

Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages

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Abstract

Species Temporal Turnover (STT) is one of the most familiar metrics to assess changes in assemblage composition as a consequence of climate change. However, STT mixes two components in one metric, changes in assemblage composition caused by a process of species loss or gain (i.e. the nestedness component) and changes in assemblage composition caused by a process of species replacement (i.e. the species replacement component). Drawing on previous studies investigating spatial patterns of beta diversity, we propose measures of STT that allow analysing each component (species replacement vs. nestedness), separately. We also present a mapping strategy to simultaneously visualize changes in species richness and assemblage composition. To illustrate our approach, we used the Mediterranean coastal fish fauna as a case study. Using Bioclimatic Envelope Models (BEMs) we first projected the potential future climatic niches of 288 coastal Mediterranean fish species based on a global warming scenario. We then aggregated geographically the species-level projections to analyse the projected changes in species richness and composition. Our results show that projected changes in assemblage composition are caused by different processes (species replacement vs. nestedness) in several areas of the Mediterranean Sea. In addition, our mapping strategy highlights that the coastal fish fauna in several regions of the Mediterranean Sea could experience a ‘cul-de-sac’ effect if exposed to climate warming. Overall, the joint exploration of changes in species richness and composition coupled with the distinction between species replacement and nestedness bears important information for understanding the nature of climate change impacts on biodiversity. These methodological advances should help decision-makers in prioritizing action in the areas facing the greatest vulnerability to climate.

Keywords: beta diversity, Bioclimatic Envelope Model, Mediterranean coastal fish, Mediterranean Sea, nestedness, Nestedness, Species Temporal Turnover, turnover, Turnover

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Introduction

Climate change is already affecting species distributions and species composition within assemblages (Tingley *et al.*, 2009; Hillebrand *et al.*, 2010), and deeper changes are expected during the 21st century (Hoegh-Guldberg & Bruno, 2010; Thuiller *et al.*, 2011). The most commonly used method to forecast climate change impacts on biodiversity is bioclimatic envelope models (BEMs, Araújo

& Peterson, 2012). BEMs describe associations between current species distribution and climate, and use these associations to forecast changes in species distribution under climate change scenarios. The structure and composition of local assemblages are then inferred by geographically aggregating the results of species-level projections (the ‘predict first, assemble later’ strategy from Ferrier & Guisan, 2006).

How can such changes in biodiversity be measured? The most familiar metric of compositional change is species temporal turnover (STT, Peterson *et al.*, 2002; Thuiller *et al.*, 2005). STT counts the numbers of species gained and lost within each geographical unit and

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compares them with the total number of species recorded in the baseline period (Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Buisson *et al.*, 2008). Both conceptually and numerically, STT is a metric of temporal beta diversity equivalent in its formulation to the Jaccard's dissimilarity index (see methods; Anderson *et al.*, 2011).

As with several measures of beta diversity (Baselga, 2010, 2012), STT (or the Jaccard's dissimilarity index) mixes two components that are relevant to understand climate change impacts on biodiversity at a given location: (i) changes in assemblage composition caused by the loss or gain of species (i.e. the nestedness component of beta diversity); and (ii) changes in assemblage composition caused by a process of species replacement (i.e. the species replacement component of beta diversity). Consequently, using broad-sense measures of STT that account for differences in both species richness and species identities (e.g. the Jaccard's dissimilarity index, see Koleff *et al.*, 2003) may confound very different situations that can be expected under climate change (see Fig. 1). For instance climate warming may induce large reshufflings of local communities (e.g. cases A and D, Fig. 1). This may be due to a total extinction of the local pool of warm-sensitive species (case A, species 1 and 2; case D, species 1); those species being in turn replaced by either less (case A, Fig. 1) or more (case D, Fig. 1) warm-tolerant species tracking their climatic niches and not limited in their dispersion (Somero, 2012). In contrast, climate warming may cause the loss of species without replacement if the new environmental conditions are too harsh or if the location is too isolated for the establishment of potential colonizers (Novak *et al.*, 2011). This scenario implies a nested subset pattern in species composition over time (case B, Fig. 1). Nested patterns of species composition over time can also result from species gains in localities (or regions) where the future environmental conditions are suitable to both resident and incoming species not limited in their dispersion (case C, Fig. 1).

