

Climate change hastens the turnover of stream fish assemblages

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Abstract

Stream fish are expected to be significantly influenced by climate change, as they are ectothermic animals whose dispersal is limited within hydrographic networks. Nonetheless, they are also controlled by other physical factors that may prevent them moving to new thermally suitable sites. Using presence–absence records in 655 sites widespread throughout nine French river units, we predicted the potential future distribution of 30 common stream fish species facing temperature warming and change in precipitation regime. We also assessed the potential impacts on fish assemblages' structure and diversity. Only cold-water species, whose diversity is very low in French streams, were predicted to experience a strong reduction in the number of suitable sites. In contrast, most cool-water and warm-water fish species were projected to colonize many newly suitable sites. Considering that cold headwater streams are the most numerous on the Earth's surface, our results suggested that headwater species would undergo a deleterious effect of climate change, whereas downstream species would expand their range by migrating to sites located in intermediate streams or upstream. As a result, local species richness was forecasted to increase greatly and high turnover rates indicated future fundamental changes in assemblages' structure. Changes in assemblage composition were also positively related to the intensity of warming. Overall, these results (1) stressed the importance of accounting for both climatic and topographic factors when assessing the future distribution of riverine fish species and (2) may be viewed as a first estimation of climate change impacts on European freshwater fish assemblages.

Keywords: climate change, fish assemblages, GAM, predictive models, species distribution, species turnover, stream fish, upstream–downstream gradient

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Introduction

To evaluate the impacts of climate change on animal and plant species distribution, correlative models relating species distribution to their environment have been developed, progressively improved (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003; Guisan & Thuiller, 2005) and applied to a large diversity of taxa (e.g. Sætersdal *et al.*, 1998; Berry *et al.*, 2002; Peterson *et al.*, 2002; Peterson, 2003; Thuiller *et al.*, 2006a; Levinsky *et al.*, 2007). Nevertheless, such approaches have been

rarely applied to predict the impacts of the ongoing climate change on fish species, although both marine and freshwater fish represent a major food resource for the human population (Millennium Ecosystem Assessment, 2005a,b). Fish distribution could be strongly affected by climate warming, as most fish species have no physiological ability to regulate their body temperature (Wood & McDonald, 1997). Recent studies have shown special concern for ecological and economic impacts on marine fish and fisheries (Perry *et al.*, 2005; Arnason, 2007; Mackenzie *et al.*, 2007). However, freshwater fish could be even more highly vulnerable to broad-scale environmental changes, because their dispersal ability is constrained by the network structure of the drainage basins (Grant *et al.*, 2007). Indeed, fish cannot disperse across terrestrial areas and are

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consequently limited to the river basin they currently live in. Most of the previous studies exploring climate change impacts on freshwater fish have been conducted in North America (Minns & Moore, 1995; Eaton & Sheller, 1996; Magnuson *et al.*, 1997; Jackson & Mandrak, 2002; Mohseni *et al.*, 2003; Chu *et al.*, 2005; Sharma *et al.*, 2007) and frequently concerned only cold water species (salmonids) (Keleher & Rahel, 1996; Nakano *et al.*, 1996; Rahel *et al.*, 1996) or recreational species such as smallmouth bass (*Micropterus dolomieu*) (Peterson & Kwak, 1999). Moreover, most of these studies were focused on determining the thermal habitat suitable under climate change scenarios, assuming that species would be able to survive in that habitat or to colonize it without giving consideration to the other local factors that could influence fish species distribution (Eaton & Sheller, 1996; Rahel *et al.*, 1996; Mohseni *et al.*, 2003; Sharma *et al.*, 2007). Indeed, although climate largely influences fish species distribution (e.g. Minns & Moore, 1995; Buisson *et al.*, 2008), it is well known that many other abiotic factors as well as biotic interactions are also determinant (reviewed in Matthews, 1998). The geographical position along the upstream–downstream gradient is particularly important for most fish species distribution (e.g. Buisson *et al.*, 2008).

To our knowledge, compared with other organisms such as plants or birds, there is a lack of studies using species distribution models to assess the impacts of the most recent climate change scenarios on both common and recreational stream fish species. In this context, we used species distribution models to predict the potential impacts of climate change on stream fish species distribution within French territorial boundaries. At this spatial level, Pearson & Dawson (2003) proposed to consider both climate and topography to predict the impacts of climate change. We thus included nonclimatic factors such as the position along the upstream–downstream gradient in order to improve the accuracy of the predicted future distributions and determine more realistic future assemblages. In addition, because freshwater fish are spatially constrained by the dendritic nature of river ecosystems, geographic and homogenous grids commonly used for other taxa (e.g. Thuiller *et al.*, 2005a; Araujo *et al.*, 2006) were not appropriate. Therefore, fish records at the scale of local stream reaches were needed. Such variation in the spatial cover could thus result in a differential response to climate change of stream fish and terrestrial organisms.

The main objectives of this study were (1) to predict the potential changes in fish species distribution in France under different climate change scenarios, then (2) to relate these potential changes to ecological niche parameters in order to highlight species sensitivity to

climatic modifications, and finally (3) to assess the potential impacts of climate change on fish assemblages' structure and diversity.

Materials and methods

Materials

Sites selection. Data were extracted from the Office National de l'Eau et des Milieux Aquatiques (ONEMA) database. This national fisheries organization is in charge of the protection and conservation of freshwater ecosystems in France and monitors fish assemblages in French rivers yearly. Among the surveyed sites, we selected 655 reference (i.e. least impacted by anthropic perturbations) sites to avoid biased results due to nonclimatic disturbances. These sites were widespread throughout nine large river units (Fig. 1).

Species datasets. A standardized electrofishing protocol conducted during low-flow periods (May–October) was used for each fish sampling. Most sites were sampled by two-pass removal electrofishing. Two different sampling methods were used depending on the river depth and width: smaller rivers were sampled by wading and larger ones by boat. Caught fish were identified to the species level, and then released back

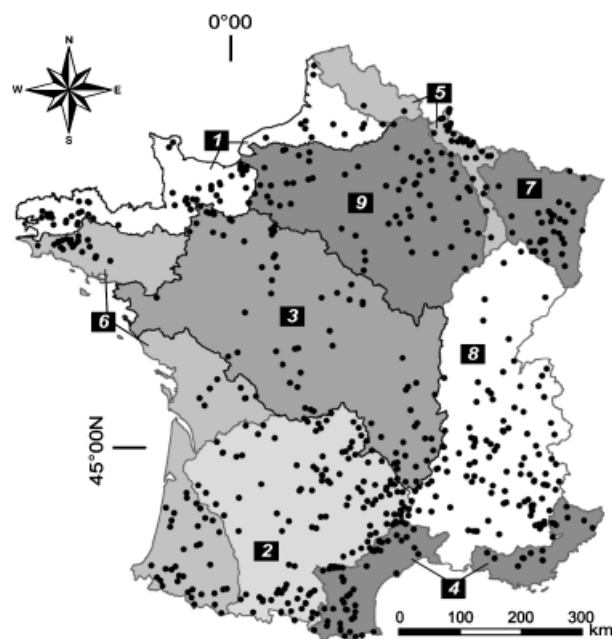


Fig. 1 Spatial distribution of fish sampling sites in nine river units in France. River unit codes: 1, English Channel; 2, Garonne; 3, Loire; 4, Mediterranean sea; 5, Meuse; 6, North Atlantic Ocean; 7, Rhine; 8, Rhone; 9, Seine.

into the river. To reduce errors associated with small sample sizes (Stockwell & Peterson, 2002), only data of fish species that occurred in more than 25 sites were retained. This resulted in a dataset of 30 fish species belonging to 11 families (Table 2).

