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Strengthening the link between climate, hydrological and species distribution modeling to assess the impacts of climate change on freshwater biodiversity

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A B S T R A C T

To understand the resilience of aquatic ecosystems to environmental change, it is important to determine how multiple, related environmental factors, such as near-surface air temperature and river flow, will change during the next century. This study develops a novel methodology that combines statistical downscaling and fish species distribution modeling, to enhance the understanding of how global climate changes (modeled by global climate models at coarse-resolution) may affect local riverine fish diversity. The novelty of this work is the downscaling framework developed to provide suitable future projections of fish habitat descriptors, focusing particularly on the hydrology which has been rarely considered in previous studies. The proposed modeling framework was developed and tested in a major European system, the Adour–Garonne river basin (SW France, 116,000 km^2), which covers distinct hydrological and thermal regions from the Pyrenees to the Atlantic coast. The simulations suggest that, by 2100, the mean annual stream flow is projected to decrease by approximately 15% and temperature to increase by approximately 1.2 °C, on average. As consequence, the majority of cool- and warm-water fish species is projected to expand their geographical range within the basin while the few cold-water species will experience a reduction in their distribution. The limitations and potential benefits of the proposed modeling approach are discussed.

1. Introduction

Freshwater ecosystems are threatened by climate change through increased air temperature and altered flow regimes (Heino et al., 2009; Pachauri and Reisinger, 2007; Schindler, 1997; Whitehead et al., 2009). Riverine fish are good model organisms with which to assess the impact of climate change on freshwater ecosystems because most fish species have no physiological ability to regulate their body temperature and they are the most widely monitored freshwater organisms (Wood and McDonald, 1997). Global warming is expected to shift cold-water fish species towards higher latitudes and altitudes, while warm-water species are expected to expand their geographical distribution (Heino et al., 2009). Moreover, declining river flows are thought to affect freshwater biodiversity, both at the species-level through reduced breeding success and post-spawning recruitment, and the community-level, through modified biotic interactions (Jackson, 1989; Walsh and Kilsby, 2007).

To date, most future climate change impact studies on freshwater fish developed at large scales (>50,000 km²) have focused on air temperature and precipitation without explicitly considering river flow (e.g., Buisson et al., 2008; Buisson and Grenouillet, 2009; Filipe et al., 2010; Lassalle and Rochard, 2009; Sharma et al., 2007). However, river flow is recognized as a crucial component of species habitat that should be considered when determining future freshwater species distribution (Gibson et al., 2005; Lamouroux et al., 1999; Poff and Zimmerman, 2010). Only a few studies have considered river flow in projecting future fish species distribution patterns but these have focused either on smaller spatial scales (<10,000 km²; Battin et al., 2007; Matulla et al., 2007; Walsh and Kilsby, 2007), on species richness modeling approaches (Döll and Zhang, 2010) or on a restricted number of fish species (Wenger et al., 2011). The main reason for not considering hydrology is the uncertainty in future projections of precipitation modeled by Global Climate Models (GCMs) leading to important errors and biases in hydrological projections (Fowler et al., 2007; Xu, 1999). Furthermore, hydrological models which are usually set up for limited

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geographic areas, often have high data requirements and require expert-knowledge for their calibration.

The aim of this work is to overcome this limitation by using downscaling techniques to estimate future hydro-climatic conditions at a fine resolution (e.g., site scale) based on coarser-resolution GCM outputs (typically 250 km × 250 km). Developed in the last decade mainly, downscaling methods are commonly separated into two categories (Fowler et al., 2007). The first category includes statistical approaches that establish an empirical relationship between GCMs outputs and local climate or river flows. The second category corresponds to dynamical approaches involving regional climate models (RCM) nested within a GCM to increase the spatial resolution of projections, typically 50 km × 50 km down to 5 km × 5 km. Here we focus on statistical downscaling approaches because they are less computer-intensive and easier to develop at different spatial resolutions than dynamical approaches.

A modeling framework is proposed which combines statistical downscaling and fish species distribution modeling, to simulate the effects of projected air temperatures and flow conditions on fish species distributions. The novelty of this work is the downscaling framework developed to provide suitable future projections of fish habitat descriptors, focusing particularly on the hydrology. There are two main objectives. The first is to calibrate and test the modeling framework for a major European system, the Adour–Garonne river basin (SW France) which displays a wide range of hydrological and climatic conditions that support a diverse fish community (Mastrorillo et al., 1998). The second objective is to use the modeling framework to estimate the potential future habitat suitability for fish communities during the 21st Century.

2. Material and methods

The five main steps of the modeling framework were the following: (1) to collate climatic, flow, environmental and biological data (Section 2.1) to describe the fish hydrological and thermal habitat (Section 2.2); (2) to calibrate the statistical downscaling models by linking GCMs outputs and fish habitat descriptors (Fig. 1a; Section 2.3); (3) to calibrate the species distribution models by developing relationships between the habitat descriptors and species distributions (Fig. 1b; Section 2.4); (4) to validate the full model under current climate by integrating the downscaling and species distribution models into a common framework, and (5) to determine the impact of climate changes on the local hydrological and thermal conditions and on the future distribution of fish species (Section 2.5).

2.1. Data sources

Fifty sites were selected over the Adour Garonne basin (Fig. 2a). For each site, data comprised fish occurrence (presence–absence) collated from the Office National de l'Eau et des Milieux Aquatiques (ONEMA) for the 13 most prevalent species during the period 1992–2000. The most prevalent fish species are defined as those present at more than 15 sites during the 1992–2000 survey period and are listed in Table 1. In addition, data characterizing fish habitat conditions comprised daily river flow records collated from the Hydro2 database (Ministère de l'Ecologie, de l'Energie, du Développement durable et de la Mer; http://www.hydro.eaufrance.fr/) and daily near-surface air-temperature provided by Météo-France for the period 1971–2000. As done in most fish species distribution modeling studies, air temperature was considered as a proxy for water temperature given that water temperature records were not available for all sampling sites and that both temperature metrics are generally highly correlated (Buisson et al., 2008; Sharma et al., 2007; Lassalle and Rochard, 2009). Finally data describing the physical characteristics at each of the 50 sites were also collated, characterizing the following: the distance from the river source (km), the upstream drainage area (km²), the longitude (degree W) and latitude (degree N), the elevation (m), the mean river slope (‰), the mean river width (m) and the mean water depth (m).