These four extreme scenarios also show that beyond change in species composition, the amount of temporal change in species richness is a crucial and complementary facet to fully investigate biodiversity changes caused by climate change (Thuiller *et al.*, 2005). Yet, previous BEM-based studies commonly analysed separately the projected changes in species richness and composition (e.g. Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Buisson & Grenouillet, 2009), although they are clearly not trivially independent patterns. For instance, changes in species composition due to full species replacement can be coupled with either a decrease or increase of species richness over time (cases A and D respectively, Fig. 1). Similarly, changes in species composition due to nestedness can be coupled

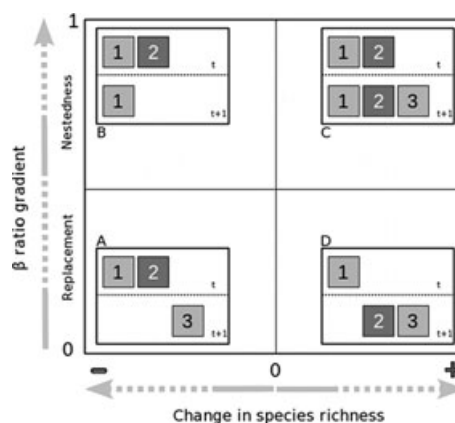


Fig. 1 Conceptual diagram describing the different scenarios of change in species richness and assemblage composition expected under global change. The horizontal axis represents the change in species richness and the vertical axis represents the gradient of β_{ratio} (representing the relative contribution of species replacement vs. nestedness in explaining species temporal turnover STT, see main text). Boxes (A, B, C, D) are divided into two parts that represent two time periods (*t* and *t + 1*). Numbered squares represent different species. Scenario A illustrates a decrease in species richness over time (*t* to *t + 1*) coupled to a full species replacement (species 1 and 2 are replaced by a new species 3) thus corresponding to a low value of β_{ratio} . Scenario B also represents a decrease in species richness between the two time periods, but in this scenario the assemblage at *t + 1* is completely nested in the assemblage at *t*, resulting in a high value of β_{ratio} . Scenarios C and D depict the same processes responsible for assemblage turnover as in B (nestedness) and A (replacement), but with an increase in species richness between the two time periods.

with either a decrease or increase of species richness over time (cases B and C respectively, Fig. 1).

In the present study, we present a strategy to improve the interpretation of BEMs forecasts by two means. First, we propose that changes in species richness and changes in species composition are being analysed together to fully apprehend the potential effects of climate change on species assemblages, and highlight a bivariate mapping strategy to picture simultaneously the spatio-temporal trend of both processes. Second, drawing on previous studies investigating spatial patterns of beta diversity (Baselga, 2010, 2012), we propose modifications in the usually used metric of temporal beta diversity (STT). We exemplify this strategy using coastal fish assemblages in the Mediterranean Sea as a case study. The region accounts for just 0.32% of the global oceanic volume, but it hosts high densities of species and endemism (Coll *et al.*, 2010). Fish assemblages are also expected to be deeply modified as a result of climate change (Giorgi, 2006; Ben Rais Lasram *et al.*, 2010; Azzurro *et al.*, 2011). For these reasons, the Mediterranean Sea provides a good template to investigate

21st century impacts of climate change on spatial and temporal components of coastal fish diversity.

Material and methods

Methodological developments

Equivalence between the species temporal turnover index and the Jaccard's dissimilarity index. In studies assessing climate change effects on species distributions, temporal modifications of species assemblages are measured using the species temporal turnover index (STT, Peterson *et al.*, 2002) as follows:

$$\text{STT} = \frac{G + L}{SR + G} \quad (1)$$

where L is the number of species lost, G is the number of species gained, and SR is the baseline species richness. Rearranging eqn (1) leads to a temporal version of the long known pairwise Jaccard's dissimilarity index (Anderson *et al.*, 2011):

$$\beta_{\text{jac}} = \frac{b + c}{a + b + c} \quad (2)$$

where a is the number of species present at both time steps, b is the number of species present in time step one but not in time step two (equivalent to L in eqn 1), and c is the number of species present at time step two but not at time step one (equivalent to G in eqn 1) with $a+b$ being equal to SR in eqn 1. β_{jac} ranges from 0 (species composition does not change between time periods) to 1 (species composition completely changes between time periods).

Decoupling the species replacement and nestedness components of species temporal turnover. To distinguish between the species replacement and nestedness components of STT, we apply the partitioning framework proposed by Baselga (2010, 2012), which consists in decomposing the pair-wise Jaccard's dissimilarity index (β_{jac} , eqn 2) into two additive components. The species replacement component of the Jaccard's dissimilarity index (β_{itu} , eqn 3) describes species replacement without the influence of richness difference between time periods. This index is formulated as follows:

$$\beta_{\text{itu}} = \frac{2 \min(b, c)}{a + 2 \min(b, c)} \quad (3)$$

where a , b and c are like in eqn 2.