Species presence–absence data were used to describe fish assemblages.

Climate data. The CRU CL 2.0 (Climatic Research Unit Climatology 2.0 version) dataset (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 (Table 1): mean annual precipitation (PAN), mean annual air temperature (TAN), mean air temperature of the coldest month (MTC) and mean air temperature of the warmest month (MTW). Indeed, the precipitations partly determine the amount of flowing waters and act consequently on the microhabitat structure available for fish species. In addition, fish species are ectothermic animals and tolerate a range of temperatures in which they are able to achieve breeding and development (Mills & Mann, 1985; Mann, 1991). Larvae and juvenile survival is also dependent on maximum temperatures. Air temperature was used as a substitute for water temperature, as both are strongly correlated (Caissie, 2006). Climate data for the current period were obtained from the average of the period 1961–1990.

Future climate predictions were calculated and averaged for the time period 2051–2080 (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 emission scenarios from the Special Report on Emission Scenarios of the Intergovernmental Panel on Climate Change (IPCC SRES) were used, A2 and B1 (Nakicenovic & Swart, 2000). The A2 storyline describes a very heterogeneous world preserving local identities and resulting in continuously increasing population. Economic development is primarily regionally oriented and *per capita* economic growth and technological change more fragmented and slower than other storylines. The B1 storyline describes a convergent world with the same global population that peaks in mid-century and declines thereafter, but with rapid change in economic structures with reductions in material intensity and the introduction of clean and resource-efficient technologies.

Values of the studied climatic variables for current and future scenarios were extracted for all the grid cells containing the 655 sites. PAN was log-transformed to correct for normal distribution.

Environmental characteristics. Six environmental descriptors were available at each site (Table 1): 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). They were called 'environmental descriptors' in opposition to the 'climate descriptors'. All the environmental descriptors were log-transformed to check the normality hypothesis.

Both DS and SDB describe the position of sites along the upstream–downstream gradient. A principal component analysis (PCA) was used to eliminate the colinearity between these two variables. The first axis of the PCA was kept as a synthetic variable describing the longitudinal gradient G :

$$G = -3.1 + 0.59 \log DS + 0.38 \log SDB. \quad (1)$$

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:

$$V = \log WID + \log DEP + \log SLO - \log(WID + 2DEP). \quad (2)$$

Methods

Fish species niche separation along environmental and climatic gradients. To identify the main environmental gradients separating fish species niches and structuring fish assemblages, we first used a multivariate approach, the outlying mean index (OMI; Dolédec *et al.*, 2000) analysis. OMI analysis allows to separate species niches and to measure two niche descriptors: niche position (i.e. marginality) and niche breadth (i.e. tolerance). The marginality of species habitat distribution measured the distance between the mean habitat conditions used by a species and the mean habitat conditions across the 655 studied sites. Species tolerance, a variance term, measured the amplitude of the distribution of each species along the sampled environmental gradients. A Monte-Carlo permutation test was used to check the statistical significance of the two niche parameters for each species. We compared the observed marginality and tolerance values with the frequency distribution of 1000 random values obtained with the random permutations of the rows of datasets.

Fish species – environment modelling

Model construction. Predicting the potential impacts of climate change on species distribution has been done by using a large variety of modelling techniques (e.g. Elith *et al.*, 2006; Pearson *et al.*, 2006; Broennimann *et al.*, 2007). Among them, generalized additive models

Table 1 Environmental and climatic variables

River unit	Environment							Climate				
	<i>n</i>	SDB	DS	WID	DEP	SLO	ELE	MTC	MTW	TAN	PAN	
English Channel	65	37 2-4000	8 1-103	4 0.5-35	0.4 0.2-1.9	6.6 0.5-20	65 10-240	3.2 1.7-5.7	17.2 16.3-18	10.4 9.6-11.5	819.6 688.6-1170.8	
Garonne	124	35.5 2-13672	11.1 0.4-284	5.4 2.2-101	0.3 0.1-1.8	10 0.3-130	560 12-1800	1.2 -4.8-5.1	18.2 11.8-21.8	9.5 2.9-13.1	919.7 763.9-1383.1	
Loire	71	75 1-20358	14 1-316	4.1 0.9-120	0.4 0.2-1.1	4.7 0.3-60	220 15-1200	2 -2-4.1	18.1 14.9-19.8	10.1 6.3-11.9	798.8 657.9-1069.4	
Mediterranean	77	25 2-2770	10 1-130	5.3 1-75	0.4 0.1-5	11 0.3-85	350 2-1540	3.3 -4.5-7.2	20.4 11.8-23.6	11.3 2.9-14.9	864.2 639.3-1355.6	
Meuse	42	50 3-4145	9 1-337	5 0.8-40	0.5 0.2-1.9	3.3 0.3-54	186 105-315	0.1 -0.3-1.6	17.9 16.9-18.3	9.2 8.4-9.9	1109.5 719-1221.9	
North Atlantic Ocean	72	100.5 2-1163	16.5 1-186	7.6 1.1-40	0.4 0.2-1.1	3.7 0.2-52	98 10-1520	4.6 -5.1-6.9	20 12-21.7	11.6 2.7-13.8	1043.5 847.3-1455.5	
Rhine	32	63 5-36832	15.5 3-422	6 1-50	0.4 0.1-1	6.6 0.6-60	337 163-638	-1.3 -3.2 to -0.1	17.7 15.2-19.6	8.6 6.4-10.1	855.4 633.4-1011.6	
Rhone	111	31 2-6960	10 1-420	6 0.8-80	0.3 0.1-1.5	19 0.2-180	659 40-1945	-0.3 -7.9-4.5	17.8 9.1-23.3	8.6 0.3-13.8	975.8 690.2-1442.2	
Seine	61	400 5-30800	26 2-395	10 1-150	0.7 0.2-4.5	1.5 0.1-11	89 22-340	1.3 -0.3-2.5	18.5 17.2-19.7	10 9.2-11.1	689.3 614.9-966.6	

Given are the median, minimum and maximum values for the environmental and climatic variables for each river unit (*n* is the number of sites within each river unit). SDB, surface of drainage basin above the site (km²); DS, distance from the source (km); WID, stream width (m); DEP, stream depth (m); SLO, slope (%); ELE, elevation (m); MTC, mean air temperature of the coldest month (°C); MTW, mean air temperature of the warmest month (°C); TAN, mean annual air temperature (°C); PAN, mean annual precipitation (mm).

(GAM; Hastie & Tibshirani, 1990) allow the combination of both linear and complex additive responses within the same model in a simple way and have greater efficiency than other approaches (e.g. linear approaches) (e.g. Araujo *et al.*, 2005). Nevertheless, they assume that the independent variables are uncorrelated (Graham, 2003). The three environmental variables were not highly correlated among themselves, but remained correlated with the climatic variables, especially with TAN. To avoid problems in regression fitting caused by the strong correlations between TAN and *G*, *V* and *ELE*, we adjusted these variables for TAN by fitting GAMs with four degrees of freedom (Leathwick *et al.*, 2006; Thuiller *et al.*, 2006c). We then used the residuals of each of the GAMs as individual predictors (called *resG*, *resV* and *resELE*). These residuals indicated the deviation from the average *G*, *V* and *ELE* expected at its TAN level. Thus, we eliminated the effect of TAN in each of the environmental descriptors and supposed that the residuals of *G*, *V* and *ELE* were independent of thermal variables. After this correction, all the seven predictors were poorly correlated except the three thermal variables.

