

Projected impacts of climate change on spatio-temporal patterns of freshwater fish beta diversity: a deconstructing approach

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ABSTRACT

Aim To assess the potential impacts of future climate change on spatio-temporal patterns of freshwater fish beta diversity.

Location Adour-Garonne River Basin (France).

Methods We first applied an ensemble modelling approach to project annually the future distribution of 18 fish species for the 2010–2100 period on 50 sites. We then explored the spatial and temporal patterns of beta diversity by distinguishing between its two additive components, namely species turnover and nestedness.

Results Taxonomic homogenization of fish assemblages was projected to increase linearly over the 21st century, especially in the downstream parts of the river gradient. This homogenization process was almost entirely caused by a decrease in spatial species turnover. When considering the temporal dimension of beta diversity, our results reveal an overall pattern of decreasing beta diversity along the upstream–downstream river gradient. In contrast, when considering the turnover and nestedness components of temporal beta diversity we found significant U-shaped and hump-shaped relationships, respectively.

Main conclusions Future climate change is projected to modify the taxonomic composition of freshwater fish assemblages by increasing their overall similarity over the Adour–Garonne River Basin. Our findings suggest that the distinction between the nestedness and turnover components of beta diversity is not only crucial for understanding the processes shaping spatial beta-diversity patterns but also for identifying localities where the rates of species replacement are projected to be greatest. Specifically we recommend that future conservation studies should not only consider the spatial component of beta diversity but also its dynamic caused by climate warming.

Keywords

Beta diversity, ensemble forecasting, France, freshwater fish, nestedness, species distribution model, temporal changes, turnover.

INTRODUCTION

Quantifying the change in species composition along spatiotemporal gradients (i.e. beta diversity) of ecosystems is important for understanding and conserving patterns of biodiversity (Wiersma & Urban, 2005). Recent studies of the impact of climate change on biodiversity have mainly focused on the temporal dimension of beta diversity, for instance by assessing changes in species composition over time (Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Hillebrand *et al.*, 2010). In contrast, future projections of beta diversity have been much less investigated from a spatial perspective, i.e. assessing if assemblages are likely to become more similar or diversified in the future (Jurasinski & Kreyling, 2007; Buisson & Grenouillet, 2009). Yet, broad-scale environmental changes in the future are expected to cause tremendous shifts in both species distributions in space and

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community turnover over time (Hillebrand *et al.*, 2010). From a conservation perspective, considering both the spatial and temporal dimensions of beta diversity in the future could help decision-makers to prioritize action plans on vulnerable zones expected to change the most rapidly (Hillebrand *et al.*, 2010).

Patterns of beta diversity are commonly quantified using broad-sense measures such as the Jaccard and Sørensen dissimilarity indices (Qian et al., 2009). These beta-diversity measures incorporate richness gradients (Koleff et al., 2003) and hence do not distinguish between the true spatial turnover and nestedness components of beta diversity (Baselga, 2010). Yet recent studies have shown that not distinguishing between these two components may blur our understanding of the process involved (Leprieur et al., 2011; Svenning et al., 2011), species turnover and nestedness being two antithetic phenomena (Baselga, 2010; Almeida-Neto et al., 2011; Carvalho et al., 2011). Spatial nestedness occurs when assemblages in depauperate sites are subsets of species of successively richer sites, hence reflecting a spatial pattern of species loss that results from different processes (i.e. selective colonization, selective extinction, nestedness of habitats, inter-specific variation in tolerance to environmental conditions) (Whittaker & Fernández-Palacios, 2007). On the other hand, spatial species turnover implies the gains and losses of species from place to place (species replacement) as a consequence of environmental sorting and/or spatial and historical constraints, including geographic isolation due to dispersal barriers (Gaston et al., 2007; Leprieur et al., 2011). Transposed to a temporal perspective, patterns of beta diversity caused by nestedness and turnover at a given location are thus reflecting a temporal process of species loss (or gain) and species replacement, respectively.

