

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

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Abstract

Current ecological changes makes it important to be able to predict how interactions will occur in emerging ecosystems. Most of the current methods to predict the existence of interactions between two species require a good knowledge of their traits, or rely on previous observations. In this paper, we overcome these limitations by developing a method, inspired from the niche model of food webs, which uses the statistical relationships between species trophic properties to infer a set of potential interactions. Our method works with a reduced set of information, namely the body size or body mass of species for which we want to estimate the interactions, and enough observations of interactions between these species to have a robust allometric scaling. 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 illustrate its ability to forecast the impact of global changes on ecosystem by predicting the properties of the mediterranean fishes metaweb under different fishing pressure scenarios.

1 Introduction

One of ecology's current challenges is to understand how communities will re-assemble following independent 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 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) for competitive communities, 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* (Poisot et al. 2012). 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 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; Poisot et al. 2012), 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 (Canard 2011; “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 species trophic interactions could greatly improve our understanding of large scale food web structure and our capacity to anticipate major changes in ecosystem functioning. 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 simple rules are sufficient to generate realistic food web structures that fit most documented food webs (Dunne 2006). The niche model was a substantial improvement of the previous cascade model (Cohen 1990) and subsequent models (e.g. the nested hierarchy - (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). 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 (Allesina et al. 2008; Williams 2011; Williams et al. 2010). The methods developed in these studies provide, for each species of the food web, the optimal parameters to fit the empirical web structures, given the hypothesized underlying rules. Despite their theoretical interest, these methods however come with several drawbacks at the time to perform biodiversity scenarios: i) they

are difficult to apply at large scale because of the technical and logistical requirements of metaweb data collection; ii) once the model is parameterized, it could only be used to infer feeding interactions between species with already documented interactions (i.e. impossible to infer potential interactions among species that do never co-occurred) and iii) the model optimization is a serious challenge for large datasets with 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 metaweb from incomplete data on species interactions. We do so by a parameterization of the niche model, based on the well-known 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 Mediterranean sea and the consequences of alteration of body size distribution by global changes or anthropic forcings.

2 Model description

2.1 Inferring parameters from the niche model

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

Assuming that body size is the main niche axis responsible for trophic interactions, the parameter n_i corresponds simply to the log of body size of species i . Though only the relative position of all species along the body size gradient needs be respected, we suggest 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). 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. Once these parameters are calculated from field data, even with a subsample of species from the regional pool, it is straightforward to obtain estimates of the parameters for all species and thus to reconstruct the metaweb.

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 systems, but also to vary 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 and we thus regrouped 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) and -1 (inverted forecast) (Allouche et al. 2006).

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

177 The parameterized niche model tends to overestimate the number of links in a web
 178 (see the example at Fig. 2). This result is significant but not surprising, given that these
 179 datasets do not necessarily contain all links, as they were not designed with this purpose,
 180 and thus some of the links might have been missed. It is also well known that the niche
 181 model predicts a continuous diet along the niche axis (the webs are said to be interval
 182 (Cohen et al. 1990; Stouffer et al. 2006)) while real food webs do not have this characteristic.
 183 We thus might over predict link density within the niche of a given species. Previous
 184 studies (Allesina et al. 2008) and the Application 1 however show this problem is easily
 185 circumvented when a second niche axis, *e.g.* an environmental niche, comes into play.

186 3.2 Sensitivity to sampling effort

187 We subsequently explored the impact of sampling effort on the accuracy of the model pre-
 188 dictions. To do so, we selected a species rich food web ($S = 67$), with 601 observed feeding
 189 links and a good TSS (0.51). We randomly removed from 0 to 90% of the observed links
 190 when parameterizing the niche model and then calculated the TSS for the full web with
 191 these parameters (100 randomizations per removal category). This numerical simulation
 192 reproduces incomplete sampling in the process of building the food web. We find that the
 193 TSS remains constant up until 80% of the observed links are removed (Fig. 4). At this

level, the TSS starts to decline drastically and its variance increases. This result shows that our parameterization of the niche model is robust to the sampling effort.