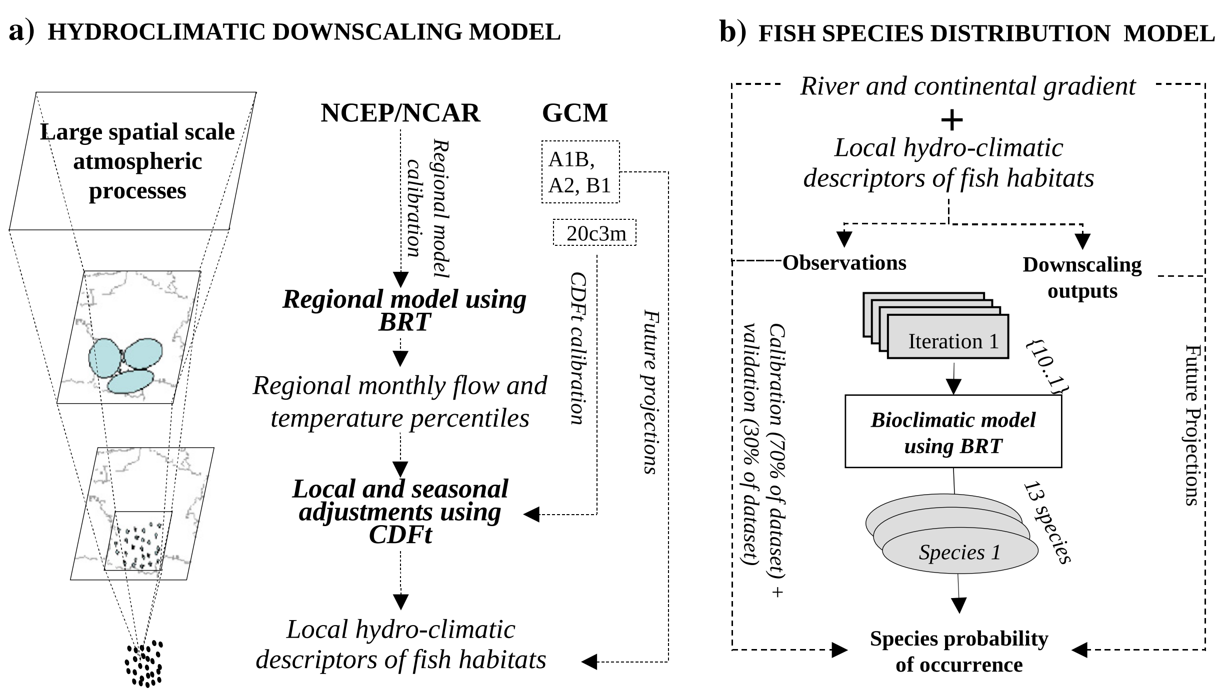

Fig. 1. Modelling framework linking (a) statistical downscaling of GCMs atmospheric processes to model local fish habitat descriptors to (b) the distribution of 13 fish species. In (a), the statistical downscaling models are built upon a regional component which links the GCM atmospheric processes to the regional variations in near surface air temperature and flow using boosted regression trees statistical models (BRT), and a local component that adjust the regional projections to explain local and seasonal hydro-climatic conditions based on the cumulative distribution function transformation approach (CDF-t; see Section 2 for more details). In (b), fish species distribution is modelled using BRT statistical models relating fish species occurrence to environmental and downscaled fish hydro-climatic habitat descriptors.

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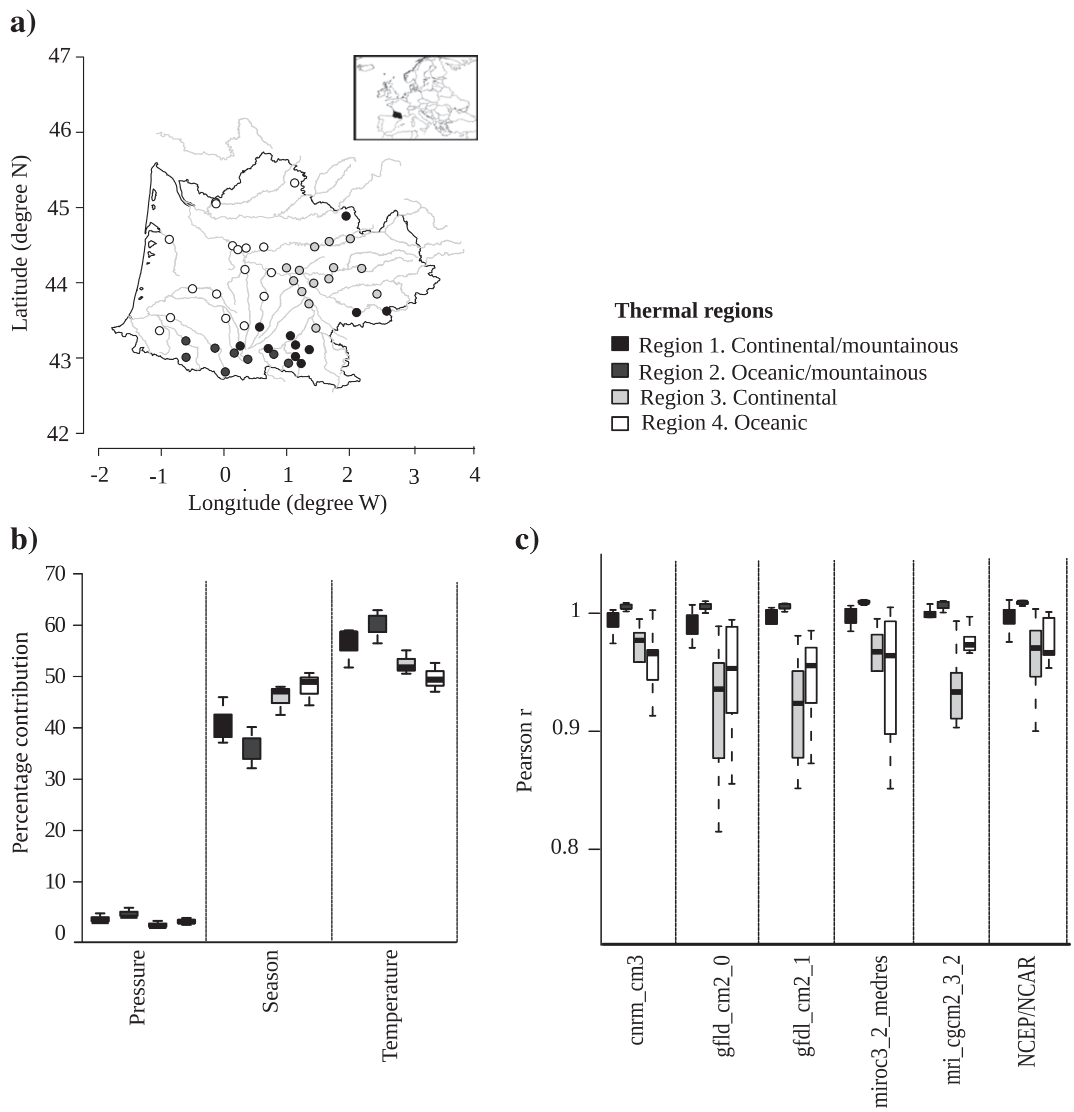