Species-specific GAMs were then built relating the current fish species occurrence as the dependent variable to the seven environmental and climatic variables as independent variables. The geographical position of the 655 sites in one of the nine river units (BASIN) was also included into the models as a dummy variable. It appeared to be a good synthetic descriptor of regional environmental constraints not explained by the seven studied variables (e.g. geological background, geographical barriers, past glaciations). Moreover, when integrated into the models, the dispersal of species outside their initial current basins may be limited. A binomial distribution of errors was assumed and the probability of species occurrence was related to the set of environmental and climatic variables via a logistic link function. GAMs were performed using the 'gam' library in the R software (R Development Core Team, 2007).

Model evaluation. To maintain an equal repartition of each of the river units in the calibration and validation dataset, we randomly selected 70% of the sites within each river unit to calibrate the GAMs, leading to a set of 458 sites. A stepwise selection procedure was performed using the Akaike Information Criterion (AIC) to select the most parsimonious model (Akaike, 1974).

The explanatory power of the models was evaluated by calculating the percentage of deviance explained by each of the species models. The current predictive power was evaluated on the remaining 30% of the initial dataset (197 sites) using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot

(Fielding & Bell, 1997; Pearce & Ferrier, 2000). The AUC ranges between 0.5 for models that discriminate no better than random sorting would, and 1 for models that discriminate perfectly (Swets, 1988). We used AUC as a performance measure, because it does not require transformation of the predicted probability of occurrence in binary data. It is consequently independent of an artificial threshold value. In addition, it is not biased by species prevalence unlike the Kappa index (Fielding & Bell, 1997).

The current predicted probability of occurrence of each species was calculated for the 655 sites and converted into presence-absence using a threshold maximizing the sum of two measures: sensitivity, which measures the percentage of presence correctly predicted, and specificity, which measures the percentage of absence correctly predicted (Fielding & Bell, 1997). Below the threshold value, a fish species was considered as absent and above as present.

Model projections. Models calibrated under current conditions were then used to generate projections of future potential distributions for 2080 under both scenarios A2 and B1. Only climatic variables were changed because the other environmental factors were expected to be independent from climate. The future probabilities of occurrence were transformed into presence-absence values by using the same threshold value as for current predictions.

Ensemble forecasting. All the procedure, from the separation of the calibration and validation datasets to the predictions of future distributions, was repeated 100 times in order to ensure the robustness of the results (Broennimann *et al.*, 2007). Therefore, a mean value and its standard deviation were calculated for AUC, percentage of explained deviance, threshold, as well as current and future predictions for each of the 655 sites.

Assessment of the potential impacts of climate change

Fish species sensitivity to climate change. Our first goal was to evaluate the impacts of climate change on stream fish species distribution. We therefore compared the current distribution with the potential future distribution for each species. We calculated the change in probability of occurrence between the current situation and the 2080 scenarios for all 655 sites. A negative value indicated that the site would be less suitable than at present and a positive value more suitable. The latter could thus be considered as a potential favourable habitat for species in the future. This comparison was done for scenarios A2 and B1. We tested whether the A2 projected changes differed from the B1 projected changes with a paired-difference permutation test. The sign of the 655 paired-differences between the projected future probabilities A2 and B1 was permuted

1000 times. The observed statistics was then compared with the frequency distribution of these 1000 permuted values.

We also grouped together species with common responses to climate change by using a hierarchical clustering method. Euclidean distances between species responses were calculated and the Ward's minimum variance method was used to determine fish species clusters.

Then, from the probabilities of occurrence transformed into 0–1, we calculated for each species the percentage of sites where the species was currently absent but predicted to be present in the future (sites gained) and the percentage of sites where the species was currently present but predicted to be absent in the future (sites lost). Lastly, the difference between these two measures was calculated and defined as the change in prevalence, namely the change in the percentage of sites occupied by the species. We also tested whether the A2 results were different from those of B1 using the same paired-difference permutation test. We ran this test after calculating 1000 random values of percentages of sites gained, sites lost and change in prevalence obtained from a random sample of 500 sites from the dataset.

The influence of ecological niche parameters on species sensitivity to climate change was assessed by fitting linear relationships between the niche parameters and changes in prevalence.

Impacts of climate change on fish assemblage structure. Predicted current and future local species richness was calculated by summing the predicted current and future present species, respectively, for each of the 655 sites. We also calculated the number of SG of species predicted to newly arrive (species gain, SG) and the num-

ber of species predicted to no longer be present in the future (species loss, SL) in each site. We, thus estimated the percentage of species turnover as

$$\text{turnover} = 100 \times \frac{\text{SG} + \text{SL}}{\text{SR} + \text{SG}}, \quad (3)$$

where SR is the current species richness (Peterson *et al.*, 2002; Broennimann *et al.*, 2006). A turnover value of 0 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. The difference in turnovers predicted for scenarios B1 and A2 was tested by the same paired-difference permutation test as previously.

We then tested the hypothesis that turnover would increase with the intensity of climate change. For each climatic scenario, a GLM was used to relate the percentage of species turnover to the climatic anomalies for the 655 sites. The differences between the current and the future climatic conditions were named ΔPAN , ΔTAN , ΔMTC and ΔMTW . A stepwise selection procedure was used to select the most explanatory variables within each model (AIC; Akaike, 1974).

Results

Niche species separation along environmental and climatic gradients

The first two axes of the OMI analysis accounted for 97% of the explained variability in species niche separation. The first axis (92.6% of the variability) distinguished the well-known upstream–downstream gradient characterizing river watersheds (Fig. 2a). The most upstream sites were defined by high altitude, steep slopes

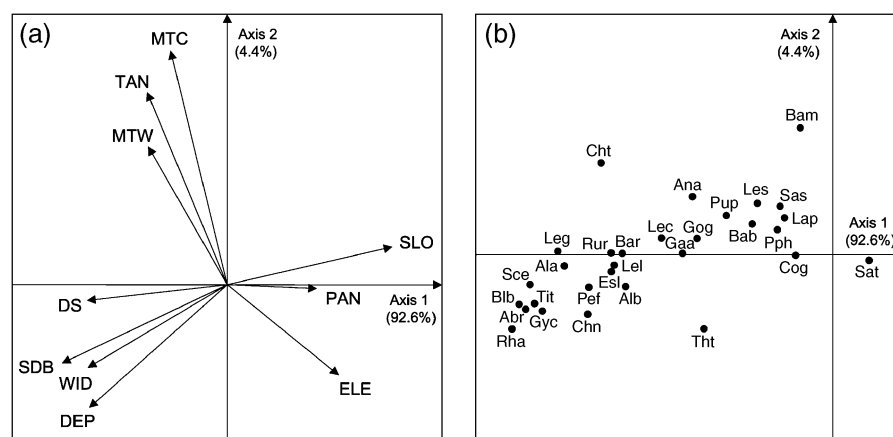


Fig. 2 Results of the outlying mean index (OMI) analysis used to investigate fish assemblages. (a) Canonical weights of environmental and climatic variables. (b) Distribution of species on the first two axes of the OMI analysis (codes as in Tables 1 and 2).