Baselga (2012) showed that β_{jac} is equal to β_{itu} in the absence of nestedness (i.e. $a = 0$). The nestedness component of the Jaccard's dissimilarity index (β_{jne} , eqn 4) is therefore simply the difference between β_{jac} and β_{itu} ($\beta_{\text{jne}} = \beta_{\text{jac}} - \beta_{\text{itu}}$). This index that accounts for the fraction of dissimilarity due to richness difference is formulated as follows:

$$\beta_{\text{jne}} = \frac{\max(b, c) - \min(b, c)}{a + b + c} \times \frac{a}{a + 2 \min(b, c)} \quad (4)$$

where a , b and c are like in eqn 2. In eqn 4 the first term expresses a measure of richness difference, whereas the second part corresponds to the similarity version of β_{itu} that is independent of richness difference ($1 - \beta_{\text{itu}}$; Baselga, 2010). β_{jac} ,

β_{itu} and β_{jne} can be studied separately, however, the ratio between β_{jne} and β_{jac} ($\beta_{\text{ratio}} = \beta_{\text{jne}} / \beta_{\text{jac}}$; Dobrovolski *et al.*, 2011) is useful to describe the relative contribution of each component (species replacement vs. nestedness) in explaining the overall amount of STT. Values smaller than 0.5 indicate that species replacement is the main driver of STT, whereas values greater than 0.5 indicate that STT is mostly caused by nestedness. For a β_{ratio} value equal to 1, the nestedness component is the sole driver of STT. When β_{ratio} equals 0 this indicates that the species replacement component is the sole driver of STT. β_{jac} equals 0 when b and c are both null in eqn 2, which means that no change in species composition occurred between time periods (implying no change in species richness, thus a null β_{jne}), in this rare case β_{ratio} is not defined.

Mapping changes in species richness and assemblage composition. To map the continuum of situations bracketed by the extreme cases illustrated in Fig. 1, we propose to picture simultaneously the β -values (β_{jac} or β_{ratio}) and the temporal changes in species richness on the same map. To do so, two different 3-colour linear ramps describing the gradients in β -values for positive vs. negative changes in species richness are required. In this article we used a green to blue to purple colour ramp matching, respectively, the 0, 0.5 and 1 β -values for cells showing a decrease in species richness and a yellow to red to brown colour ramp (matching the 0, 0.5 and 1 β -values) for cells showing an increase in species richness.

The R functions required to calculate β_{jac} , β_{itu} , β_{jne} and β_{ratio} values as well as to map simultaneously β -values and changes in species richness are available in the 'betapart' package for the R (R 2.13.0, R Development Core Team, 2011) statistical and programming environment (<http://CRAN.R-project.org/package=betapart>).

Case study: the future of the Mediterranean coastal fish fauna

We exemplify the approach by exploring the potential effects of climate change on Mediterranean coastal fish assemblages for the mid and late 21st century. Using BEMs we projected the potential future climatic niches of 288 coastal Mediterranean fish species based on a global warming scenario implemented with the Mediterranean model NEMOMED8. We then aggregated geographically the species-level projections to analyse the projected changes in species richness and assemblage composition. We used eqns 3 and 4 to characterize the two components (species replacement vs. nestedness) of expected species temporal turnover. Using the strategy highlighted above we mapped simultaneously changes in species richness and β_{ratio} values to discuss the changing biogeography of coastal Mediterranean fishes. In addition, we analysed patterns of STT (species replacement vs. nestedness) at a finer spatial scale using the marine ecoregions defined by Spalding *et al.* (2007).

Species Data. We used the geographical distributions (extent of occurrence maps) of 288 endemic and native coastal fish species on the continental shelf of the Mediterranean Sea (Ben Rais Lasram *et al.*, 2009, 2010; Coll *et al.*, 2010). Data were

compiled from the atlas of fishes of the Northern Atlantic and Mediterranean (FNAM; Whitehead *et al.*, 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 geographical ranges of all Mediterranean Sea fish species (Ben Rais Lasram *et al.*, 2009).

The above-mentioned atlas does 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 range (minimum–maximum) known for the species (Froese & Pauly, 2010). Species' bathymetric ranges were obtained from fishbase and Louisy (2005). The bathymetry of the Mediterranean Sea was obtained from the ETOPO2v2 (ETOPO2v2, 2010) Global Gridded 2-min Database. Exotic species were discarded from our analyses since the equilibrium with environmental conditions is a required assumption for predicting and projecting species distributions (Guisan & Thuiller, 2005). In addition, we did not consider potential colonizations of fish species from neighbouring regions (i.e. the Atlantic ocean and the Red Sea). We therefore explored a scenario of climate change impact on the native coastal Mediterranean fish fauna only. We acknowledge that this scenario is restrictive but most of range maps of Lessepsian and Atlantic fish species are currently not available. Overall, our final data set contained the occurrences of 288 strictly coastal fish species on a 0.1° resolution grid system covering the whole continental shelf of the Mediterranean Sea (8154 cells).