Fig. 2. (a) Sampling sites grouped into four homogeneous thermal regions using hierarchical agglomerative clustering (with Euclidean distance and Ward criterion) applied to monthly air-temperature statistics. (b) For each region, the relative contribution to the regional temperature variability explained by the atmospheric temperature, pressure as well as seasons, was derived from the regional downscaling. (c) For each region, the Pearson *r* correlation between observed and downscaled thermal descriptors of fish species habitat was calculated over the period 1971–2000.

Monthly reanalysis data from the National Centre for Environmental Prediction and the National Centre for Atmospheric Research (NCEP/NCAR; Kalnay et al., 1996) were also collated for the period 1971–2000. Reanalysis data were used as coarse-resolution records of atmospheric variables (250 km × 250 km) to calibrate the statistical downscaling models (Wilby et al., 1998; Fowler et al., 2007). To model future local temperature and hydrological conditions, an ensemble approach was applied by downscaling a combination of five GCMs and three scenarios downloaded from the Program for Climate Model Diagnosis and Inter-comparison (PCMDI) website at https://esg.llnl.gov:8443/index.jsp (Table 2). GCMs data were collated for the period 1971–2000 (control scenario 20c3m) and the A1B, A2 and B1 scenarios of future greenhouse gas emissions (period 2010–2100; Pachauri and Reisinger, 2007).

Nine atmospheric variables available from both reanalysis and the outputs of the GCMs were selected and interpolated at the 50 sites location using bilinear interpolation. These atmospheric variables represent key atmospheric processes influencing the regional near-surface temperature and hydrological variability, namely precipitation, temperature, solar radiation and pressure (Table 3). For each of the five GCMs, each atmospheric variable was standardized over the period 1971–2000, by subtracting the mean and dividing by the standard deviation. A Hierarchical Agglomerative Clustering (HAC) was applied to the standardized atmospheric variables to identify four groups of atmospheric processes related to precipitation, temperature,

Table 1
Prevalence of 13 studied fish species over the studied region.

Species name	Common name	Code	Ichthyological zones	Actual prevalence
Perca fluviatilis	Perch	Pef	4	0.30
Parachondrostoma toxostoma	Soufie	Cht	3	0.30
Leuciscus leuciscus	Dace	Lel	3	0.36
Lepomis gibbosus	Pumpkinseed	Leg	4	0.36
Salmo trutta non-migratory form	Brown trout	Sat	1	0.49
Anguilla anguilla	European eel	Ana	4	0.51
Alburnus alburnus	Bleak	Ala	4	0.54
Barbatula barbatula	Stone loach	Bab	2	0.55
Barbus barbus	Barbel	Bar	4	0.59
Rutilus rutilus	Roach	Rur	4	0.62
Phoxinus phoxinus	Minnow	Php	2	0.63
Squalius cephalus	Chub	Lec	4	0.69
Gobio gobio	Gudgeon	Gog	3	0.77

Table 2
Names and origin of the five GCMs tested for the modelling framework.

Originating Group(s)	Acronyms	Country
Météo-France/Centre National de Recherches Météorologiques	cnrm_cm3	France
US Dept. of Commerce/NOAA/Geophysical Fluid Dynamics Laboratory	gfdl_cm2_0	USA
US Dept. of Commerce/NOAA/Geophysical Fluid Dynamics Laboratory	gfdl_cm2_1	USA
Center for Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change (JAMSTEC)	miroc3_2_medres	Japan
Meteorological Research Institute	mri_cgcm2_3_2a	Japan

solar radiation and pressure (Table 3; Tisseuil et al., 2010). For each group, a Principal Component Analysis was applied and the first principal component of each group (synthesizing more than 90% of the atmospheric process of interest) was used as the predictor in the downscaling framework (Fig. 1a).

2.2. Identification of fish hydro-climatic habitat descriptors

The downscaling framework was developed to explicitly model the fish species' hydrological and thermal habitat suitability. To this end, GCM outputs were downscaled locally to the 50 sites to derive 18 hydrological and thermal habitat descriptors of biological relevance in the life-history of fish. These descriptors characterized the seasonal mean, and extreme, flows and air temperatures. The extremes were calculated as the 10th, 50th and 90th percentiles of river flow and near-surface air temperature (hereafter referred to as P10, P50 and P90) for three biological periods of major importance in fish life cycles (Fig. 1; Table A.1). Except for Salmonids (e.g. *Salmo trutta*) which are autumn spawners, the three biological periods were defined as (1) the period of low activity (from October to February), (2) the spawning season (from March to June) encompassing the major part of the reproduction time, and (3) the growth season (from July to September) during which fishes actively feed (e.g., Beard and Carline, 1991; Cattanéo, 2005; Cattanéo et al., 2002; Crisp, 1996).

