

From projected species distribution to food-web structure under climate change

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Abstract

Climate change is inducing deep modifications in species geographic ranges worldwide. However, the consequences of such changes on community structure are still poorly understood, particularly the impacts on food-web properties. Here, we propose a new framework, coupling species distribution and trophic models, to predict climate change impacts on food-web structure across the Mediterranean Sea. Sea surface temperature was used to determine the fish climate niches and their future distributions. Body size was used to infer trophic interactions between fish species. Our projections reveal that 54 fish species of 256 endemic and native species included in our analysis would disappear by 2080–2099 from the Mediterranean continental shelf. The number of feeding links between fish species would decrease on 73.4% of the continental shelf. However, the connectance of the overall fish web would increase on average, from 0.26 to 0.29, mainly due to a differential loss rate of feeding links and species richness. This result masks a systematic decrease in predator generality, estimated here as the number of prey species, from 30.0 to 25.4. Therefore, our study highlights large-scale impacts of climate change on marine food-web structure with potential deep consequences on ecosystem functioning. However, these impacts will likely be highly heterogeneous in space, challenging our current understanding of climate change impact on local marine ecosystems.

Keywords: climate change, connectance, fish body size, food-webs, generality, Mediterranean Sea, metaweb, niche model, vulnerability

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Introduction

There has been impressive progress in biogeography over the last 15 years to predict the impact of climate change on species geographic range shifts, extinction risks, and biodiversity patterns (Thuiller, 2004; Araújo & New, 2007; Albouy *et al.*, 2013; Thuiller *et al.*, 2013). Future ecosystems are, however, unlikely to be a simple collection of independent species that will co-occur according to their future geographic distributions. Indeed, novel ecosystems will emerge with assemblages that have never been observed before and, most likely, with species that have not been known to interact yet. One of the greatest challenges that ecology and biogeography are facing today is thus to understand

how current assemblages, forming complex interaction networks, will be reorganized following individual species responses to climate change and how these emergent ecosystems will function (Montoya *et al.*, 2009; Woodward *et al.*, 2010).

Food webs are central to ecosystem functioning since their structure governs fluxes of energy and underpins key processes such as productivity (Chassot *et al.*, 2010) and resilience (Loreau & Behera, 1999). The biomass produced by basal species is distributed across the food web via trophic interactions toward apical species (Cury *et al.*, 2003; Allesina & Bodini, 2004; Colloca *et al.*, 2010). This flux of matter is, however, far from a linear chain from primary producers to top carnivores, with frequent omnivory, feeding loops, intraguild predation, and cannibalism (Polis & Strong, 1996; Thompson *et al.*, 2007). Network-level responses to climate change are thus likely to be more than simply the aggregate sum of all species-level responses. Spatial mismatch may

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separate previously interacting species (Schweiger *et al.*, 2008), while novel interactions may appear thanks to new spatial co-occurrences (Gilman *et al.*, 2010). Consequently, understanding the patterns and processes that govern food-web assembly remains crucial to predict the impacts of climate change on ecosystem functioning (Woodward *et al.*, 2010). To this aim new modelling frameworks need to consider species as potential interacting components of a wider ecological network.

The major recent breakthrough in food-web theory has been the attempts to parameterize food-web models from field data and to compare their fit through likelihood methods (Allesina *et al.*, 2008; Williams *et al.*, 2010). Once the model is parameterized, the principal drawback of these methods at the time to perform biodiversity scenarios is the impossibility to infer potential interactions between species that have never co-occurred. There is consequently a need for a method that could rapidly and easily provide an estimate of potential interactions in a metaweb based on incomplete data.

Here, we assume a positive relationship between predator and prey body size, an ubiquitous pattern found in most terrestrial and marine ecosystems (Brose *et al.*, 2006), to infer potential interactions among species and predict large-scale alterations of food-web structure under climate change. Such a simple rule has been largely employed to infer realistic food-web structures (Shin & Cury, 2001; Dunne, 2006) and to predict trophic relationships that closely match empirical data (Cattin *et al.*, 2004; Allesina *et al.*, 2008; Williams *et al.*, 2010). Inferring global change impacts on both network structure and functioning is a tremendous task to achieve and we made some assumptions for this first approximation. We considered a binary food web approach at species level and did not model species abundances, neither ontogenetic shifts. We simulated range shifts independently of biotic interactions and secondly we inferred interactions based on the expected species assemblage composition.

The general objective of this study is to assess the impact of climate change on the food-web structure of coastal Mediterranean fish assemblages. Our analysis should be viewed as a network-level interpretation of global change impacts on body size frequency distribution at a large scale. Indeed the Mediterranean Sea is one of the most responsive regions to climate change (Giorgi, 2006), with a Sea Surface Temperature (SST) expected to warm with an average of 2.8 °C by 2080–2099 under the SRES A2 IPCC scenario (Somot *et al.*, 2006). Marine species may respond to this modification by shifting their geographic range (Cheung *et al.*, 2009; Albouy *et al.*, 2013). The question is no longer whether

marine species assemblages will be modified under increasing climate change, but whether such expected changes may modify ecosystem structure and functioning and to which extent. We therefore used body size distribution within coastal Mediterranean fish assemblages to predict and map the structure of future food webs following climate change. To do so, we calibrated a niche model using three well-studied local trophic networks of the Mediterranean Sea. The model was then used to infer a 'metaweb' describing potential trophic interactions among the 256 fish species for the whole Mediterranean continental shelf. Finally, we estimated the potential effects of climate change on the trophic structure of fish assemblages by calculating food-web descriptors under current and predicted climate conditions across the whole Mediterranean continental shelf.