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 threaten 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 Mediterranean fishes

We estimated parameters n , c and r for each of the 557 species and inferred the potential interactions among all of them. 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

216 links between species having no range overlap. Data on the extent of occurrence of fish
217 species were compiled from a published atlas of fishes of the northern Atlantic and the
218 Mediterranean (Whitehead & Unesco 1986). This atlas is based on regional data sets and
219 expert knowledge and was edited between 1984 and 1986. It currently provides the only
220 available basin-wide information on the extent of occurrence of all Mediterranean Sea fish
221 species. The above mentioned atlas do not account for the bathymetric distribution of
222 Mediterranean fish species, yet bathymetry is considered as one of the main factors ac-
223 counting for marine fish distributions (Louisy 2005). We therefore refined the extent of
224 occurrence maps by clipping off areas with depths that fall outside the minimum or max-
225 imum known for the species. Species' bathymetric ranges were obtained from FishBase
226 (Froese 2010; Louisy 2005). The resulting metaweb has a total of 95 989 links, for a con-
227 nectance of $C = 0.31$. This metaweb is less interval and there are modules (groups of
228 species sharing similar interactions) emerging (Fig. 5B).

229 **4.3 Impact of fishing pressure**

230 Our method to parameterize the niche model has a unique feature relative to the original
231 niche model (Williams & Martinez 2000): the network properties of the original model,
232 such as the number of links, food chain length and degree distribution (the number of in
233 and out feeding links per species), are controlled by the input parameters (species richness
234 and connectance), while the properties of our parameterized niche model are emergent
235 features of the predator-prey body size relationship and the frequency distribution of body
236 size. This feature is particularly important when comes the time to understand global
237 change impacts on community structure. For instance, a common prediction of the impact
238 of fisheries on the body size distribution is reduction in the average and variance of body
239 size (Jackson et al. 2001). We explored by simulations the impact of these changes on the
240 degree distribution of the Mediterranean metaweb. Results are illustrated at Fig. 6. 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. It is obvious from Fig. 6 that reduction in the average body size will decrease the average number of preys per predator. 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 has considerable impacts on the expected persistence of these species (Gravel et al. 2011a,b).

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 body size of a large number of species are available, 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 conservation opportunity, 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.

The method should be completed with other sources of informations to better understand holes in the interaction matrix. The original niche model was definitely inspired by the predator-prey body size relationship, but was intended to be more general and eventually deal with several niche axis (Williams & Martinez 2000). Allesina et al. (Allesina et al.

2008) indeed found that adding a second axis, creating holes into the first axis interaction matrix, increases the fit of the model to real data. It also makes the network less interval, a structural issue of the niche model that was reported by Cattin et al (Cattin et al. 2004) and Bersier et al. (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 Mediterranean pelagic fish food web provides a great example of how easily additional information could be added to the parameterization. A similar approach such as the one we described could also build on the compatibility 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. 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 closer to ecosystem functioning.

6 Acknowledgements

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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 than 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 a given predator, we consider that the niche centroid (c) is the average prey size, given by the linear relationship between predator and prey size (black line). The boundaries of the feeding range (r) 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 observation ("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

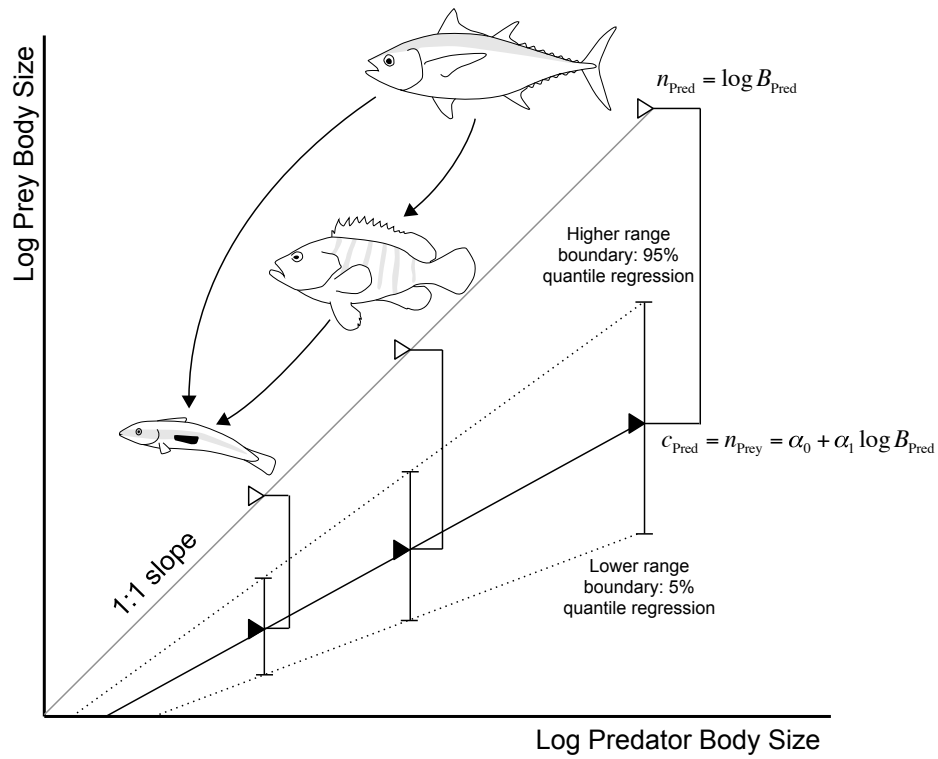
Illustration of the metaweb of the Mediterranean pelagic fishes. Panel A) represents the full metaweb and B) the same metaweb for which links between species not co-occurring together were removed (their range overlap for less than 0.1% of the Mediterranean sea).