Table 2 Niche parameters for the 30 fish species

Code	Species	Family	OMI	Tol
Abr	<i>Abramis brama</i>	Cyprinidae	69.1	12.4
Ala	<i>Alburnus alburnus</i>	Cyprinidae	60.1	13.8
Alb	<i>Alburnoides bipunctatus</i>	Cyprinidae	53.8	12.8
Ana	<i>Anguilla anguilla</i>	Anguillidae	29.7	19.0
Bab	<i>Barbatula barbatula</i>	Balitoridae	13.2	31.5
Bam	<i>Barbus meridionalis</i>	Cyprinidae	42.8	15.9
Bar	<i>Barbus barbus</i>	Cyprinidae	46.2	20.2
Blb	<i>Blicca bjoerkna</i>	Cyprinidae	68.4	12.9
Chn	<i>Chondrostoma nasus</i>	Cyprinidae	61.3	12.5
Cht	<i>Chondrostoma toxostoma</i>	Cyprinidae	64.4	11.9
Cog	<i>Cottus gobio</i>	Cottidae	3.9	28.7
Esl	<i>Esox lucius</i>	Esocidae	48.7	19.6
Gaa	<i>Gasterosteus aculeatus</i>	Gasterosteidae	35.8	13.0
Gog	<i>Gobio gobio</i>	Cyprinidae	26.0	30.2
Gyc	<i>Gymnocephalus cernuus</i>	Percidae	68.6	10.2
Lap	<i>Lampetra planeri</i>	Petromyzontidae	10.6	20.6
Lec	<i>Leuciscus cephalus</i>	Cyprinidae	36.3	23.4
Leg	<i>Lepomis gibbosus</i>	Centrarchidae	53.3	21.0
Lel	<i>Leuciscus leuciscus</i>	Cyprinidae	51.5	15.2
Les	<i>Leuciscus souffia</i>	Cyprinidae	23.5	29.1
Pef	<i>Perca fluviatilis</i>	Percidae	53.6	19.9
Pph	<i>Phoxinus phoxinus</i>	Cyprinidae	7.0	36.6
Pup	<i>Pungitius pungitius</i>	Gasterosteidae	42.7	6.9
Rha	<i>Rhodeus amarus</i>	Cyprinidae	71.3	10.2
Rur	<i>Rutilus rutilus</i>	Cyprinidae	50.3	17.3
Sas	<i>Salmo salar</i>	Salmonidae	28.4	15.9
Sat	<i>Salmo trutta fario</i>	Salmonidae	2.4	40.3
Sce	<i>Scardinius erythrophthalmus</i>	Cyprinidae	60.9	18.1
Tht	<i>Thymallus thymallus</i>	Thymallidae	38.0	15.9
Tit	<i>Tinca tinca</i>	Cyprinidae	64.9	13.7

The outlying mean index (OMI) and the tolerance index (Tol) are given as percentages of the total variability. Statistical significance of each niche parameter was tested by a Monte-Carlo permutation test; significant niche parameters ($P < 0.05$) are in bold.

and a large amount of rainfall, whereas downstream sites were located in large and deep rivers far from the source. Niche fish species were distributed along this longitudinal gradient, *Salmo trutta fario* (Sat) occupying the most upstream sites and a group of species with the highest marginality values on the other extremity of the gradient (e.g. Rha, Abr, Blb, Gyc – Fig. 2b, Table 2). The second axis explained 4.4% of the variability in marginality and was related to the three thermal variables. Three species had their ecological niche mainly influenced by this thermal gradient (Fig. 2b): *Barbus meridionalis* (Bam) whose distribution was limited to upstream but relatively warm sites, *Thymallus thymallus* (Tht) which inhabited intermediate streams but with cold waters and *Chondrostoma toxostoma* (Cht) which preferred warmer downstream sites than the other downstream species.

Niche position and niche breadth were highly variable between species (Table 2). The most uniformly distributed species were Sat, *Cottus gobio* (Cog) and *Phoxinus phoxinus* (Pph). *Rhodeus amarus* (Rha) was the species whose niche position was the most distant from the 'mean habitat' calculated from the environmental conditions of the 655 sites. *Pungitius pungitius* (Pup) had a low tolerance, indicating that it was a highly specialized species.

Modelling of current species distribution

The explanatory power of the 30 species models was relatively good, because GAMs globally explained 51% of the variability in species probability of occurrence (Table 3). Percentage of explained deviance ranged from 27% for Pph to 65% for Bam and was higher than 50% for 19 species.

Predictive performances were considered as excellent because AUC values for the evaluation dataset equalled 0.91, on average, and were higher than 0.8 for all 30 species (Table 3).

For both explained deviance and AUC, standard deviations calculated from the 100 repetitions were relatively low (Table 3) strengthening the robustness of the predictions.

Impacts of climate change on potential future fish species distribution

For both scenarios of climate change, all 30 fish species were positively or negatively affected by climate (Fig. 3, Table 4). For the most pessimistic scenario A2, changes in predicted probability of occurrence ranged on average from -34% for Sat to 47.7% for *Barbus barbus* (Bar). These changes were slightly less important for the B1 scenario, but they were significantly different from changes predicted under the A2 scenario for all species except *Gymnocephalus cernuus* (Gyc) which was equally affected by both scenarios.

Four groups of responses to climate change were identified both in scenarios B1 and A2 (Fig. 3). The first fish cluster grouped three species [Sat, Cog and *Lampetra planeri* (Lap)] that responded negatively. These species were also predicted to lose more previously suitable sites than to gain newly suitable habitats, presenting consequently a negative change in prevalence (Table 4, Fig. 4). In some sites, Sat could decrease its probability of occurrence by 77% resulting in a loss of 55% of the currently suitable sites under the most pessimistic scenario A2. The second fish cluster consisted of 12 species that had a median predicted change close to 0 but with some sites becoming less suitable and some others more suitable (Fig. 3 – for the B1

Table 3 Current prevalence of the fish species across the 655 sites, and explanatory and predictive performances of the generalized additive models

Code	Prevalence	Explained deviance ± SD	AUC ± SD
Abr	0.05	0.55 ± 0.04	0.95 ± 0.03
Ala	0.14	0.61 ± 0.03	0.95 ± 0.02
Alb	0.09	0.59 ± 0.03	0.94 ± 0.02
Ana	0.33	0.55 ± 0.03	0.93 ± 0.01
Bab	0.50	0.40 ± 0.02	0.87 ± 0.02
Bam	0.08	0.65 ± 0.04	0.96 ± 0.02
Bar	0.19	0.50 ± 0.03	0.91 ± 0.02
Blb	0.05	0.56 ± 0.06	0.91 ± 0.07
Chn	0.06	0.57 ± 0.05	0.93 ± 0.05
Cht	0.04	0.52 ± 0.06	0.91 ± 0.06
Cog	0.52	0.35 ± 0.02	0.84 ± 0.02
Esl	0.14	0.51 ± 0.03	0.91 ± 0.03
Gaa	0.06	0.36 ± 0.04	0.85 ± 0.04
Gog	0.40	0.47 ± 0.03	0.90 ± 0.02
Gyc	0.05	0.58 ± 0.06	0.91 ± 0.06
Lap	0.25	0.30 ± 0.02	0.81 ± 0.03
Lec	0.33	0.57 ± 0.03	0.93 ± 0.02
Leg	0.07	0.58 ± 0.04	0.89 ± 0.05
Lel	0.19	0.48 ± 0.03	0.91 ± 0.02
Les	0.06	0.62 ± 0.03	0.96 ± 0.01
Pef	0.14	0.52 ± 0.03	0.93 ± 0.02
Pph	0.57	0.27 ± 0.02	0.82 ± 0.03
Pup	0.05	0.47 ± 0.05	0.89 ± 0.05
Rha	0.06	0.64 ± 0.06	0.94 ± 0.04
Rur	0.22	0.62 ± 0.03	0.95 ± 0.01
Sas	0.07	0.59 ± 0.04	0.93 ± 0.04
Sat	0.86	0.54 ± 0.03	0.92 ± 0.02
Sce	0.05	0.41 ± 0.05	0.89 ± 0.06
Tht	0.04	0.38 ± 0.07	0.83 ± 0.06
Tit	0.06	0.55 ± 0.06	0.92 ± 0.04