Materials and methods

Food-web data

The interaction data set was composed of three finely resolved food webs from different regions of the Mediterranean Sea: the Bonifacio Strait Natural Reserve (Albouy *et al.*, 2010), the Southern Catalan Sea (Coll *et al.*, 2006), and the Tyrrhenian Sea (Colloca *et al.*, 2010). Feeding interactions were mainly determined from stomach contents and completed by information from FishBase (Stergiou & Karpouzi, 2001; Froese & Pauly, 2012).

For each studied site x , we obtained a prey/predator interaction matrix M_x of dimension $S_x \times S_x$, with S_x being the total number of species. Trophic interactions m_{ij} between species i and j are indicated by either 1 or 0 (1 if species j eats species i and 0 if not). The Bonifacio Strait Natural Reserve, the Southern Catalan Sea and the Tyrrhenian Sea data sets were composed of 58 (1 mammal), 82 (2 mammals and 1 marine turtle), and 35 species respectively. We focused on the fish/fish interactions: there were 185, 264, and 82 in the Bonifacio Strait Natural Reserve, the Southern Catalan Sea and the Tyrrhenian Sea matrix respectively. All these interactions were aggregated in a single matrix M_A , that contains a final data set of 126 species plus two compartments that represent the primary and secondary producers ($S = 128$). In M_A we observed 635 realized interactions among 16384 potential interactions (S^2).

Actual and future species geographic distributions

We collected actual geographical distributions (extent of occurrence maps) for 256 endemic and native coastal fish species on a 0.1° resolution grid system covering the whole continental shelf of the Mediterranean Sea (Albouy *et al.*, 2012). We restricted our analyses to the continental shelf of the Mediterranean Sea (200 m depth limit) because climate change is more likely to affect coastal species that are not benefiting from the temperature inertia of deep waters (Lloyd

et al., 2012). For instance, Stefansdottir *et al.* (2010) show that fish assemblages in hydrographically stable deep waters have not changed substantially over the last decade whereas assemblages in more variable shallow waters underwent a clear shift toward species representative of warmer temperatures.

To model future fish species distributions under climate change, we used Sea Surface water Temperature (SST) as the main forcing variable (Azzurro *et al.*, 2011; Albouy *et al.*, 2013). We employed a Mediterranean regional marine model (NEMOMED8) that predicts observed and future SST based on the following drivers: water energy fluxes, river discharges, and water exchanges with the surrounding seas (Beuvoir *et al.*, 2010). Observed SST values were extracted for the period 1961–1980 and projected SST values were extracted for the end of the 21st century (2080–2099) from NEMOMED8 outputs, based on the SERS IPCC A2 scenario. This scenario is conservative but not the most pessimistic (IPCC, 2007). The daily data were averaged to infer monthly data, leading to 15 variables: 12 monthly averaged SST values, the absolute minimum SST, the absolute maximum SST, and the absolute range of SST. The set of predictive variables was reduced to 15 variables to height on the basis of a k-means partitioning method to avoid model over parameterization for more details see (Albouy *et al.*, 2013).

Using actual geographical distributions transformed into presence/absence data and height climatic variables we conducted an ensemble forecasting approach (Araújo & New, 2007), based on seven statistical algorithms (Generalized Linear models, Generalized Additive models, Classification Tree Analysis, Random Forests, Boosted Regression Trees, Multivariate Adaptive Regression Splines, and Surface Range Envelope). Analyses were implemented using the BIOMOD package (Thuiller *et al.*, 2009) from the R statistical and programming environment (R Development Core Team, 2010). Each model in the ensemble was weighted according to the True Skill Statistic (TSS) criterion (Allouche *et al.*, 2006). TSS assesses 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). TSS was then calculated as $TSS = (ad - bc) \times [(a + c) \times (b + d)]^{-1}$ where a is the number of cells for which presence was correctly predicted by the model; b the number of cells for which the species was not found but the model predicted presence; c the number of cells for which the species was found but the model predicted absence; d the number of cells for which absence was correctly predicted by the model.

Species presences/absences were derived from probabilistic model outputs using the threshold that maximized the TSS (Thuiller *et al.*, 2009).

Food-web modelling

Despite their theoretical interest, the recently developed methods to parameterize food-web models offer several drawbacks to implement robust biodiversity scenarios at large scales since the model optimization remains challenging with rough likelihood surfaces and the optimization is time consuming. To overcome these drawbacks, (Gravel *et al.*, 2013), proposed

a method to infer a master web that includes all the taxa that would potentially co-occur in a single habitat as well as all their possible feeding links, coined as the metaweb (Dunne, 2006). This method predicts the links between species that have not interacted previously by parameterizing the niche model based on observed relationships between predator and prey body size.

The niche model (Williams & Martinez, 2000) predicts the food-web structure from a three species-specific parameters: the niche position n , the feeding niche centroid c (the niche optimum), and a range of suitable prey r . Gravel *et al.* (2013) developed a method assuming that body size is the main niche axis responsible for trophic interactions and then inferred all these parameters. They demonstrated that their approach was robust to the sampling effort. The method assumes a linear relationship between the niche position n and the log of body size. This assumption was confirmed by recent studies with a determinant role of body size in shaping the structure of food webs (Colloca *et al.*, 2010; Williams *et al.*, 2010; Riede *et al.*, 2011). The species-specific niche centroid c was estimated for each species by fitting a linear model between the log body size of predators and the log body size of prey. The range r was obtained by the difference between the 5% and 95% quantile regressions of this relationship. The three parameters (n , c , r) were evaluated for the 256 fish species. Primary and secondary producers were assumed present at all locations and nonlimiting on the whole Mediterranean Sea, and their parameters fixed at $n = 0$, $c = 0$ and $r = 0$.

We calibrated the food-web model using the three resolved Mediterranean food webs pooled into the matrix M_A (see Fig. S1). An evaluation of the model was done by adapting the TSS method used previously. TSS was calculated as $TSS = (dg - ef) \times [(d + f) \times (e + g)]^{-1}$ where the component d reports the number of links that are both predicted and observed, e reports predicted links with no observation, f reports predicted absences of links while observed, and g reports the number of predicted and observed absences of links. We removed the impossible predicted links where species do not co-occur in the field (bathymetric and spatial constraints were taken into account) and we recalculated the TSS to increase the realism of our niche model.

