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Predicting the Potential Impacts of Climate Change on Stream Fish Assemblages

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Abstract.—Stream fish are expected to be influenced by climate change as they are ectothermic animals living in lotic systems. Using fish presence–absence records in 1,110 stream sites across France, our study aimed at (1) modeling current and future distributions of 35 stream fish species, (2) using an ensemble forecasting approach (i.e., several general circulation models [GCM] × greenhouse gas emission scenarios [GES] × statistical species distribution models [SDM] combinations) to quantify the variability in the future fish species distribution due to each component, and (3) assessing the potential impacts of climate change on fish species distribution and assemblage structure by using a consensus method that accounted for the variability in future projections.

We found that future projections of fish species distribution were relatively consistent among GCM × GES × SDM combinations, with 57% of the total variability between projections being consensual. The statistical method used was the main driver of the variability between future projections, accounting for 70% of the total variation. The projections were next influenced by the GCMs, whereas the importance of GES was weak. Nonetheless, both the amount of consistency among projections and the relative contribution of each uncertainty component to the variability in projections were different depending on the species considered. Concerning the impacts of climate change, only the scarce coldwater species (e.g., brown trout *Salmo trutta fario*) were predicted to experience a strong reduction in their distributional area, whereas most coolwater and warmwater fish species (e.g., barbel *Barbus barbus,* European chub *Leuciscus cephalus*) were predicted to colonize many newly suitable sites located in intermediate streams or upstream. As a result, local species richness was forecasted to increase greatly, and high turnover rates indicated fundamental changes in the structure of assemblages in the future. Moreover, we found that climate change could result in remarkably different impacts on the structure of fish assemblages depending on their position along the upstream–downstream gradient.

These findings may be viewed as a first estimation of climate-change impacts on European freshwater fish biodiversity. They also illustrate the need to account for different sources of uncertainty when estimating the potential impacts of climate change on species distribution modifications.

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Introduction

There is now ample evidence that the on-going climatic change will irreversibly affect natural species across the globe (Hughes 2000; Sala et al. 2000; McCarthy 2001; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Among the predicted changes, climate change is expected to induce diverse functional (e.g., phenology, physiology) and structural (e.g., changes in species distribution, range contractions, poleward movements) ecological responses among organisms (Parmesan et al. 1999; Thomas and Lennon 1999; Beaugrand et al. 2002; Hickling et al. 2006; Menzel et al. 2006; Jetz et al. 2007; Levinsky et al. 2007; Parmesan 2007). Responses of single species to future changes would result in progressive species association shifts and potentially cause fundamental changes in the structure and composition of current assemblages (Hughes 2000; Walther et al. 2002).

To date, many studies have attempted to predict the future distribution of animal and plant species by relating species distribution and climate-change scenarios (e.g., Berry et al. 2002; Peterson et al. 2002). Such correlative models have been applied to a large diversity of taxa, including plants (e.g., Sætersdal et al. 1998; Thuiller 2004; Ohlemüller et al. 2006), insects (e.g., Peterson et al. 2004), mammals (e.g., Thuiller et al. 2006a; Levinsky et al. 2007), herptiles (e.g., Araujo et al. 2006), and birds (e.g., Peterson 2003; Jensen et al. 2008; Virkkala et al. 2008). Nevertheless, most of these previous studies only used a single statistical modeling technique, whereas a wide range of these models have now been developed and are easily applied to large data sets.

In recent years, some studies have questioned the errors and uncertainties embedded in such statistical models (Thuiller 2004; Araujo et al. 2005; Hartley et al. 2006; Heikkinen et al. 2006; Lawler et al. 2006; Araujo and New 2007). Indeed, projections of the future distribution of a single species could differ considerably depending on the statistical models, and different models could even predict opposing outcomes (Araujo et al. 2005; Lawler et al. 2006; Pearson et al. 2006). Consensus methods and ensemble forecasting represent approaches to explore the range of resulting projections and to reduce the model-based uncertainty in predictions of species distribution (Thuiller 2004; Araujo and New 2007; Marmion et al. 2009). They are based on the combinations of different single-models and are very attractive because they have the advantages of taking into account the variability of the predictions derived from the individual models.

Nevertheless, other sources of uncertainty may lead to contrasting projections of future species distribution. Indeed, through the Intergovernmental Panel on Climate Change framework, several general circulation models (GCM) have been developed by different meteorological research centers to represent physical processes in the atmosphere, ocean, cryosphere, and land surface, thus simulating the response of the global climate system to increased greenhouse gas concentrations (IPCC 2007). Each GCM includes different storylines defined by the Special Report on Emission Scenarios (Nakicenovic and Swart 2000). Future greenhouse gas emissions will actually be the product of very complex dynamic systems, determined by driving forces such as demographic and socioeconomic developments, as well as technological change. Their future evolution is highly uncertain, and scenarios are thus alternative images of how the future might unfold.

Although crucial when forecasting species distributions under climate change, the relative importance of these different sources of uncertainty remains poorly investigated.

Thus, combining different statistical modeling techniques, GCM and gas emission scenarios (GES) may increase the reliability of the predictions and greatly enhance our understanding of the potential impacts of climate change on species distribution.

In that context, this study focused on applying a range of species distribution models (SDM), GCM, and GES to a set of fish species occurring in French streams. Compared to other organisms such as birds or plants, species distribution modeling approaches have been applied less often to predict the impacts of the on-going climate change on freshwater fish species, except in North America (e.g., Minns and Moore 1995; Eaton and Sheller 1996; Magnuson et al. 1997; Jackson and Mandrak 2002; Mohseni et al. 2003; Chu et al. 2005; Sharma et al. 2007). Stream fish could yet be highly vulnerable to broadscale environmental changes as most fish species have no physiological ability to regulate their body temperature (Wood and McDonald 1997).

Thus, this study has three main objectives: (1) to model current and future distributions of the most common stream fish species in France, (2) to use an ensemble forecasting approach (several GCM × GES × SDM combinations) to quantify the uncertainty in the future fish species distribution due to each component, and (3) to assess the potential impacts of climate change on fish species distribution, and on structure and diversity of species assemblages, by using a consensus method that accounted for the uncertainties in future projections.

Fish Data

Data were extracted from the ONEMA (Office National de l'Eau et des Milieux Aquatiques) database. ONEMA is the national fisheries organization in charge of the protection and conservation of freshwater ecosystems in France. Among the surveyed sites, 1,110 reference (i.e., least impacted by anthropogenic perturbations) sites were selected. These sites were widespread throughout the national boundaries and they covered all types of streams, from small headwaters to large lowland rivers. Two standardized electrofishing methods were used depending on the river depth and width: smaller rivers were sampled by wading and larger ones by boat. Species presence–absence data were used to describe fish assemblages, and only data of fish species that occurred in at least 25 sites were retained to reduce errors associated with excessively small sample sizes (Stockwell and Peterson 2002; Barry and Elith 2006). This resulted in a data set of 35 fish species.

Current and Future Climate Conditions

Three variables related to fish ecological requirements were used to describe climate conditions: mean annual precipitation, mean annual air temperature, and annual air temperature amplitude derived from the difference between mean air temperature of the warmest month and mean air temperature of the coldest month. Only mean annual precipitation was log-transformed to correct for nonnormal distribution. The CRU CL 2.0 (Climatic Research Unit Climatology 2.0 version) data set (New et al. 2002) at a resolution of $10' \times 10'$was chosen to describe the current climate. Climate conditions were averaged for the period 1961–1990.