2.3. Hydro-climatic downscaling models

The downscaling model structure was devised in two parts to derive the 18 fish hydrological and thermal habitat descriptors (Fig. 1a). A "regional" part makes the link between the four atmospheric predictors (i.e., the first principal components related to precipitation, temperature, solar radiation and pressure) and the monthly statistic (i.e., P10, P50 and P90) of daily mean flow and air temperature for a different group of sites having similar hydro-climatic characteristics. For this regional part, hydrological and thermal regions were defined separately using HAC with Euclidean distance and Ward criterion, to group sites having similar monthly P10, P50 and P90 values of daily flows and air temperatures. For each region, the regional downscaling was done using boosted regression tree statistical models (Elith et al., 2008; Friedman, 2001) to model each monthly statistic (P10, P50 and P90) as a function of the four coarse-resolution atmospheric predictors. Two seasonal predictors describing cyclic variations for each three biological periods were also included as predictors in this regional downscaling models to improve goodness-of-fit.

In addition to the regional component, a 'Cumulative Distribution Function — transform' approach (CDF-t; Michelangeli et al., 2009) was used to modify the regional projections to explain 'local' and seasonal hydro-climatic variations (i.e., monthly P10, P50 and P90) at each site. CDF-t consists of adjusting the cumulative distribution of regional downscaling projections for the 1971–2000 (20c3m) control period to that of local observations, conditionally for each biological period.

The calibration and validation of hydro-climatic downscaling models were based on three independent time periods (denoted *a*, *b*, *c*) of approximately 10 years, between 1971 and 2000. This was done to account for non-stationarity in the observed daily mean air-temperature and flow time series over 1971–2000. Period *a* was used to calibrate the regional downscaling model using NCEP/NCAR data. Period *b* was used to calibrate the local downscaling part. Finally, the validation period *c* was used to compare the results of the downscaling process with observed local data to test the model behavior. The process was then repeated so that overall, six combinations of calibration/validation periods were generated, namely *abc*, *acb*, *bac*, *bca*, *cab*, *cba*. Hydro-climatic projections from the six combinations of validation periods were assembled and averaged, so that a single validation period was derived for each year over the period 1971–2000. This validation period was used to estimate the goodness-of-fit of the downscaling models to the observed data.

To derive future hydro-climatic projections, a simplified procedure was developed in three steps. First, the period 1971–2000 was split into two consecutive time periods of 15 years, labeled periods *e* and *f*. Secondly, these two periods were used, respectively to calibrate the regional and local (CDF-t) aspects of the modeling framework. Thus, two combinations of regional and local calibration periods, namely *ef* and *fe*, were generated and the two associated downscaling models were used to project the future hydro-climatic variability under A1B, A2 and B1 scenarios for the five GCMs. These two downscaling projections were averaged, so that a single future climate projection was derived for each year over the period 2010–2100.

Table 3
Description of the nine atmospheric variables used to drive the hydro-climatic downscaling models.

Full name	Short name	Unit	Atmospheric group
Mean daily air temperature 2 m above surface	air.2m	K	Temperature
Mean daily air temperature at 500 hPa	air.500	K	Temperature
Mean daily air temperature at 850 hPa	air.850	K	Temperature
Mean daily clear sky downward longwave flux at surface	csdlf	$W\,m^{-2}$	Temperature
Mean daily clear sky upward solar flux at surface	csusf	$W\,m^{-2}$	Solar radiation
Mean daily precipitation rate at surface	prate	$kg\,m^{-2}\,s^{-1}$	Precipitation
Mean daily surface pressure	pres	Pa	Pressure
Mean daily SST/land skin Temperature	skt	K	Temperature
Mean daily upward solar radiation flux at surface	uswrf	$W\,m^{-2}$	Solar Radiation

2.4. Fish distribution modeling

To understand how fish assemblages were currently distributed over the region, HAC (with Euclidean distance and Ward criterion) was applied to the observed fish occurrences at the 50 sites to highlight different groups of sites having similar fish assemblages. In this way ichthyological regions were identified. The 'Indicator Values' approach was then used to identify key indicator species for each ichthyological region (IndVal; Dufrene and Legendre, 1997).

Fish species distributions were modeled using twenty six predictors, characterizing the seasonal hydrological and air temperature variability at each site as well as environmental habitat characteristics (Table A.1). Apart from the 18 previously downscaled predictors, six predictors related to seasonal hydro-climatic variability (VAR, defined

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as the difference between P90 and P10) were included to characterize the amplitude of the shift between low (P10) and high (P90) hydro-climatic conditions. Finally, two environmental predictors describing the position of sites along the upstream–downstream river continuum and along the SW–NE gradient were also considered to highlight the physical structure of the basin potentially influencing fish distribution. These last two predictors were represented by the first two axes of a PCA performed on the sites physical descriptors.

A species-specific boosted regression tree model was built for each of the 13 fish species. A binomial distribution of errors was assumed and the probability of species occurrence was related to the twenty-six predictors via a logistic link function. The dataset was first randomly divided into two subsets, as typically done in most species distribution modeling studies (Buisson et al., 2008; Guisan and Thuiller, 2005). One subset representing 70% of the dataset was used to calibrate the regression tree models and the remaining 30% was used for validation. The procedure of calibration and validation was repeated ten times to account for variability in the simulated species occurrence.

For each species distribution model driven by GCMs or reanalysis data, presence–absence data were derived from the projected probability of occurrence of each species from 1992 to 2000. Presence and absence were derived by identifying an optimal threshold that maximized the sum of two measures, namely the "sensitivity", which gives the percentage of presence correctly predicted, and the "specificity", which measures the percentage of absence correctly predicted (Fielding and Bell, 1997). Below the optimal threshold value, a given species was considered as absent and as present above the value. Future fish distribution was then projected annually for the period 2010–2100 according to the five GCMs and A1B, A2 and B1 scenarios, based on the downscaled fish hydrological and thermal habitat descriptors.

2.5. Validation and future projections of the modeling framework

For the validation of the framework, the downscaled fish hydro-climatic habitat descriptors and the resultant probability of occurrence for the 13 fish species were averaged per site from 1992 to 2000. The spatial correlation between the observed and the projected results was assessed using permutation tests with a 5% level of confidence. This was done by randomly permuting 1000 times the projected results between the 50 sites, and then comparing the observed statistics to those calculated from the 1000 random permutations (Legendre and Legendre, 1998).

The downscaled fish hydro-climatic habitat descriptors were analysed according to each hydrological and climatic region. For each region, the Pearson r correlation values between the downscaled and observed data were considered as significant if the null hypothesis of spatial independence was rejected with a 5% level of confidence. The overall spatial consistency between the downscaled and observed descriptors over the region was tested using the Mantel R correlation test from the 50×50 Euclidean dissimilarity of sites based on hydro-climatic descriptors (Legendre and Legendre, 1998).