Current and projected Sea Surface Temperatures (SST). Water temperature is one of the main drivers shaping marine fish species distributions and thus the composition of local assemblages (Dulvy *et al.*, 2008; ter Hofstede & Rijnsdorp, 2011), especially in the Mediterranean (Raitso *et al.*, 2010; Azzurro *et al.*, 2011). We used a Mediterranean regional marine model (NEMOMED8) that predicts SST based on the following drivers: water energy fluxes, river discharges and water exchanges with the surrounding seas (Beuvier *et al.*, 2010). We used daily SST values predicted by NEMOMED8 for the period 1961–1980 as a baseline to calibrate the species distribution models (Beuvier *et al.*, 2010). 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 (i.e. the difference between the absolute maximum and minimum SST). Several SST variables were considered because fish are ectothermic and thus highly dependent on their thermal environment for critical life-history steps such as breeding and developmental success (Mann & Blackburn, 1991). For instance, larvae and juvenile recruitment is strongly dependent on maximum temperatures (Burreson & Sypek, 1981) while growth rate may be limited by increased metabolic costs above a certain SST (Neuheimer *et al.*, 2011).

However, to avoid model over-parameterization and strong collinearity among predictor variables (Thuiller *et al.*, 2005), we aggregated redundant temperature variables. To do so, we reduced the set of predictive variables on the basis of a

k-means partitioning method (Legendre & Legendre, 1998). The optimal number of groups was determined according to the highest Simple Structure Index (SSI) following Dolnicar *et al.* (1999). We obtained eight synthetic variables by averaging inside each group determined by the k-means clustering. Projected SST values were extracted for the middle (2040–2059) and end of the 21st century (2080–2099) from NEMOMED8 outputs, based on the IPCC A2 scenario (the only scenario implemented in NEMOMED8); this scenario is conservative and not the most pessimistic regarding future prediction of global warming (IPCC, 2007).

Bioclimatic envelope modelling. To account for model-based uncertainties in the modelling process, we applied an ensemble forecasting approach (Araújo & New, 2007) based on seven statistical algorithms: (1) Generalized Linear Models, (2) Generalized Additive Models, (3) Classification Tree Analysis, (4) Random Forests, (5) Boosted Regression Trees, (6) Multivariate Adaptive Regression Splines and (7) Surface Range Envelope. Analyses were implemented with the BIOMOD package (Thuiller *et al.*, 2009) for the R statistical and programming environment (R Development Core Team, 2011). Each model in the ensemble was weighted according to the True Skill Statistic (TSS) criterion (Allouche *et al.*, 2006). Species presences/absences were derived from probabilistic model outputs using the threshold that maximized the TSS (Thuiller *et al.*, 2009). The predictive accuracy was classified as 'fair' to 'good' for the seven BEMs, with a mean TSS of 0.61. However, overall no clear evidence of model superiority emerged. We therefore implemented ensemble forecasts (Weighted Average Consensus) to project potential thermal niches in the future.

Using the projected temperatures for 2040–2059 and 2080–2099, we predicted the geographical location of the potential climatic niche (as inferred by the WAC) for each species. We assumed no dispersal limitation towards new climatically suitable areas because recent invasions show that fish may reach a mean dispersal rate of $221 \pm 5.4 \text{ km yr}^{-1}$ on the northern side of Mediterranean Sea (Ben Rais Lasram *et al.*, 2008). However, we imposed some bathymetric limitations by not allowing a species to be present in a cell if that cell's depth did not fall inside the species' known bathymetric range (Froese & Pauly, 2010). In addition, we estimated the potential dispersal distances travelled by species under climate warming by measuring changes in the geographical position of species range centroids (Tingley *et al.*, 2009).

Results

When considering the whole continental shelf of the Mediterranean Sea, species replacement contributes more than nestedness in explaining the temporal pattern of coastal fish turnover (2040–2059: mean $\beta_{\text{ratio}} = 0.36$; 2080–2099: mean $\beta_{\text{ratio}} = 0.315$). Indeed, nestedness contributes more than 75% to the total amount of STT in only 1053 cells (12.9%) and 184 cells (2.3%) of the continental shelf for the first and the second modelled periods respectively.