Future climate predictions were averaged for the time period 2051–2080 (referred to as the 2080 scenario) for each of the three climatic descriptors. These predictions were derived from three GCM: HadCM3 (Hadley Centre for Climate Prediction and Research), CGCM2 (Canadian Centre for Climate Modeling and Analysis), and CSIRO2 (Commonwealth Scientific and Industrial Research Organisation). Four GES from the *Special Report on Emission Scenarios* of the Intergovernmental Panel on Climate Change (Nakicenovic and Swart 2000) were used for each of the GCM. These four GES were chosen to represent different degrees of climate change severity with expected concentrations in CO_2 by the year 2100 of 960, 840, 620, and 550 ppm for the A1FI, A2, B2, and B1, respectively. The A1FI scenario may be viewed as the "high emission" scenario and is mainly fossil-fuel intensive. The A2 scenario ("medium-high") represents high human population growth and slow technological advancement, whereas the B2 scenario ("medium-low") has moderate population growth with more environmental protection. The B1 scenario is considered as the "low emission" scenario with particular emphasis on global solutions to economic, social, and environmental sustainability. For each sampling site, values of the three studied climatic variables were extracted for all GCM × GES combinations, thus providing 12 different projections for future climate conditions.

Environmental Characteristics

Although a large number of studies applied strictly bioclimatic models to predict the future impacts of climate change (e.g., Sætersdal et al. 1998; Berry et al. 2002; Thuiller et al. 2005; Virkkala et al. 2008), recent studies have demonstrated that large-scale modeling studies, which did not account for nonclimatic variability (e.g., topography), may have underestimated the potential impacts of climate change (Trivedi et al. 2008). As stream ecosystems have great variability in their environmental conditions, ranging from small headwater streams to large lowland channels, it is crucial to take into account such local factors when addressing the potential impacts of climate change. Therefore, we included both climatic and nonclimatic factors in our species-models, allowing us to assess the potential responses of fish assemblages both at the large scale (i.e., all of France) and along the upstream–downstream gradient.

At each site, six variables were measured to describe environmental conditions: SDB (surface area of the drainage basin above the sampling site, km^2), DS (distance from the headwater source, km), WID (mean stream width, m), DEP (mean water depth, m), SLO (river slope, %), and ELE (elevation, m). A principal component analysis (PCA) was used to summarize the covariation between DS and SDB, and the first axis was kept as a synthetic variable describing the position of sites along the upstream–downstream gradient G. Following Oberdorff et al. (2001), a rough approximation of local velocity (V) derived from the Chezy formula was calculated from WID, DEP, and SLO. Thus, three variables (i.e., ELE, G, and V) were used to describe environmental characteristics at each site.

Because these three environmental variables were correlated with climatic variables, we adjusted these variables for the three climatic variables by fitting generalized additive models (GAM) with four degrees of freedom (Leathwick et al. 2006; Thuiller et al. 2006b). The residuals of each of the GAM indicated the deviation from the average G, V, and ELE expected with their climatic conditions. We used these three residuals as individual predictors.

Species Distribution Modeling

For each fish species, seven statistical methods were used to model fish distribution: (1) generalized linear models (GLM) are extensions of linear models able to handle nonlinear relationships by fitting parametric terms (McCullagh and Nelder 1989); (2) GAM are nonparametric extensions of GLM using a smoother to fit nonlinear functions (Hastie and Tibshirani 1990); (3) multivariate adaptive regression splines

(MARS) are an alternative regression-based method for fitting nonlinear responses, using piecewise linear basis functions (Friedman 1991); (4) linear discriminant analysis (LDA) finds the linear combination of predictor variables that best discriminates between the defined groups; (5) classification and regression trees (CART) use recursive binary partitioning to split the data into increasingly smaller, homogenous, subsets until a termination is reached (Breiman et al. 1984); (6) aggregated boosted trees (ABT) compute a sequence of single regression trees by combining a boosting algorithm and a regression-tree algorithm (Friedman 2001; De'ath 2007); and (7) random forests (RF) are a model-averaging approach generating hundreds or thousands of random trees built from a set of randomly selected predictors and observations (Breiman 2001). Each modeling technique was implemented using the same six input variables and following the same modeling procedure (summarized in Figure 1).

First, we randomly selected 70% of the sites within each river unit to calibrate the models,

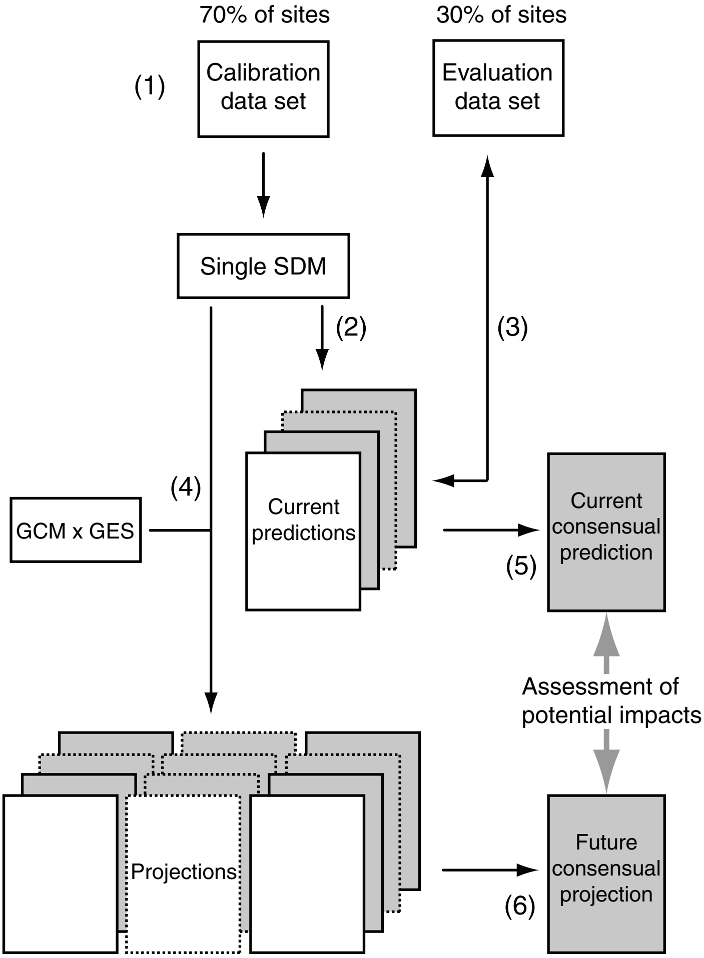

Figure 1. Modeling procedure (see text for details). It indicates the division of data into training and validation sets followed by its use in various general circulation models (GCM) and greenhouse gas emission scenarios (GES) models. SDM: species distribution models.

allowing us to maintain an equal proportion of each river unit in the calibration (777 sites) and validation (333 sites) data set (step 1, Figure 1). Then, we calibrated each SDM using the calibration data set. Current predictions were subsequently calculated from the calibrated models for all of the 1,110 sites (step 2, Figure 1). These predictions of probability of occurrence of each species were converted into presence–absence using a threshold maximizing the sum of two measures: sensitivity (i.e., the percentage of presence correctly predicted) and specificity (i.e., the percentage of absence correctly predicted).

