BIODIVERSITY RESEARCH

Contrasted impacts of climate change on stream fish assemblages along an environmental gradient

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ABSTRACT

Aim To investigate the potential impacts of climate change on stream fish assemblages in terms of species and biological trait diversity, composition and similarity.

Location One-thousand one-hundred and ten stream sections in France.

Methods We predicted the future potential distribution of 35 common stream fish species facing changes in temperature and precipitation regime. Seven different species distribution models were applied and a consensus forecast was produced to limit uncertainty between single-models. The potential impacts of climate change on fish assemblages were assessed using both species and biological trait approaches. We then addressed the spatial distribution of potential impacts along the upstream–downstream gradient.

Results Overall, climate change was predicted to result in an increase in species and trait diversity. Species and trait composition of the fish assemblages were also projected to be highly modified. Changes in assemblages' diversity and composition differed strongly along the upstream–downstream gradient, with upstream and midstream assemblages more modified than downstream assemblages. We also predicted a global increase in species and trait similarity between pairwise assemblages indicating a future species and trait homogenization of fish assemblages. Nevertheless, we found that upstream assemblages would differentiate, whereas midstream and downstream assemblages would homogenize. Our results suggested that colonization could be the main driver of the predicted homogenization, while local extinctions could result in assemblage differentiation.

Main conclusions This study demonstrated that climate change could lead to contrasted impacts on fish assemblage structure and diversity depending on the position along the upstream–downstream gradient. These results could have important implications in terms of ecosystem monitoring as they could be useful in establishing areas that would need conservation prioritization.

Keywords
Climate change, ensemble forecasting, environmental gradient, homogenization, stream fish assemblages.

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INTRODUCTION

There is now ample evidence that the on-going climate change will irreversibly affect natural species across the globe (Sala *et al.*, 2000; Root *et al.*, 2003) and significant changes have already been demonstrated at different scales (Hughes, 2000; McCarty, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003). Among them, climate change is expected to induce diverse functional (e.g. phenology, physiology) and structural (e.g. changes in species distribution, range contractions, latitudinal movements) ecological responses among organisms (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Beaugrand *et al.*, 2002; Hickling *et al.*, 2006; Menzel *et al.*, 2006; Jetz *et al.*, 2007; Levinsky *et al.*, 2007; Parmesan, 2007).

Many studies have investigated climate-induced effects for a large panel of single species. Idiosyncratic responses of species to future changes would result in progressive species association shifts and potentially cause fundamental changes in the structure and composition of current assemblages (Hughes, 2000; Walther *et al.*, 2002). Such changes have already been observed for butterflies (Menendez *et al.*, 2006; Wilson *et al.*, 2007; Gonzalez-Megias *et al.*, 2008), freshwater macroinvertebrates (Burgmer *et al.*, 2007) and freshwater and marine fish (Daufresne & Boët, 2007; Hiddink & ter Hofstede, 2008) assemblages.

To date, many studies have aimed at predicting the future distribution of individual species by using species distribution models and climate change scenarios (e.g. Berry *et al.*, 2002; Peterson *et al.*, 2002). These models relating the present-day species distribution to climate and other environmental descriptors have been developed for species from a variety of major taxonomic groups, including plants (e.g. Saetersdal *et al.*, 1998; Thuiller, 2004; Ohlemüller *et al.*, 2006), insects (e.g. Peterson *et al.*, 2004), mammals (e.g. Thuiller *et al.*, 2006a; Levinsky *et al.*, 2007), herptiles (e.g. Araujo *et al.*, 2006) and birds (e.g. Peterson, 2003; Jensen *et al.*, 2008; Virkkala *et al.*, 2008). During the last few decades, a large number of statistical methods allowing to model species distribution have been developed, progressively improved and are now applied routinely. Recent studies have demonstrated that projections of the future distribution of a single species could be much contrasted depending on the statistical models applied (Thuiller, 2004; Araujo *et al.*, 2005; Lawler *et al.*, 2006; Pearson *et al.*, 2006; Crossman & Bass, 2008). Therefore, calls have been made to fit a number of alternative models and to explore the resulting range of projections. Although very common in various fields such as meteorology (e.g. Weigel *et al.*, 2008) or economics (e.g. Gregory *et al.*, 2001), these consensus methods and ensemble forecasting approaches have been only recently applied in ecology (Thuiller, 2004; Araujo *et al.*, 2005, 2006; Araujo & New, 2007; Crossman & Bass, 2008; Roura-Pascual *et al.*, 2008; Marmion *et al.*, 2009). Based on the central limit theorem in statistics, where central limits of particular projections are expected to be more likely than extremes (Araujo *et al.*, 2006), such methods are very attractive as they reduce the predictive uncertainty in single-models by combining their predictions. To date, most available studies have demonstrated that the accuracy of species distribution predictions could be substantially improved by applying consensus methods (Araujo *et al.*, 2005; Crossman & Bass, 2008; Marmion *et al.*, 2009).

Like single species distribution models, these ensemble forecasting and consensus approaches may be used to apply an assemblage-level analysis to the resulting set of species distributions ('predict first, assemble later' strategy from Ferrier & Guisan, 2006). Assemblage-level modelling aggregates predictions obtained from multiple species distribution models in a simple manner and produces information on spatial pattern in the distribution of biodiversity. It also allows synthesizing complex data into a form more readily interpretable by scientists and decision-makers (Ferrier & Guisan, 2006). The studies that have applied this technique have mainly used measures such as species richness or species turnover to address the potential changes in assemblages' structure induced by future climate change (Peterson *et al.*, 2002; Thuiller *et al.*, 2005, 2006c; Broennimann *et al.*, 2006).