The goodness-of-fit between the projected and observed fish distributions was evaluated using the area under the curve (AUC) method of a receiver operating characteristic (ROC) plot (Fielding and Bell, 1997; Pearce and Ferrier, 2000). For each species, the AUC value was assumed as significant if rejecting the null hypothesis that the projected distribution of species was not better projected than by chance, namely if the simulated AUC was higher than 0.5 with a 5% level of confidence. The overall spatial consistency between the projected and observed fish assemblages (i.e., the aggregation of the 13 species probability of occurrence at the 50 sites) was tested using Mantel R correlation test from the 50×50 Euclidean dissimilarity of sites based on fish assemblages.

Future projections of the modeling framework were analysed for each ichthyological region, by calculating the annual mean absolute and relative changes in future fish hydrological and thermal habitat descriptors, for the period 2010–2100. Similarly, the absolute change in fish prevalence was calculated for each species as well as the mean absolute and relative change in the total species richness.

3. Results

3.1. Validation of downscaling models outputs

Four thermal regions showing distinct seasonal patterns in air-temperature were defined from the HAC analysis: continental/mountainous (region 1), oceanic/mountainous (region 2), continental (region 3) and oceanic (region 4) regions (Fig. 2a). The calibration of the regional downscaling component revealed that atmospheric temperature processes and seasons contributed to approximately 50% and 37% of the explained variance in the regional monthly statistics of temperature, respectively (Fig. 2b). For each GCM and NCEP/NCAR-driven models, the downscaled thermal habitat descriptors for fish were significantly spatially correlated to observations in each thermal region. (Fig. 2c; 1000 permutations Pearson r correlation test, $r \sim 0.90$, $p\text{-value} < 0.05$). Spatial correlation between observed and downscaled thermal conditions was marginally higher in mountainous (in mean, $r \sim 0.91$ in regions 1 and 2) than in continental and oceanic regions (in mean, $r \sim 0.88$ in regions 3 and 4).

Five hydrological regions were also defined from the HAC analysis, representing a marked transition from nival- (i.e., regions characterized by maximum annual flows in spring; region 1) to pluvial-dominated hydrological (i.e.; regions characterized by maximum annual flow in winter; region 5) regimes (Fig. 3a). With the transition from nival to pluvial regimes, the contribution of short-wave solar radiation to the regional monthly flow statistics decreased from 47 to 13% while that of atmospheric temperature gradually increased from 13 to 50% and that of atmospheric precipitation and pressure predictors was similar across hydrological regimes, ranging between 10% and 18% (Fig. 3b). For each hydrological region, the spatial correlation between the observed and downscaled fish hydrological habitat descriptors was significant (Fig. 3c; 1000 permutations Pearson r correlation test, $r \sim 0.89$, $p\text{-value} < 0.05$). When considering the overall fish hydrological and thermal habitat descriptors, the spatial structure of the downscaled results was significantly consistent with observations for the five GCMs and NCEP/NCAR data (1000 permutations Mantel R correlation test, $R \sim 0.93$, $p\text{-value} < 0.05$).

3.2. Validation of species distribution models outputs

Four ichthyological regions were defined and the 'Indicator Values' approach identified key indicator species for each region (Fig. 4a): headwater species in region 1 (*S. trutta* non-migratory form) and region 2 (*Barbatula barbatula*, *Phoxinus phoxinus*), and lowland species in region 3 (*Parachondrostoma toxostoma*, *Leuciscus leuciscus*, *Gobio gobio*) and region 4 (*Perca fluviatilis*, *Lepomis gibbosus*, *Anguilla anguilla*, *Alburnus alburnus*, *Barbus barbus*, *Rutilus rutilus*, *Squalius cephalus*).

Fish thermal and environmental habitat descriptors explained the majority of fish species occurrence (40% and 34%, respectively), whereas hydrological descriptors explained approximately 26% (Fig. 4b). Furthermore, thermal habitat descriptors particularly had more influence on headwaters species (region 1) than lowlands species (region 4; Fig. 4b). However, each species displayed a different modeled response to the prevailing hydro-climatic and environmental habitat descriptors (Fig. B.1). The projected distribution for all 13 fish species was better modeled than by chance when driven by the five GCMs or NCEP/NCAR datasets, since AUC scores were significantly higher than 0.5 for all 13 fish models (Fig. 4c and Fig. B.2; 1000 permutations AUC test, $AUC \sim 0.93$, $p\text{-value} < 0.05$). When combining the 13 species-level projections, the overall spatial structure in fish assemblages was consistently modeled by both GCMs- and reanalyses-driven models (1000 permutations Mantel R correlation test, $R \sim 0.84$, $p\text{-value} < 0.05$).