Figure 6

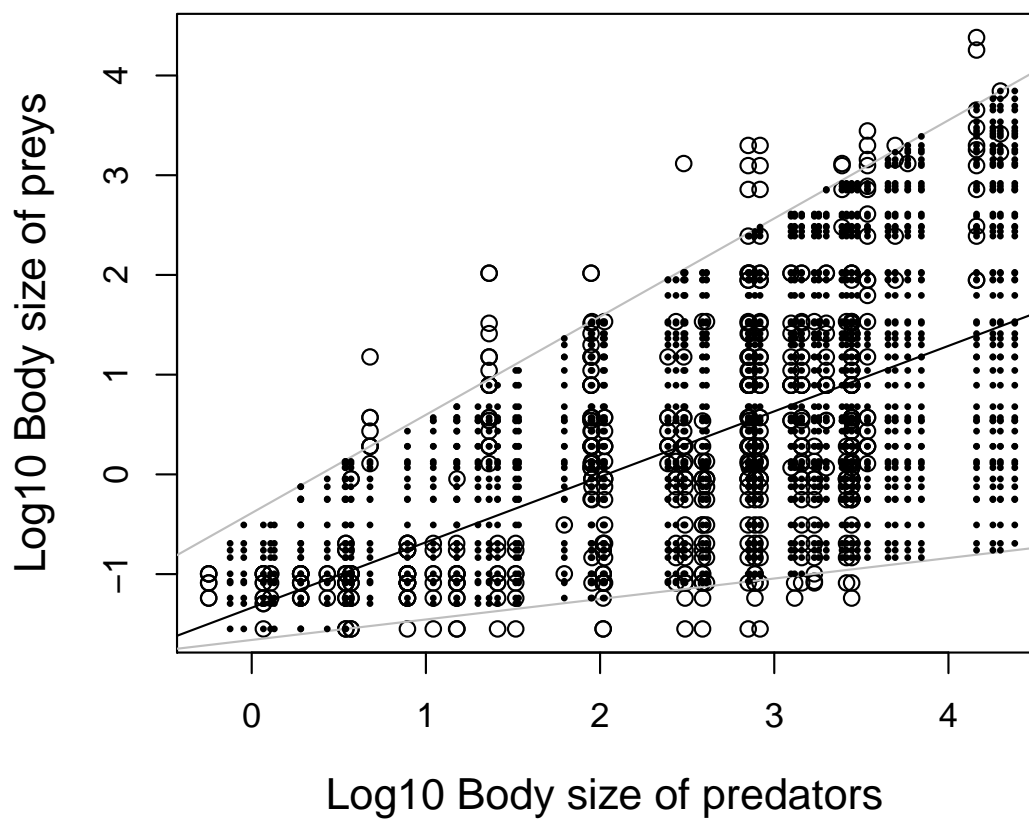
Impacts of altering the body size distribution of Mediterranean fishers on the degree distribution of the metaweb. The black line corresponds to the original metaweb degree distribution. For the first scenario, we simulated a 40% reduction in body size and recalculated the metaweb properties, keeping 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).