In recent years, a growing concern has been to highlight the potential ecosystem impacts of changes in functional diversity due to climate change (Thuiller *et al.*, 2006b). Indeed, functional approaches are increasingly applied to assess ecological responses to anthropogenic perturbations (Poff & Allan, 1995) or as a tool for the biomonitoring of ecosystem functions (e.g. Gayraud *et al.*, 2003; Doledec & Statzner, 2008). In studies assessing the impacts of climate change, species are often predicted to change their present-day distribution. Thus, a species may be replaced by another species in a particular assemblage. If this new species is redundant (in terms of functional traits) to the replaced species, the impact on the assemblage structure would be minimal compared to the replacement by a functionally dissimilar species (Díaz & Cabido, 1997; Rosenfeld, 2002). Therefore, the prediction of the potential effects of climate change on functional assemblages rather than on species assemblages could be more helpful to evaluate the impacts of species range shifts on ecosystem functioning (Thuiller *et al.*, 2004, 2006b).

To our knowledge, there are at present very few studies which have addressed this issue. Most of them have concerned plants or biomes and used plant functional types (Díaz & Cabido, 1997; Lavorel *et al.*, 1997; Calef *et al.*, 2005; Thuiller *et al.*, 2006b,c) which allow simplifying complex plant communities. Some studies have also pooled species according to their feeding group, degree of habitat specialization or climate requirements (Beaugrand *et al.*, 2002; Andrew & Hughes, 2005; Golicher *et al.*, 2008) to analyse the potential impacts of climate change on these functional groups.

In this context, the purpose of our study was therefore to predict the impacts of climate change on stream fish assemblages for both taxonomic and trait approaches by using an ensemble forecasting framework. Fish, having no physiological ability to regulate their body temperature (Wood & McDonald, 1997), could be highly sensitive to climate warming. In recent years, it has been found that freshwater fish species could greatly change their present-day distribution in response to climate change (e.g. Eaton & Sheller, 1996; Mohseni *et al.*, 2003; Chu *et al.*, 2005; Buisson *et al.*, 2008). However, the impacts of climate modifications on fish assemblages' structure and diversity remain to be investigated.

Therefore, the main objectives of this study were: (1) to predict the future potential distribution of 35 stream fish species by using several species distribution models and consensual predictions; (2) to aggregate these individual predictions to assess the potential impacts of climate change on stream fish assemblages in terms of composition, diversity and similarity; and (3) to compare the effects for both taxonomic and trait approaches.

METHODS

Description of the data

Fish data

Fish data were extracted from the Office National de l'Eau et des Milieux Aquatiques (ONEMA) database. The ONEMA is the national fisheries organization in charge of the conservation of freshwater ecosystems in France. We selected a set of 1110 sites spread over nine French river units. A standard electrofishing protocol was conducted during low-flow periods in these 1110 sites. Presence and absence of the 35 most common species were used in this study.

Fish autecological characteristics were described using 19 biological traits that we thereafter coded in 67 modalities. Traits coding was derived from the literature and FishBase website. These biological traits described body length, shape and swimming factors, reproduction habitat, absolute and relative fecundity, number of spawning events, egg diameter, age at female maturity, life span, larval length, presence or absence of parental care, duration of the incubation period, feeding habitat and diet, rheophily and salinity preferences, habitat and migration behaviour (see Appendix S1 in Supporting Information).

Environmental data

Six environmental variables measured by the ONEMA were used to describe the 1110 studied sites: surface area of the drainage basin above the sampling site (SDB, km^2), distance from the headwater source (DS, km), mean stream width (WID, m), mean water depth (DEP, m), river slope (SLO, ‰) and elevation (ELE, m).

To eliminate the colinearity between DS and SDB which both describe the position of sites along the upstream–downstream gradient, we used a principal component analysis (PCA). The first axis of the PCA was kept as a synthetic variable describing the longitudinal gradient G. It accounted for 93.2% of the total variability.

WID, DEP and SLO influence water velocity and current characteristics. Following Oberdorff et al. (2001), a rough approximation of local velocity derived from the Chezy formula was calculated:

$$V = \log \text{WID} + \log \text{DEP} + \log \text{SLO} - \log(\text{WID+2DEP}). \quad (1)$$

Climate data

The CRU CL 2.0 dataset (Climatic Research Unit Climatology 2.0 version) (New et al., 2002) at a resolution of $10' \times 10'$ was chosen to describe the current climate. Four variables related to fish ecological requirements were extracted: mean annual precipitation (PAN, mm), mean annual air temperature (TAN, °C), mean air temperature of the coldest month (MTC, °C) and mean air temperature of the warmest month (MTW, °C).

MTC and MTW were grouped in a single variable describing the annual thermal range (TAM, °C):

$$\text{TAM} = \text{MTW} - \text{MTC}. \quad (2)$$

Climate data for the current period were obtained from the average of the period 1961–90. Future climate predictions were calculated and averaged for the time period 2051–80 (referred to as the 2080 scenario) and derived from HadCM3 (Hadley Centre for Climate Prediction and Research's General Circulation Model) for each of the four selected climatic descriptors. Two greenhouse gas emissions scenarios from the Special Report on Emission Scenarios of the Intergovernmental Panel on Climate Change (IPCC SRES) were used, B2 and A1FI (Nakicenovic & Swart, 2000). The CO_2 levels under the B2 and A1FI scenarios are expected to be respectively around 550 and 800 p.p.m. in 2080, an increase of 150% and more than 200% in comparison with the levels measured in 2000 (IPCC, 2001). The A1FI scenario is mainly fossil-fuel intensive and is thus more pessimistic about future climate warming than the B2 scenario.

Ensemble forecasting and consensus

First, we randomly split the dataset into two subsets: the model calibration dataset including 70% of the sites (i.e. 777 sites) and the evaluation dataset containing 30% of the 1110 sites (i.e. 333 sites).

We then simulated the distribution of 35 fish species using seven different statistical methods: three regression methods (generalized linear models, generalized additive models, multivariate adaptive regression splines), two machine learning methods (random forest, general boosted models) and two classification methods (factorial discriminant analysis, classification tree analysis). We restricted our attention to these seven methods because they are amongst the most widely applied methods to model species distributions based on presence–absence data (see Heikkinen et al., 2006, for a review).

