator and prey log body size and r_i from the quantile regressions.

The next step of the methodology is to reconstruct the metaweb. Once these parameters are calculated from a subsample of species from the regional pool, the coefficients of the different linear models are used to infer the niche parameters of each species of the species pool. Again, the niche parameter for any species i, n_i, is given by the log of body size. The centroid of the niche is obtained by the relationship $c_i = \alpha_0 + \alpha_1 \times n_i$, the lower boundary of the niche is $r_{low,i} = \beta_{0,low} + \alpha_{1,low} \times n_i$ and the upper boundary $r_{high,i} = \beta_{0,high} + \alpha_{1,high} \times n_i$. A feeding link from species j to species i occurs if $n_j > r_{low,i} \& n_j < r_{high,i}$. We provide an example at Fig. 2.

3 Method accuracy

3.1 Predictive performance

We illustrate the method with the food web datasets of Brose et al. (Brose et al. 2005). The meta-analysis of Brose (Brose et al. 2006) was conducted on this dataset to test the generality of the predator-prey body size relationship across different systems (terrestrial, aquatic and marine). The relationship was found to be very strong across all systems despite exhibiting variability from one to another. Each web has between 26 and 380 species and 18 and 1466 feeding links. Several of these webs are repetitions over time at a single location, in which cases we pooled the data for each of the 15 different locations to calculate the predator-prey body size relationship. We removed 4 datasets that had a non-significant predator-prey relationship and were thus useless with our approach. The links are not systematically sampled, meaning that any absence of a link between two species for a given dataset could either be a real absence or due to insufficient sampling or lack of information. While the predator-prey body size relationship is very strong over all datasets (Brose2006), there is quite substantial variation among them, enabling us to assess the sensitivity of the method to the strength of this relationship.

We assessed the performance of our method using the True Skill Statistic (TSS). The TSS is based on the partition of events (the prediction of a trophic interaction) between four components: the component a reports the number of links that are both predicted and observed, b reports predicted links with no corresponding observation, c reports the number of observed links that are predicted absent, and d reports the number of predicted and observed absences of links. The TSS is then calculated as $TSS = (ad - bc)/[(a + c)(b + d)]$. The TSS quantifies the proportion of prediction success relative to false predictions and returns values ranging between 1 (perfect predictions)

8

and -1 (inverted forecast) (Allouche et al. 2006).

We calculated the TSS for each of the 11 different webs and related it to the strength of the predator-prey body size relationship, measured by the R^2 of the linear model. We find that the TSS is positive for all webs, ranging from 0.13 to 0.76 (Fig. 3A). We find a positive relationship between the R^2 of the linear model and the TSS ($R^2 = 0.50$, $p = 0.016$). When we decompose the different components of predictions and observations, we find that the fraction of prediction match is high, with an average of $(\overline{a} + \overline{d})/S^2 = 0.58$, Fig. 3B). The fraction of wrong predictions is lower, at $\overline{b + c}/S^2 = 0.40$, and decreases with the R^2 of the predator-prey body size relationship.

The parameterized niche model tends to overestimate the number of links in a web (see the example at Fig. 2). This result is significant but not surprising, given that these datasets do not necessarily contain all links, as they were not designed with this purpose, and thus some of the links might have been missed. This interpretation is also reminiscent of previous debates on the difficulty to sample all links in a web (Martinez et al. 1999). It is also well known that the niche model predicts a continuous diet along the niche axis (the webs are said to be interval (Cohen et al. 1990; Stouffer et al. 2006)), while real food webs do not have this characteristic. We thus might over predict link density within the niche of a given species. Previous studies (Allesina et al. 2008) and the Application 1 however show this problem is easily circumvented when a second niche axis, *e.g.* an environmental niche, comes into play. A recent study on dimensionality of networks shown that most webs have between 3 and 7 dimensions (Eklöf et al. 2013), meaning that adding a few more niche axes can greatly improve the accuracy of predictions.