The estimated coefficients n , c , r were then used to infer the feeding niche of the 256 coastal osteichthyan species of the Mediterranean Sea. Chondrichthyans, mammals, and turtles were under-represented in the three trophic networks and were removed from the analyses. Invertebrates were considered as a 'black box' because we only had information on species distribution for highly commercial species (Coll *et al.*, 2012). Exotic species were discarded as well because they are not at equilibrium with environmental conditions, an assumption required for species distribution models (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005).

Impact of climate change on food-web structure

We generated actual and future trophic networks for each of the 8154 cells of the Mediterranean continental shelf based on actual and future fish occurrences, respectively, and the

metaweb describing potential trophic interactions among the 256 fish species. A local (cell) trophic interaction between species i and j was considered to occur if the two species were predicted to co-occur, considering their observed bathymetry and their habitat, and if they were potentially interacting in the metaweb.

We then calculated descriptors of local food-web structure for current and predicted fish assemblages (Williams & Martinez, 2000; Bersier *et al.*, 2002; Dunne *et al.*, 2002). To assess the food-web structure at cells scale and ecoregions scale (Spalding *et al.*, 2007) we used the number of species (S), the number of actual links (L), and the fraction of all possible links (S^2) that are realized in the network, called connectance ($L * S^{-2}$). These indices have been highlighted as important in terms of population stability and community structure (Petchey *et al.*, 2010). To assess the modification of trophic network at species level we also calculated the vulnerability, i.e. the mean number of consumer species per prey species and the generality, i.e. the mean number of prey species per predator species. We calculated and mapped the difference between the baseline period 1961–1980 and the future period 2080–2099 for each index of food-web structure.

Results

Calibration of the metaweb

We calibrated a metaweb for 256 fish species of the continental shelf of the Mediterranean Sea using three empirical food webs pooled into the matrix M_A and the allometric niche model. Approximately half of the 256 fish species (52.37%) are feeding on primary and secondary producers and do not have fish prey. One third of the species (33.50%) are top predators and the remaining 14.13% are intermediate consumer species.

The comparison between observed and modelled trophic links for the three empirical food-webs shows a TSS value of 0.51. After removing the links between species that cannot co-occur, the TSS reached a value of 0.67. This improvement was mainly due to the decrease of the f fraction into the TSS calculation, which reports the predicted absences of links while observed.

The inferred corrected metaweb yields a realistic relationship between predator and prey body sizes, indicating that our parameterization captures some essential aspects of this food-web structure (Fig. 1). The Mediterranean metaweb constrained by bathymetric and spatial mismatch between species pairs contained 11 055 potential interactions and the directed connectance (number of links divided by the number of potential links; S^2) had a value of 0.17. On average, species had 76.7 potential predator species and 54.7 potential prey species (Table 1).

Mapping current food-web structure

Food-web descriptors for the baseline period (1961–1980) were calculated and mapped at the cell scale (Fig. 2). On average, there were 79 species per cell (SD = 41.12) with the highest value (181 species) in the Tyrrhenian Sea and the lowest (8 species) in the Levantine basin (Fig. 2a). There were on average 2128 feeding links between fish species (SD = 1891) per cell with the highest density (7158 links) in the Alboran Sea and the lowest (22 links) in the Levantine basin (Fig. 2b; Table 2). The mean connectance per fish assemblage was 0.26 (SD = 0.048) with highest values (0.43) in the western Mediterranean basin, the Tyrrhenian Sea, the Adriatic Sea, the gulf of Gabès, and in the Aegean Sea (Fig. 2c). The lowest connectance values (lower than 0.15) were inferred in the Levantine basin. On average, there were 24 predator species per prey species (vulnerability, SD = 12.9; Fig. 2d) and 30 prey species per predator species (generality, SD = 17.8 Fig. 3e). The highest values for both generality (67) and vulnerability (48) were observed in the Adriatic Sea (Table 2). The lowest values for both generality (2.75) and vulnerability (2.75) were observed in the northern part of the Levantine basin.

Projected changes in food-web structure

The projected species distributions according to climate change revealed that 54 species of 256 would disappear by 2080–2099 from the Mediterranean continental shelf with a widespread decrease of local species richness (Fig. 3a). The number of feeding links would also decrease on 73.39% of the continental shelf (Fig. 3b). On the contrary, the number of links would increase in the Gulf of Lion, the Adriatic Sea, the Aegean Sea, and the Levantine basin. By 2080–2099, the decrease in species richness would be faster than the decrease in link density for the 44.0% of fish assemblages which will have higher connectance than current values, like the North western part of the Mediterranean Sea, the south of the Adriatic Sea, a large part of the Aegean Sea, and the northern part of the Levantine basin (Fig. 3c). On average the connectance between the two time periods would increase by 0.037. The generality of predator species would decrease between the two periods, from 30 to 25.4 prey species by predator in each local assemblage on average. Consequently, 82.8% of fish species would have a lower value of predator generality in the future than currently observed (Fig. 3d). Overall, 73.9% fish assemblages of the continental shelf would experience a decreasing vulnerability in the future, particularly in the western basin, the Gulf of Gabès, the