The next step was to evaluate the current predictive performance of each SDM using the validation set (step 3, Figure 1). Two measures of performance were used: the area under the curve (AUC) of a receiver operating characteristic plot (Fielding and Bell 1997; Pearce and Ferrier 2000) and the overall accuracy of each model. 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). The AUC does not require transformation of the predicted probability of occurrence in binary data and it is not biased by species prevalence (Fielding and Bell 1997). The accuracy is based on binary predictions and measures the percentage of both presence and absence correctly predicted, thus allowing one to quantify the match between predicted and observed distributions using an independent data set.

Overall, the performances of the individual models in predicting current distributions were good (Figure 2). Across the 35 species, the mean AUC ranges from 0.72 ± 0.08 for the CART to 0.85 ± 0.05 for the RF method, and the mean accuracy from 74.50 ± 4.64% for the MARS to 79.50 ± 6.57% for the CART method. This last result indicated that around 75% of the sites were predicted in agreement with the observations. Performance measures were coarsely equivalent for all the seven statistical method (except the AUC of the CART method), whereas they differed greatly depending on fish species (Figure 2).

Given their good predictive performances, the calibrated models were then used to project fish species distributions for year 2080 under each of 12 GCM × GES combinations, assuming unlimited dispersal capacity of fish species (step 4, Figure 1). The future probabilities of occurrence were then transformed into presence–absence values by using the same threshold value as for current predictions.

All procedures were repeated 100 times in order to increase the robustness of the results.

Quantifying Uncertainty in Species Distribution Forecasting

The three factors tested here (seven SDM × three GCM × four GES) resulted in 84 projections for each 35 species, each of which representing a possible state of future species distributions in 2080. Following Thuiller (2004), we used a PCA on the projected presence–absence of fish species resulting from the 84 combinations of SDM, GCM, and GES. Although the use of PCA is faulted when used with binary data (e.g., nonlinear relationships), PCA using presence–absence data has been shown to perform well and to provide useful and informative results (Hirst and Jackson 2007). These authors suggested that other multivariate ordination methods could be used (e.g., principal coordinates analysis) to permit the use of resemblance measures more adapted to presence–absence data. To date, only PCA has been performed to summarize the outputs of species distribution model (i.e., probability of occurrence, Marmion et al. 2009) or species range shifts (Thuiller 2004; Araujo et al. 2005), and additional research is clearly needed.

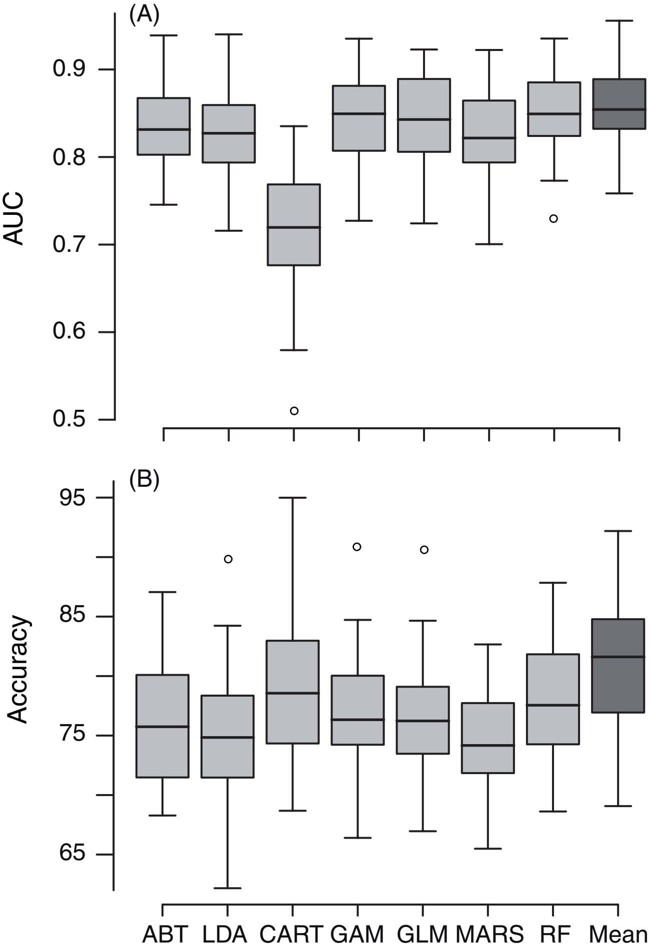

Figure 2. Predictive performance of statistical models based on the predictions of current distributions: (a) area under the curve (AUC), and (b) accuracy (i.e., percentage of correctly predicted presence and absence) for the 35 fish species. Individual statistical methods (light gray) and consensus approach based on the averaging of the whole ensemble of predictions (dark gray—Mean) are presented. For each box plot, the median (line within the box), first and third quartiles (box), non-outlier range (wiskers), and outliers (dot) are shown. ABT = aggregated boosted trees; LDA = linear discriminant analysis; CART = classification and regression trees; GLM = generalized linear models; MARS = multivariate adaptive regression splines; and RF = random forests.

Here, the first PCA axis is equivalent to a line that goes through the centroid of all sets of model projections and minimizes the square of the distance of each set of projections to that line (Araujo et al. 2005). This axis thus captured consistent patterns in fish species distributions across the different projections. If the 84 projections were perfectly unrelated (i.e., all pairwise comparisons equal zero), each axis would explain 1/84 of the total variation. The variability explained by the first axis represented the consensus (i.e., the shared information) among the whole set of projections (Thuiller 2004). This percentage of consensus was related to species occurrence using a generalized additive model.

Globally, the first axis of the consensus PCA explained 57% of the total variability among projections across all fish species. As most other studies dealing with consensus projections under different combinations of uncertainty sources have not quantified this consensus (e.g., Marmion et al. 2009; Roura-Pascual et al. 2009), comparisons with other taxonomic groups remain difficult. However, our result was consistent with the few studies that described consensus responses in predicting impacts of climate change. For instance, Thuiller (2004) found a consensus axis accounting for 56.1% of the variability in species turnover across projections for 1,350 European plant species for 2050. Araujo et al. (2006) showed higher percentage of consensus in European amphibian and reptile responses with 80% of variability across the projections captured by the first axis, whereas only 29.9% of this variability could be summarized by a consensus axis for bird species in Great Britain (Araujo et al. 2005).

In this study, we also found that the percentage of consensus across projections varied greatly depending on fish species. It ranged from 30.8% (threespine stickleback *Gasterosteus aculeatus*) to 69.9% (gudgeon *Gobio gobio*) (Table 1). For 12 (i.e., one-third) of the studied fish species, the consensus was higher than 60%, whereas it was lower than 50% for 14 fish species. This result indicated that the three uncertainty sources studied here (SDM, GCM and GES) could lead to very different projections in some cases (e.g., threespine stickleback, burbot *Lota lota*, and European bullhead *Cottus gobio*), whereas other species show very consistent projected distributions (e.g., gudgeon, roach *Rutilus rutilus*, and European chub *Leuciscus cephalus*). Moreover, it appeared that the percentage of consensus was significantly ($P = 0.011$) related to fish occurrence. The percentage of consensus was the lowest for the rarest fish species (Figure 3), indicating that predicted future distributions of uncommon species would be more variable depending on the selected SDM × GCM × GES combination. This trend could be explained by the small number of occurrences used to calibrate the distribution models of rare species. Statistical methods may actually vary in how they model the shape, nature, and complexity of species' response (Guisan and Zimmermann 2000). When few records are available, a species ecological niche may be difficult to model and divergences between statistical methods may increase.

To quantify the relative contribution of each of the three uncertainty sources to the variability in projections of fish distribution, we related the entire set of projections to the three factors using a generalized linear model. We assessed the proportion of variability explained by each factor as the ratio between the deviance explained by one factor and the null deviance. This procedure was performed for each fish species separately.