3.2 Sensitivity to sampling effort

We subsequently explored the impact of sampling effort on the accuracy of the model predictions. We assumed a random subsampling of all the interactions occurring in the food web. To do so, we selected a species rich food web ($S = 67$) from the Brose et al. dataset, with 601 observed feeding links and a good TSS (0.51). We randomly removed from 0 to 90% of the observed links to do the evaluation of the parameters of the linear regressions (i.e. e decrease the quantity of information used to calibrate the model). We then after compared the empirical web (with all species) to the inferred web with these parameters (all species also). The comparison was done again with the TSS. We performed 100 randomizations per number of removed links. This numerical simulation reproduces incomplete sampling in the process of building the food web. We find that the TSS remains constant up until 80% of the observed links are removed (Fig. 3). At this level, the TSS starts to decline drastically and its variance increases.

This result shows that our method of parameterization of the niche model is robust with regard to sampling effort. Note however that a biased sampling with respect to body size (e.g. sampling of the largest species) might be more likely to reduce the fit of the predator-prey body size relationship. The aggregation intro trophic species that do have the same body size and the same diet should not impact the prediction since it will not affect parameter evaluation. It will however reduce the fit of the predator-prey body size relationship and therfore the accuracy of the method if the species do have different body sizes. The same artifact will be observed if there is strong intraspecific variation in body size (see the Discussion).

10

4 Application: Mediterranean food web structure under fishing pressure

4.1 Dataset

We now present an application of the method to infer the metaweb of interactions among fishes of the Mediterranean sea. The Mediterranean is known as a hotspot of fish diversity that is severely threatened by climate change and overfishing (Mouillot et al. 2011).There are 557 fish species in the regional pool, with a maximum body size ranging from 2.3 cm to 1100 cm (Froese & Pauly 2011; Louisy 2005; Whithead et al. 1986). Chondrichthyans, mammals and turtles were under represented in the two trophic networks and were removed from the analyses. We parameterized the niche model with a subset of species, from two different highly resolved food webs from the Catalan area (Coll et al. 2006) (82 species) and Corsica (Albouy et al. 2010) (58 species).

4.2 Inferring the metaweb for Mediterrannean fishes

We estimated parameters n, c and r for each of the 557 species and inferred the potential interactions among all of them (the example in the Supplementariy code is based on this dataset). The metaweb has a total of 126 501 links, for a connectance of 0.41 (Fig. 5A). The metaweb is also highly nested (specialist species feed on a subset of prey of the most generalist species. Fig. 5A). We also considered a second niche axis related to species spatial distribution. Most fish species have restricted geographic range within the Mediterranean sea because of specific response to temperature and other environmental variables (Albouy et al. 2012). We therefore removed from the metaweb all links between species having no range overlap. Data on the extent of oc-

11

currence of fish species were compiled from a published atlas of fishes of the northern Atlantic and the Mediterranean (Whitehead & Unesco 1986). This atlas is based on regional data sets and expert knowledge and was edited between 1984 and 1986. It currently provides the only available basin-wide information on the extent of occurrence of all Mediterranean Sea fish species. The above mentioned atlas do not account for the bathymetric distribution of Mediterranean fish species, yet bathymetry is considered as one of the main factors accounting for marine fish distributions (Louisy 2005). We therefore refined the extent of occurrence maps by clipping off areas with depths that fall outside the minimum or maximum known for the species. Species' bathymetric ranges were obtained from FishBase (Froese 2010; Louisy 2005). The resulting metaweb has a total of 95 989 links, for a connectance of $C = 0.31$. Connectance decreases because links are removed by incomptabilities in bathymetry but the total number of species stays constant. This metaweb is clearly less interval (Fig. 5B). Contiguous gaps in the diet are likely to emerge from modularity in the co-occurrence matrix (Araújo et al. 2011).

4.3 Impact of global changes

Our method to parameterize the niche model has a unique feature relative to the original niche model (Williams & Martinez 2000): the network properties of the original model, such as the number of links, food chain length and degree distribution (the number of in and out feeding links per species), are controlled by the input parameters (species richness and connectance), wherea all properties of our parameterized niche model are emergent features of the predator-prey body size relationship and the frequency distribution of body size. The connectance in the niche model is fixed by the user; in our case it strongly depends on the scaling of the feeding range with body size and the frequency of larger body species.