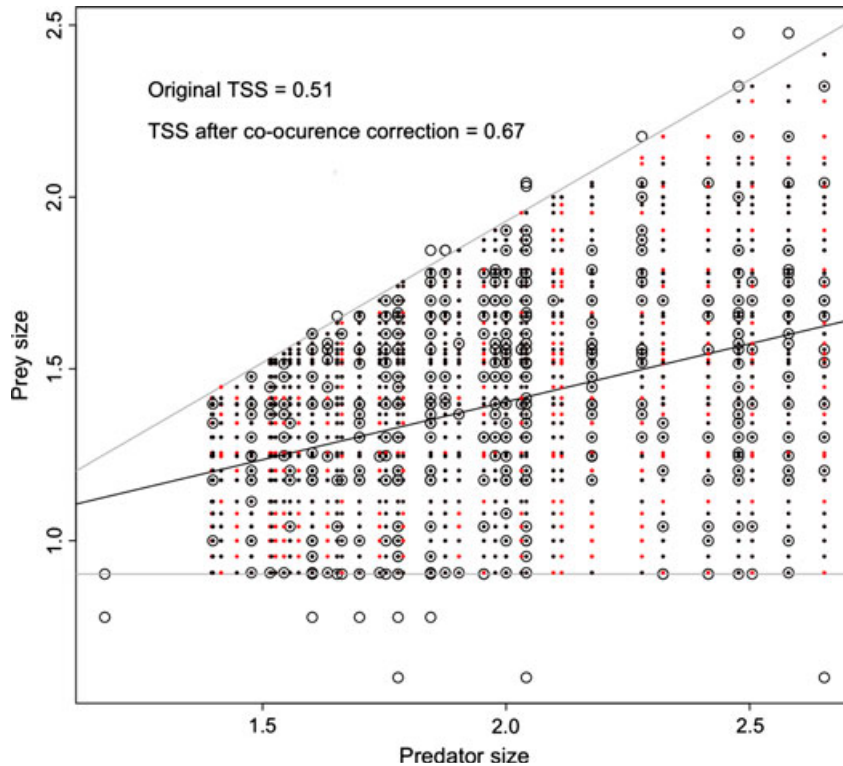


Fig. 1 Relationship between prey and predator body size for the compilation of the three observed Mediterranean food-webs (Bonifacio Strait Natural Reserve, the Southern Catalan Sea, and the Tyrrhenian Sea). The circles represent the observed links between prey and predator species, the black dots represent the links predicted by the allometric model and the red dots represent the removed links due to absence of co-occurrence between species pairs either to habitat or bathymetric mismatch. TSS represents the True Skill Statistic and assesses the proportion of prediction success relative to false predictions.

Table 1 Food-web structural indicators calculated for the Bonifacio Strait Natural Reserve, the Southern Catalan Sea, the Tyrrhenian Sea, and the metaweb for the Mediterranean Sea. *S* is the number of species, *L* the link between two species, *C* is the connectance value ($L S^{-2}$), *Gen* the generality value that represent the mean number of prey by predator, and *Vul* the vulnerability that represent the mean number of predator by prey

	<i>S</i>	<i>S</i> ²	<i>L</i>	<i>C</i>	<i>Gen</i>	<i>Vul</i>
Bonifacio	58	3364	185	0.05	7.1	4.1
S. Catalan Sea	82	6724	295	0.04	6.8	4.9
Tyrrhenian Sea	35	1225	82	0.07	5.9	2.9
Metaweb	256	65536	18968	0.29	93.4	131.7
Metaweb corrected by bathymetry	256	65536	12961	0.20	64.1	90
Metaweb corrected by preferred habitats	256	65536	11055	0.17	54.7	76.7

Peloponnese, and the Tyrrhenian Sea, and a large part of the Adriatic Sea (Fig. 3e; Table 2). On average, vulnerability values would decrease by 10.7% (from 24 to 21.1) over all fish assemblages between 1961–1980 and 2080–2099.

Covariation between species generality, vulnerability, and range size

Beyond changes of generality and vulnerability, we investigated the relationship of these two food-web components with the change in range size of the

species. We should be concerned by scenarios such as a joint reduction in generality and range size, or an increase in vulnerability and a decrease of generality. We first assessed the covariation in vulnerability and generality to determine whether some species would be under both stresses, i.e. expected to have less prey and more predator species in the future (Fig. 4). The majority of species (113 of 256) would have less prey at the end of the 21st century than in the baseline period (1961–1980), while a low number of species (11 of 256) would have more prey. In parallel, 50 species would have more predators while 65 would have fewer