Overall, variability in species projections was mainly explained by the statistical modeling technique (69.7%), followed by the GCM (24.4%), whereas variability across climate-change scenarios was weak (5.9%) (Figure 4).

Here again, it is worth noting that the proportion of variability explained by each factor varied greatly among fish species (Table 1). Indeed, for 5 of the 35 fish species, GCM appeared to be the primary source of uncertainty in future species distribution, and emission scenarios were the secondary source of uncertainty for six fish species. Addressing the relationships between fish species characteristics and the relative importance of different uncertainty sources in species projections should thus be helpful to better predict the potential impacts of climate change on fish species distributions. To date, the paucity of similar studies precludes a wider comparison, and additional investigations are thus clearly needed.

Table 1. Consensus analysis and sources of variability in fish species projections under climate change for 2080. Given are the percentage of consensus among the different projections and the percentage of variability in projections explained by the species distribution model (SDM), the global circulation model (GCM), and the greenhouse gas emission scenario (GES) for each fish species. Higher percentages of consensus indicate a high degree of consistency between projections. Higher percentages of source of variability indicate that most of the variability in projections is due to the considered source of uncertainty.

				Source of variability		
Family	Fish species	Code	Consensus	SDM	GCM	GES
Anguillidae	European eel *Anguilla anguilla*	Ana	68.10	55.82	14.10	30.07
Balitoridae	Stone loach *Barbatula barbatula*	Bab	62.38	93.56	6.03	0.41
Centrarchidae	Pumpkinseed *Lepomis gibbosus*	Leg	55.39	85.15	11.26	3.59
Cottidae	European bullhead *Cottus gobio*	Cog	41.45	78.72	4.97	16.31
Cyprinidae	Bream *Abramis brama*	Abb	62.69	97.16	2.00	0.85
	Spirlin *Alburnoides bipunctatus*	Alb	53.53	48.66	48.00	3.34
	Bleak *Alburnus alburnus*	Ala	69.86	87.98	11.04	0.98
	Barbel *Barbus barbus*	Bar	62.36	55.37	35.35	9.28
	Mediterranean barbel *B. meridionalis*	Bam	45.08	96.34	0.13	3.53
	White bream *Blicca bjoerkna*	Blb	49.94	66.98	29.68	3.34
	Crucian carp *Carassius carassius*	Cac	45.18	93.35	2.06	4.60
	Nase *Chondrostoma nasus*	Chn	50.35	60.58	38.12	1.30
	French nase *C. toxostoma*	Cht	44.31	80.12	7.49	12.39
	Common carp *Cyprinus carpio*	Cyc	58.90	88.68	8.11	3.21
	Gudgeon *Gobio gobio*	Gog	69.91	94.76	2.45	2.79
	European chub *Leuciscus cephalus*	Lec	68.72	30.24	53.81	15.94
	Eurasian dace *L. leuciscus*	Lel	65.12	61.82	35.19	2.99
	Blageon *L. souffia*	Les	48.04	37.89	47.58	14.52
	Eurasian minnow *Phoxinus phoxinus*	Php	56.00	62.16	35.41	2.43
	European bitterling *Rhodeus amareus*	Rha	58.18	43.95	54.85	1.20
	Roach *Rutilus rutilus*	Rur	69.46	48.37	47.99	3.64
	Rudd *Scardinius erythrophthalmus*	Sce	45.23	58.05	39.64	2.31
	Tench *Tinca tinca*	Tit	58.18	61.23	36.39	2.38
Esocidae	Northern pike *Esox lucius*	Esl	64.97	79.45	20.27	0.28
Gasterosteidae	Threespine stickleback *Gasterosteus aculeatus*	Gaa	30.82	75.55	23.42	1.03
	Ninespine stickleback *Pungitius pungitius*	Pup	41.38	87.10	7.86	5.04
Ictaluridae	Black bullhead *Ameiurus melas*	Amm	41.32	77.48	21.78	0.75
Lotidae	Burbot *Lota lota*	Lol	35.52	88.03	11.67	0.30
Percidae	Ruffe *Gymnocephalus cernuus*	Gyc	59.42	94.25	5.60	0.16
	Eurasian perch *Perca fluviatilis*	Pef	60.50	52.09	32.78	15.13
	Zander *Sander lucioperca*	Sal	45.44	88.13	11.00	0.86
Petromyzontidae	European brook lamprey *Lampetra planeri*	Lap	45.63	38.57	43.93	17.51
Salmonidae	Atlantic salmon *Salmo salar*	Sas	51.52	70.01	23.69	6.30
	Brown trout *S. trutta fario*	Sat	62.54	60.65	24.47	14.88
	Grayling *Thymallus thymallus*	Tht	42.26	41.20	54.50	4.30

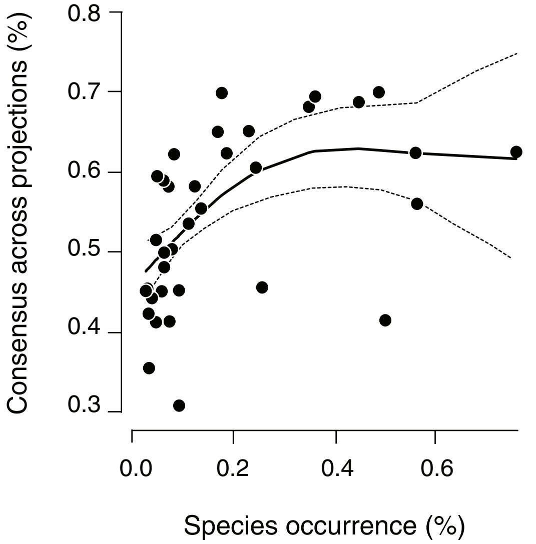

Figure 3. Consensus across future projections of fish species distribution resulting from the 84 combinations of species distribution models, general circulation models, and greenhouse gas emission scenarios for each 35 fish species as a function of the observed fish species occurrence. A generalized additive model (GAM) was fitted to model this relationship. Values predicted by this GAM are plotted (solid line) as well as their associated standard error estimates (dashed lines).

Recently, it has become clear that species projections are sensitive to the statistical methods used to calibrate the models (Araujo et al. 2005; Elith et al. 2006; Pearson et al. 2006). Here, our results are consistent with those of previous studies that showed that variability across projections from different modeling techniques could be large and may even hide the variability of using a range of climate-change scenarios (Thuiller 2004). Therefore, these results demonstrate that care must be taken when assessing the potential impacts of climate change from species distribution forecasting and that special attention should be paid to choose the projections with best consensus, that is those that best summarize agreements among ensemble projections generated under different uncertainty sources.

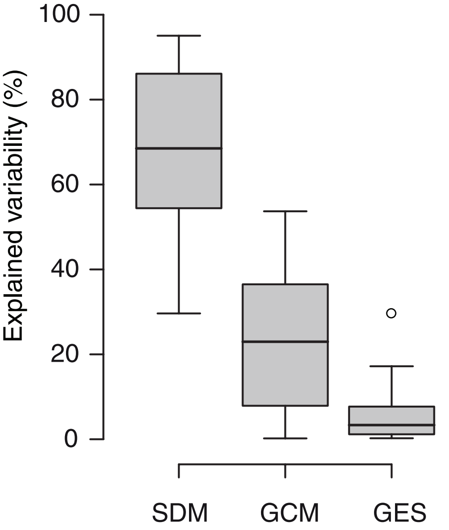

Figure 4. Percentage of variability among all projections explained by the three different uncertainty sources tested: species distribution model (SDM), general circulation model (GCM), and greenhouse gas emission scenario (GES). See Figure 2 for details.