The calibrated models were then used to predict the current distribution of the 35 fish species for the 1110 studied sites and to generate projections of future potential distributions for 2080 under both A1FI and B2 scenarios. These predicted current and future probabilities of occurrence were converted into binary values using a cut-off threshold. Two measures of performance, sensitivity (i.e. the percentage of presence correctly predicted) and specificity (i.e. the percentage of absence correctly predicted), were calculated for a large range of threshold values between 0 and 1. We selected the accurate threshold as the one which maximized the sum of these two measures (Fielding & Bell, 1997). If the probability of occurrence of a given species in a site was above this threshold, it was considered as present, and below as absent.

We used a consensus method based on the computation of the average value of the ensemble of predictions. Indeed, several studies have suggested that this method provides significantly more robust predictions than all the single-models

and other consensus methods (e.g. Clemen, 1989; Araujo *et al.*, 2005; Marmion *et al.*, 2009). To test whether this hypothesis was true in our study, we evaluated the predictive accuracy of both the seven single-models and the 'consensual model' (i.e. average of the current predictions across the seven single-models), by using the computation of the rate of prediction errors (i.e. the rate of observed presence and absence wrongly predicted) on the remaining 30% of the initial dataset. We found that the prediction errors calculated for the 'consensual model' were lower on average across the 35 species (mean prediction error ± SD: 18.92 ± 5.44%) than prediction errors calculated for the single-models, which ranged from 20.51 ± 6.57 to 25.50 ± 4.63%. It indicated that current consensual predictions of fish species distribution were more accurate than predictions coming from the single-models. Therefore, we also averaged the predictions across the seven statistical modelling techniques for both future scenarios. This resulted in a single prediction at each site for each species, for current and both climate change scenarios, which we thereafter transformed into presence–absence values following the previously mentioned method.

Combining predicted future species distributions

To determine the predicted species richness and other variables describing fish assemblages, we overlapped all the individual species distributions. Although summing distributions of individual species has become a widely used approach for obtaining estimates of species richness and composition (e.g. Thuiller *et al.*, 2005, 2006c; Broennimann *et al.*, 2006), recent studies have highlighted the need to provide measures of uncertainty along with the species distribution models (Hortal & Lobo, 2006; Pineda & Lobo, 2009). According to these authors, overlapping individual models to predict species richness can magnify the bias and overestimation of the prediction of individual distributions. This may result in a spatial aggregation of model errors, mainly at the edges of the observed distributions and also in other parts of the environmental spectrum (reviewed in Hortal & Lobo, 2006). This issue thus needed to be addressed before predicting changes in future assemblages. Therefore, we first quantified the prediction errors for each fish species by examining separately errors of commission and omission (i.e. observed absence predicted as presence and observed presence predicted as absence respectively) calculated on the evaluation dataset. Quite similar patterns were observed across all species (see Appendix S2), with a mean commission error of 18.90 ± 5.95% (SD) and a mean omission error of 24.34 ± 7.62%. Half of the species were wrongly predicted as absent in < 25% of the sites where they currently occur. We then found that the correlation between observed and predicted species richness values was high ($R^2 = 0.704$), suggesting that combining predicted distributions across all species provided a reliable representation of the spatial pattern of fish species richness. Finally, we tested for spatial autocorrelation in prediction errors of this relationship (i.e. the residuals of the relationship between predicted versus observed species richness) using Mantel tests and correlograms. Mantel tests showed that prediction errors were not correlated to geographical distance ($r_M = -0.008$, $P = 0.785$) or to the distance between sites along the upstream–downstream gradient ($r_M = 0.005$, $P = 0.360$). For both Mantel correlograms, none of the r_M-values in the different distance-classes was statistically significant at a 5% significance level. These results thus indicated that prediction errors of species richness were not spatially autocorrelated. We can therefore reject the hypothesis of a spatial aggregation of model errors, which could have been due to the combination of individual species distributions to derive information about future assemblages. Thus, the 'predict first, assemble later' strategy used to assess fish species richness and the other fish biological variables was strengthened.

Change in assemblages' diversity

We assessed the changes in fish species diversity by comparing the predicted species richness for current and future climate conditions at each of 1110 sites. To measure fish trait diversity, we followed Champely & Chessel (2002) by using biological information about the dissimilarity between species. Each of the 35 species being assigned to one modality of each of the 19 biological traits (see Appendix S1), we first computed the dissimilarity among fish species for each biological trait using the Jaccard distance (Gower & Legendre, 1986). The resulting dissimilarity matrix $\mathbf{D}_i$ contained the pairwise distance between species for trait i. Dissimilarity between two species for a given biological trait equalled zero, if the two species were coded in the same way and one, if they were assigned to different modalities of the given trait. We then combined the 19 resulting dissimilarity matrices through their quadratic mean (Hartl & Clark, 1989) to derive a global dissimilarity matrix of biological traits (**D**) as follows:

$$\mathbf{D} = \sqrt{\frac{1}{t}\sum_{i=1}^{t}\mathbf{D}_i{}^2}, \tag{3}$$

where t is the number of biological traits (i.e. $t = 19$).

Finally, trait diversity (TD) for a given site j was computed by the product:

$$\mathrm{TD}_j = \mathbf{P}_j \times \left(\frac{1}{2}\mathbf{D}^2\right) \times \mathbf{P}_j{}^T, \tag{4}$$

where **P** is the table describing fish species prevalence in the 1110 sites and $\mathbf{P}^T$ was the transpose of **P**. Trait diversity was calculated for both predicted current and future assemblages.

Both changes in species and trait diversity were related to the upstream–downstream gradient G using generalized additive models.

Change in assemblages' composition

Change in fish assemblages' composition was assessed both for fish species and fish trait composition. For fish species

composition, we calculated the number of species predicted to appear (species gain, SG) and the number of species predicted to be no longer present in the future (species loss, SL) in each site. We thus estimated the percentage of species turnover as:

$$\text{Species turnover} = 100 \times \frac{\text{SG} + \text{SL}}{\text{SR} + \text{SG}}, \tag{5}$$

where SR is the current species richness (Peterson *et al.*, 2002).