Recently, a number of studies showed that the present-day distributions of freshwater fish could be greatly affected by climate change (Buisson et al., 2008; Buisson & Grenouillet, 2009). However, the impacts of climate change on riverine fish assemblages remain poorly investigated, whereas riverine ecosystems are among the most threatened ecosystems of the world (Sala et al., 2000). The identification of priority sites for the conservation of riverine fish biodiversity is therefore urgently needed (Olden et al., 2010). In that context, recent studies have extended the systematic conservation planning approach to riverine ecosystems by selecting a set of areas that ensure the adequate representation of all the riverine biodiversity and its long-term persistence (Hermoso et al., 2009). However, designing efficient conservation area networks in freshwater ecosystems is challenging because of the spatial hierarchies of riverine ecosystems (Olden et al., 2010). More importantly, the presentday composition of freshwater fish assemblages is expected to greatly evolve as a result of future climate change (Buisson et al., 2008; Heino, 2008), which implies that the current design of reserves will be inappropriate at the end of the 21st century. The design of conservation area networks should therefore not solely account for species distributions in space but also for species turnover in time. For instance, species replacement over time has been empirically observed in coastal ecosystems as a result of climate warming (Hillebrand et al., 2010).

In the present study, we explored potential impacts of climate change on the spatial and temporal components of beta diversity in freshwater fish assemblages by comparing and discussing the framework proposed by Baselga (2010) and Almeida-Neto *et al.* (2011). As a case study, we analysed fish distributions in a major European river system, the Adour–Garonne River Basin (south-west France). The main objectives of this study were: (1) to project the potential future distribution of the most prevalent fish species over the Adour–Garonne River Basin; (2) to analyse the projected patterns of spatial and temporal beta diversity by disentangling the contributions of species turnover and species nestedness; (3) to discuss the relevance of approaches decomposing beta diversity, especially in a context of climate change impact studies; (4) to discuss potential implications for the design of conservation area networks.

MATERIALS AND METHODS

Data resources

This study focused on a major European system, the Adour–Garonne River Basin in south-west France (drainage basin area 53540 km²; elevational range 2576 m), which displays a wide range of hydrological and climatic conditions. Fifty sites comprising readily available data for fish species, air temperature, river flow and river physical characteristics were selected throughout the Adour–Garonne River Basin (Fig. 1a). Fish occurrences (presence–absence) were collated from the Office National de l'Eau et des Milieux Aquatiques (ONEMA) for 24 native strictly freshwater fish species occurring in more than 5% of the overall study sites (Table 1) to warranty the applicability of species distribution models (SDMs) with sufficient species occurrences.

Thirty variables were considered to characterize the environmental conditions at each site. Among them, 18 hydroclimatic variables were derived from daily time series of river discharge (Ministère de l'Ecologie, de l'Energie, du Développement durable et de la Mer; http://www.hydro.eaufrance.fr/) and nearsurface air temperature (MeteoFrance). These variables correspond to the 10th, 50th and 90th percentiles (hereafter referred to as P10, P50 and P90) of river flow and air temperature for three important periods in the life cycle of fish (Cattaneo, 2005): low activity (November–February), reproduction (March–June) and growth (July-October). Six other hydroclimatic variables related to seasonal hydroclimatic variability (VAR, defined as the difference between P90 and P10) were also considered to characterize the amplitude of the shift between low (P10) and high (P90) hydroclimatic habitat conditions. Finally, we extracted six physical variables that are commonly used to characterize environmental gradients in riverine ecosystems (Buisson et al., 2008), i.e. the distance from the river source (km), upstream drainage area (km²), altitude (m), mean river slope (‰), mean site width (m) and depth (m).