When analysing patterns of STT at a finer spatial scale (i.e. marine ecoregions, see Fig. 2 for more details), the relative contribution of species replacement vs. nestedness differs markedly among marine ecoregions. For instance, STT in the Alboran Sea for both the first (2040–2059: mean $\beta_{jac} = 0.498$) and second (2080–2099: mean $\beta_{jac} = 0.417$) periods is mostly caused by nestedness ($\beta_{ratio} > 0.5$) (see Table 1 and Fig. 2) with a clear decrease in species richness (the case B in Fig. 1). In contrast, the low levels of STT in the Adriatic (mean $\beta_{jac} = 0.356$) and Aegean Seas (mean $\beta_{jac} = 0.322$) for the first modelled period are associated with species replacement ($\beta_{ratio} < 0.5$). This replacement of species is accompanied by an overall increase in species richness

(the case D in Fig. 1), more particularly in the northern and central parts of the Adriatic and Aegean Seas (Fig. 2c). For the second modelled period, similar patterns emerge in these two regions (Table 1), except that patterns of species replacement are associated to a net decrease in species richness (the case A in Fig. 1) on almost all the continental shelf of the Adriatic Sea (Fig. 2b, d).

The other marine ecoregions of the Mediterranean Sea also provided contrasting results. The low levels of STT observed in the Levantine basin ($\beta_{jac} = 0.158$) are equally explained by both species replacement and nestedness ($\beta_{ratio} \sim 0.5$ for both the first and second modelled periods, see Table 1, Fig. 2). The Levantine

Table 1 Values of the Jaccard index (β_{jac}) measuring temporal turnover and the β_{ratio} index measuring the relative contribution of species replacement vs. richness difference to the total turnover in seven Mediterranean marine ecoregions (Fig. 2) calculated between the baseline time period (1961–1980) and two future periods (2040–2059; 2080–2099); n is the number of grid cells in each marine ecoregion

Ecoregion	n	2040–2059		2080–2099	
		β_{jac}	β_{ratio}	β_{jac}	β_{ratio}
Alboran Sea	250	0.498 ± 0.135	0.659 ± 0.156	0.417 ± 0.10	0.530 ± 0.157
Western Mediterranean	1958	0.345 ± 0.104	0.322 ± 0.236	0.411 ± 0.09	0.400 ± 0.146
Tunisian Plateau/Gulf of Sidra	1359	0.199 ± 0.09	0.55 ± 0.321	0.232 ± 0.09	0.353 ± 0.226
Ionian Sea	770	0.376 ± 0.09	0.435 ± 0.181	0.407 ± 0.08	0.339 ± 0.179
Adriatic Sea	1373	0.356 ± 0.120	0.179 ± 0.130	0.462 ± 0.106	0.187 ± 0.109
Aegean Sea	1481	0.322 ± 0.117	0.282 ± 0.188	0.351 ± 0.105	0.172 ± 0.137
Levantine Sea	944	0.158 ± 0.09	0.396 ± 0.259	0.167 ± 0.09	0.415 ± 0.248