The percentage of explained deviance and AUC are calculated for each 100 repetitions from the calibration and validation dataset, respectively. Given are the mean values and standard deviations obtained from the 100 repetitions. Species codes as in Table 2.

scenario, Rha was included in this group, whereas Bam was excluded). This group was also characterized by a change in prevalence, which was slightly negative or positive (except for Bam), with site losses often compensated by newly gained sites (Fig. 4). For this group, the mean change in prevalence was $9.3 \pm 13.7\%$ and $4.2 \pm 7.7\%$ for the A2 and B1 scenarios, respectively. The third fish cluster grouped species that would experience an increase in their probability of occurrence in almost all the sites where they were already present (Fig. 3 – for the B1 scenario, Bam was included in this group, whereas Rha was excluded). Change in prevalence for this group was 36% and 28.4% on average for the A2 and B1 scenarios, respectively. Finally, *Gobio gobio* (Gog), *Leuciscus cephalus* (Lec) and Bar formed the last fish

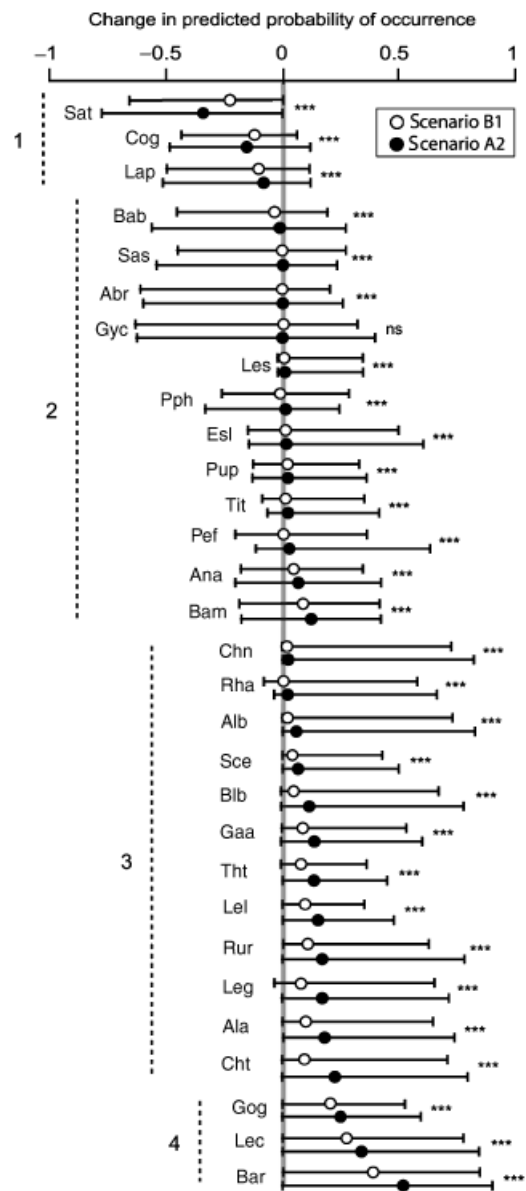


Fig. 3 Changes in the probability of occurrence for each of the 30 fish species for scenarios B1 (white circles) and A2 (black dots). Change is expressed as the difference between the current and future predictions. The medians of the changes in probability over the 655 sites are shown (dots), as well as the minimum and maximum changes predicted for each species. The statistical significance of the differences between scenarios B1 and A2 was evaluated through a paired-difference permutation test (** $P < 0.01$; ns, nonsignificant). Fish species were grouped according to the results of a hierarchical clustering based on general dissimilarity matrices for A2 scenario (groups 1–4). Fish clusters were identical for the B1 scenario except for *Barbus meridionalis* (Bam) and *Rhodeus amarus* (Rha) which were inverted (see Table 2 for species codes).

Table 4 Number of occurrences predicted for current, B1 and A2 scenarios, percentages of gained and lost sites and difference between the predicted future and current percentages of sites occupied by species for both scenarios B1 and A2

Code	No. of occurrences			Sites gained (%)			Sites lost (%)			Δ prevalence (%)		
	Current	B1	A2	B1	A2	<i>P</i>	B1	A2	<i>P</i>	B1	A2	<i>P</i>
Abr	108	55	69	1.4	3.5	***	9.5	9.5	ns	-8.1	-6.0	***
Ala	159	327	407	25.6	37.9	***	0	0	ns	25.6	37.9	***
Alb	142	289	320	22.4	27.2	***	0	0	ns	22.4	27.2	***
Ana	263	313	338	7.9	11.6	***	0.3	0.2	***	7.6	11.5	***
Bab	318	286	308	2.3	4.0	***	7.2	5.5	***	-4.9	-1.5	***
Bam	121	374	402	38.8	43.1	***	0.2	0.2	ns	38.6	42.9	***
Bar	197	499	547	46.1	53.4	***	0	0	ns	46.1	53.4	***
Blb	102	288	390	28.4	44.0	***	0	0	ns	28.4	44.0	***
Chn	98	250	281	23.2	27.9	***	0	0	ns	23.2	27.9	***
Cht	79	339	453	39.7	57.1	***	0	0	ns	39.7	57.1	***
Cog	279	204	167	0.2	0.2	ns	11.6	17.3	***	-11.5	-17.1	***
Esl	186	239	253	8.4	10.2	***	0.3	0	***	8.1	10.2	***
Gaa	162	352	381	29.0	33.4	***	0	0	ns	29.0	33.4	***
Gog	266	436	468	26.0	30.8	***	0	0	ns	26.0	30.8	***
Gyc	99	92	95	4.7	5.2	***	5.8	5.8	**	-1.1	-0.6	***
Lap	309	100	127	0	0	ns	31.9	27.8	***	-31.9	-27.8	***
Lec	253	489	522	36.0	41.1	***	0	0	ns	36.0	41.1	***
Leg	99	319	432	33.7	50.8	***	0.2	0	***	33.6	50.8	***
Lel	201	322	369	18.5	25.6	***	0	0	ns	18.5	25.6	***
Les	110	128	142	2.7	4.9	***	0	0	ns	2.7	4.9	***
Pef	155	184	224	5.8	10.7	***	1.4	0.2	***	4.4	10.5	***
Pph	357	366	386	6.3	7.0	***	4.9	2.6	***	1.4	4.4	***
Pup	100	211	232	17.3	20.3	***	0.3	0.2	***	16.9	20.2	***
Rha	86	158	219	11.0	20.3	***	0	0	ns	11.0	20.3	***
Rur	198	329	391	20.0	29.5	***	0	0	ns	20.0	29.5	***
Sas	98	87	66	1.2	0	***	2.9	4.9	***	-1.7	-4.9	***
Sat	497	226	137	0	0	ns	41.4	55.0	***	-41.4	-55.0	***
Sce	114	272	343	24.1	35.0	***	0	0	ns	24.1	35.0	***
Tht	159	403	441	37.3	43.1	***	0	0	ns	37.3	43.1	***
Tit	136	231	269	14.5	20.3	***	0	0	ns	14.5	20.3	***

Differences in percentages of sites gained, sites lost and number of occurrences between scenarios B1 and A2 were tested by a paired-difference permutation test.