For the trait approach, we derived a 'trait modalities-by-site' table (presence or absence of trait modalities in each site) for current and future scenarios, upon which the formula of species turnover was applied.

For both species and trait approaches, a turnover value of zero indicated that the predicted assemblage in the future would be the same as the current assemblage, whereas a turnover value of 100 indicated that the assemblage would be completely modified under climate change.

As for change in assemblages' diversity generalized additive models were used to relate the turnover rates to the upstream–downstream gradient G.

Change in assemblages' similarity

We evaluated the changes in similarity between assemblages under climate change scenarios for both species and trait approaches using the Jaccard similarity index. Previous authors have shown that this index could reflect a general size effect (Jackson *et al.*, 1989), similar species richness leading to similar Jaccard index values even when the sets of species are quite random. To limit this effect, as fish species richness has been shown to increase with increasing stream size (reviewed in Matthews, 1998), we grouped sites according to their positions along the upstream–downstream gradient G. A hierarchical clustering method (using the Ward's method and Euclidean distance) was applied on G and three site clusters were defined: upstream, midstream and downstream sites. Within each cluster, we computed the Jaccard similarity index for current (J_{cur}) and both future (J_{A1FI} and J_{B2}) predictions for each pair of sites. We then quantified the changes in similarity values (ΔJ) by calculating the differences between J_{A1FI} (J_{B2}) and J_{cur}. Positive values of ΔJ indicated that climate change would lead to an increase in similarity (i.e. fish assemblages would homogenize), whereas negative values indicated a decrease in similarity (differentiation of fish assemblages). Following Qian & Ricklefs (2006), we analysed ΔJ-values within three equal classes of increasing J_{cur} as ΔJ is dependent on the current similarity between assemblages. The number of classes was chosen arbitrarily.

Given this framework, testing for changes in similarity between assemblages means testing whether the mean ΔJ-value was significantly different from zero. This was performed using paired-difference permutation tests for each climate scenario, site cluster and level of initial similarity. For each test, the observed mean ΔJ-value was computed. The sign of all the pairwise combinations was then permuted and simulated mean

ΔJ-value was computed. One thousand permutations were made this way, resulting in 1000 permuted values of mean ΔJ under the hypothesis of no similarity change. The observed mean ΔJ-value was then compared with the frequency distribution of these 1000 permuted values. We distinguished two cases: (1) if the observed value was positive and < 5% of the simulated values were higher than the observed value, we concluded that there was homogenization; and (2) if the observed value was negative and < 5% of the simulated values were lower than the observed value, we concluded that there was differentiation.

Finally, changes in similarity were analysed for two theoretical scenarios, as suggested by Olden & Poff (2003) who explained that both species extinctions and invasions may drive biotic homogenization. In our first scenario, climate change could only drive colonization; no extinction would occur. The second scenario hypothesized that species would not be able to colonize new suitable habitats and thus only extinction could occur. For these two scenarios, we calculated ΔJ for both species and trait approaches and for both climate change scenarios.

RESULTS

Change in assemblages' diversity

On average, species richness was predicted to increase from the current 10.3 species per site to 15.9 and 19.5 species in 2080 under B2 and A1FI scenario respectively, leading to strong changes in local species richness (Fig. 1a). Change in species number could range from −5 species to +27 species depending on the sites and future scenarios. At the site level, the increase in species richness under the B2 scenario was predicted to be moderate compared to A1FI (Fig. 1a). For both scenarios, some sites would experience a slight decrease in species richness, especially in north-west France (Brittany), but most sites would gain fish species. The relationship between the change in species richness and the position along the upstream–downstream gradient G was slightly bell-shaped for both climate scenarios (Fig. 2a): species richness would increase the most in the midstream sites, which are mainly located in medium-sized mountains (e.g. low elevations in the Pyrenees and the Alps), whereas most upstream and downstream sites would be colonized by a limited number of species.

On average, trait diversity rose from 0.23 currently to 0.27 and 0.29 under B2 and A1FI scenarios respectively. Therefore, a slight increase in trait diversity was predicted at the scale of France and this change was predicted to be negative in more sites than species richness, especially under the scenario B2 (Fig. 1c). A negative relationship was found between the change in trait diversity and the upstream–downstream gradient, being weaker for the B2 scenario (Fig. 2c). The largest increase in trait diversity would thus occur in upstream and mountainous regions, whereas downstream and lowland sites were projected to gain very few biological trait modalities (Fig. 2c).
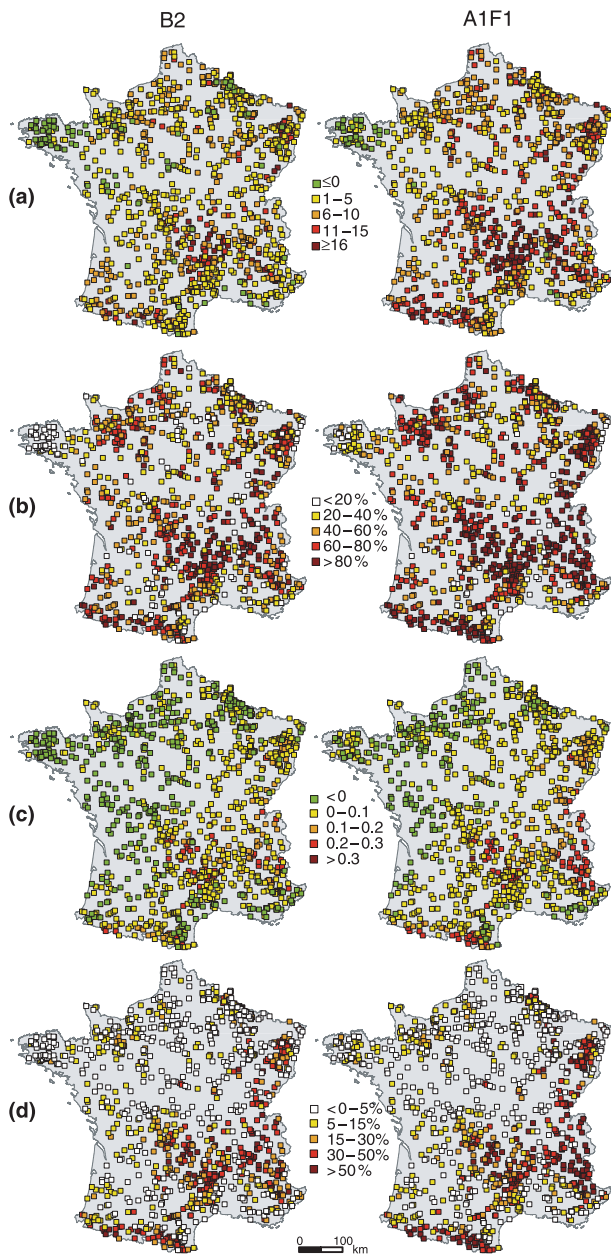
Figure 1 Spatial distribution of predicted impacts of climate change on fish assemblages under B2 (left-hand column) and A1FI (right-hand column) climate change scenarios: (a) change in species richness, (b) species turnover, (c) change in biological trait diversity and (d) trait turnover.