Consensus Forecasting

Given the relatively low percentage of variability explained by the GCM and GES in the different fish species projections, a single GCM (HadCM3), combined with a single emission scenario (A1FI), was arbitrarily chosen to assess the potential impacts of climate change on stream fish assemblages. Nevertheless, to deal with the variability resulting from the species distribution models, we used consensus predictions that combined the whole predictions ensemble obtained from single models.

Consensus methods have recently been applied in broadscale conservation studies in order to deal with the variability due to SDM (Araujo et al. 2005, 2006; Hartley et al. 2006; Roura-Pascual et al. 2009). There are many different ways to build consensus predictions. Some methods are based on global (i.e., output of several single models) median, mean, or weighted-average functions, whereas some others first retain certain methods based on selection criteria (e.g., AUC, PCA) and then combine these selected methods using an average or median function (Araujo and New 2007; Marmion et al. 2009). Marmion et al. (2009) suggested that the consensus method based on the computation of the mean value of the predictions ensemble provides significantly more robust predictions than all of the single models and other consensus methods. Thus, for both current and future periods, we averaged the current (step 5, Figure 1) and future (step 6, Figure 1) predictions across the seven statistical modeling techniques, respectively. This resulted in a single prediction at each site, for each species and for each time period. We then converted these current and future consensus predictions into binary values using a threshold selected in the same way as described for single models. As for individual statistical models, we examined the performances of this consensus approach in predicting the current distributions of fish species on the validation data set. Across the 35 species, AUC averaged 0.86 ± 0.05, and accuracy 81.08 ± 5.52% (Figure 2). Therefore, the consensus approach performed very well in predicting current distributions, even better than all the individual methods, strengthening the choice of this approach to evaluate subsequently the impacts of climate change on fish species.

Assessing the Potential Impacts of Climate Change on Stream Fish Species Distribution

First, we compared the current species distribution with the potential future distribution for each of the 35 species by calculating the change in probability of occurrence between the current situation and the 2080 scenario for all 1,110 sites. A negative value indicated that the site would be less suitable than at present and a positive indicated increased suitability.

On average, changes in probability of occurrence ranged from –36.6% for brown trout (Sat) to 44.6% for blageon (Les) (Figure 5). Like results found for many other organisms (e.g., Peterson et al. 2002; Peterson 2003), individual fish species responded idiosyncratically to climate change. Nonetheless, three groups of responses to climate change could be coarsely identified (Figure 5). A first group, including seven species such as blageon (Les), European chub (Lec), or barbel (Bar), was characterized by a global increase in the probability of occurrence (on average, +25.6%). All of these species were cool- and warmwater species with a large range of thermal tolerance. This positive response contrasted with the strong decrease in occurrence of two coldwater species—European bullhead (Cog) and brown trout (Sat)—for which none of the 1,110 sites would become more suitable in the future for this second group. Last, a third group of species composed of 26 species such as roach (Rur), black bullhead (Amm), or northern pike (Esl) could have an intermediate response to these two previous groups. On average, these fish species would change their probability of occurrence by +5.6%, indicating a slightly positive response to climate change. Nevertheless, some sites could also become less suitable in the future. For these species, local extinctions in some areas would be compensated by colonization of new thermally suitable sites.

To analyze in greater detail the changes in fish species spatial distribution and to highlight potential range reductions or expansions, we compared maps of the predicted current and future distribution of some species. The results were illustrated for one species of each group described above: barbel (Bar), northern pike (Esl), and brown trout (Sat) (Figure 6).

Barbel, a rheophilic species relatively common in French streams, was predicted to ex-

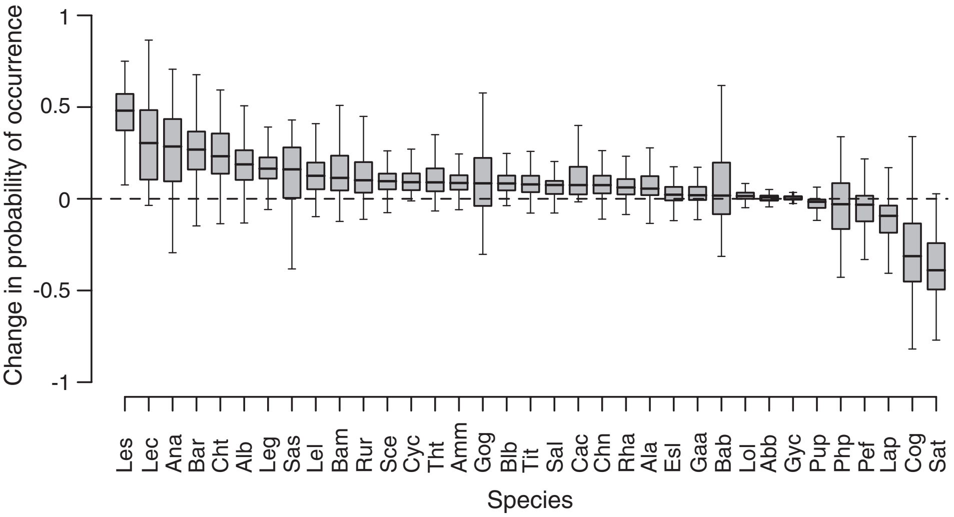

Figure 5. Changes in the probability of occurrence for each of the 35 fish species predicted for 2080 under the scenario HadCM3 A1FI. Change is expressed as the difference between the consensual current and future predictions resulting from the averaging of the seven statistical methods. See Figure 2 for details and Table 1 for species codes.

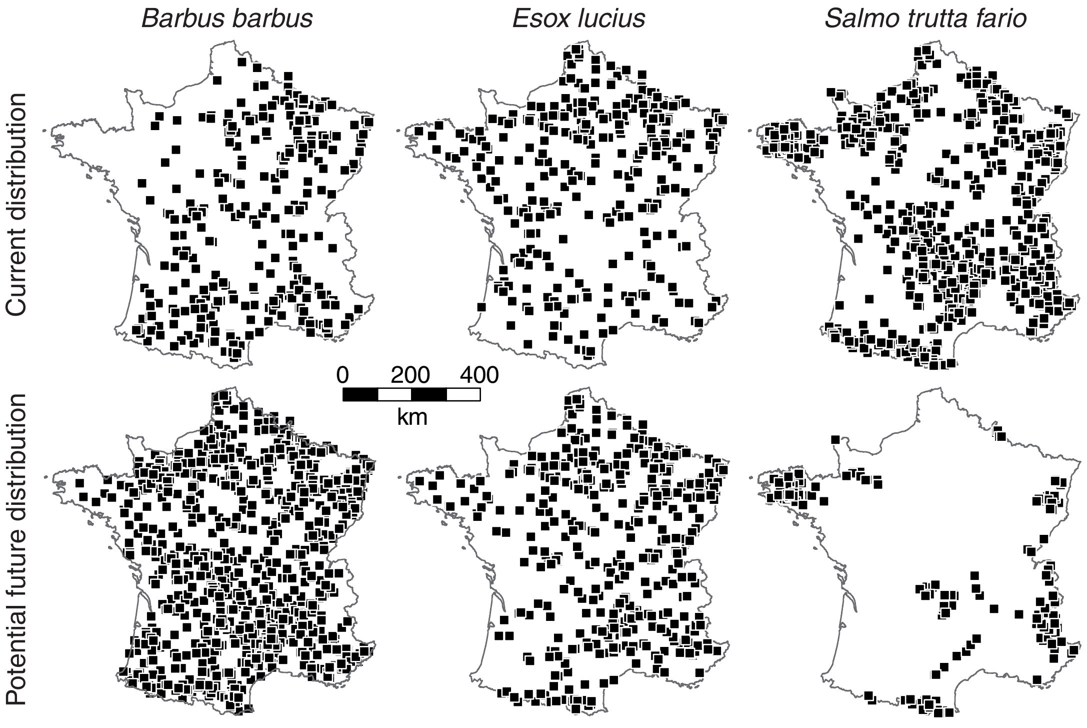

Figure 6. Predicted spatial distribution of three fish species (barbel, northern pike, and brown trout) for current (1961–1990) and future (2051–2080) periods.