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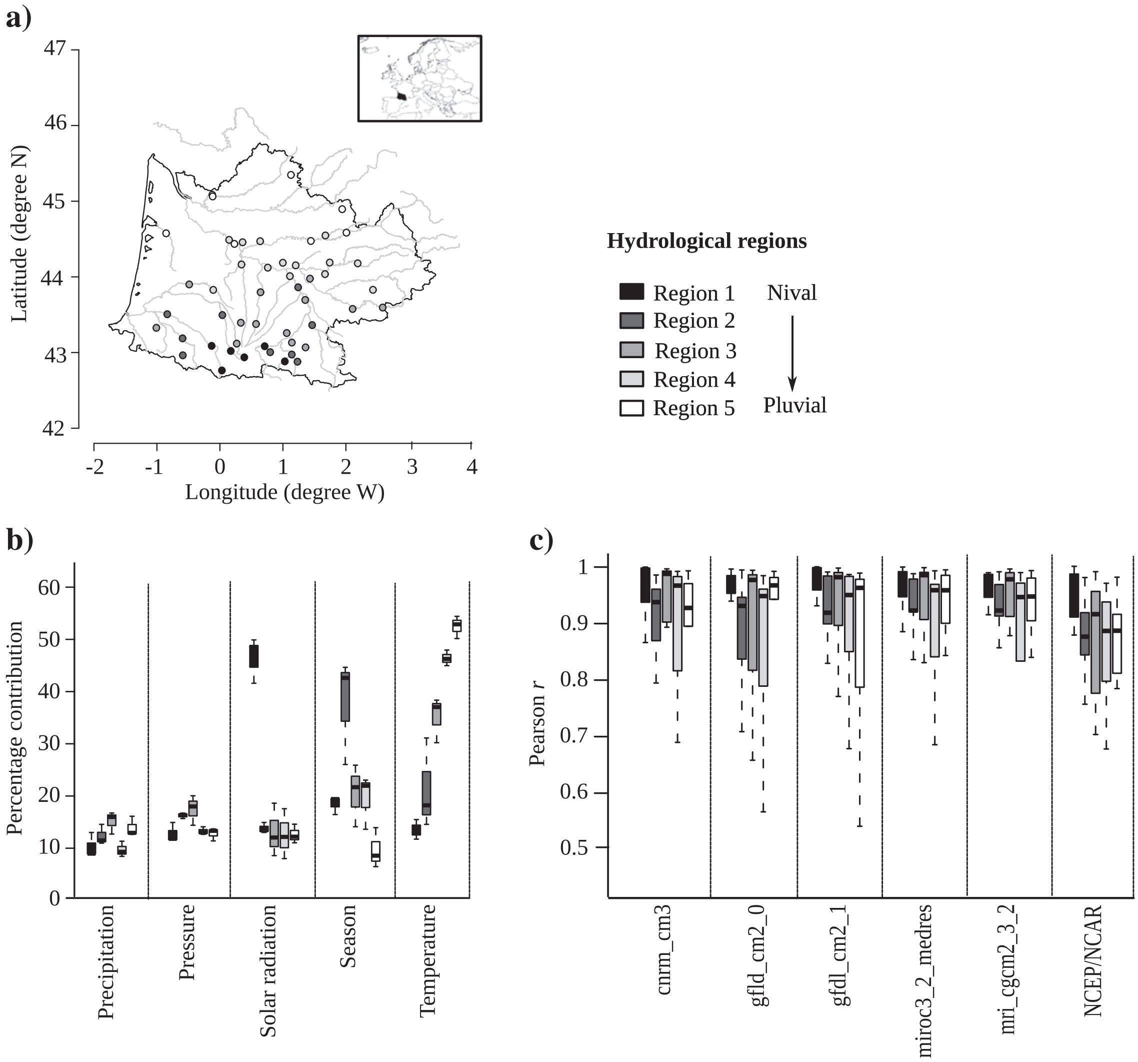

Fig. 3. (a) Sampling sites grouped into five hydrological regions ranging from nival (cluster 1) to pluvial (cluster 5) systems, identified using hierarchical agglomerative clustering applied to monthly river flow statistics. (b) For each hydrological region, the relative contribution to the local flow variability explained by the atmospheric temperature, shortwave solar radiation, pressure and precipitation as well as seasons, was derived from the regional downscaling. (c) For each region, the Pearson *r* correlation between observed and downscaled hydrological descriptors of fish species habitat was calculated over the period 1971–2000.

3.3. Future projections of the modeling framework

The future thermal habitat suitability for fish (i.e., P10, P50, P90 for the three biological seasons) was projected to increase over the region by approximately +0.7 °C, in 2040–2060, and by +1.1 °C in 2070–2090 (Fig. 5 and Fig. C.1). This increase is projected to be more important in lowlands (region 4; +1.2 °C in 2070–2090) than in headwaters (region 1; +1 °C in 2070–2090; Fig. 5a and b). On average, the standardized hydrological habitat suitability for fish could globally decrease by −0.26 (i.e., −11%) in 2040–2060 and by −0.39 (i.e., −17%) in 2070–2090, more importantly in the lowlands (region 4; −20% in 2070–2090) than in headwaters (region 1; −11% in 2070–2090; Fig. 5c).

The total number of species in the four zones was estimated to increase by +0.6 species (+13%) in 2040–2060 and by +0.9 species (+23%) in 2070–2090 (Fig. 5d). The percentage of increase in species richness is projected to be higher in headwaters (region 1; +46% in 2070–2090) than in lowlands (region 4; +7% in 2070–2090; Fig. 5d). The absolute change in fish prevalence increased for all species, except *S. trutta*, though the amplitude of these changes was different according to species (Fig. C.2). Future projections in species richness and prevalence were shown to fluctuate between years, reflecting stochastic variations in the future hydro-climatic habitat suitability for fish.

4. Discussion

The proposed downscaling framework was set up to enhance the understanding of how global climate changes, as modeled by GCMs at coarse-resolution, may affect local riverine fish diversity. We acknowledge that our projections should be interpreted cautiously as our modeling framework does not provide a holistic view of processes affecting both local hydro-climatic processes and the subsequent effects on fish species distribution. For instance, the connection between coarse-resolution atmospheric and local hydro-climatic processes is dynamic and should ideally take into account the antecedent conditions. This connection might be also influenced by a number of intermediate factors interacting on the hydrological cycle (e.g., topography, groundwater and land cover). Furthermore, our fish species distribution models did not take into account species interaction (Wenger et al., 2011), land cover alterations (Filipe et al., 2010) or other natural environmental factors (e.g., river network connectivity) that could amplify or mitigate the projected changes in species distribution and