This feature is particularly important to understand global change impacts on community structure. For instance, a common prediction of the impact of fisheries on the body size distribution is the reduction in the average and variance of body size (Jackson et al. 2001). Similarly, global warming is also expected to alter fish body size distribution towards smaller species (Cheung et al. 2012). We explored by simulations the impact of these changes on the degree distribution of the Mediterranean metaweb. Results are illustrated at Fig. 6. The shape of the cumulative degree distribution provides a visual assessment of the distribution of diet specificity in a network. The curves becomes steeper and the fall moves to the left with increasing specialization (indicative of a larger proportion of species with a low degree). Even if the simulated scenarios are crude representations of the predicted alterations of community structure, they both show that fisheries impacts on body size will substantially alter the network properties. The results at Fig. 6 show that reduction in the average body size will decrease the average number of preys per predator (there is an initial sharper decline of the cumulative distribution), but that super generalist species will also appear (because of the shift of the tail toward the right). The removal of the 40% largest species reduces much more the average generality which is expect as larger species are predators with a large feeding niche in the niche model. The two scenarios consequently increases substantially the relative abundance of species with a smaller degree, even for the average size reduction scenario where the total number of species is held constant. The change in the degree distribution is likely to reduce substantially the expected persistence and stability of these communities (Gravel et al. 2011a,b).

13

5 Discussion

In this paper, we presented a method to infer potential interactions among an arbitrary pool of species. The data required to perform this methodology are simple to obtain, as the body size of a large number of species are available from reference databases, or easy to measure. Because we rely on a robust allometric relationship, applying this method requires neither complex statistical techniques, nor an exhaustive knowledge of the realized interactions within the metaweb of interest. In addition to the opportunity to simulate biodiversity scenarios, our method can also help generating baseline expectations about the food web structure for environments which are notoriously difficult to sample, such as soils, deep-sea environments, or fossil records. 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.

Ontogenic shifts in diet are common in many size-structured populations and 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 yield in a data point for species B figuring above the 1:1 relationship. Such a data point will obviously influence the model calibration and enlarge the regime of all species. It is not obvious however that ontogenic shifts will be found 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.

The method should be completed with other sources of informations to better pre-

14

dict gaps in the interaction matrix. The original niche model was definitely inspired by the predator-prey body size relationship, but was intented to be more general and eventually deal with several niche axes (Williams & Martinez 2000). Allesina et al. (2008) indeed found that adding a second axis, creating gaps into the first axis interaction matrix, increases the fit of the model to empirical data. It also makes the network less interval (a continuous succession of species diets along the niche axis), a structural issue of the niche model that was reported by Cattin et al. (2004) and Bersier et al. (2006). There are numerous sources of information that could be used to improve the model, such as co-occurrence and functional traits.

Our application with the Mediterannean pelagic fish food web provides an example of how straightforward it is to add additional information so as to improve the parameterization. A similar approach could also build on the comptability of other traits such as phenology, location in the water column or hunting modes. While the approach we describe here is based on very simple statistics, the next methodological efforts will also have to take into account more various and heterogeneous sources of data such as phylogeny (Eklöf et al. 2012) and expert knowledge. Bayesian inference appears a good candidate to achieve this goal with the possibility to constrain the prior distribution of parameters for each species.

Adding this method to the ecologist's toolbox is a timely issue because there is an urgent need to include interactions into future biodiversity scenarios ("A road map for integrating eco-evolutionary processes into biodiversity models"). There has been impressive progress in biogeography over the last fifteen years to predict the impact of global changes on range shifts, extinction risks, and the future distribution of biodiversity, but we now face the realization that emerging ecosystems are unlikely to be a spatial displacement of the ones we currently know. This method will help assessing global change impacts of community structure, moving the field of biogeography

15

closer to ecosystem functioning.

6   Acknowledgements

16

References

Albouy, C. et al. (2010) *Simulation of the combined effects of artisanal and recreational fisheries on a Mediterranean MPA ecosystem using a trophic model.* Marine Ecology Progress Series, **412**, 207–221.

Albouy, C. et al. (2012) *Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages.* Global Change Biology, n/a–n/a.

Allesina, S., Alonso, D. & Pascual, M. (2008) *A general model for food web structure.* Science, **320**, 658–61.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) *Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS).* Journal of Applied Ecology, **43**, 1223–1232.