*** $P < 0.01$, ** $P < 0.05$; ns, nonsignificant. Species codes as in Table 2.

cluster which responded only positively to climate change. These three species would not experience any site losses in 2080 and would be able to colonize many sites, consequently increasing their mean prevalence (B1, 36%; A2, 41.8%).

Potential influence of ecological niche parameters on fish species responses to climate change

The relationships between the change in prevalence and the ecological niche parameters, namely niche position (OMI) and niche breadth (tolerance), were significant ($P < 0.05$) for both scenarios A2 and B1, although R^2 values were quite low (OMI: 0.24 and 0.3, respectively; Tol: 0.17 and 0.2, respectively – Fig. 5). Change in prevalence was positively related to niche position,

whereas its relationship was negative with niche breadth (Fig. 5).

Potential impacts of climate change on fish assemblage structure

Local species richness was predicted to experience a strong increase under climate change. Mean local species richness would increase from the current 8.3 species per site to 14 and 12.5 species in 2080 under the A2 and B1 scenarios, respectively. This mean increase was greatly variable according to the river unit (e.g. English Channel: +1.5 species, Rhine: +10.4 species). Only 37 sites had a reduction in species richness (maximum reduction of three species) and 20.6% of the sites gained more than 10 species under the A2 scenario.

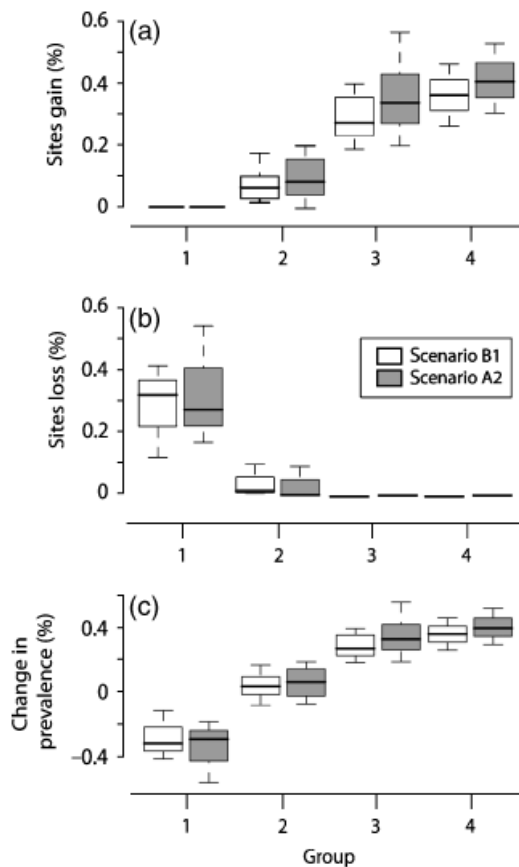


Fig. 4 Box plots representing the percentages of (a) sites gained, (b) sites lost and (c) the change in prevalence for B1 (white) and A2 (grey) scenarios for the four groups of species defined by the hierarchical clustering method (see Fig. 3).

The number of species lost was very low (between one and six) contrary to the number of species gained that was much more important, being on average 5.3 species for the B1 scenario and seven species for the A2 scenario (Table 5). Lost species mainly belonged to fish cluster 1 (see Fig. 3).

Across the 655 sites, turnover equalled 52.7% for the B1 scenario and 59.3% for the A2 scenario (Table 5). The sites of five river units (Garonne, Loire, Meuse, Rhine and Rhone) were predicted to have a high turnover rate, exceeding a median value of 60% in the B1 scenario and 70% in the A2 scenario. Very few sites would have exactly the same assemblage as today (24 sites with a turnover equal to 0 under the B1 scenario), and they would be located in four river units: English Channel, Mediterranean, North Atlantic Ocean and Seine. Nevertheless, even within one river unit, there was a strong variability in the results, and the range of possible turnovers was very large (Table 5).

The difference Δ PAN did not influence the turnover in either scenario (Table 6). Although the selected

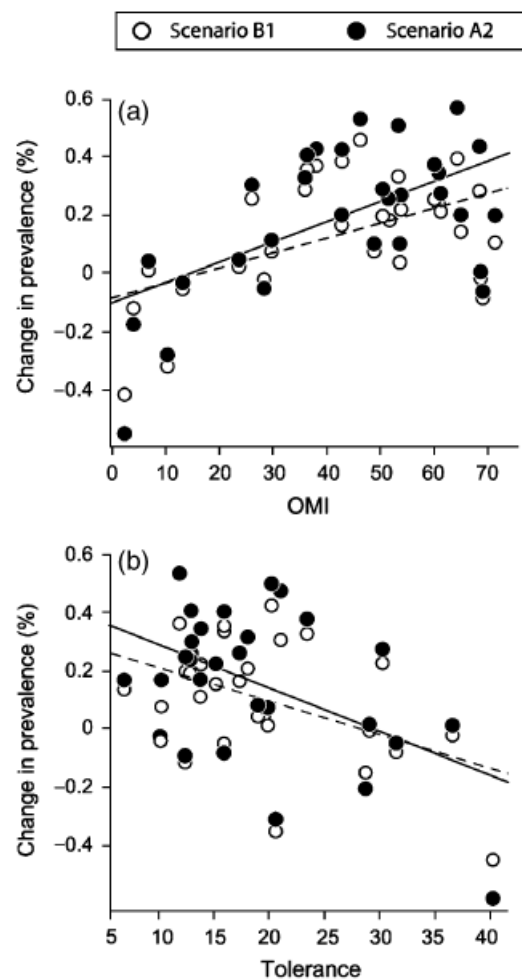


Fig. 5 Relationships between the changes in prevalence and (a) niche position (OMI), and (b) niche breadth (tolerance), for the B1 (white circles and dashed line) and A2 (black dots and line) scenarios. The linear relationship between OMI and change in prevalence was statistically significant for both scenarios ($P < 0.01$, $R^2 = 0.24$ and 0.3 for B1 and A2, respectively). The linear relationship between tolerance and change in prevalence was also statistically significant ($P < 0.05$, $R^2 = 0.17$ and 0.2 for B1 and A2, respectively).

thermal anomalies differed between both scenarios (Δ MTC and Δ MTW for A2, Δ TAN for B1), all the selected variables showed a positive relationship with species turnover.

Discussion

Fish species responses to climate change

Like many other taxa, stream fish are projected to be severely affected by climate change. Our results suggest that most of the French riverine fish species would have to face climate change by restricting their range or by

Table 5 Projected number of species lost and gained, and turnovers per site in each river unit under climate change scenarios

River unit	No. of species lost		No. of species gained		Turnover (%)	
	B1	A2	B1	A2	B1	A2
English Channel	2 (0–6)	2 (0–6)	2 (0–10)	3 (0–12)	42.9 (0–87.5)	50 (0–88.9)
Garonne	1 (0–4)	0 (0–4)	5.5 (1–12)	7.5 (1–15)	76.9 (13.6–100)	86.2 (13.6–100)
Loire	3 (0–5)	3 (0–5)	8 (1–14)	10 (2–16)	68.4 (16–100)	75 (15.4–94.4)
Mediterranean	0 (0–2)	0 (0–2)	3 (0–8)	5 (0–10)	44.4 (0–87.5)	54.5 (0–90.9)
Meuse	1 (0–2)	1 (0–2)	7.5 (1–17)	9.5 (1–19)	71.4 (4.2–84.2)	76.1 (4.2–91.7)
North Atlantic Ocean	1 (0–4)	1 (0–4)	4 (0–9)	6 (0–12)	37.8 (0–100)	42.1 (0–100)
Rhine	1 (0–2)	1 (0–2)	9 (1–18)	11.5 (1–20)	60.4 (7.7–84.2)	73.9 (7.7–85.4)
Rhone	0 (0–3)	1 (0–3)	7 (0–15)	9 (0–18)	68.4 (0–100)	80 (0–100)
Seine	1 (0–4)	2 (0–4)	3 (0–14)	5 (1–15)	24 (4–75)	28 (4–81.8)

Given are the median values (minimum and maximum values in parentheses). Differences in turnovers calculated for B1 and A2 scenarios were statistically significant ($P < 0.05$) for all river units.