Future seasonal statistics (i.e. P10, P50 and P90) of river flow and temperature conditions were derived at the 50 sites, annually from 2010 to 2100, by statistically downscaling five global



Figure 1 (a) Location of the 50 studied sites within the Garonne River Basin. The sites were grouped according to their position along the upstream–downstream gradient [first principal components analysis axis (PCA1), see Material and Methods for more details] using a hierarchical clustering analysis based on the Euclidean distance and the Ward agglomerative criterion. (b) Correlation circle showing the relationships among topographic and physical variables.

climate models (GCMs) from the Fourth Report of the Intergovernmental Panel on Climate Change (IPCC 2007); namely CNRM-CM3 (MeteoFrance, France), GFDL-CM2.0 and GFDL-CM2.1 (NOAA, USA), MRI-CGCM2.3.2 (Meteorological Research Institute; Japan) and MIROC3.2 (medres) (Center for Climate System Research; Japan) models. Three scenarios of greenhouse gas emissions described in the Special Report on Emission Scenarios (SRES) were also considered, namely scenarios A2, A1B, B1 (see Appendix S1 in the Supporting Information for further information about the downscaling approach).

Fish species distribution models

A principal components analysis (PCA) was applied to the 30 environmental variables to derive a limited number of uncorrelated predictors for fish SDMs. The first five principal components (PCs) summarized more than 70% of the total variance and were therefore retained as predictors for SDMs. Since there is still uncertainty in the modelling of climatic habitats that determine species geographic distributions, we implemented an ensemble forecasting method (Araújo & New, 2007; Marmion *et al.*, 2009). To this end, the 24 fish species distributions were modelled using four different statistical approaches: generalized linear models (GLMs; McCullagh, 1984), generalized additive models (GAMs; Hastie & Tibshirani, 1990), feedforward artificial neural networks (ANNs; Rumelhart *et al.*, 1986) and boosted regression trees (BRTs; De'ath, 2007).

We implemented a cross-validation procedure to avoid circular reasoning when the same data were used to construct and evaluate the model. For each species, models were calibrated using a random sample of the initial data (70%). Then, each model was evaluated on the remaining 30% of the initial data set for each species with the true skill statistic (TSS) criterion. The TSS scores were interpreted with the same classification as used for Kappa, according to the Landis & Koch (1977) accuracy classification scheme: TSS > 0.8 excellent; 0.6 < TSS < 0.8 good; 0.4 < TSS < 0.6 fair; 0.2 < TSS < 0.4 poor; and TSS < 0.2 no predictive ability. The predicted presence/absence of a species was derived from the predicted probability of occurrence using the threshold that maximized model accuracy; i.e. that maximized the percentage of presence and absence that could be correctly predicted (Thuiller et al., 2009). This calibration step was repeated 10 times to introduce randomness due to the calibration dataset.

Alternative SDMs may provide markedly different projections for the same dataset, and model evaluations often cannot demonstrate which projection is superior (Araújo & New, 2007). To overcome these limitations, we used the weighted average consensus (WAC) method (Marmion *et al.*, 2009; Thuiller *et al.*, 2009) that takes into account model-based uncertainty. Using the projected hydroclimatic conditions for the five GCMs and three SRES, we projected the potential thermal and hydrological habitat suitability for each species according to each of the four SDMs. We assumed no dispersal limitation towards new areas with suitable hydroclimatic conditions. Then, for each site, we