Araújo, M. B. et al. (2011) *Using species co-occurrence networks to assess the impacts of climate change.* Ecography, **34**, 897–908.

Baiser, B. et al. (2012) *Geographic variation in network structure of a nearctic aquatic food web.* Global Ecology and Biogeography, **21**, 579–591.

Bersier, L.-F. et al. (2006). Reply to Martinez and Cushing. *Ecological networks: Linking structure and dynamics* (ed. by Pascual, M & Dunne, J. a.), pp. 91–92. Oxford University Press, Oxford.

Brose, U., Williams, R. J. & Martinez, N. D. (2006) *Allometric scaling enhances stability in complex food webs.* Ecology letters, **9**, 1228–36.

Brose, U. et al. (2005) *Body sizes of consumers and their resources.* EN. Ecology, **86**, 2545–2545.

Cattin, M.-F. et al. (2004) *Phylogenetic constraints and adaptation explain food-web structure.* Nature, **427**, 835–9.

Cavender-Bares, J. et al. (2009) *The merging of community ecology and phylogenetic biology.* Ecology letters, **12**, 693–715.

Cheung, W. W. L. et al. (2012) *Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems.* Nature Climate Change, **3**, 254–258.

Cohen, J. E., Briand, F. & Newman, C. (1990) *Community food webs: data and theory,* Springer-Verlag, Berlin.

Cohen, J. E., Jonsson, T. & Carpenter, S. R. (2003) *Ecological community description using the food web, species abundance, and body size.* Proceedings of the National Academy of Sciences of the United States of America, **100**, 1781–6.

Coll, M. et al. (2006) *Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean.* Journal of Marine Systems, **59**, 63–96.

Dunne, J. A. (2006). The network structure of food webs. *Ecological networks: Linking structure and dynamics* (ed. by Pascual, M & Dunne, J. A.), pp. 27–86. Oxford University Press, Oxford.

Eklöf, A. et al. (2012) *Relevance of evolutionary history for food web structure.* Proceedings. Biological sciences / The Royal Society, **279**, 1588–96.

Eklöf, A. et al. (2013) *The dimensionality of ecological networks.* Ecology letters,

Froese, R (2010) *FishBase,*

Froese, R. & Pauly, D. (2011). *Fishbase.*

Gravel, D. et al. (2011a) *Persistence increases with diversity and connectance in trophic metacommunities.* PloS one, **6**, e19374.

Gravel, D. et al. (2011b) *Trophic theory of island biogeography.* Ecology letters, **14**, 1010–6.

Havens, K. (1992) *Scale and structure in natural food webs.* Science, **257**, 1107–1109.

Ings, T. C. et al. (2009) *Ecological networks–beyond food webs.* The Journal of animal ecology, **78**, 253–69.

Jackson, J. B. et al. (2001) *Historical overfishing and the recent collapse of coastal ecosystems.* Science, **293**, 629–37.

Lafferty, K. D. & Dunne, J. a. (2010) *Stochastic ecological network occupancy (SENO) models: a new tool for modeling ecological networks across spatial scales.* Theoretical Ecology, **3**, 123–135.

Louisy, P (2005) *Guide d'identification des poissons marins: Eirpe de l'ouest et Métitérannée,* Ulmer, Paris.

Martinez, N. D. et al. (1999) *Effects of Sampling Effort on Characterization of Food-Web Structure.* Ecology, **80**, 1044–1055.

McGill, B. et al. (2006) *Rebuilding community ecology from functional traits.* Trends in Ecology & . . . , **21**, 178–85.

Montoya, J. M. & Raffaelli, D. (2010) *Climate change, biotic interactions and ecosystem services.* Philosophical transactions of the Royal Society of London. Series B, Biological sciences, **365**, 2013–8.

Mouillot, D. et al. (2011) *Protected and threatened components of fish biodiversity in the Mediterranean sea.* Current biology : CB, **21**, 1044–50.

Mouquet, N. et al. (2012) *Ecophylogenetics: advances and perspectives.* Biological reviews of the Cambridge Philosophical Society,

Pereira, H. M. et al. (2010) *Scenarios for global biodiversity in the 21st century.* Science (New York, N.Y.), **330**, 1496–501.