Change in assemblages' composition

Species composition was predicted to be more highly modified than trait composition (Fig. 1b,d): a turnover value higher than 50% was exceeded for only 16% of the sites for the trait approach, whereas 71% of the sites exceeded this value for the species approach under the A1FI scenario. Trait turnover values could, nevertheless, be quite important in some areas, especially in mountainous regions (Fig. 1d). Furthermore, both species and trait turnover were negatively related to the upstream–downstream gradient (Fig. 2b,d).
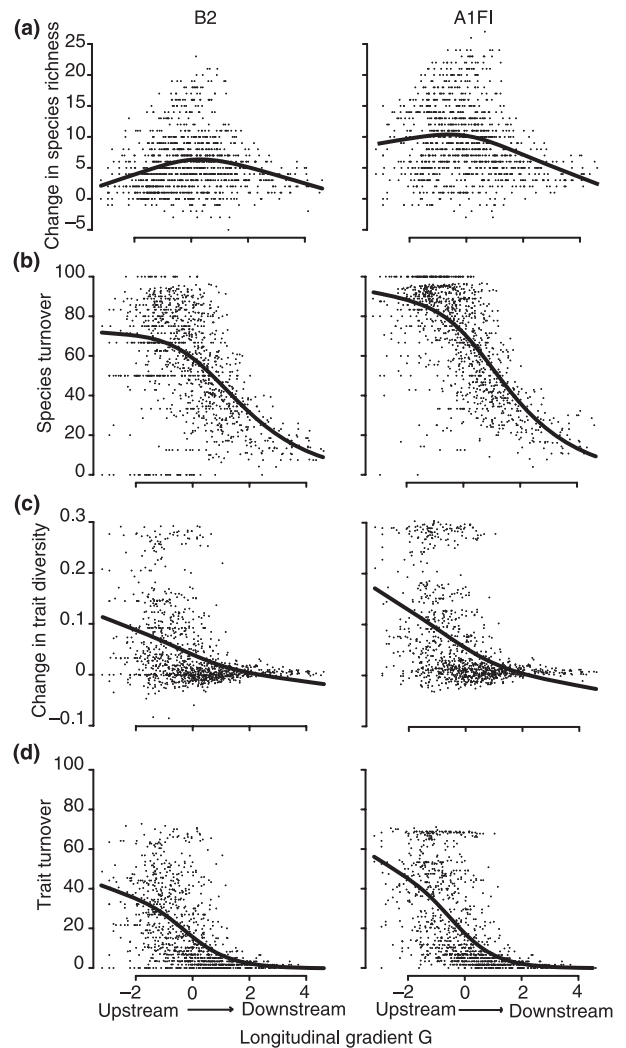
Figure 2 Predicted modifications of fish assemblages under B2 (left-hand column) and A1FI (right-hand column) scenarios along the upstream–downstream gradient. Individual observations (black dots) and predictions (solid line) from fitted generalized additive models are shown.

Change in assemblages' similarity

For the species approach, among all pairwise-site combinations, the mean Jaccard similarity index equalled 24.6% for current and 35 and 50.7% under B2 and A1FI scenarios respectively. However, changes in species similarity differed depending on the position of the sites along the upstream–downstream gradient. For example, under the B2 scenario, upstream assemblages were predicted to differentiate on average by 6.3%, whereas midstream and downstream assemblages would homogenize by 19.2 and 17.2% respectively (Table 1). For the trait approach, a global increase in trait similarity was also predicted, going from a mean J_{cur} of 69.5% to a mean J_{B2}-value of 83.2% and J_{A1FI} of 92.5%. This increase was expected regardless the position of the sites along the upstream–downstream gradient, but was slightly higher for the upstream assemblages (Table 1). For example, under the A1FI

Table 1 Mean Jaccard similarity index (%) for current and both future climate change scenarios A1FI and B2.

	Current	A1FI	B2
Species			
Upstream	31.4	39.8	25.1
Midstream	30.6	63.6	49.8
Downstream	65.4	87.7	82.6
Traits			
Upstream	62.1	87.9	74.4
Midstream	80.7	96.3	91.7
Downstream	98	99.4	99.6

Using paired-difference permutation tests, all the differences between the current and future scenarios were statistically significant ($P < 0.001$).

scenario, trait assemblages would homogenize by 25.8% on average in upstream sites, whereas downstream assemblages would homogenize by only 1.4%.

Globally, negative relationships between ΔJ and J_{cur} were found for both species and trait approaches (Fig. 3). This indicated that fish assemblages currently with low similarity would tend to be more homogenized than assemblages, which are currently more similar.