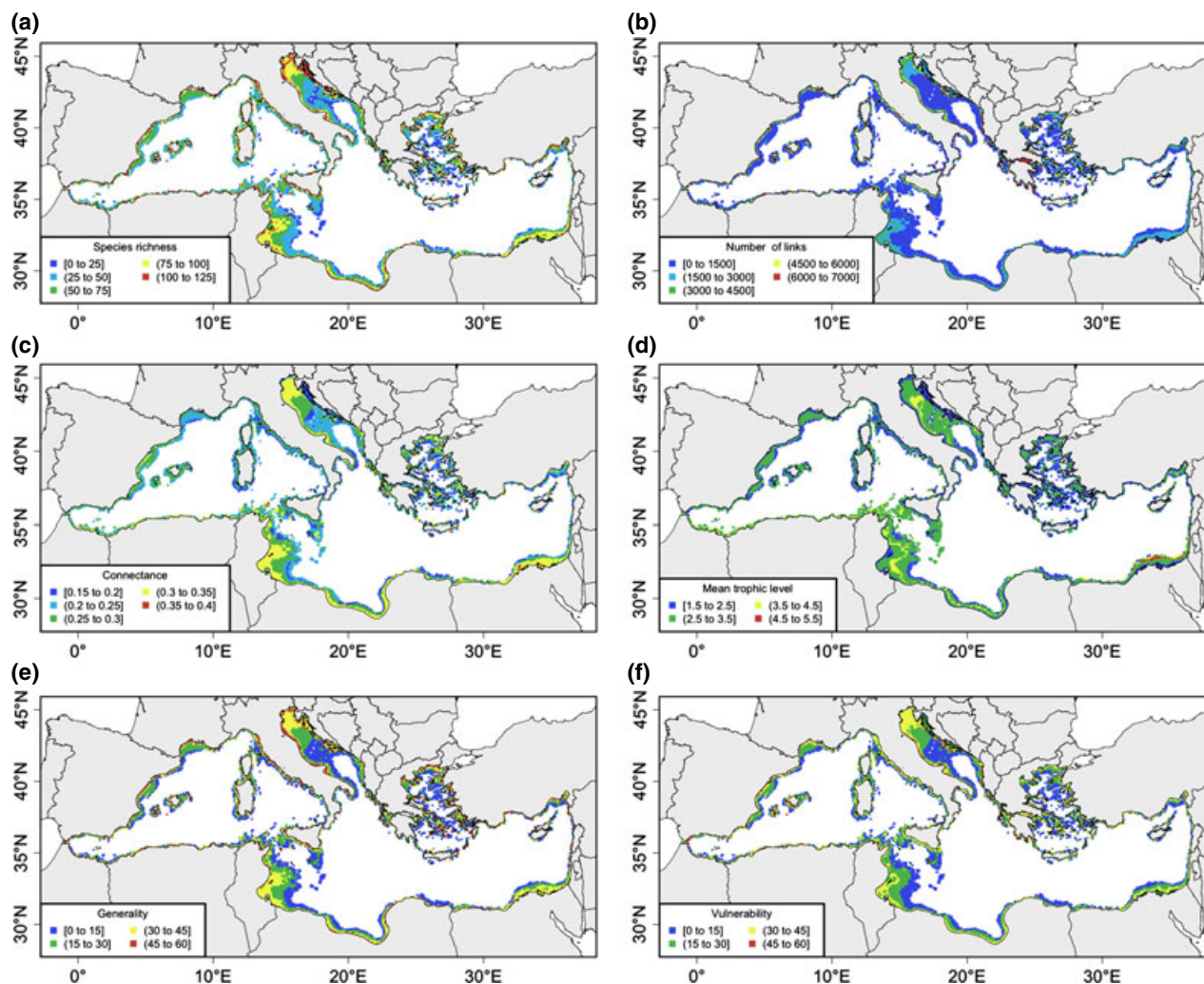


Fig. 2 Maps of species richness (a), number of links (b), connectance (c), trophic level (d), generality (e), and vulnerability (f) values for the period 1961–1980 on the continental shelf of the Mediterranean Sea.

predators. However, there was no relation between generality and vulnerability (Spearman correlation test; $\rho = -0.106$, $P = 0.16$).

We also investigated the relationship between the change in range size due to climate change and the modification of generality and vulnerability experienced by species. We found no link between the change in range size and the variation in both vulnerability (Spearman correlation test; $\rho = -0.06$, $P = 0.43$) and generality (Spearman correlation test; $\rho = 0.0046$, $P = 0.95$).

Discussion

Climate change will impose modifications of species composition and trophic structure for many ecosystems on Earth (Tingley *et al.*, 2009; Petchey *et al.*, 2010; Thuiller *et al.*, 2011). If changes in species composition have

been widely investigated and modelled, we still lack a framework to assess changes in trophic structure. In this study, we developed a flexible framework based on a hybrid model mixing climatic and trophic niches, and we predicted future fish food webs in the Mediterranean Sea.

The maps of food-web descriptors, as well as their projections under climate change, revealed potential changes of interactions in Mediterranean fish assemblages with a high spatial heterogeneity. Indeed, we found that an important part of the Mediterranean continental shelf would face a decrease in the number of links, vulnerability, and generality, while the connectance within fish assemblages would increase by the end of the 21st century. (i.e. the western part of the Mediterranean Sea without the Gulf of Lion). This increase in connectance is mainly due to a differential loss rate of realized feeding links and species richness.

Table 2 Food-web structural indicators calculated for each ecoregions of the Mediterranean Sea. S is the number of species, L the number of link between two species, C is the connectance value ($L S^{-2}$), Ntop express the number of top species, Nbas the number of basal species, Nint the number of intermediate species, TL is the trophic level, Gen the generality value that represent the mean number of prey by predator, and Vul the vulnerability that represent the mean number of predator by prey. SD means Standard deviation; max maximum and min minimum

Ecoregions	Mean S		Mean L		Mean C		Mean Ntop		Mean Nbas		Mean Nint		Mean chain length		Mean TL		Mean Omnivory index		Mean Vul		Mean Max		Mean Min		Mean Max	
	S	L	S	L	C	Ntop	Nbas	Nint	chain length	TL	Omnivory index	Vul	Max	Min	Max	Min	Max	Min	Max	Gen	Gen	Gen	Gen	Gen	Gen	
Period 1961–1980																										
Adriatic Sea	77	1947.61	6928	39	0.25	4.17	30.64	65.19	4.41	2.61	0.57	23.27	4.56	48.45	30.19	5.57	66.61									
Aegean Sea	79	2129.06	6407	27	0.25	4.63	31.52	63.85	4.16	2.39	0.45	23.11	3	45.44	30.76	3.37	62.81									
Alboran Sea	96	3079.6	7158	59	0.28	3.5	22.31	74.18	4.65	2.93	0.66	29.29	5.36	47.95	35.42	7.37	65.54									
Ionian Sea	89	2644.41	6956	37	0.25	5.26	28.52	66.22	4.42	2.59	0.53	26.14	4.08	47.82	33.25	4.82	65.01									
Levantine Sea	74	1859.57	4596	22	0.28	5.54	24.92	69.54	4.55	2.75	0.6	23	2.75	38.04	28.86	2.75	52.88									
Tunisian Plateau	65	1564.4	5496	45	0.28	5.34	20.2	74.46	4.58	2.88	0.63	20.61	4.31	43.27	24.64	4.67	54.18									
Western Mediterranean	87	2435.42	7144	51	0.25	3.72	27.9	68.39	4.35	2.62	0.55	25.07	4.21	48.18	31.64	4.92	65.76									
Difference between 2080–2099 and 1961–1980 in:																										
Adriatic Sea	-15	-470.77	-1515	-3	0.03	2.88	-10.03	7.15	0.19	0.28	0.07	-3.4	-1.29	-6.49	-6.22	-2.15	-13.55									
Aegean Sea	-5	-217.99	-1237	26	0.01	2.29	-9.43	7.15	0.59	0.51	0.21	-0.97	1.42	-4.73	-3.95	0.70	-10.7									
Alboran Sea	-27	-1498.17	-2626	22	-0.02	4.31	0.26	-4.56	0.21	0	0.02	-8.61	0.11	-10.18	-10.78	-1.90	-15.55									
Ionian Sea	-20	-920.47	-2383	56	0.01	2.22	-7.2	4.98	0.55	0.42	0.21	-5.33	1.39	-9.86	-8.22	1.38	-15.30									
Levantine Sea	9	256.82	122	103	-0.03	1.54	0.59	-2.14	0.22	0.06	0.04	1.39	4.04	0.39	1.38	4.42	-1.60									
Tunisian Plateau	0	-134.97	-778	67	-0.02	3.63	1.31	-4.94	0.54	0.2	0.14	-1.05	1.80	-4.92	-1.58	2.16	-3.28									
Western Mediterranean	-21	-764.63	-642	-11	0.03	2.38	-8.16	5.78	0.47	0.41	0.16	-4.06	-0.21	-2.39	-6.59	-1.28	-5.55									