| | | TSS | | | | | | | |
|---|---|------------------------------------|--------------------------------------|---------------------------------------|---|-------------------------------------|---|---|--|
| Species | Family | BRT | GLM | GAM | ANN | WAC | Actual prevalence | % change in prevalence (2040–60) | % change in prevalence (2080–2100) |
| Gymnocephalus cernuus | Percidae | 0.52 | 0.48 | 0.10 | 0.51 | 0.76 | 0.05 | 3 (1) | 1 (1) |
| Stizostedion lucioperca | Percidae | 0.61 | 0.66 | 0.55 | 0.72 | 0.71 | 0.08 | 17 (5) | 34(9) |
| Blicca bjoerkna | Cyprinidae | 0.53 | 0.49 | 0.17 | 0.49 | 0.54 | 0.11 | 3 (2) | 0(4) |
| Scardinius erythrophthalmus | Cyprinidae | 0.46 | 0.51 | 0.36 | 0.47 | 0.47 | 0.12 | 37 (5) | 45 (5) |
| Cottus gobio | Cottidae | 0.48 | 0.37 | 0.42 | 0.53 | 0.48 | 0.13 | -24(5) | -31(5) |
| Lampetra plane | Petromyzontidae | 0.28 | 0.33 | 0.44 | 0.37 | 0.37 | 0.15 | -20(4) | -21(4) |
| Esox lucius | Esocidae | 0.42 | 0.47 | 0.49 | 0.41 | 0.51 | 0.18 | -23(4) | -28 (3) |
| Carassius sp. | Cyprinidae | 0.31 | 0.21 | 0.26 | 0.27 | 0.31 | 0.18 | 27(7) | 39 (8) |
| Cyprinus carpio | Cyprinidae | 0.42 | 0.48 | 0.38 | 0.42 | 0.37 | 0.20 | 41 (6) | 52 (6) |
| Abramis brama | Cyprinidae | 0.59 | 0.59 | 0.58 | 0.58 | 0.51 | 0.22 | 21 (5) | 33 (8) |
| Tinca tinca | Cyprinidae | 0.38 | 0.38 | 0.43 | 0.41 | 0.34 | 0.23 | 37 (6) | 47 (8) |
| Perca fluviatilis | Percidae | 0.41 | 0.35 | 0.33 | 0.36 | 0.34 | 0.30 | 20(4) | 21(4) |
| Chondrostoma toxostoma | Cyprinidae | 0.41 | 0.30 | 0.39 | 0.28 | 0.42 | 0.31 | 25 (6) | 38 (9) |
| Lepomis gibbosus | Centrarchidae | 0.53 | 0.48 | 0.53 | 0.51 | 0.54 | 0.37 | 22 (6) | 36 (9) |
| Leuciscus leuciscus | Cyprinidae | 0.43 | 0.34 | 0.41 | 0.42 | 0.38 | 0.37 | 21 (3) | 26(4) |
| Salmo trutta fario | Salmonidae | 0.66 | 0.70 | 0.59 | 0.68 | 0.69 | 0.49 | -24(4) | -32 (5) |
| Anguilla anguilla | Anguillidae | 0.57 | 0.51 | 0.49 | 0.52 | 0.58 | 0.51 | 23 (5) | 30(7) |
| Alburnus alburnus | Cyprinidae | 0.70 | 0.59 | 0.55 | 0.60 | 0.62 | 0.54 | 22 (4) | 27 (4) |
| Barbatula barbatula | Cobitidae | 0.58 | 0.42 | 0.51 | 0.46 | 0.47 | 0.55 | 23 (2) | 30(4) |
| Barbus barbus | Cyprinidae | 0.46 | 0.52 | 0.42 | 0.50 | 0.47 | 0.59 | 28 (3) | 32(2) |
| Rutilus rutilus | Cyprinidae | 0.73 | 0.71 | 0.66 | 0.74 | 0.77 | 0.63 | 15(4) | 21 (5) |
| Phoxinus phoxinus | Cyprinidae | 0.52 | 0.36 | 0.47 | 0.45 | 0.40 | 0.63 | 13(3) | 16(4) |
| Leuciscus cephalus | Cyprinidae | 0.61 | 0.60 | 0.64 | 0.60 | 0.66 | 0.70 | 17(2) | 19(2) |
| Gobio gobio | Cyprinidae | 0.69 | 0.65 | 0.46 | 0.64 | 0.75 | 0.77 | 11(1) | 13(1) |
| In bold, the 18 species assumed as sa percentage change in fish prevalence | tisfactorily well modelled us e from the period 1990–200 | ing the WAC ap 0 and the varial | proach (i.e. TSS ility associated | greater than 0.4 with the differen | A have been used and global climate | to analyse futur. models and Spe | e projected patterns o cial Report on Emissi | f beta diversity. For each ion Scenarios (in bracket | species, the mean s) is provided for |
| periods 2040–60 and 2080–2100. | 4 | | | |) | | 4 | | 4 |