Changes in similarity were much more complex for the species approach than for the trait approach. Indeed, for the trait approach, whatever the sites' location along the upstream–downstream gradient and whatever the current similarity and climate change scenario, assemblages would tend to become homogenized in terms of trait composition and very few pairs of assemblages would be differentiated (Fig. 3d–f).

Results were quite different for the species approach. Current dissimilar assemblages were expected to be strongly homogenized in the future, especially downstream assemblages (Fig. 3a). In comparison, current similar assemblages would differently change their similarity depending on the position along the upstream–downstream gradient. Upstream sites would tend to be differentiated, whereas midstream and downstream assemblages would be homogenized, but to a lesser extent than current dissimilar sites (Fig. 3c).

Finally, both theoretical scenarios gave contrasting results (Table 2). Under the colonization-only scenario, fish assemblages of upstream, midstream and downstream sites were predicted to homogenize both in terms of species and trait composition. Indeed, high percentage values (i.e. between 68 and 95.9% for the species approach; between 60.6 and 92.5% for the trait approach) indicated that more pairwise-site combinations would increase their similarity rather than keep it unchanged or decrease it. Homogenization was stronger for
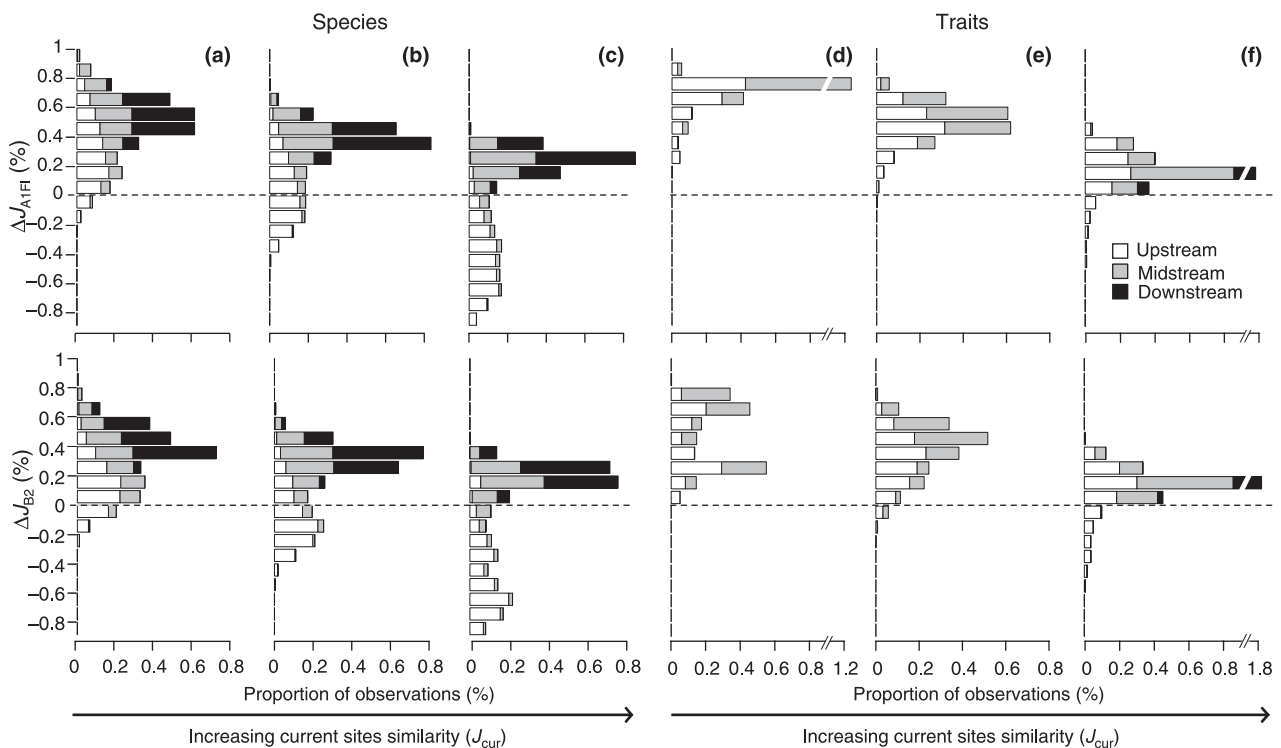
Figure 3 Distribution of changes in Jaccard similarity index (ΔJ) between pairs of sites under A1FI (above) and B2 (below) scenarios, for both species (left) and trait (right) approaches. The pairs of sites are grouped by (1) degree of current similarity: (a,d) low similarity between pairwise sites ($J_{cur} < 0.33$), (b,e) medium similarity ($0.33 \leq J_{cur} < 0.66$), (c,f) high similarity ($0.66 \leq J_{cur}$); and by (2) position along the upstream–downstream gradient: upstream (white), midstream (grey) and downstream (black). Using paired-difference permutation tests, mean ΔJ-value was significantly different from zero ($P < 0.001$) for each level of initial similarity, each site cluster and each climate scenario.

Table 2 Percentage of pairwise-site combinations for which change in Jaccard similarity index is strictly positive (homogenization) for colonization-only and extinction-only, under both climate change scenarios.

	Colonization		Extinction	
	A1FI	B2	A1FI	B2
Species				
Upstream	68	46.9	10.3	18
Midstream	95.4	87.2	22.7	29.2
Downstream	98.3	95.9	69.2	66.7
Traits				
Upstream	91.9	82.9	14.7	18
Midstream	92.5	86.1	10.3	8.3
Downstream	60.6	61.4	0.7	1.3

the A1FI scenario especially for the species approach. The single exception was the upstream assemblages for the species approach under the scenario B2. Only 46.9% of the pairwise-site combinations presented homogenization, suggesting that the majority of the assemblages would not change or would differentiate. Under the extinction-only scenario, changes in species and trait similarity were different according to the position along the upstream–downstream gradient. Under both climate change scenarios, low percentage values were found for upstream and midstream sites for both species and trait approaches. Under this extinction-only hypothesis, differentiation would thus occur more often than homogenization in these assemblages. However, downstream assemblages exhibited a different trend for the species approach as more than two-thirds of the pairwise-site combinations would increase their similarity in the future, indicating a taxonomic homogenization of these assemblages.