Table 6 Results of the stepwise GLM relating species turnover and climatic anomalies Δ TAN, Δ PAN, Δ MTC, Δ MTW for scenarios B1 and A2

Scenario	B1	A2
Δ TAN	<0.001	ns
Δ PAN	ns	ns
Δ MTC	ns	<0.001
Δ MTW	ns	<0.001
Explained deviance (%)	21.2	24.2

Given are P -values of each variable (ns, nonsignificant) and the percentage of explained deviance by the GLM, retaining only statistically significant variables.

colonizing new climatically suitable habitats. Responses to climate change were idiosyncratic (Peterson *et al.*, 2002; Peterson, 2003; Broennimann *et al.*, 2006), but some of them were similar enough to be grouped together. These groups, although identified irrespective of fish thermal tolerances, corresponded reasonably well to the known thermal guilds (Magnuson *et al.*, 1979). Cold-water species (i.e. *S. trutta fario*, *C. gobio*, *Barbatula barbatula* and *L. planeri*) would suffer from the warming and reduce their distributional area. Their future distribution would be restricted to the most upstream sites. Most cool- and warm-water species would tend to expand their range by colonizing new suitable sites in intermediate streams or upstream if the physical conditions (hydraulic conditions, elevation) were to suit them. However, some warm-water species were predicted to respond to climate change in a direction opposite to that expected on the basis of known physiological constraints (e.g. *Abramis brama*, *G. cerneuus*). This may be due to the inclusion in the models of nonclimatic factors that may have restricted the

amount of suitable sites for these species. Overall, our results were consistent with those obtained in previous studies conducted in North America, which predicted a decrease in salmonids distribution and more contrasted results for cool- and warm-water species (Eaton & Sheller, 1996; Rahel *et al.*, 1996; Mohseni *et al.*, 2003; Chu *et al.*, 2005; Sharma *et al.*, 2007).

Our results also confirmed that the impacts of climate change would be different according to the future climatic scenario, as predicted changes in prevalence or in probability of occurrence were significantly different between both scenarios for most species. Considering that we have chosen one moderate (B1) and one pessimistic (A2) climatic scenario, we assume that the real future climate would result in an in-between situation. The magnitude of future changes is therefore predicted to be within the range of values obtained here (Thuiller *et al.*, 2005b).

In the OMI analysis, we found that the least marginal species with the broadest niche were cold-water species (Sat, Cog, Pph, Lap), whereas marginal and specialized species were cool- and warm-water species (e.g. Blb, Gyc, Sce, Tit). Considering the consistent responses to climate change within each thermal guild, the positive relationship between OMI and change in prevalence and the negative relationship between tolerance and change in prevalence found in our results were not surprising. Nonetheless, they contrasted with numerous studies dealing with other flora and fauna, where species having the narrowest niche were found to be the most affected by climate change in terms of habitat loss (Swihart *et al.*, 2003; Thuiller *et al.*, 2005a; Broennimann *et al.*, 2006; Menendez *et al.*, 2006; Wilson *et al.*, 2007). Such a difference between our results and those found in previous studies can be explained by several factors. First, fish live in hydrographic networks that are orga-

nized according to a dendritic structure where the number of small streams is much more important than of large channels. Headwater streams actually compose over two-thirds of total stream length in typical river drainage systems (Horton, 1945; Leopold *et al.*, 1964; Freeman *et al.*, 2007). In our dataset, headwater streams were also in great number. The 'mean habitat' defined in the OMI analysis was thus rather typical of small, cold headwater streams where dominant species are cold-water fish such as *S. trutta fario* or *C. gobio*. In addition, as headwater streams are known to be the coldest and the most dependent on the amount of precipitation (snow or rainfall), they would be the most affected by climate change. Therefore, in stream ecosystems, species classified as 'generalists' because occurring in common habitats are projected to suffer from range contractions and local extinctions. On the contrary, downstream species classified as 'specialists' would expand their range and colonize many newly suitable sites.

Compared with other taxa for which the impacts of climate change could be very detrimental (Thomas *et al.*, 2004, 2006; Jetz *et al.*, 2007; Levinsky *et al.*, 2007), the global assessment for French stream fish species was rather positive. For example, nine species would increase their probability of occurrence in all the sites and 16 species would not experience any site loss under either B1 scenario or A2 scenario. On the contrary, these species would find many potential suitable habitats under climate change by moving to streams where the current temperature is too cold. Some other studies demonstrated that the sole effect of climate change could lead to positive effects on biological traits (Chamaille-Jammes *et al.*, 2006), availability of reproductive habitats (Jensen *et al.*, 2008) or range expansions (Araujo *et al.*, 2006). The global positive impact of climate change on stream fish distribution may be caused by the fact that, in temperate stream systems, there are more cool- and warm-water species than cold-water species (e.g. Magnuson *et al.*, 1979; Eaton & Sheller, 1996: 10 cold-water species out of 57). French fish assemblages contain few cold-water species (e.g. *S. trutta fario*, *C. gobio*) that are predicted to be negatively affected by climate change. All other species living in intermediate streams or downstream have a large range of thermal tolerance, and even under the most pessimistic scenario, maximum thermal tolerance would not be reached.

Changes in fish assemblages' diversity and structure

The large increase in fish species richness in most sites was very likely the result of the large number of positive individuals responses of fish species to climate change. This increase in species richness was also

observed (e.g. Grabherr *et al.*, 1994; Menendez *et al.*, 2006) or projected for the future (e.g. Sætersdal *et al.*, 1998; Brown *et al.*, 2007) for other organisms. However, previous studies have shown contrasted results, as species richness has also been predicted to be strongly reduced or unchanged depending on latitude, altitude, geographical area or organisms (Andrew & Hughes, 2005; Broennimann *et al.*, 2006; Levinsky *et al.*, 2007; Wilson *et al.*, 2007). For freshwater fish, our results are overall concordant with those found by Minns & Moore (1995) in Canada, where a global average increase in species richness of 31.8 species for the studied tertiary watersheds was predicted. Interestingly, the increase in fish species richness found here was also concordant with the result obtained in a recent study aiming at evaluating the impact of recent past climate warming on global abundance, structure and diversity of fish communities in large French rivers (Daufresne & Boët, 2007). The authors reported a significant increase in specific richness and proportion of warm-water species over the last 25 years, which experienced a gradual increase in upstream water temperature. Thus, their paper states that climate warming is already having an effect on fish species richness, and our results suggest that the assemblages' diversity is predicted to carry on changing in the same direction as during the last 25 years. An identical trend was also observed for marine fishes of the North Sea (Hiddink & ter Hofstede, 2008).