Petchey, O. L. et al. (2008) *Size, foraging, and food web structure.* Proceedings of the National Academy of Sciences of the United States of America, **105**, 4191–6.

Piechnik, D. A., Lawler, S. P. & Martinez, N. D. (2008) *Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order.* Oikos, **117**, 665–674.

Pillai, P., Loreau, M. & Gonzalez, A. (2009) *A patch-dynamic framework for food web metacommunities*. Theoretical Ecology, **3**, 223–237.

Poisot, T. et al. (2012) *The dissimilarity of species interaction networks.* Ecology letters, **15**, 1353–61.

Riede, J. O. et al. (2010) *Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems*. Ecology Letters, no–no.

Stanko, M. et al. *Mammal density and patterns of ectoparasite species richness and abundance*. eng. Oecologia, **131**, 289–295.

Stouffer, D. B., Camacho, J. & Amaral, L. a. N. (2006) *A robust measure of food web intervality.* Proceedings of the National Academy of Sciences of the United States of America, **103**, 19015–20.

Stouffer, D. B. et al. (2005) *Quantitative patterns in the structure of model and empirical food webs*. Ecology, **86**, 1301–1311.

Thuiller, W. et al. *A road map for integrating eco-evolutionary processes into biodiversity models*. Ecology Letters,

Tylianakis, J. M. et al. (2008) *Global change and species interactions in terrestrial ecosystems*. Ecology Letters, **11**, 1351–1363.

Whitehead, P. & Unesco (1986) *Fishes of the North-eastern Atlantic and the Mediterranean*,

Whithead, P. et al. (1986) *Fishers of the north eastern Atlantic and the Mediterranean*, UNSECO, Paris.

Williams, R. J. (2011) *Biology, methodology or chance? The degree distributions of bipartite ecological networks*. PloS one, **6**, e17645.

Williams, R. J., Anandanadesan, A. & Purves, D. (2010) *The probabilistic niche model reveals the niche structure and role of body size in a complex food web*. PloS one, **5**, e12092.

Williams, R. J. & Martinez, N. D. (2000) *Simple rules yield complex food webs*. Nature, **404**, 180–183.

Figure legends

Figure 1

Schematic representation of the niche model and its application to the predator-prey body size relationship. Three consumer species are represented. The white triangles correspond to the niche position of predators (their position on the X axis is transposed along the Y axis). For most cases, prey size is smaller that the predator size and thus fall under the 1:1 relationship. In some occasions, however, the feeding range can overlay the 1:1 relationship, for instance in presence of ontogenic shifts in diet. For a given predator, we consider that the niche centroid (c_i) is the average prey size, given by the linear relationship between predator and prey size (black line). The boundaries of the feeding range (r_i) are given by the 5% and 95% quantile regression lines (dotted lines). A predator feeds on all prey species which their niche lies between these boundaries. In this specific example, the largest predator feeds on the two smaller species (the white triangles depicting the niche lies between range boundaries) and the intermediate size predator feeds on the smallest species.

Figure 2

Example of predator-prey body size relationship and predictions from the parameterized niche model. Black dots represent observed links while open dots are predicted interactions based on the parameterization of the niche model. The bullseye symbols thus correspond to a match between predicted occurrence of a link and the real data (the "a" classification in the calculation of the TSS, see main text), a black dot a predicted link with not pbservation ("b") and an open circle a non-predicted and observed link ("c"). Data from a creek bed located in Australia (Brose et al. 2005).

Figure 3

Performance of the parameterized niche model to predict food web structure for the 11 food webs. A) Relationship between the TSS and the R^2 of the predator-prey body size relationship. B) Partitionning of the different components of the TSS.