pand its range greatly under climate change. The consensus model did not predict any extinction, but rather, barbel may be able to colonize a large number of areas where it does not currently occur, for example the Pyrenees, Massif Central, and the Jura mountains. It could also expand its range to northwestern France. Northern pike, a predatory species living among dense vegetation, was predicted to move to new suitable habitats mainly in eastern France and in mountainous areas, whereas it could suffer from local extinctions in the western part of France where it currently occurs in many sites. Finally, brown trout was predicted to be the most severely affected by climate change and to be most restricted relative to its current distributional area. Indeed, brown trout is a salmonid species living in cold and well-oxygenated waters mainly in the head of the watersheds. The consensus model predicted this species to be currently distributed in mountainous regions (e.g., Pyrenees, Alps, Massif Central, and Jura) and also in coastal streams of northwestern France. But in 2080, brown trout may become extinct in a large number of these areas and restrict its distribution to the most upstream sites of the mountainous regions and some streams of northwestern France, where habitats could remain suitable for the ecological requirements of this species.

Our results thus illustrated that coldwater species living in headwater streams would undergo a very deleterious effect of climate change by reducing their distributional area, whereas cool- and warmwater fish species occurring currently downstream would expand their range by migrating to sites located in intermediate streams and upstream.

Overall, these results were in agreement with those obtained in North America, which consistently predicted a decrease in salmonid distribution but divergent results for cool- and warmwater species. Those species could actually increase or decrease their distribution depending on species and studies (Eaton and Sheller 1996; Rahel et al. 1996; Mohseni et al. 2003; Chu et al. 2005; Sharma et al. 2007). Nevertheless, compared with other taxa for which the impacts of climate change could be very detrimental (e.g., Thomas et al. 2004, 2006; Jetz et al. 2007), the global assessment for French stream fish species was rather positive as most fish were predicted to expand their distributional area. This global positive impact of climate change on stream fish distribution may result from the scarce diversity of coldwater species in French fish assemblages compared to cool- and warmwater species, which have a larger range of thermal tolerance.

Assessing the Potential Impacts of Climate Change on Stream Fish Assemblages

Two measures were used to assess the potential impact of climate change on fish assemblages in French streams. First, we calculated the predicted current and future local species richness in each of the 1,110 sites by summing the predicted current and future present species obtained from the consensus predictions, respectively. Current and future species richness were then compared. Second, we calculated the number of species predicted to newly arrive (species gain [SG]) and the number 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

$$\text{Species turnover} = 100 \times \frac{SG + SL}{SR + SG}, \quad (1)$$

where SR is the current species richness (Peterson et al. 2002). A turnover value of zero indicated that the predicted assemblage in the future would be the same as the current assemblage, whereas a turnover value of 100 indicated that the assemblage would be completely modified under climate change.

Both the change in species richness and the turnover rate were related to the upstream–downstream gradient *G* using generalized additive models in order to highlight potential spatial patterns in the response of fish assemblages to future climate change. Indeed, the upstream–downstream gradient, which structures watersheds, is known to influence greatly the distribution of individual fish species (Buisson et al. 2008) and, thus, the structure of fish assemblages.

Mean local species richness was predicted to increase strongly from the current 10.3 ± 8.0 species per site to 19.5 ± 7.3 species in 2080. Only 20 sites would show a decline in species number, whereas at least 10 species would be gained in 43% of the 1,110 sites. The change in species richness would vary according to the position along the upstream–downstream gradient. Indeed, the relationship between the change in species richness and the position along the upstream–downstream gradient *G* was slightly bell-shaped (Figure 7). This indicated that species richness would have the largest increase in the midstream sites, which are mainly located at medium elevations (e.g., foothills at the base of the Pyrenees and the Alps mountains), whereas downstream sites would be colonized by a limited number of species. The most upstream sites would also gain new species, but more moderately than midstream sites.

On average, turnover equaled 67.0 ± 26.2% (mean ± SD across the 1,110 sites). A turnover value higher than 50% (i.e., at least half of the current pool of species in a site could be changed in the future) was achieved in more than two-thirds of the sites. Species turnover was negatively related to the upstream–downstream gradient (Figure 7), indicating that upstream assemblages would be highly modified due to the arrival and/or the local extinction of species. On the contrary, very few changes would occur in the composition of downstream assemblages.

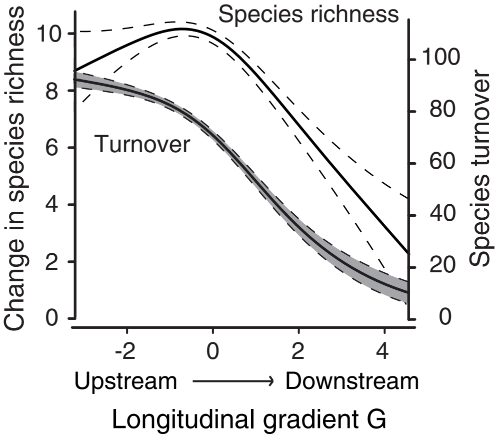

Figure 7. Predicted modifications of fish assemblages along the upstream–downstream gradient for 2080 under the scenario HadCM3 A1FI. Predictions (solid line) and associated standard error estimates (dashed lines) from fitted generalized additive models are shown.

The predicted large increase in fish species richness in French streams very likely resulted from the great number of positive individual responses of cool- and warmwater fish species to climate change. As French fish assemblages contain few coldwater species, more fish species would expand their distribution to newly suitable areas than reduce it. This result is in agreement with the increase in species richness, which has already been observed for marine (Hiddink and ter Hofstede 2008) and freshwater fish species (Daufresne and Boët 2007) during the past decades, but also for other organisms (e.g., plants: Grabherr et al. 1994; butterflies: Menendez et al. 2006). However, results are more contrasted when predicting species richness in future (e.g., plants: Broennimann et al. 2006; mammals: Levinsky et al. 2007; butterflies: Wilson et al. 2007). For freshwater fish, our results are overall concordant with those found by Minns and Moore (1995) in Canada, where an average increase in species richness of 31.8 species for the studied tertiary watersheds was predicted.

Although appearing as a fairly positive aspect for fish fauna diversity, an increase in species richness may, however, hide local extinctions of species and lead to great changes in the structure of fish assemblages. Our findings suggested that fish assemblages' composition in French streams could be strongly modified under climate change. The species turnover rate was slightly higher than 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. 2005). Despite the small loss of fish species from their current suitable sites, severe ecological perturbations may thus occur in future and species' association shifts may cause substantial changes in assemblage structure and function.