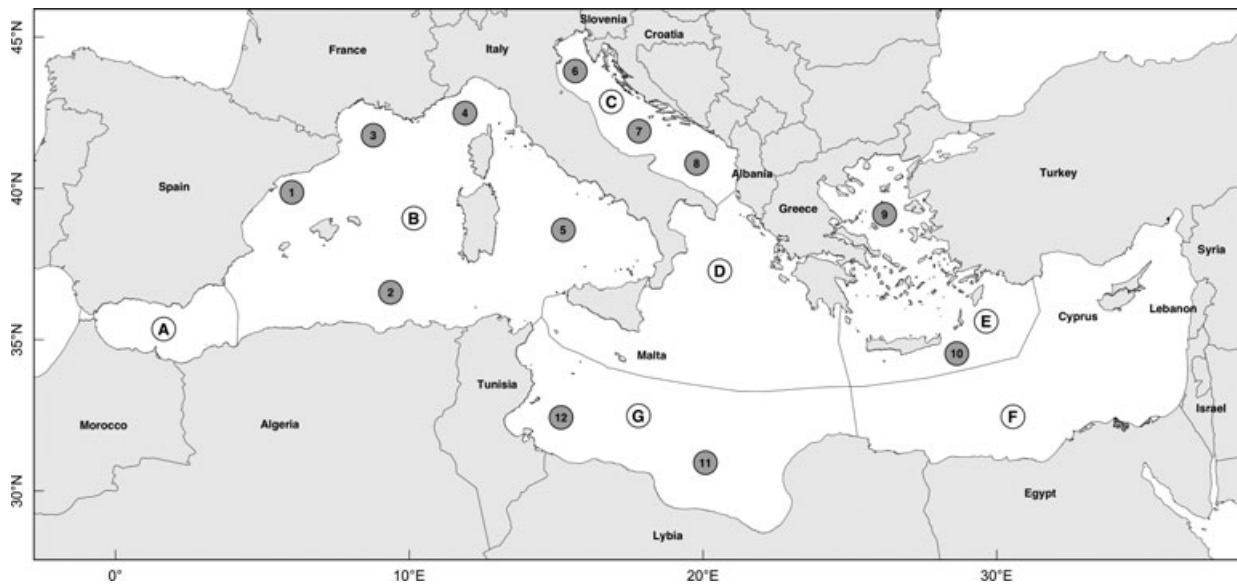


Fig. 2 Main marine ecoregions (Spalding *et al.*, 2007) and basins in the Mediterranean Sea. Ecoregions: A, Alboran Sea; B, Western Mediterranean; C, Adriatic Sea; D, Ionian Sea; E, Aegean Sea; F, Levantine Sea; G, Tunisian shelf/Gulf of Sidra. Basins: 1, Balearic Sea; 2, Algerian and Tunisian waters; 3, Gulf of Lions; 4, Ligurian Sea; 5, Tyrrhenian Sea; 6, North Adriatic Sea; 7, Central Adriatic Sea; 8, South Adriatic Sea; 9, North Aegean Sea; 10, South Aegean Sea; 11, Gulf of Sidra; 12, Gulf of Gabès.

basin also shows a net increase in species richness, in contrast to the Algerian and Tunisian coasts and the Gulf of Gabès (see Fig. 1 for localization) that experience similar levels of STT but mainly caused by nestedness ($\beta_{\text{ratio}} \sim 0.75$, see Fig. 2c, d).

Finally, 61.11% of the 288-modelled fish species are predicted to experience a shift towards the northern part of the Mediterranean Sea during the first period (Fig. 4). On average, for the first period, the overall fish assemblage moves to *c.* 70 km northwards and 30 km eastwards. More particularly, species range centroids move to north-eastwards for 37.85% of the modelled species. A similar trend emerges when considering the second period: 53.82% of the species shift in their geographical ranges towards the northern part of the Mediterranean Sea. On average, for the second period, the overall fish assemblage moves to *c.* 140 km westwards and 90 km northwards.

Discussion

Previous studies assessing climate change impacts on species assemblages typically measured changes in species richness, STT, or both (Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Araújo *et al.*, 2006; Ben Rais Lasram *et al.*, 2010; Garcia *et al.*, 2011). Here we showed that changes in assemblage composition over time can be caused by either species replacement or nestedness or combinations of both, which may hence reflect different impacts impinging on local assemblages when they are exposed to climate change (Fig. 1). Recent works highlighting the effect of past glaciations on large-scale biodiversity patterns have successfully demonstrated that disentangling the species replacement and nestedness components of beta diversity improves understanding of past environmental changes on species assemblages (Baselga, 2010; Dobrovolski *et al.*, 2011; Leprieur *et al.*, 2011). The same may apply for biodiversity forecast. Yet, those advances have not been incorporated into climate change impact assessments on species assemblages. Here, we illustrate how such developments in macroecology can offer insights for understanding impacts of climate change on local species assemblages.

The results related to our case study demonstrate that temporal turnover in projected coastal fish assemblages are caused by different processes (species replacement vs. nestedness related to species loss or gain), with different relative magnitudes in several areas of the Mediterranean Sea. For instance, the Jaccard's dissimilarity index, usually used to measure species temporal turnover in climate change studies (Peterson *et al.*, 2002), shows that the extreme north of the Adriatic Sea and the Gulf of Gabès would display similar turnover

levels (Fig. 3a, b). However, changes in fish fauna composition on the northern part of the Adriatic Sea are almost entirely driven by species replacement (see Figure S1), whereas those projected in the Gulf of Gabès are mainly caused by species loss (Fig. 2c, d). We thus suggest that a measure of STT emphasizing species replacement (e.g. β_{ju}) is more suitable for the identification of areas that would gain and lose species as a result of climate change than the traditional Jaccard's dissimilarity index.

A complementary approach is to map changes in species richness and assemblage composition altogether (e.g. Williams *et al.*, 1999). Using a mapping tool allowing the joint exploration of changes in richness and assemblage composition, we show that the coastal fish fauna in several regions of the Mediterranean Sea could experience a 'cul-de-sac' effect if exposed to climate warming (see also Ben Rais Lasram *et al.*, 2010). By the mid-21st century, high levels of species replacement associated to an increase in species richness are projected in most of the Aegean and Adriatic Seas (see Fig. 3c). This increase in species richness can be explained by the immigration of many coastal fish species that track their climate niches from the different parts of the Mediterranean Sea (Azzurro *et al.*, 2011), including the Gulf of Gabès that would experience a net loss of species (Fig. 3c). Our results (see Fig. 4) demonstrate that species ranges are expected to move northwards and eastwards, i.e., in direction of the Aegean and Adriatic Seas. In contrast, by the end of 21st century, most of the Gulf of Lion as well as the Adriatic and Aegean Seas are projected to experience a net decrease in species richness resulting from a loss of thermal niche for numerous fish that are not balanced by the arrival of other species from the south (Fig. 3d). Such a 'cul-de-sac' effect has been already described as the upward altitudinal response of terrestrial organisms to climate change (Tingley *et al.*, 2009); initially mountains might act as refugia for species, but as temperature increases, species have nowhere to migrate being trapped in the mountain tops and tends to disappear (Parmesan & Yohe, 2003).