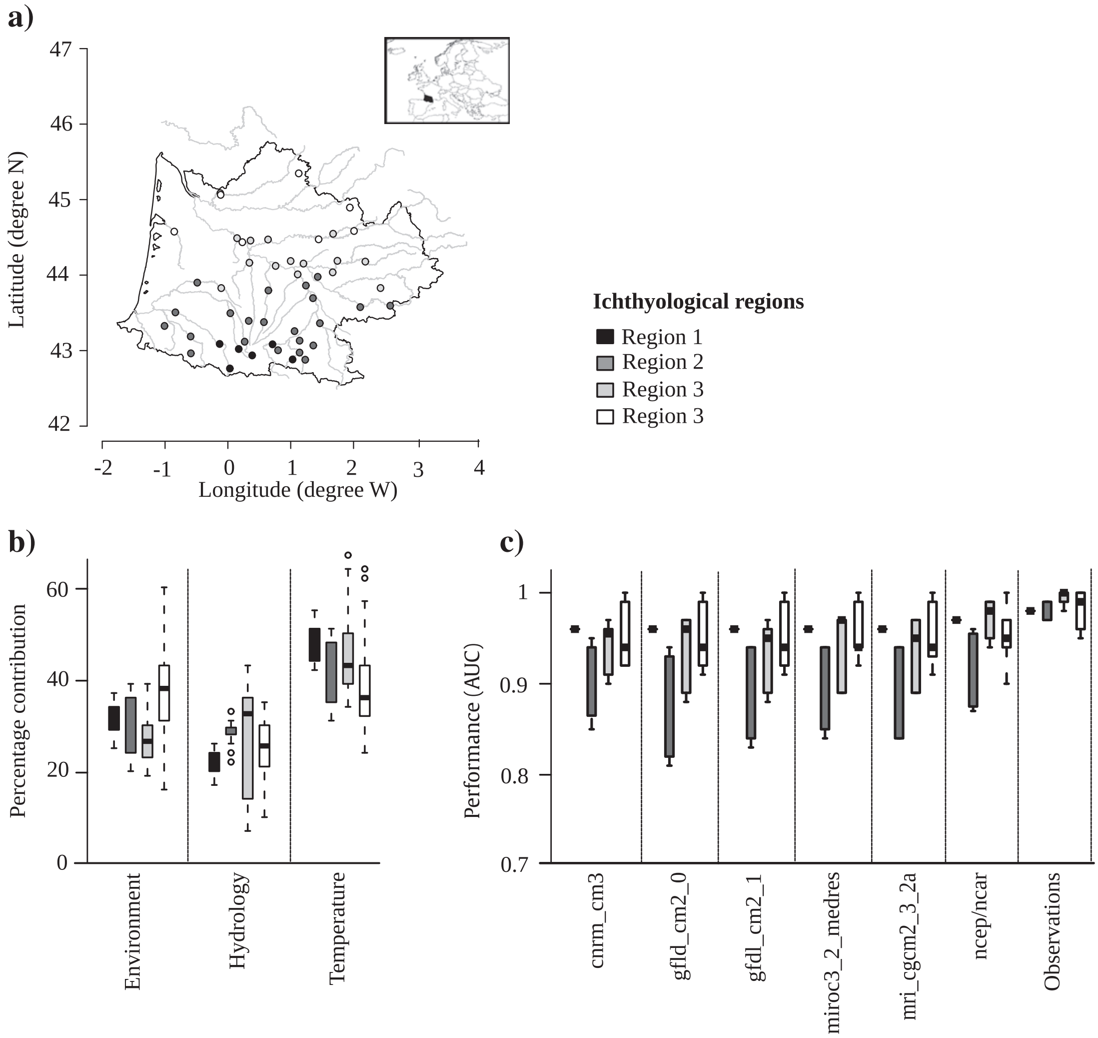

Fig. 4. (a) Sampling sites grouped into the four ichthyological regions identified using hierarchical agglomerative clustering applied to fish species occurrence records. (b) For each ichthyological region, the relative contribution to the fish occurrence explained by thermal, hydrological and environmental descriptors of species habitat, was derived from species distribution modeling. (c) For each region, AUC between the observed and simulated fish species probability of occurrence was calculated over the period of fish sampling.

community structure at both local and regional scales (Heino et al., 2009). Our results should be thus interpreted as a preliminary attempt to understand the hierarchical impacts of climate changes on freshwater biodiversity throughout an integrated multiple-scale approach.

The regional component of the downscaling framework links GCMs atmospheric predictors to the regional variations in near-surface air temperature and river flow. The validation of this regional component corroborates the results obtained in previous downscaling studies (Phillips et al., 2003; Tisseuil et al., 2010; Wilby et al., 1998) and goes a further step by incorporating them in a single framework. Specifically, we show that the coarse-resolution atmospheric processes may have contrasting effects on the regional hydrology and temperature, which stresses the need to account for regional specificities in hydro-climatic downscaling models. Coarse-resolution temperature is shown to be the most influential process acting on near surface air temperature for the overall thermal regions, despite the fact that local temperature exhibited different seasonal patterns among thermal regions. By contrast, the influence of coarse-resolution atmospheric processes on regional hydrology displays regional nuances. For instance, the contribution of atmospheric temperature to the regional flow variability gradually increases from 13 to 50% with the transition from nival to pluvial regimes, while the contribution of short-wave solar radiation decreases from 47 to 13%. Although atmospheric processes influence the water cycle through evapotranspiration, the particularly high influence of shortwave solar radiations on nival regimes may be due to the influence on the snowmelt process (Li and Williams, 2008; Tisseuil et al., 2010). Interestingly, the unexpectedly weak effects of coarse-resolution precipitation (ranging between 10% and 18% between hydrological regimes) on regional pluvial hydrological regimes should be put in the context of the modeling framework attempting to model river flows through coarse-resolution processes. Thus, GCMs do not account for regional-scale features, such as orography and convective rainfall that may influence river flows. Furthermore, the temporal resolution of our model is the season, whereas precipitation influence on streamflow variability is recognized as particularly significant at higher temporal resolution, namely at the daily, or sub-daily time scales.

The local component of the modeling framework adjusts the regional projections to explain local and seasonal hydro-climatic variations at each site and their subsequent effects on fish distribution. The local component was satisfactorily validated for the 1992–2000 control period, which builds confidence in the ability of the modeling framework to provide consistent local projections of future hydrological and thermal habitat suitability for fish. By 2080, the mean annual stream flow is projected to decrease (by approximately −10% and −20% in nival and pluvial systems, respectively) and temperature to increase over the region (by approximately 1.2 °C). This result agrees with the works of Caballero et al. (2007) and Boe et al. (2009) who projected a similar amplitude of hydro-climatic changes over the Adour–Garonne using