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 Table 1
 Validation of fish species distribution models based on the true skill statistic (TSS) criterion applied to the four statistical models (boosted regression trees, BRT; generalized linear model, GLM; generalized additive model, GAM; artificial neural network, ANN) and the weighted averaging consensus (WAC) approach, respectively.

calculated a probability of occurrence according to the weight of each SDM model, based on TSS values. The future weighted probabilities of occurrence were then transformed into presence/absence values according to the same threshold values as were used for the current predictions (Thuiller *et al.*, 2009).

Future patterns of spatial and temporal beta diversity

To analyse future beta-diversity patterns, we first selected species fairly well modelled by SDMs under current climate (i.e. species for which TSS values were greater than 0.4). From the aggregation of the species-level projections, we then applied an assemblage-level analysis (the 'predict first, assemble later' strategy from Ferrier & Guisan, 2006) to derive future patterns of spatial and temporal beta diversity.

Here we used the additive partitioning framework proposed by Baselga (2010) to distinguish the two major processes shaping the differences in communities occurring across space and time; namely species substitution (or turnover) and species loss (or gain) (Baselga, 2010; Carvalho et al., 2011). According to Baselga (2010), the Sørensen multiple-site dissimilarity index (β_{SOR}) was used characterize the total amount of beta diversity among localities, ranging from 0 to 1 for communities being strongly to weakly similar in species composition. The multiplesite Simpson dissimilarity index (β_{SIM}) is a narrow-sense measure of beta diversity that describes true patterns of species turnover (i.e. species replacement) without the influence of richness gradients (Koleff et al., 2003). Using basic operations on fractions, Baselga (2010) proposed a nestedness multiple-site dissimilarity index (β_{NES}), as the difference between β_{SOR} and β_{NES} (i.e. $\beta_{SOR} = \beta_{SIM} + \beta_{NES}$). As the β_{NES} index is intended to measure how dissimilar the sites or the years are due to increase in change in species richness among nested assemblages, it does not measure how perfect the nested pattern is (Baselga, 2012). To measure a true pattern of nestedness that represents a special case of an ordered pattern of differences in species richness, we used the NODF index (Almeida-Neto et al., 2008) that depends both on paired overlap and matrix filling (Almeida-Neto et al., 2011; Baselga, 2012). This measure ranges from 0 (non-nested) to 100 (the matrix is perfectly nested) and was rescaled in the present study from 0 to 1 to allow comparisons with β_{NES} .

Spatial beta diversity was quantified annually over the period 2000–2100, hence reflecting how differences in species composition among sites will change over time. Temporal beta diversity was also quantified for each site, separately, hence reflecting how differences in species composition among years (i.e. for the period 2000–2100) will change at each site. To test whether temporal beta diversity varies along environmental (i.e. related to river size, topography) gradients, we first applied a PCA on the physical and spatial data matrix. The first PCA axis accounted for 80% of the total variability in the original variables and was mainly related to the upstream–downstream gradient (see Fig. 1b). This is currently the most well-known, world-wide, large-scale environmental gradient in riverine ecosystems, characterized by a continuous (or discontinuous) gradient of physical conditions (e.g. stream slope, stream width and depth) from headwaters to large rivers (Allan, 1995).

RESULTS

The predictive accuracy over all four SDMs was classified as 'good' or 'fair' for 18 species out of 24 (i.e. TSS values for 75% of species were greater than 0.4), whereas the predictive accuracy for the remaining six species was classified as 'poor'. On average, the WAC approach revealed better predictive performance than the four models considered separately (TSS_{WAC} = 0.52; TSS_{ANN} = 0.50; $TSS_{BRT} = 0.50$; $TSS_{GAM} = 0.44$; $TSS_{GLM} = 0.47$; Table 1). We thus used the WAC method to project potential hydrological and climatic niches for the 18 best-modelled species while limiting uncertainty in projections due to SDM variability. By 2100, the projected increase in seasonal temperature (+2.2 \pm 0.5°C) and decreasing seasonal river flows (-0.6 ± 0.2 standardized; Appendix S1, Fig. S2) was likely to increase the prevalence and the probability of occurrence for 80% of the modelled species, although each species showed contrasting patterns (Table 1, Fig. 2).