These results have important fundamental and applied implications. For instance, the very high STT predicted in the Adriatic and Aegean Seas during the 21st century may have marked consequences on ecosystem functioning (Hillebrand *et al.*, 2010; Wardle *et al.*, 2011). However, previous studies have mostly focused on ecosystem impacts of species gain and loss in isolation from each other (see Vaughn, 2010; Wardle *et al.*, 2011). Yet, both species gain and loss are frequently encountered simultaneously in ecological communities (Jackson & Sax, 2010). Empirical approaches evaluating the functional roles of species

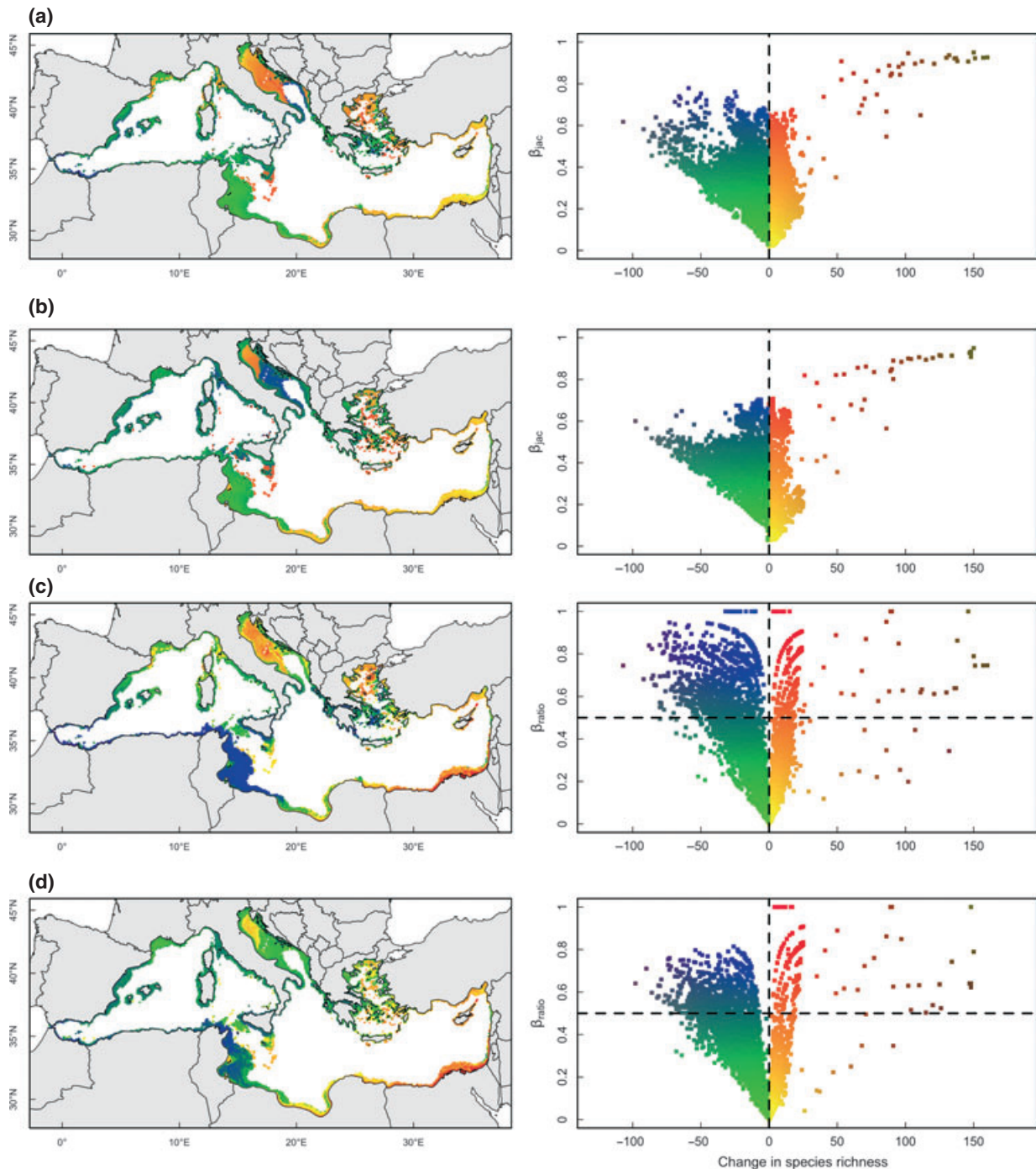


Fig. 3 Changes in species richness and composition between the baseline time period (1961–1980) and the future (2040–2059 (a, c); 2080–2099 (b, d)) for the fish assemblages of the Mediterranean continental shelf. Changes in species composition are quantified using the Jaccard's dissimilarity index β_{jac} (a, b) and the β_{ratio} index (c, d).