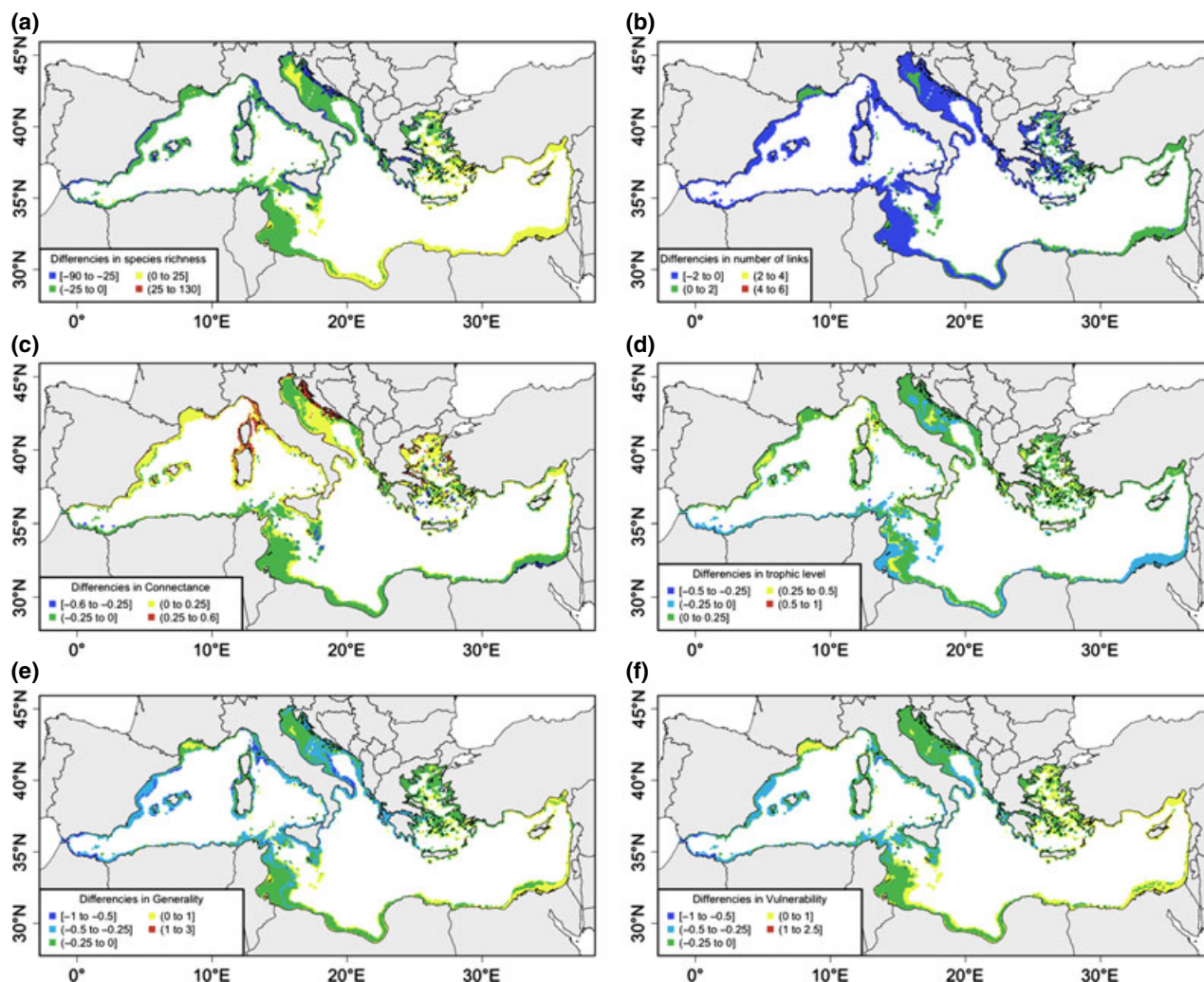


Fig. 3 Differences in species richness (a), number of links (b), connectance (c), trophic level (d), generality (e), and vulnerability (f) predicted on the continental shelf of the Mediterranean Sea considering all fish species between the baseline scenario (1961–1980) in comparison with the end of the 21st century scenario (2080–2099). For a better representation we present the logarithm of the values plus one of the relative difference between the future and observed periods.

In fact, climate change could drive 54 species to lose their suitable climatic niche and 159 species toward a geographic range contraction. Among those loser species most are basal fish species which are only linked to fish predators in our network (Albouy *et al.*, 2013). In parallel, we observed an increase of intermediate and top predator fish species, which make many trophic links.