423 **Figures**

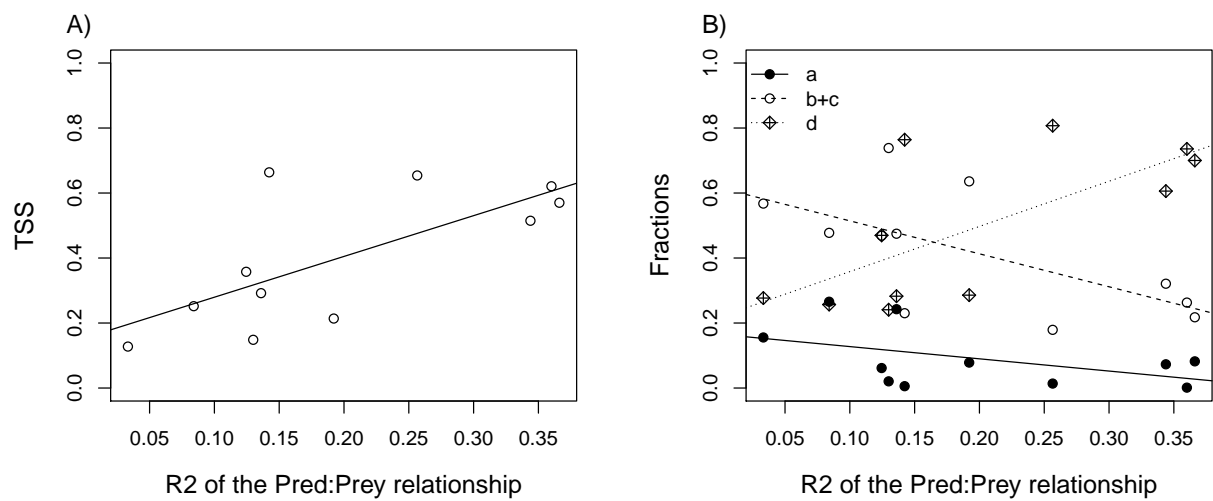
424 **Figure 1**



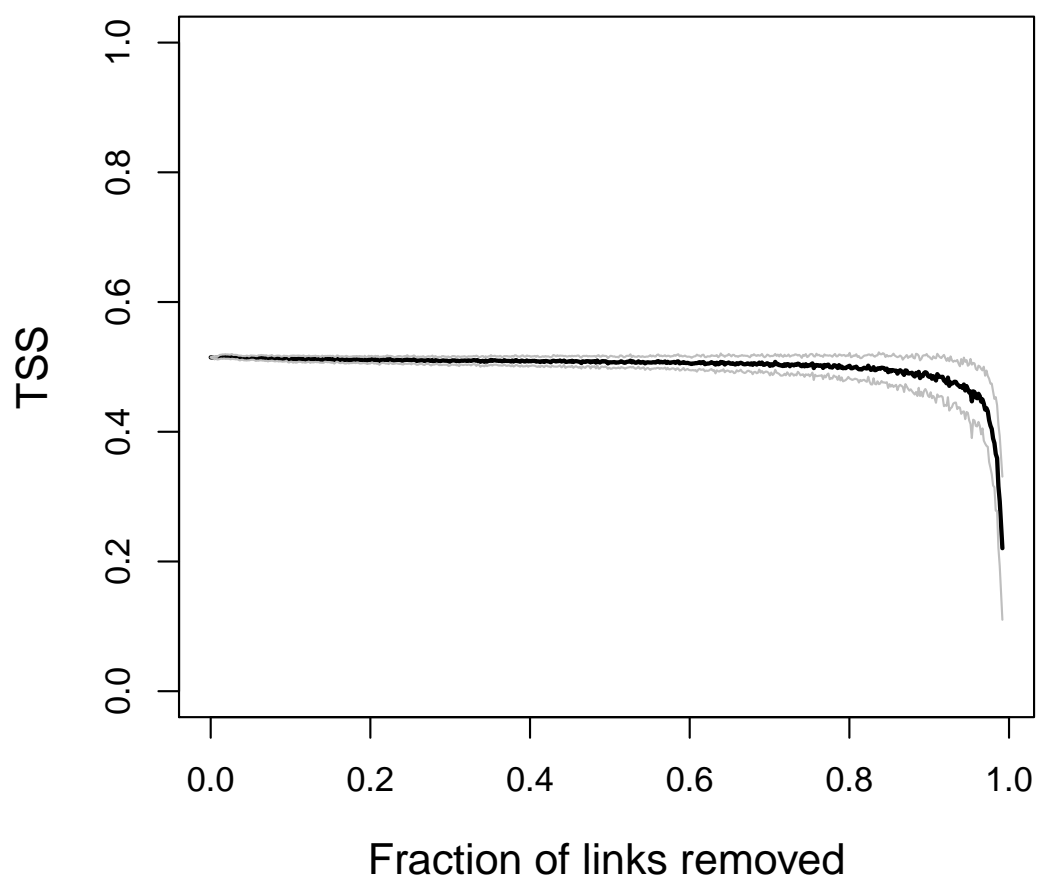
425 **Figure 2**