Figure 4

Effect of the sampling effort on the accuracy of the parameterized niche model to predict food web structure. The simulation was conducted with the same data as Fig. 2.
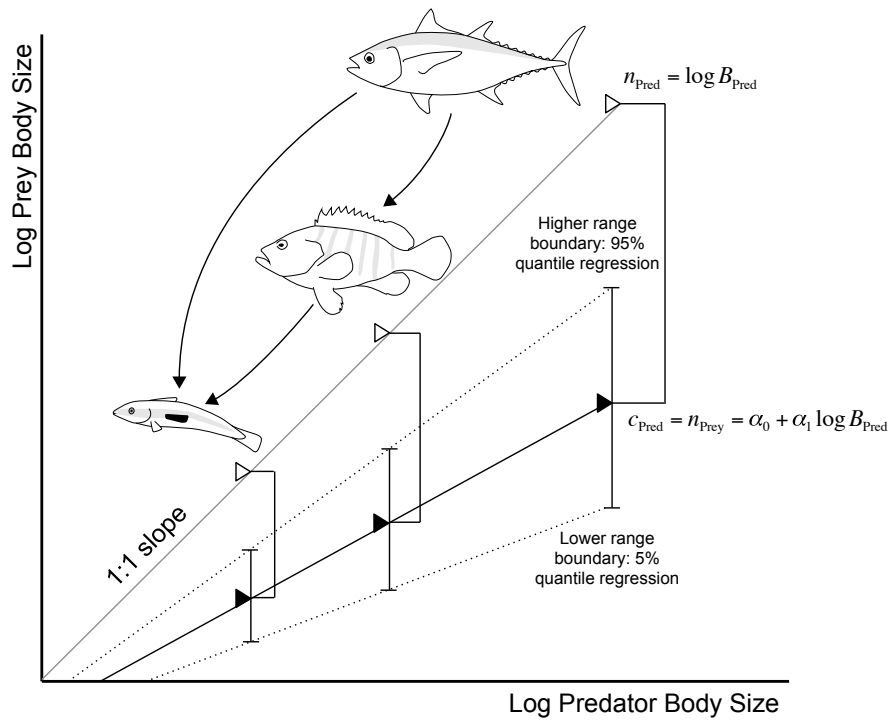
Figure 5

Illustration of the metaweb of the Mediterannean pelagic fishes (interactions in black). Panel A) represents the full metaweb and B) the same metaweb for which links between species not co-occuring together were removed (their range overlap for less than 0.1% of the Mediterannean sea).
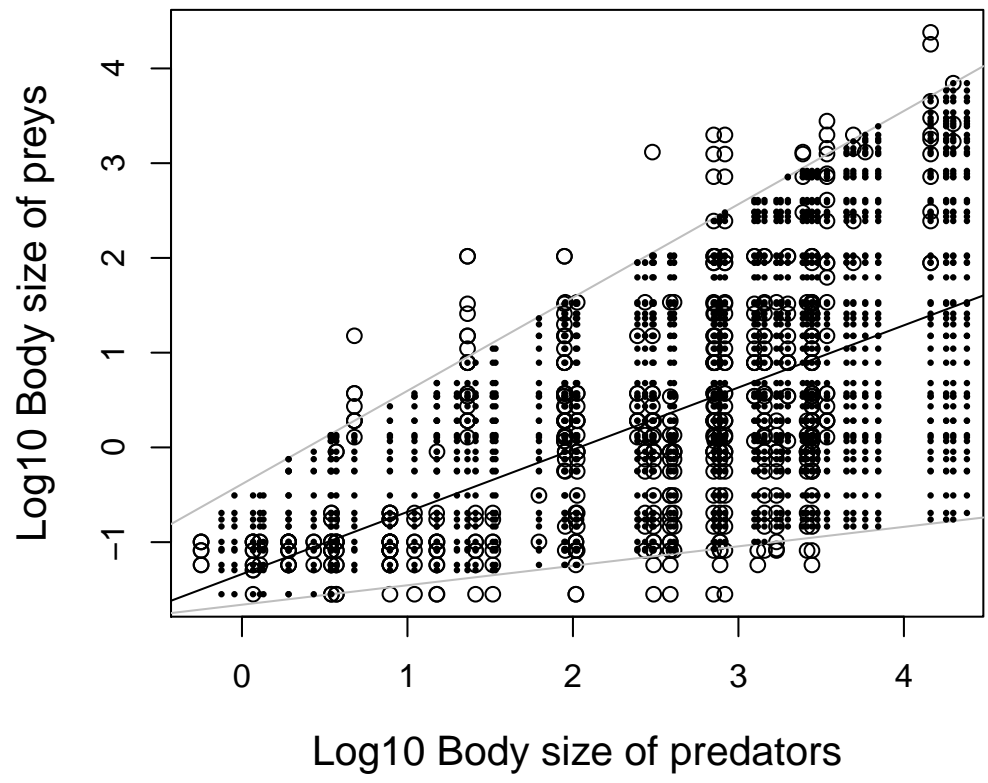
Figure 6