that are both lost and gained are therefore urgently needed (Suding *et al.*, 2008). For instance, the degree of functional redundancy between loser and winner species is a key issue for understanding the consequences of high STT on ecosystem properties and functioning. In the best-case scenario, remaining or

arriving species in local assemblages after global change impact would share combinations of functional traits with lost species, thereby maintaining ecosystem functioning. In the worst-case scenario, lost species would have functional traits distinct from those of remaining or arriving species, hence the functions they

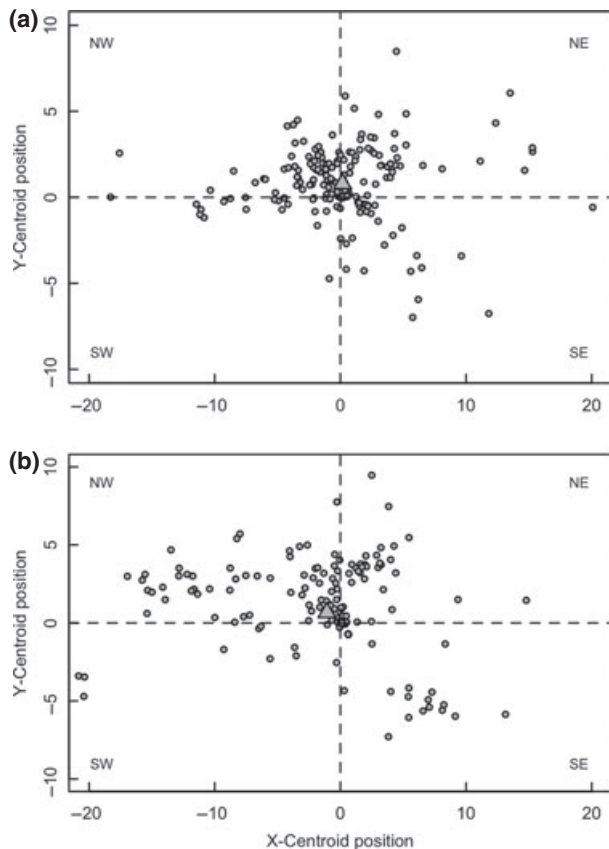


Fig. 4 Expected geographical species shifts for the 288 coastal Mediterranean fish species for both periods (a: 2040–2059; b: 2080–2099). Shifts were calculated from geographic range centroids and are expressed in degrees (NW: North West, NE: North East, SE: South East, SW: South West). Triangles represent the overall displacement of the fish assemblage calculated as the average centroid geographical shift.

support would go extinct and would imperil ecosystem functioning. Functional redundancy is also recognized as an important feature of communities insuring ecosystem resilience (Rosenfeld, 2002). This is particularly important since coastal ecosystems are facing multiple anthropogenic perturbations (e.g. habitat loss due to urbanization, overexploitation, human-mediated species invasion and toxic pollution) that may act in synergy with climate change towards local extinctions (Crain *et al.*, 2009).

From a conservation perspective, distinguishing between the different scenarios that can be expected under climate change (Fig. 1) may reveal further challenges for the evaluation and the optimal design of protected areas network in a changing world. For example, a recent macroecological evaluation of the Mediterranean system of protected areas investigated the overlap of protected areas with hotspots (areas of exceptionally high diversity) of total, endemic,

threatened coastal fish species richness as well as with hotspots of functional and phylogenetic diversity (Mouillot *et al.*, 2011). They showed that the fish biodiversity components are spatially mismatched and that protected areas, mainly situated along the north coast, are spatially congruent with the hotspots of all taxonomic components of fish diversity but misses hotspots of functional and phylogenetic diversity. Our results suggest that the composition of coastal fish assemblages in the Mediterranean Sea will be deeply modified during the 21st century, more particularly in the current areas of high fish species richness (Ben Rais Lasram *et al.*, 2009). The high projected level of species replacement in these regions, coupled with species richness decline, may therefore make current assessment of protected area networks obsolete in the future, challenging the future extension of the Mediterranean system of protected areas.

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Supporting Information

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

Figure S1. Representation of the species replacement component (β_{jtu}) of STT between the baseline time period (1961–1980) and the future (2040–2059 (a); 2080–2099 (b)) for the fish assemblages of the Mediterranean continental shelf.

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