Nevertheless, although the local increase in species richness could appear as a fairly positive aspect *per se*, fish assemblage structure in French streams could be strongly modified under climate change. Indeed, turnover rates could exceed 50% on average, indicating that more than half of the 655 studied sites would have at least half of the current pool of species changed. This rate is comparable to the turnover rate predicted for the Mexican fauna (Peterson *et al.*, 2002), the endemic flora in southern Africa (Broennimann *et al.*, 2006), the mammals in African national parks (Thuiller *et al.*, 2006a) or the European plants (Thuiller *et al.*, 2005b). This suggests that, despite the small loss of fish species from their current suitable sites, severe ecological perturbations may occur in the future and species' association shifts may cause fundamental change in assemblage structure. The aim of our approach was to evaluate the impacts of climate change at a taxonomic level. Nevertheless, recent studies have highlighted the potential ecosystem impacts of changes in functional diversity due to climate change (Thuiller *et al.*, 2006b). Changing fish assemblage structure may also have important effects on assemblage functioning. Further studies dealing with the ecological attributes of fish species are thus needed to assess the functional impacts of species range shifts associated with climate change.

Lastly, we validated the hypothesis that turnover rates were positively related to the intensity of temperature change but not to precipitation anomalies. Highly modified assemblages would thus be located at sites where warming would be the greatest.

Some limitations to the assessment of the impacts of climate change

Our species-models were enhanced compared with strictly bioclimatic models because they considered both climate and physical factors as drivers of fish species distribution. Nevertheless, none of the climatic variables considered took into account the potential effects of the increased climate variability. For instance, mean precipitation was used as a surrogate variable to describe stream flows, but increase in hydrological variability may also have great effects on stream fish assemblages. Nonetheless, the good predictive quality of our models suggested that mean climate variables were a quite good alternative to predict fish species distributions. Still, the predicted future fish distributions and assemblages may be considered only as 'potential assemblages under altered environmental conditions' (Dormann, 2007) without taking into account the numerous other factors that could hinder these assemblages to be established. Indeed, it is now well recognized that many other factors acting at different spatial or temporal scales may also influence species distribution and block some of the projected displacements (Pearson & Dawson, 2003; Dormann, 2007). For stream fish species, such factors include (1) biotic interactions, (2) barriers to natural displacements and (3) biological ability to disperse.

The first limitation is that the species-specific modelling approach used here did not allow us to include the effects of the potential biotic interactions that are nevertheless recognized as being of great importance in structuring species assemblages, especially at the local scale (Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Araujo & Luoto, 2007). Future fish assemblages are predicted to be strongly modified. However, some of these new assemblages are composed of species that did not occur together historically. Therefore, the sustainability of such assemblages in the long-term is questionable. Nonetheless, Oberdorff *et al.* (1998) reported that species interactions are negligible in structuring stream fish assemblages in France, relating it to the fact that the European freshwater fish fauna is currently unsaturated following past glaciations (Nahon, 1984). We can thus assume that the potential biotic interactions existing between fish species would not greatly alter the predictions of our models.

The second limitation to the predicted changes in fish species distribution and assemblage structure is the barriers to fish dispersal. To deal with this dispersal problem, studies usually propose two extreme assumptions: 'universal dispersal' opposed to 'no dispersal' (e.g. Peterson, 2003; Thuiller *et al.*, 2006a). It has also been suggested to consider the distance that could be reasonably covered by species (Peterson, 2003; Midgley *et al.*, 2006; Ohlemüller *et al.*, 2006). In this study, all the future predictions assumed that there would not be any constraint to the dispersal, but this assumption is questionable. Indeed, both natural and physical barriers could hinder fish displacements to newly suitable sites. Adjacent rivers may be disconnected if they are not included in the same watershed. The insular nature of watersheds thus stops the natural dispersal of fish species to river units where those species are nonnative. To limit dispersal to unattainable sites, a river unit effect was included in the species-models, which hindered to predict suitable habitats in river units where the species was first absent (e.g. Les, Gaa, Pup, Chn, Leg, Alb). However, despite this effect, some species were expected to gain many suitable habitats in river units where they do not currently occur (e.g. Bam, Tht, Cht). Many habitats would consequently be suitable in the future but impossible to be colonized via natural dispersal means. Stream and river fragmentation could also be an artificial obstacle to fish dispersal. Indeed, streams worldwide have been fragmented by man-made barriers such as dams or flood control structures. These alterations would hinder the ability of fishes to move upstream to new habitats that could otherwise become suitable under climate change (Gosset *et al.*, 2006; Fukushima *et al.*, 2007).

The third limitation to dispersal would be the inability of species to disperse at a sufficient rate to keep up with the changing climate. In the present study, it was assumed that all the 30 fish species have the same dispersal ability. However, it is known that fish dispersal ability is related to the species' biological characteristics and life-history traits, such as size (Jenkins *et al.*, 2007) or reproductive strategies (e.g. seed production or dispersal mode for plants: Pearson, 2006; Van der Veken *et al.*, 2007). Further studies allowing quantification of the true dispersal capacity of fish are thus needed to improve the accuracy of future fish species distributions.

Lastly, our results could be questioned in the context of biological invasions. Indeed, fish invasions have often caused local extirpations of native fish species (e.g. Mercado-Silva *et al.*, 2006; Olden *et al.*, 2006). Here, the predicted expansion of many French species may have an additional effect on species already suffering from range reductions caused by climate change, by an

increase in competitive interactions. Thus, 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. For example, Jackson & Mandrak (2002) demonstrated that smallmouth bass, a predatory fish species, would largely expand its distributional area in Ontario under climate change and cause the extirpation of more than 25 000 populations of four cyprinid species. As a direct consequence, our results should be viewed in terms of ecosystem services and supplies. Indeed, species predicting to invade French streams are either exotic species (e.g. *Lepomis gibbosus*) or common species with low ecological or commercial importance (e.g. *L. cephalus*). The species with the highest risk of local extinction is *S. trutta fario*, which has a high recreational and commercial value and is also considered as a good biological indicator of river health. If our predictions are accurate, French streams and rivers could thus lose a large part of their supply of economic and ecological resources.

Conclusion

To our knowledge, this study is one of the first ones to assess the potential impacts of climate change on stream fish species and assemblages for a large number of species including not only recreational or commercial fish, on the European continent. Compared with bioclimatic envelope models applied to many other taxa at a large scale, the inclusion of additional nonclimatic factors into our species distribution models allowed us to project the future distributions more precisely. It also allowed us to consider the upstream–downstream gradient, which is a major determinant of local structure of fish assemblages. Our results suggest that stream fish species and assemblage structure would be affected by climate change even for moderate scenarios. Overall, fish species diversity is likely to increase, but this probably would be at the expense of cold-water species such as *S. trutta fario*. This may be due to two factors that are characteristic of French watersheds in aquatic environments. First, fish species diversity is dominated by cool- and warm-water species which would be favoured by the increase in temperature. Secondly, French hydrographic networks are mainly constituted of small, cold-water streams that would become warmer and thus suitable for most species.

It would also be interesting to generate comparative studies with other systems. In particular, stream fish species from North America are characterized by many specialized and highly sedentary species. On the contrary, European fauna is marked by the abundance of generalist species, often capable of extensive movement

within the hydrographic network (Belliard *et al.*, 1997). Such differences may affect the responses of stream fish species to climate change, and inter-continental comparisons would probably reveal different patterns of future fish assemblage modifications. Taking into account ecological characteristics of species should be helpful to identify similar responses across contrasted assemblages (Thuiller *et al.*, 2004, 2006b) and should thus enhance our understanding of potential impacts of climate change on stream fish assemblages.

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