DISCUSSION

Like in many other organisms, individual responses of fish species to climate change would result in significant modifications of assemblages' structure. Our findings highlighted that both structural and functional changes in fish assemblages could occur when facing climate change. Nevertheless, the changes concerning species richness, composition and similarity appeared to be larger and more pronounced than the functional changes. Bonada et al. (2007) found a similar result when comparing stream macroinvertebrate communities of Mediterranean and temperate regions. They suggested that climate change could produce large modifications in the taxonomic but rather weak changes in the trait composition. Indeed, biological traits aggregate information shared among different species. This functional redundancy is based on the observation that some species perform similar roles in the assemblages and may therefore be replaceable with little impact on ecosystem functioning (Lawton & Brown, 1993; Rosenfeld, 2002; Micheli & Halpern, 2005).

Contrary to other studies that applied strictly bioclimatic models to predict the future impacts of climate change at a large scale (e.g. Saetersdal et al., 1998; Berry et al., 2002; Thuiller et al., 2005; Virkkala et al., 2008), we enhanced our species-models by including non-climatic factors. Pearson & Dawson (2003) recommended accounting for topography when studying the impacts of climate change at a regional or local scale. Trivedi et al. (2008) have also recently demonstrated that large-scale modelling studies, which did not account for topography, may have underestimated the potential impacts of climate change on mountain plants. As the studied sites covered different types of streams, they offered a large variability in environmental conditions ranging from small headwater streams in mountain areas to large lowland channels downstream. Taking into account such local factors in this study allowed us to describe the potential responses of fish assemblages both at the scale of France and along the upstream–downstream gradient.

Changes in fish assemblages at the scale of France

Fish assemblages were predicted to modify their composition, diversity and similarity for both species and trait approaches. Overall, we found an increase in species and trait diversity. This result is concordant with the increase in species richness, which has already been observed for marine (Hiddink & ter Hofstede, 2008) and freshwater fish species (Daufresne & Boët, 2007) during the last decades and also for other organisms (e.g. plants: Grabherr et al., 1994; butterflies: Menendez et al., 2006). Results are more contrasted when predicting species richness in the future (e.g. plants: Broennimann et al., 2006; mammals: Levinsky et al., 2007; butterflies: Wilson et al., 2007). However, for freshwater fish, our results are in accordance with those found by Minns & Moore (1995) in Canada, where an average increase in species richness of 31.8 species for the studied tertiary watersheds was predicted. As French fish assemblages contain few cold-water species, more fish species (cool- and warm-water species) would expand their range than reduce it under climate change. Thus, more species would locally occur, leading to this predicted rise in species richness.

While the effects of climate change on taxonomic diversity have been widely documented through the use of measures such as species richness (e.g. Broennimann et al., 2006; Thuiller et al., 2006c), few studies have focused on changes in trait diversity. Here we showed that fish assemblages could become more functionally diverse under climate change as globally a slight increase in trait diversity was predicted. It is commonly assumed that changes in species diversity lead to changes in functional diversity (Díaz & Cabido, 1997; Micheli & Halpern, 2005), which appears to be the case in our study. Indeed, fish species expanding their distributional area to newly suitable sites may be functionally different from species occurring currently in these sites, increasing thus assemblage trait diversity.

Species turnover rates indicated that at least half of the current pool of species would be changed in more than

two-thirds of the studied sites. This taxonomic turnover rate is slightly higher than the rate found for other organisms (Peterson *et al.*, 2002; Thuiller *et al.*, 2005, 2006a; Broennimann *et al.*, 2006; Buisson *et al.*, 2008). Most of these previous studies have discussed the potential consequences of high species turnover rate, which could cause fundamental change in assemblage functioning. Our results confirmed that changes in fish trait composition could be globally important at the scale of France and they could induce substantial effects on stream fish assemblages functioning. As biotic interactions may undergo alterations, the sustainability of these future assemblages in the long term remains questionable.

This study also aimed at comparing the similarity between the 1110 fish assemblages at present and in the future. Overall, our findings suggested that the similarity between fish assemblages would be higher in the future for both species and trait approaches. Under the most pessimistic climate change scenario, fish assemblages may homogenize on average by 26.1 and 23% for the species and trait approaches respectively. This potential biotic homogenization of fish assemblages would be mainly caused by the future potential colonizations of fish species that would expand their distributional area to move to new habitats suiting their ecological requirements. The question of taxonomic homogenization has been largely documented in the context of biological invasions, especially for freshwater fishes and plants. Investigations have been carried out to verify whether the human-mediated introduction of exotic species has tended to homogenize historical assemblages from which native species were extirpated (e.g. Rahel, 2002; Olden, 2006; Olden & Rooney, 2006; Leprieur *et al.*, 2008b). Most studies have shown that assemblages become more homogeneous when facing exotic species invasions and extirpations of native species (Rahel, 2000; McKinney, 2004; Qian & Ricklefs, 2006; Olden *et al.*, 2008). To date, a few studies have investigated the effects of the recent observed climate modifications on the similarity between assemblages (e.g. macroinvertebrates: Burgmer *et al.*, 2007; plants: Jurasinski & Kreyling, 2007). Jurasinski & Kreyling (2007) found that the upward shift of plant species during the last century has led to the homogenization of the vegetation in Alpine summit regions. Nonetheless, to our knowledge, no study has focused on predicting changes in similarity and potential biotic homogenization in the future climate via a species-distribution-modelling approach. In our study, we predicted that climate change could lead to both taxonomic and functional homogenization. The predicted functional homogenization could have important consequences for the fish assemblages' functioning. Future stream fish assemblages could actually increase their vulnerability to other large-scale environmental events as local assemblages would have synchronized and identical biological responses (Olden, 2006). Regarding taxonomic homogenization, we found that the value of homogenization for French fish assemblages in 2080 would be much higher than values of change in similarity observed among freshwater fish communities in recent decades and due to the invasions by alien species (Rahel, 2000; Taylor, 2004; Leprieur *et al.*, 2008b; Olden *et al.*, 2008). Therefore, this result suggests that climate change would tend to exacerbate the biotic homogenization, which has already started because of human-mediated introductions of invasive species (Leprieur *et al.*, 2008a).