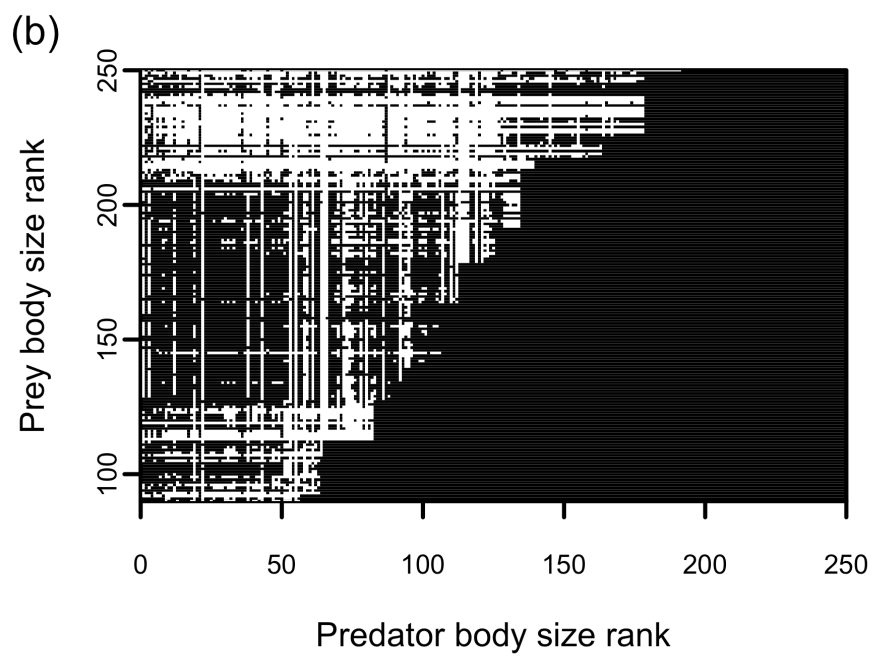
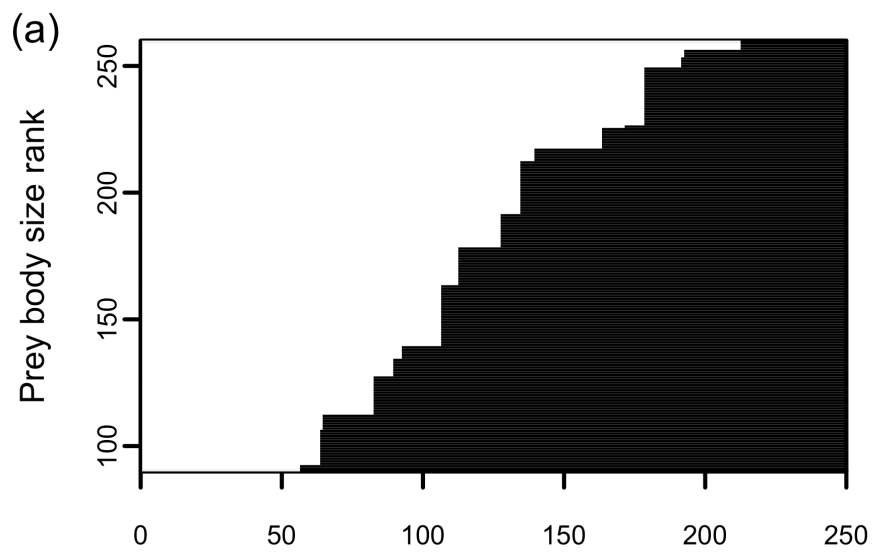


426 **Figure 3**



427 **Figure 4**





429 **Figure 6**