Impacts of altering the body size distribution of Meditarrennean fishes on the degree distribution of the metaweb. The black line corresponds to the original metaweb degree distribution. For the first scenario, we simulated a 40% reduction in average body size and recalculated the metaweb properties, keeping the predator-prey body size relationship constant (dotted line). For the second scenario we eliminated the top 40% largest species and recalculated the metaweb properties (dashed line).
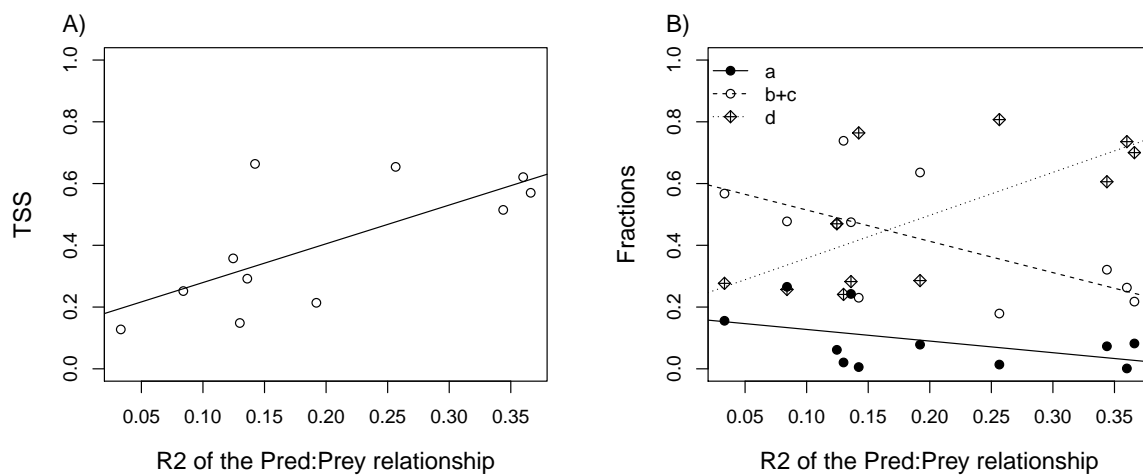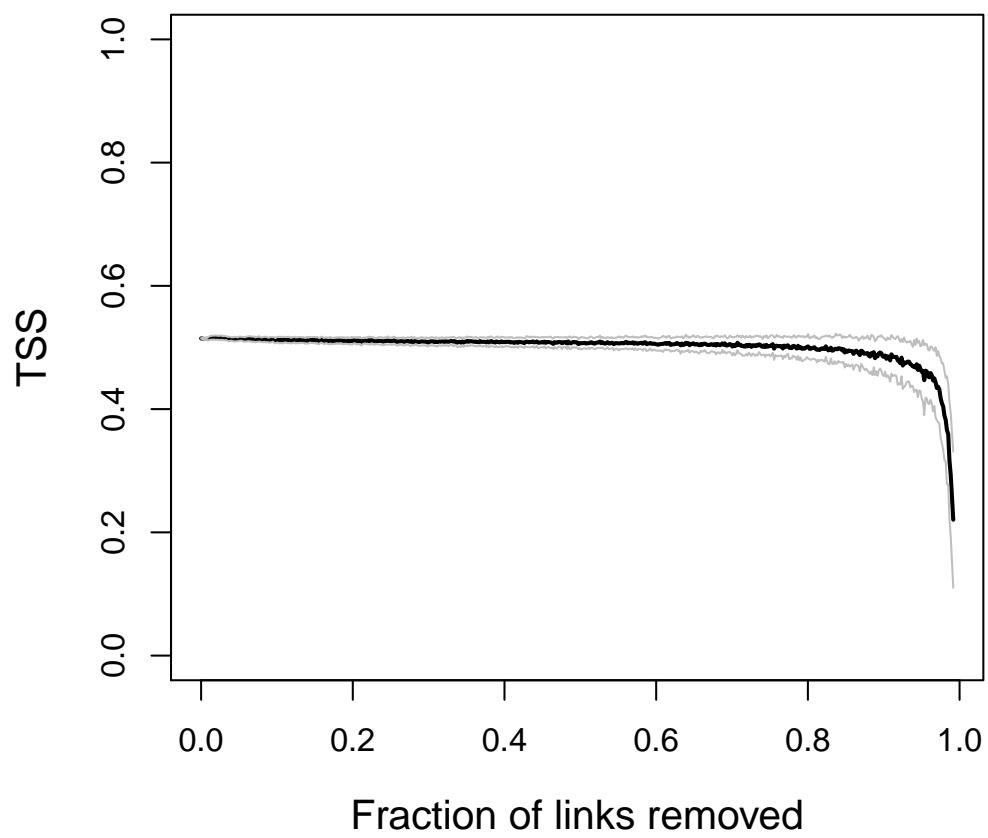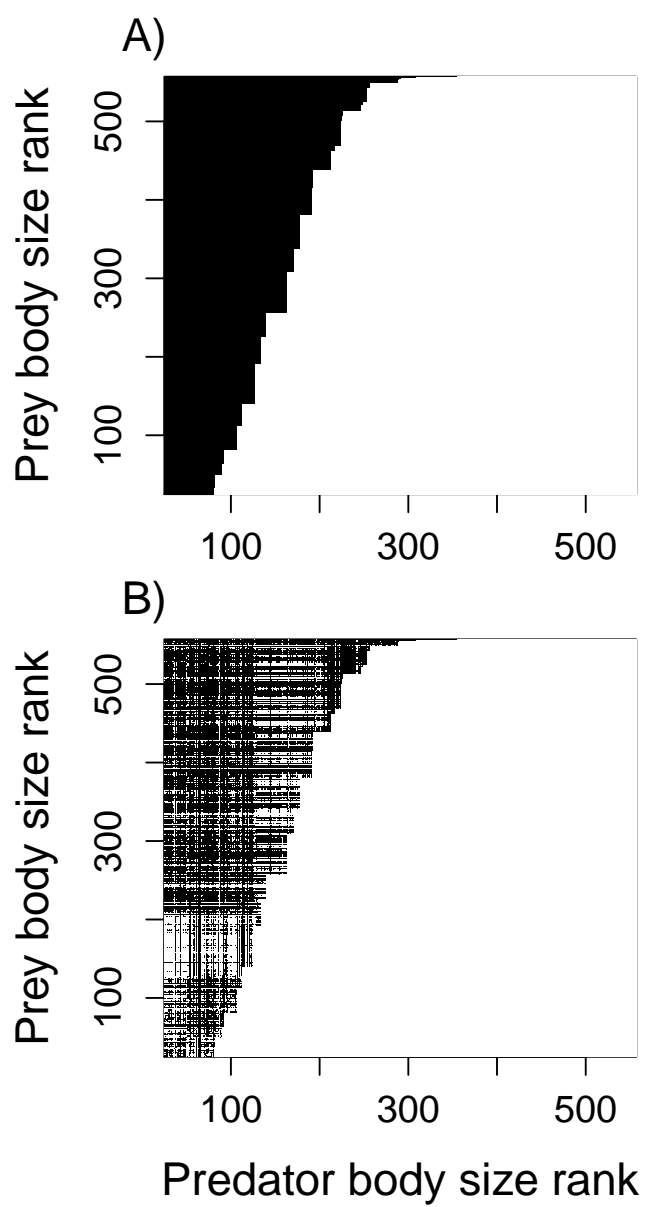
Figures

Figure 1

The figure shows a plot with "Log Prey Body Size" on the y-axis and "Log Predator Body Size" on the x-axis. Labels include:

$n_{\mathrm{Pred}} = \log B_{\mathrm{Pred}}$

Higher range boundary: 95% quantile regression

$c_{\mathrm{Pred}} = n_{\mathrm{Prey}} = \alpha_0 + \alpha_1 \log B_{\mathrm{Pred}}$

Lower range boundary: 5% quantile regression

1:1 slope

Figure 2

Figure 3

Figure 4

Figure 5

A)

B)

Prey body size rank

Prey body size rank

Predator body size rank

Figure 6