Changes in fish assemblages along the upstream–downstream gradient

Despite the global pattern of changes in fish assemblages' structure under climate change, one of the key results of our study was that these predicted changes could be highly contrasted depending on the position of the sites along the upstream–downstream gradient. This gradient is probably the most well-known, large-scale pattern in stream fish assemblages, generally reflecting an increase in fish species richness with increasing stream size (reviewed in Matthews, 1998). This typical longitudinal pattern has been well discussed, with different explanations being advanced such as differential rates of migration and extinction (Power *et al.*, 1988), habitat diversity (Gorman & Karr, 1978) or sampling phenomenon (Angermeier & Schlosser, 1989). Although various competing factors (i.e. biotic, abiotic and spatial) have been identified in structuring stream fish assemblages (Jackson *et al.*, 2001), much of the debate on the mechanisms responsible for such a large-scale pattern has focused on the concepts of 'addition' versus 'replacement' of species from headwaters to lower mainstreams (Matthews, 1998).

In the present study, upstream sites were predicted to suffer the most from the effects of climate change. Species richness and trait diversity in these sites were predicted to increase strongly and those sites would have the most changed species and trait composition. Moreover, the similarity between some upstream assemblages could decrease indicating a taxonomic differentiation. On the contrary, downstream sites would mainly lose a few species and biological traits leading to a predicted biotic homogenization.

Therefore, upstream assemblages would markedly respond to climate change by strongly modifying fish species and trait structure. In a previous study, Buisson *et al.* (2008) found that the most modified fish assemblages would be located at sites where climate warming would be the greatest. Both results are thus concordant as upstream sites are globally located in mountainous regions, which are expected to face more rapid and intense climate changes than other regions (Beniston, 2003; Schroter *et al.*, 2005).

Our findings would benefit from being compared with other studies dealing with the potential consequences of climate change along other environmental gradients such as altitudinal or latitudinal gradient. However, the lack of other studies precludes a wider comparison and additional investigations are thus urgently necessary.

Some limitations

Although our results were obtained from an ensemble forecasting approach, which appears to be a robust predictive method

(Araujo & New, 2007), the predicted patterns in assemblages' diversity, composition and similarity may only be viewed as 'future potential assemblages' and may be greatly overstated or understated. Indeed, many factors acting at different spatial or temporal scales could hinder these assemblages to be established (Pearson & Dawson, 2003; Dormann, 2007).

First, both natural and physical barriers may obstruct fish displacements to newly suitable sites. In this study, a fundamental assumption is that a given species could reach every site that would become suitable in the future (universal dispersal), but this assumption is questionable. Indeed, although France has a large system of canals linking the internal river units and thus allowing potential inter-watershed transfer of aquatic organisms, adjacent rivers may be disconnected if they are not included in the same watershed. The insular nature of watersheds may thus stop the natural dispersal of fish species to river units where those species are not currently present. Stream fragmentation by weirs or dams could also be an artificial obstacle to fish dispersal.

Secondly, fish species may be unable to disperse at a sufficient rate to keep up with the changing climate. In this study, it was assumed that all the 35 fish species have the same dispersal ability. However, this assumption, although very common, is critical as dispersal ability is related to species' biological characteristics (i.e. size: Jenkins et al., 2007) and life-history traits (i.e. reproduction).

Moreover, species could also adapt to future climate by modifying their behaviour. Such behavioural modifications have already been shown for amphibians and birds (earlier breeding: Beebee, 1995; Dunn & Winkler, 1999) or plants (earlier flowering: Bradley et al., 1999). To our knowledge, no similar studies have illustrated such behavioural changes for stream fish.

Lastly, expected changes in mean precipitation have been used as a surrogate variable to describe stream flows and hydrological conditions. However, hydrology is a much more complex parameter, which concerns diverse fields such as meteorology, geomorphology, geology or geography. Thus, to assess the effects of hydrology on fish assemblages, including many more variables would certainly improve our species distribution models. Fish will certainly respond to changes in hydrological conditions, as these conditions determine the micro-structure of the habitat and also influence fish life cycles, especially reproduction and migration. Taking into account changes in hydrology, mainly the possibility of increased hydrological variability, when assessing the impacts of climate change on fish assemblages is an issue that would need to be addressed in further studies to enhance the accuracy of the predictions.

CONCLUSION

Our results indicated that the forecasted climate change could lead to both structural and functional changes in stream fish assemblages. The local fish species richness and trait diversity could increase in parallel with a global fish species and trait

homogenization, raising interesting issues in terms of ecosystem conservation and management.

One of the key issues of this study was that the impacts of climate change on stream fish assemblages may be highly contrasted depending on the position along the upstream–downstream gradient. Thus, it revealed the importance of accounting for environmental gradients (e.g. altitudinal gradient) to predict more accurately the response of fauna and flora to climate change in future studies.

Such an approach allowed us to highlight the high sensitivity of upstream fish assemblages to the forecasted climate change compared to downstream assemblages, which could be more resilient. Upstream areas would be refuge areas for cold-water species as well as thermally suitable regions for cool- and warm-water species, leading to substantial changes in fish assemblages. These results may have important implications for identifying stream reaches and geographical areas that would need priority conservation measures in response to global climate change.

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SUPPORTING INFORMATION

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

Appendix S1 Fish species biological traits.

Appendix S2 Errors of prediction, commission and omission for the 35 studied species calculated from the consensus method and evaluation dataset (333 sites).

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