The 18 best-modelled species were then used to estimate future spatial and temporal beta-diversity components. The total amount of spatial beta diversity (β_{SOR}) and its turnover component (β_{SIM}) were projected to decrease linearly during the 21st century, hence highlighting that future local fish assemblages would become more and more similar over the Adour River Basin (Fig. 3a). By contrast, the significant increase in dissimilarity due to nestedness (β_{NES} , Fig. 3a) reflected an overall increase of the regional species richness (i.e. three additional species per site in 2100 on average, Fig. 3b), as approximately 80% species would increase their prevalence and probability of occurrence over the region (Table 1, Fig. 2). It is worth noting that the level of nestedness (NODF) was found to be relatively constant (c. 0.6) over the studied period. Finally, spatial beta diversity was mainly explained by a process of species replacement as the ratio $\beta_{\text{NES}}/\beta_{\text{SOR}}$ was greatly inferior to 0.5 in average $(\beta_{\text{NES}}/\beta_{\text{SOR}} = 0.16 \pm 0.01).$

The total amount of temporal beta diversity was projected to be particularly higher in the upstream ($\beta_{SOR} = 0.9 \pm 0.1$) than in the downstream ($\beta_{SOR} = 0.5 \pm 0.1$) parts of the river gradient (Fig. 3c), hence revealing an overall pattern of decreasing temporal beta diversity along this gradient. When considering the turnover and nestedness components of beta diversity, we found significant hump-shaped and U-shaped relationships, respectively. For instance, temporal beta diversity in the midstream part of the river gradient was found to be mainly caused by species turnover ($\beta_{\text{NES}}/\beta_{\text{SOR}} < 0.25 \pm 0.02$; Fig. 3c). In contrast, the contribution of nestedness in explaining temporal beta diversity is gaining importance in the upstream and downstream parts of the river gradient ($\beta_{\text{NES}}/\beta_{\text{SOR}} > 0.70$). This means that the extreme parts of the river gradient displayed the greatest changes in species composition due to richness differences among nested assemblages (see Fig. 3c). The midstream part of the river gradient was also projected to host an increasing number of species (an extra three species on average by



Figure 2 Mean change in the probability of species occurrence at sites from the period 1990–2000 projected by the weighted average consensus (WAC) approach for the 18 fish species. For each species, mean changes are represented annually for the 21st century and along the downstream–upstream river gradient. The horizontal dotted line represents no changes in the projected probability of species occurrence.

2080–2100; Fig. 3d). This may explain the hump-shaped pattern of NODF along the river gradient, indicating that the level of nestedness is higher in the midstream sites (Fig. 3c).

DISCUSSION

Our results indicate that 80% of the studied fish species are projected to increase their probability of occurrence over the region, thus reflecting an overall range expansion of most species in response to projected changes in hydrological and thermal habitat conditions. Moreover, the projected range expansion of species is not spatially uniform over the region, as local changes in species occurrence are found to be greatest in the midstream parts of the river gradient. This emphasizes the necessity of using individual- rather than community-level modelling approaches to account for local and species-specific response to climate changes (see also Buisson *et al.*, 2008; Baselga & Araújo, 2010). However, we acknowledge that our projections should be interpreted cautiously as our modelling framework does not provide a holistic view of processes



Temporal beta diversity

0.6

0.4

0.2

0

5

4

3

2

1

0

Upstream

1 -4

(d) 6

A local species richness

Upstream

-4

Midstream

-2

0

River gradient

Downstream

2

4

Downstream

2

4

turnover (β_{SIM} ; black) and the nestedness component, which is compared between the Baselga's (2010) (β_{NES} ; green online/light grey in print) and Almeida-Neto et al.'s (2011) (NODF; red online/mid-grey in print) approaches. Smoothed lines are estimated using generalized additive models with a smooth term of third degree. affecting fish species distribution (Heino et al., 2009). For