Last, we predicted that changes in species richness and assemblages' composition could be highly contrasted depending on the location along the upstream–downstream gradient. Upstream assemblages could be the most sensitive to climate change as species richness was predicted to increase greatly and the assemblages' composition to be highly modified, whereas presently, these assemblages have low diversity. In comparison, downstream assemblages could be more resilient. These findings highlighted the importance of topography and local factors when assessing the effects of climate change on species. They could have important implications for identifying stream reaches and geographic areas that would need priority conservation measures.

Some Limitations to the Assessment of Potential Impacts of Climate Change

Although the predicted impacts of climate change on stream fish species and assemblages were obtained from an ensemble forecasting approach, which appears a robust predictive method (Araujo and New 2007), they should only be viewed as potential future impacts. Indeed, we only identified the future habitat suitability for fish species, and its possible consequences on fish assemblages, without taking into account many factors acting at different spatial or temporal scales which could hinder these changes to occur (Pearson and Dawson 2003; Dormann 2007).

First, both natural and physical barriers may obstruct fish displacements to newly suitable sites. In this study, we assumed that a given species could reach every site within France that would become suitable in the future. Although France has a large system of canals linking the internal river units, thus allowing potential interwatershed transfer of aquatic organisms, adjacent rivers may, however, be disconnected if they are not included in the same watershed. Natural dispersal of fish species to river units where they do not occur at present may thus be limited by the insular nature of watersheds, but also by artificial obstacles such as weirs or dams, which result in stream fragmentation. Moreover, fish species may be unable to disperse at a sufficient rate to keep up with the changing climate. In the present study, we assumed that all the 35 fish species have the same dispersal ability. Although very common, this assumption is critical as dispersal ability is related to species' biological characteristics (i.e., size: Jenkins et al. 2007) and life history traits (i.e., reproduction).

Second, we evaluated the potential impacts of climate change on fish species occurring within French boundaries. An underlying assumption was that there was a barrier around France, thus preventing any other species from colonizing French streams regardless of whether suitable habitat could appear under climate change. Predicted changes in species richness and assemblages' composition could be greatly underestimated if suitable habitat for species outside France would exist in future, especially in downstream parts of river units where very few changes are expected. These nonnative species could also become invasive and, like nonnative species occurring presently in French streams, have an additional negative effect on species already suffering from range reductions or displacements caused by climate change. Indeed, these nonnative species have often wider environmental tolerances and may be more resilient to climate modifications than native species. Jackson and Mandrak (2002) illustrated this effect by showing that smallmouth bass *Micropterus dolomieu,* 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. In our study, the five nonnative species occurring in French streams (i.e., black bullhead, crucian carp, common carp, pumpkinseed *Lepomis gibbosus,* and zander) were not among the fish species that were projected to colonize the largest number of sites under climate modifications (except pumpkinseed, Figure 5). Nonetheless, even slight changes in their distribution should be watched in future as they could cause local extirpations of species already vulnerable to climate change by increasing competitive interactions. Besides, taking into account such biotic interactions in the assessment of future impacts of climate change should urgently be addressed (Pearson and Dawson 2003; Guisan and Thuiller 2005). Here, we used a species-specific modeling approach and then combined the individual predictions to evaluate the impacts on fish assemblages. We thus assumed that the habitat suitability for a species was independent from the presence of other species. However, some of the predicted future assemblages are composed of species that did not occur together, historically. Therefore, the sustainability of such assemblages in the long term remains questionable.

Conclusions and Implications

The ensemble forecasting framework and consensus approach used in this study allowed us to assess the potential impacts of the ongoing climate change on French stream fish species by considering uncertainty due to some methodological issues such as the choice of the statistical methods. The predictions indicated that climate change will very likely affect fish species and thus result in fundamental changes in the composition and structure of fish assemblages. As expected, coldwater species would suffer from range reductions and local extinctions, whereas cool- and warmwater species would expand their range to newly suitable habitat, provided that they could be able to disperse to these areas. Given the small number of coldwater species in French streams, fish fauna could be more diverse in future, but fish assemblages completely modified. Nonetheless, many obstacles will arise before the existence and sustainability of such predicted assemblages. Contrasting impacts of climate change on stream fish assemblages along the upstream–downstream gradient revealed the importance of accounting for environmental gradients (e.g., altitudinal gradient) to predict more accurately the response of fauna and flora to climate change in forthcoming research.

Last, these findings should be viewed in terms of conservation and management strategies. Upstream areas would actually serve as refuge areas for coldwater species as well as new thermally suitable regions for cool- and warmwater species, whereas fish assemblages located downstream would be more resilient. This could have important implications in identifying stream reaches and geographic areas that would need priority conservation measures in response to climate modifications. Moreover, species predicted to be the most favored by climate change are either common species with low ecological or commercial importance (e.g., European chub) or exotic species (e.g., pumpkinseed). The species with the highest risk of local extinction is brown trout, which has a high recreational and commercial value and is also considered as a good biological indicator of river health. French streams and rivers could thus lose a large part of their supply of economic and ecological resources.

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References

Araujo, M. B., R. J. Whittaker, R. J. Ladle, and M. Erhard. 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14:529–538.

Araujo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712–1728.

Araujo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22:42–47.

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. Journal of Applied Ecology 43:413–423.

Beaugrand, G., P. C. Reid, F. Ibanez, J. A. Lindley, and M. Edwards. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692–1694.

Berry, P. M., T. P. Dawson, P. A. Harrison, and R. G. Pearson. 2002. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. Global Ecology and Biogeography 11:453–462.

Breiman, L. 2001. Random forests. Machine Learning 45:5–32.

Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth and Brooks, Pacific Grove, California.

Broennimann, O., W. Thuiller, G. Hughes, G. F. Midgley, J. M. R. Alkemade, and A. Guisan. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? Global Change Biology 12:1079–1093.

Buisson, L., L. Blanc, and G. Grenouillet. 2008. Modelling stream fish species distribution in a river network: the relative effects of temperature versus physical factors. Ecology of Freshwater Fish 17:244–257.

Chu, C., N. E. Mandrak, and C. K. Minns. 2005. Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. Diversity and Distributions 11:299–310.

Daufresne, M., and P. Boët. 2007. Climate change impacts on structure and diversity of fish communities in rivers. Global Change Biology 13:2467–2478.

De'ath, G. 2007. Boosted trees for ecological modeling and prediction. Ecology 88:243–251.

Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. Basic and Applied Ecology 8:387–397.

Eaton, J. G., and R. M. Sheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41:1109–1115.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, W. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Friedman, J. H. 1991. Multivariate adaptive regression splines. Annals of Statistics 19:1–141.

Friedman, J. H. 2001. Greedy function approximation: a gradient boosting machine. The Annals of Statistics 29:1189–1232.

Grabherr, G., M. Gottfried, and H. Pauli. 1994. Climate effects on mountain plants. Nature (London) 369:448.

Guisan, A., and N. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Hartley, S., R. Harris, and P. J. Lester. 2006. Quantifying uncertainty in the potential distribution of an invasive species: climate and the Argentine ant. Ecology Letters 9:1068–1079.

Hastie, T., and R. Tibshirani. 1990. Generalized additive models. Chapman and Hall, London.

Heikkinen, R. K., M. Luoto, M. B. Araujo, R. Virkkala, W. Thuiller, and M. T. Sykes. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30:751–777.

Hiddink, J. G., and R. ter Hofstede. 2008. Climate induced increases in species richness of marine fishes. Global Change Biology 14:453–460.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12:450–455.