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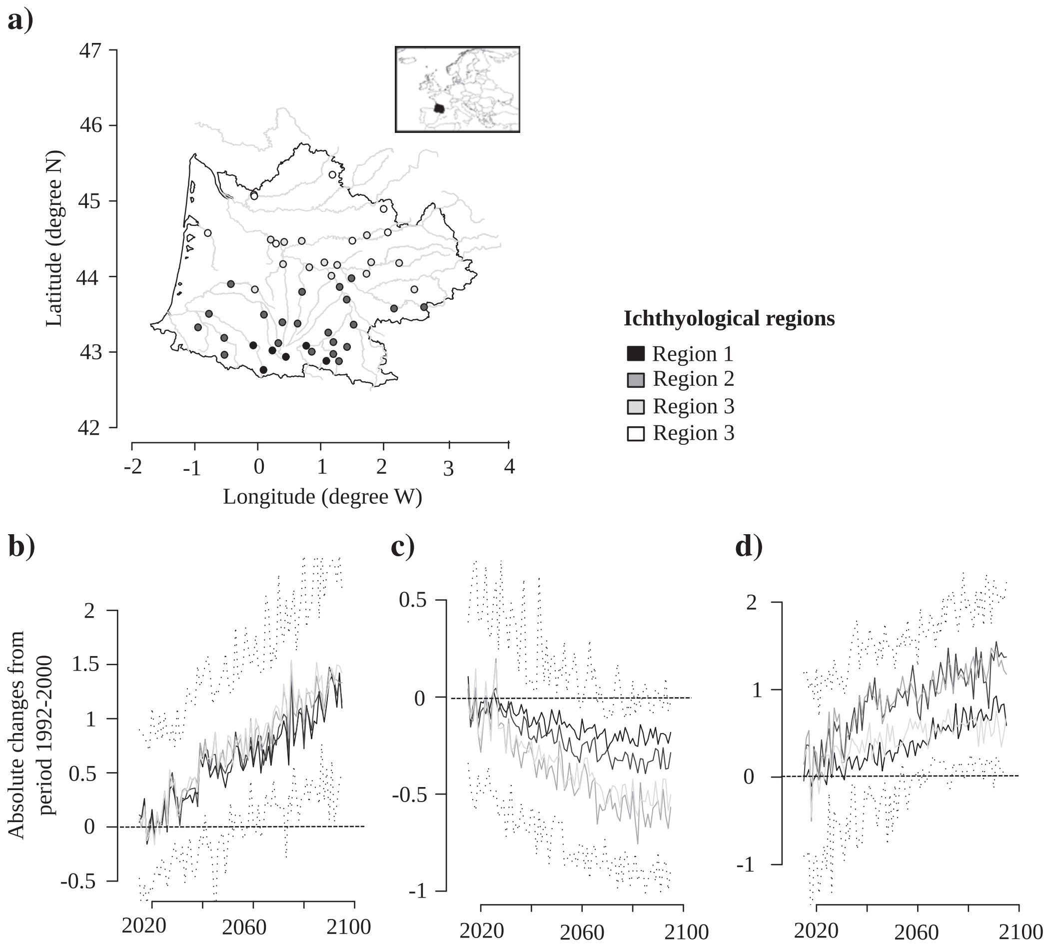

Fig. 5. Projected impacts of climate change on the four ichthyological regions identified over the Adour Garonne basin using hierarchical agglomerative clustering applied to fish species occurrence records. For each ichthyological region shown in (a), the mean absolute changes in fish (b) thermal and (c) hydrological habitat descriptors and (d) fish species richness is projected for the period 2010–2100. Uncertainty in projections is represented with dotted lines by the 10th and 90th percentiles estimated from the ensemble projections including five GCMs, three SRES scenarios and ten species distribution model runs.

mechanistic (process-based) hydrological modeling approaches. The projected hydro-climatic changes could lead to an overall increase in the local species richness, as noticed by previous studies applied in Europe (e.g., Buisson et al., 2008; Buisson and Grenouillet, 2009; Daufresne and Boet, 2007; Matulla et al., 2007) and in North America (e.g., Chu et al., 2005; Sharma et al., 2007). This increase is linked to a change in the composition of species through a colonization process by warm-water species that are expected to expand their geographical range. However, the strength of changes in community composition could be markedly more pronounced in the lowlands than in headwaters. Thus, in headwaters of the Adour Garonne, overall species richness should increase slightly, but the occurrence of cold-water species, such as *S. trutta*, is projected to decrease.

The inclusion of fish hydrological preferences is a key feature of our modeling framework. It is noteworthy that our results do not show strong evidence of predictive superiority in comparison with others studies that used precipitation as a proxy for fish hydrological preferences (e.g., Buisson et al., 2008; Buisson and Grenouillet, 2009; Filipe et al., 2010; Lassalle and Rochard, 2009; Sharma et al., 2007). However, accounting for flow in the modeling framework is likely to improve the reliability of interpretation of the future impacts of climate change on freshwater fish biodiversity; river flow conditions are known to have important effects on species life-history processes (Daufresne et al., 2004; Mills and Mann, 1985; Tedesco et al., 2008). For instance, the projected decrease of mean flow conditions during the spawning season in all hydrological regions of the Adour Garonne could directly promote the development of early-life stages for species with a medium fecundity such as *L. leuciscus* or *B. barbatula* (Cattanéo, 2005). In addition, the projected decrease of low flows could be detrimental for many organisms particularly for lithophilic spawners (e.g., *S. trutta*, *S. cephalus*, *P. phoxinus* and *B. barbus*) by increasing the clogging of their spawning habitat (Filipe and Cowx, 2002). Finally, the synergistic effects of hydrology and temperature could have complex effects on the different stages of species life-histories as the survival rate of juvenile fish could decrease markedly with the combination of higher temperatures and lower flows leading to greater oxygen depletion (Gibson et al., 2005). Thus, hydrology plays a non-negligible role which cannot be ignored by both theoretical and applied ecologists in studying the potential impacts of climate change on the distribution of species, especially to anticipate the potential species loss due to extreme hydro-climatic events such as droughts or floods (Filipe and Cowx, 2002).

5. Conclusions

The proposed downscaling approach provides promising perspectives for climate change impact studies on freshwater biodiversity that have, until now, rarely accounted for the future hydrological habitat suitability of organisms. The framework is adjustable and could be extended to other spatial scales, ecosystems and organisms. The framework also provides spatially and temporally explicit projections, which will help to develop dynamic approaches of species distribution accounting for demographic processes, such as migration, mortality and fecundity (e.g., Anderson et al., 2009; Morin et al., 2007; Zurell et al.,

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2009). The framework could therefore have important implications for conservation issues by helping river managers to prioritize their action for mitigating the effects of climate change on freshwater biodiversity.

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