2020

(a) 1

Spatial beta diversity

0.8

0.6

0.4

0.2

0

(b)

3

2

1

0

-1

-2

Δ local species richness

2020

2060

2060

Years

Years

2100

2100

Figure 3 Weighted average consensus (WAC) projections of spatio-temporal beta diversity and changes in species richness at sites from the period 1990–2000. The temporal trend in the spatial beta diversity (a) and changes in species richness (b) are projected annually over the 21st century. The spatial trend in the temporal beta diversity (c) and the mean changes in species richness (d) are projected along the longitudinal river gradient. Fish beta-diversity projections are decomposed into total beta diversity (\$\beta_{SOR}\$; blue online/dark grey in print),

instance, we did not take into account species interactions or other environmental stressors (e.g. eutrophication and landcover alterations) that could amplify or mitigate the projected changes in species distribution and community structure at both local and regional scales (Heino et al., 2009). Our results should thus be interpreted as a preliminary attempt to assess the strength of spatial and temporal changes in riverine fish community structure facing climate changes.

Midstream

-2

0

River gradient

Future hydroclimatic changes are projected to strongly affect both spatial and temporal patterns of freshwater fish beta diversity in the Adour-Garonne River Basin. For instance, we found a significant temporal trend of spatial homogenization of fish assemblages over the 21st century, which directly reflects the range expansion of 80% of the studied species as result of climate change. Buisson & Grenouillet (2009) found a similar projected trend of spatial homogenization of fish assemblages, although these authors identified this trend between only two time periods, as is commonly done in most climate change impact studies. Climate change could therefore exacerbate the process of biotic homogenization, which has already started because of human-mediated introductions of exotic species (e.g. Leprieur et al., 2008; Olden et al., 2008). In addition, the predicted range expansion of many species may have an additional effect on species already suffering from range reductions caused by climate change, e.g. by increasing competitive interactions. Overall, in the long term, potential extirpation of vulnerable species may occur as a consequence not only of the direct effect of climate change but also of the invasion of species favoured by climate warming (see Sharma et al., 2009).

With regard to temporal beta diversity, we also showed that the composition of local fish assemblages will greatly change over the 21st century, which is consistent with previous studies on riverine fish faunas (e.g. Buisson et al., 2008), Mexican fauna (Peterson et al., 2002), endemic flora in southern Africa (Broennimann et al., 2006), mammals in African national parks (Thuiller et al., 2006) and European plants (Thuiller et al., 2005). However, compared with these previous studies, we provided new insights and understanding of the processes shaping temporal beta diversity by distinguishing between its turnover and nested components. We indeed showed that temporal beta diversity caused by species turnover and nestedness displayed contrasting patterns along an environmental gradient, i.e. the well-recognized upstream-downstream gradient in riverine ecosystems. For instance, the changes in species composition projected in upstream and downstream sites were mainly caused by differences in richness among nested assemblages, whereas those projected in midstream sites were almost entirely caused by a process of species replacement.

Two non-mutually exclusive explanations can be proposed. First, higher temporal changes in thermal conditions may explain the higher temporal species turnover projected in the midstream sites (see Hillebrand et al., 2010). Accordingly, we found a weak but significant correlation (Spearman rank correlation test: $r_s = 0.31, P < 0.05$) between temporal species turnover and temporal changes in thermal conditions. Second, middomain or boundary constraint models assume that hard boundaries constrain the size and placement of species ranges, which may cause randomly distributed species ranges to cluster near the centre of the domain. In riverine ecosystems, such geometric effects have been demonstrated for riparian plants (i.e. the river domain; Dunn et al., 2006). One might therefore expect, by chance alone, the greatest shifts in species range boundaries in the centre of the river domain, which may explain the projected unimodal distribution of temporal species turnover along the upstream-downstream gradient. Further works using null models would be particularly useful to tease apart the relative role of geometric vs environmental constraints in shaping the placement of riverine fish species ranges (see Dunn et al., 2006).