Increasing number of links, vulnerability, and generality are also predicted while connectance could decrease in some regions such as the Levantine basin. This situation is expected to occur when the rate of realized feeding links could increase faster than species richness. We observe it in the Levantine basin and in a small area of the Adriatic Sea and it is most likely because few top predator species with many links such

as Yellowmouth barracuda (*Sphyraeana viridensis*) or Haifa grouper (*Epinephelus haifensis*), would move to new areas tracking their climate niche across the Mediterranean Sea (Araújo & New, 2007; Albouy *et al.*, 2013). Alternatively, realized feeding links could also decrease faster than species richness. Under this second scenario (decrease in both connectance and species richness), which was predicted in the Gulf of Gabès, we observed an increase of top predator and a decrease in intermediate and basal species.

The analysis of the biogeography of food-web descriptors is the first step to understand the consequences of climate change on ecosystem functioning. Binary food-web descriptors such as connectance, link density, vulnerability, and generality are related to several ecosystem functions. For instance, it was

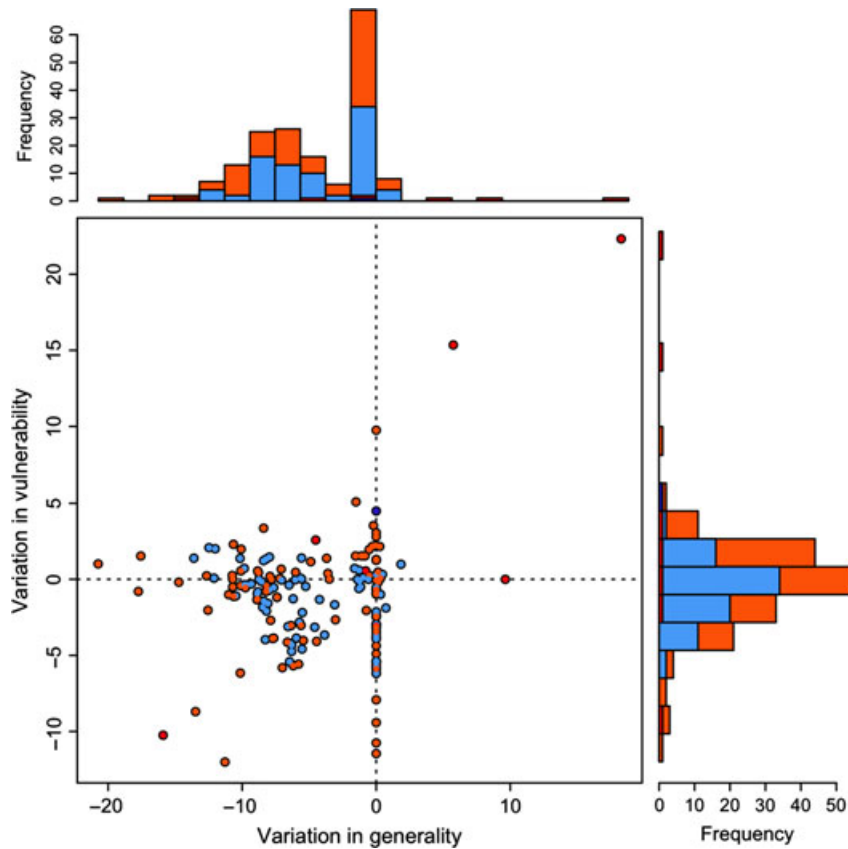


Fig. 4 Relationship for each modeled species (except those species with no links in the created food-web), between the variation in generality, vulnerability, and range shift. The color gradient for points (red to blue) represents the variation (loss, gain) in range between the baseline scenario (1961–1980) in comparison with the end of the 21st century scenario (2080–2099).

previously shown that the degree distribution is fundamental to metapopulation persistence (Holt & Hoopes, 2005; Gravel *et al.*, 2011; Pillai *et al.*, 2011). The number of prey species per predator also strongly impacts species geographic distribution (Gravel *et al.*, 2011) and the immigration–extinction dynamics at large spatial scales (Piechnik *et al.*, 2008). Network robustness to node deletion is also first order property of network stability (Dunne *et al.*, 2002). Recently, the contribution of individual nodes to the topological structure of mutualistic networks was linked to network persistence (Saavedra *et al.*, 2011). Motifs frequency distribution is also driving persistence (Stouffer & Bascompte, 2010). In our case, the number of links per species is expected to decrease with climate change. Based on food-web theory, we presumed that the altered structure could make fish assemblages more sensitive to disturbances. Mediterranean fish species may have less prey and less predator species by the end of the 21st century, which may further enhance their extinction probability (Petchey *et al.*, 2010). But this result should be moderated because species may develop an adaptive trophic behavior due to variation in their trophic environment,

and this adaptation may play a key role in modulating the dynamics of feeding relationships within natural communities (Valdovinos *et al.*, 2010).

The modification of trophic structure can have some impact on ecosystem functioning, too. Even if primary production is mainly driving fishery yields (Chassot *et al.*, 2010), this relationship is, however, not consistent when global patterns are examined across 52 large marine ecosystems (Friedland *et al.*, 2012). Indeed, the relationship between net primary productivity and upper trophic levels is strongly influenced by processes determining movement of energy toward high trophic levels (Friedland *et al.*, 2012). However, it is challenging at this stage to infer the direction of the change in functioning from the alteration of food-web structure we documented since there is not yet a complete predictive theory linking network structure and ecosystem functioning (Thompson *et al.*, 2012). The current theory on biodiversity and ecosystem functioning in food webs revealed all the complexity of the problem (Duffy *et al.*, 2007) and the inexistence of any general mechanistic complete approach linking structure to functioning. There are nevertheless some findings that could

potentially guide intuitions. In small food webs with low trophic redundancy, the impact of species loss is highly variable because of the unique contribution of each species to the topological structure. There is, however, considerable predictability in larger networks attributable to considerable distance-decay of the interaction strength between pairs of species (Berlow *et al.*, 2009). Because many biological rates scale with body size (Brown *et al.*, 2004), and also because of the important structuring role of body size, this functional trait appears as a potentially powerful variable to develop general predictions on ecosystem functioning. This is particularly relevant given the well-established relationship between climate and ecosystem fluxes in size-structured communities (Brose *et al.*, 2012). A recent modelling study revealed that climate change would cause a decline of primary and fish production in many areas via an effect on body-size distribution (Blanchard *et al.*, 2012).