Hirst, C. N., and D. A. Jackson. 2007. Reconstructing community relationships: the impact of sampling error, ordination approach, and gradient length. Diversity and Distributions 13:361–371.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution 15:56–61.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Cambridge University Press, Cambridge, UK.

Jackson, D. A., and N. E. Mandrak. 2002. Changing fish biodiversity: predicting the loss of cyprinid biodiversity due to global climate change. Pages 89–98 *in* N. A. McGinn, editor. Fisheries in a changing climate. American Fisheries Society, Symposium 32, Bethesda, Maryland.

Jenkins, D. G., C. R. Brescacin, C. V. Duxbury, J. A. Elliott, J. A. Evans, K. R. Grablow, M. Hillegass, B. N. Lyon, G. A. Metzger, M. L. Olandese, D. Pepe, G. A. Silvers, H. N. Suresch, T. N. Thompson, C. M. Trexler, G. E. Williams, N. C. Williams, and S. E. Williams. 2007. Does size matter for dispersal distance? Global Ecology and Biogeography 16:415–425.

Jensen, R. A., J. Madsen, M. O'Connell, M. S. Wisz, H. Tommervik, and F. Mehlum. 2008. Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. Global Change Biology 14:1–10.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. Plos Biology 5:1211–1219.

Lawler, J. J., D. White, R. P. Neilson, and A. R. Blaustein. 2006. Predicting climate-induced range shifts: model differences and model reliability. Global Change Biology 12:1568–1584.

Leathwick, J. R., J. Elith, M. S. Francis, T. Hastie, and P. Taylor. 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. Marine Ecology Progress Series 321:267–281.

Levinsky, I., F. Skov, J. C. Svenning, and C. Rahbek. 2007. Potential impacts of climate change on the distributions and diversity patterns of European mammals. Biodiversity and Conservation 16:3803–3816.

Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler, and F. H. Quinn. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. Hydrological Processes 11:825–871.

Marmion, M., M. Parviainen, M. Luoto, R. K. Heikkinen, and W. Thuiller. 2009. Evaluation of consensus methods in predictive species distribution modelling. Diversity and Distributions 15:59–69.

McCarthy, J. P. 2001. Ecological consequences of recent climate change. Conservation Biology 15:320–331.

McCullagh, P., and J. Nelder. 1989. Generalized linear models, 2nd edition. Chapman and Hall, London.

Menendez, R., A. G. Megias, J. K. Hill, B. Braschler, S. G. Willis, Y. Collingham, R. Fox, D. B. Roy, and C. D. Thomas. 2006. Species richness changes lag behind climate change. Proceedings of the Royal Society B 273:1465–1470.

Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kübler, P. Bissolli, O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, A. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatczak, F. Måge, A. Mestre, O. Nordli, J. Peñuelas, P. Pirinen, V. Remisova, H. Scheifinger, M. Striz, A. Susnik, A. J. H. Van Vliet, F.-E. Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12:1969–1976.

Minns C. K., and J. E. Moore. 1995. Factors limiting the distributions of Ontario's freshwater fishes: the role of climate and other variables, and the potential impacts of climate change. Pages 137–160 *in* R. J. Beamish, editor. Climate change and northern fish populations. Canadian Special Publication of Fisheries and Aquatic Sciences 121.

Mohseni, O., H. G. Stefan, and J. G. Eaton. 2003. Global warming and potential changes in fish habitat in US streams. Climatic Change 59:389–409.

Nakicenovic, N., and R. Swart, editors. 2000. Special report on emissions scenarios. Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

New, M., D. Lister, M. Hulme, and I. Makin. 2002. A high-resolution data set of surface climate over global land areas. Climate Research 21:1–25.

Oberdorff, T., D. Pont, B. Hugueny, and D. Chessel. 2001. A probabilistic model characterizing fish assemblages of French rivers: a framework for environmental assessment. Freshwater Biology 46:399–415.

Ohlemüller, R., E. S. Gritti, M. T. Sykes, and C. D. Thomas. 2006. Quantifying components of risk for European woody species under climate change. Global Change Biology 12:1788–1799.

Parmesan, C., N. Ryrholm, C. Stefanescu, J. Hill, C. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and N. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature(London) 399:579–583.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature(London) 421:37–42.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13:1860–1872.

Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Pearson, R. G., W. Thuiller, M. B. Araujo, E. Martinez-Meyer, L. Brotons, C. McClean, L. Miles, P. Segurado, T. P. Dawson, and D. C. Lees. 2006. Model-based uncertainty in species range prediction. Journal of Biogeography 33:1704–1711.

Peterson, A. T., M. Ortega-Huerta, J. Bartley, V. Sanchez-Cordero, J. Soberon, R. H. Buddemeier, and D. R. B. Stockwell. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature(London) 416:626–629.

Peterson, A. T. 2003. Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. Global Change Biology 9:647–655.

Peterson, A. T., E. Martinez-Meyer, C. Gonzalez-Salazar, and P. W. Hall. 2004. Modeled climate change effects on distributions of Canadian butterfly species. Canadian Journal of Zoology 82:851–858.

Rahel, F. J., C. J. Keleher, and J. L. Anderson. 1996. Potential habitat loss and population fragmentation for cold water fish in the North Platte River drainage of the Rocky Mountains: response to climate warming. Limnology and Oceanography 41:1116–1123.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature(London) 421:57–60.

Roura-Pascual, N., L. Brotons, A. T. Peterson, and W. Thuiller. 2009. Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. Biological Invasions 11:1017–1031.

Sætersdal, M., H. J. B. Birks, and S. M. Peglar. 1998. Predicting changes in Fennoscandian vascularplant species richness as a result of future climatic change. Journal of Biogeography 25:111–122.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Sharma, S., D. A. Jackson, C. K. Minns, B. J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biology 13:2052–2064.

Stockwell, D. R. B., and A. T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. Ecological Modelling 148:1–13.

Swets, K. 1988. Measuring the accuracy of diagnostic systems. Science 240:1285–1293.

Thomas, C. D., and J. J. Lennon. 1999. Birds extend their ranges northwards. Nature(London) 399:213.

Thomas, C. D., A. Cameron, and R. E. Green. 2004. Extinction risk from climate change. Nature(London) 427:145–148.

Thomas, C. D., A. M. A. Franco, and J. K. Hill. 2006. Range retractions and extinction in the face of climate warming. Trends in Ecology and Evolution 21:415–416.

Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. Global Change Biology 10:2020–2027.

Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America 102:8245–8250.

Thuiller, W., O. Broennimann, G. Hughes, J. R. M. Alkemade, G. F. Midgley, and F. Corsi. 2006a. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Global Change Biology 12:424–440.

Thuiller, W., G. F. Midgley, M. Rouget, and R. M. Cowling. 2006b. Predicting patterns of plant species richness in megadiverse South Africa. Ecography 29:733–744.

Trivedi, M. R., P. M. Berry, M. D. Morecroft, and T. P. Dawson. 2008. Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. Global Change Biology 14:1089–1103.

Virkkala, R., R. K. Heikkinen, N. Leikola, and M. Luoto. 2008. Projected large-scale range reductions of northern-boreal land bird species due to climate change. Biological Conservation 141:1343–1353.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature(London) 416:389–395.

Wood, C. M., and G. McDonald, editors. 1997. Global warming: implications for freshwater and marine fish. Cambridge University Press, Cambridge, UK.

Wilson, R. J., D. Gutierrez, J. Gutierrez, and V. J. Monserrat. 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. Global Change Biology 13:1873–1887.