Overall our results could have important fundamental and applied implications. Regarding fundamental issues, our results are relevant to recent debates on the consistency of approaches proposed to decompose beta diversity, especially in the context of climate change. The approach proposed by Baselga (2010) received much criticism from Almeida-Neto et al. (2011) and Carvalho et al. (2011), especially about the estimation of nestedness. In reply, Baselga (2012) addressed the problems by reaffirming that β_{NES} is intended to account for the patterns of beta diversity caused by nestedness and not to measure nestedness in absolute terms. The author stresses that nestedness patterns should be assessed using consistent measures that depend both on paired overlap and matrix filling, as for example NODF (Almeida-Neto et al., 2008). This understanding is fundamental and well exemplified by our study showing the contrasting patterns between NODF and β_{NES} along the river gradient. For instance in the midstream river gradient, while the projected increase of species richness coincided with an overall increase of nestedness (i.e. NODF), the contribution of nestedness to the overall beta-diversity (i.e. $\beta_{\text{NES}})$ was markedly low due to the predominant contribution of species turnover (i.e. β_{SIM}).

Regarding applied issues, the very high temporal turnover predicted in the midstream sites during the 21st century may have marked consequences for ecosystem functioning (Hillebrand et al., 2010; Wardle et al., 2011) and the design of future conservation areas. For instance, the projected results could serve the development of empirical approaches incorporating the functional traits of species that are both lost and gained. This could help to quantify the degree of functional redundancy between loser and winner species affecting ecosystem reliability (Rosenfeld, 2002), as communities with higher levels of redundancy would be less susceptible to disturbance by providing higher resistance (Forys & Allen, 2002). In regard to reserve design, previous studies mostly focused on where reserves should be placed in order to protect regional species pools (i.e. by maximizing spatial beta diversity) (e.g. Harborne et al., 2006; Wu et al., 2010). However, these studies did not explicitly account for the local influence of community dynamics over time (but see Felinks et al., 2011) or consider only temporal species turnover between two time periods (D'Amen et al., 2011). Thanks to an inter-annual approach, our projected results could thus be incorporated in conservation planning algorithms in order to identify conservation priority areas (Cabeza et al., 2010).

To conclude, future climate change is projected to substantially modify freshwater fish assemblages by increasing their overall similarity over the Adour–Garonne River Basin (i.e. homogenization process); this has already been observed in several temperate riverine ecosystems (Buisson & Grenouillet, 2009). In contrast with previous studies, our study has provided new insights into the future temporal patterns of beta diversity in riverine ecosystems by explicitly considering community dynamics over time. Our results thus reinforce the idea that future conservation studies focusing on riverine ecosystems should not only consider the spatial component of beta diversity (Olden *et al.*, 2010) but also its dynamics caused by climate warming. Furthermore, our findings suggest that the distinction between the nestedness and turnover components of beta diversity is not only crucial for understanding the processes shaping spatial beta-diversity patterns (Baselga, 2010; Leprieur *et al.*, 2011) but also for identifying localities (or regions) where the rates of species replacement are greatest. This is an important issue, as temporal species turnover has been, to date, commonly quantified using broad-sense measures of beta diversity such as the Jaccard and Sørensen indices (e.g. Korhonen *et al.*, 2010). Considering the Sørensen index, one might conclude that upstream sites will experience the greatest species replacement over time, which is not the case as shown in this study. We therefore urge future studies to use narrow-sense measures of beta diversity (e.g. the Beta-sim index; Koleff *et al.*, 2003) when analysing patterns and processes of temporal species turnover.

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SUPPORTING INFORMATION

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Appendix S1 Statistical downscaling framework to project future hydroclimatic conditions from global climate model outputs.

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BIOSKETCH

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