The approach we developed here is not limited to fish and could be useful for a variety of size-structured ecosystems. This framework may also be applied in contexts where interactions can be confidently inferred from individual traits or other biological features. For instance, the topology of complex interaction networks such as plant-pollinator can be predicted from a small set of traits (Santamaria & Rodriguez-Girones, 2007). Mouillot *et al.* (2008) also showed that phylogenetic constraints on host-parasite links produced webs very similar to empirical, and every trait related to the niche of a species could be used to reconstruct realistic food-webs. To improve our modelling approach, and consider the fact that shifts in diet during ontogenetic development commonly occurred in fish assemblage, we propose to consider different life stages as different entities in the metaweb in the future. Then, ontogenetic shifts in diet could be modelled along the trophic niche axis to infer unobserved interactions. This ontogenetic shift is observed in many fish species occurring in the Mediterranean Sea (Stergiou & Karpouzi, 2001).

Since the Mediterranean Sea is subjected to a diverse human activity that impacts its diversity in an heterogeneous way (Coll *et al.*, 2012), the next step to our approach will be the integration of climate change in conjunction with fisheries to determine the nature of interaction between these two perturbations (additive, synergetic, or antagonist effects) and the consequence of the interactions on food-web structure. Invasive species coming from the Atlantic Ocean and the Red Sea are also an important element shaping the current biodiversity of the Mediterranean Sea (Coll *et al.*, 2010). Thus, they should also be integrated because they are susceptible to modify trophic structures (Ben Rais Lasram *et al.*, 2008). Our modelling approach for trophic

interactions allow the exploration of the possible feeding links that these new species could have based on their body size, probability of occurrence, and their bathymetric ranges. Consequently, our approach may allow testing the potential impact of the introduction of a species or a pool of species by analysing the potential feeding links that these species could create within local assemblages. Our approach can be also used to determine the robustness to cascading secondary extinctions and to identified overlap species that are expected to mitigate the environmental change on ecosystem (Staniczenko *et al.*, 2010).

Moreover, similar methods to ours here approximating potential interactions and their sensitivity to global changes can be developed for other systems, such as host-parasite and plant-pollinator systems. Global change first influence demography of individuals, then species ranges and eventually the interactions within assemblages. Ecologists are currently challenged to develop general methods flexible enough to be applied across ecosystems and able to better predict global change impacts on ecosystem functioning. Knowledge of individual species traits and life history is necessary to drive conservation practices, but integrative tools at the ecosystem scale are also of need. Our study aims at going a step forward with a novel methodology accounting for both climatic and trophic niches. Our approach could be useful to any other ecosystem where interactions are also constrained by species traits or phylogeny and are facing perturbations under climate change.

Our approach paves the way to integrate the complexity of ecological interactions into species distribution models. Our analysis was limited to binary interactions and presence-absence predictions. We did interpret the network-level consequences of previously documented impacts of global change on body size frequency distribution (Albouy *et al.*, 2013). This approach is a first step to identify potential biotic multipliers of global change impacts (Zarnetske *et al.*, 2012), but a comprehensive analysis of biomass distribution among species and fluxes of matter between them would be required to assess future primary and secondary productivity. The next step therefore requires the addition of interaction strength to predict biomass dynamics. There are some tools and data available in the literature to facilitate this development. For instance, Emmerson & Raffaelli (2004) documented that interaction strength between pairs of species is strongly related to the predator-prey body size ratio. The bio-energetic approach to consumer-resource theory (Vasseur & McCann, 2005; Brose *et al.*, 2006) could also provide valuable guidance in that direction. Ontogenetic shifts in diet also have to be integrated since they are fundamental for persistence

and energy flows in most food webs. These changes will allow shifting from a binary network to a quantitative and realistic food-web.

Such an approach would nicely complement the recent application of the metabolic theory to predict global change impacts on fisheries conducted by Cheung *et al.* (2008). In that study, the maximal catch potential was related to trophic level, biomass, and geographic ranges. More recently, (Cheung *et al.*, 2013) had quantified the tropicalization of catches as a signature of climate-change effects on global fisheries based on the thermal preference of species assessed from SDMs (Species Distribution Modelling). These studies do not consider, however, the impact of network structure on ecosystem functioning. A full understanding of global change impacts on ecosystem functioning will have to integrate such elements into our framework.

Another issue to tackle is that forecasting future species distributions should take into account biotic interactions. Here, we conducted this exercise in two steps. First we simulated range shifts independently of biotic interactions and secondly we inferred interactions based on the expected species assemblage composition. A more realistic modelling approach would be to run these two steps simultaneously to account for species interactions (Thuiller *et al.*, 2013). Current species distributions are likely to be influenced by biotic interactions (Kissling *et al.*, 2012; Wisz *et al.*, 2013), and similarly will be future distributions. Another overlooked phenomenon is the potential dependence of pairwise interactions on abiotic conditions. The integration of SDMs with community ecology is currently a very active field of research. We hope that our methodology could be used as a mean to infer biotic interactions in future SDM model projections.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Relation between prey and predator body size for the Mediterranean metaweb (a), after bathymetric correction (b), and after both bathymetric and habitat correction (c).