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Climate-induced changes in the distribution of freshwater fish: observed and predicted trends

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SUMMARY

1. Climate change could be one of the main threats faced by aquatic ecosystems and freshwater biodiversity. Improved understanding, monitoring and forecasting of its effects are thus crucial for researchers, policy makers and biodiversity managers.

2. Here, we provide a review and some meta-analyses of the literature reporting both observed and predicted climate-induced effects on the distribution of freshwater fish. After reviewing three decades of research, we summarise how methods in assessing the effects of climate change have evolved, and whether current knowledge is geographically or taxonomically biased. We conducted multispecies qualitative and quantitative analyses to find out whether the observed responses of freshwater fish to recent changes in climate are consistent with those predicted under future climate scenarios.

3. We highlight the fact that, in recent years, freshwater fish distributions have already been affected by contemporary climate change in ways consistent with anticipated responses under future climate change scenarios: the range of most cold-water species could be reduced or shift to higher altitude or latitude, whereas that of cool- and warm-water species could expand or contract.

4. Most evidence about the effects of climate change is underpinned by the large number of studies devoted to cold-water fish species (mainly salmonids). Our knowledge is still incomplete, however, particularly due to taxonomic and geographic biases.

5. Observed and expected responses are well correlated among families, suggesting that model predictions are supported by empirical evidence. The observed effects are of greater magnitude and show higher variability than the predicted effects, however, indicating that other drivers of changes may be interacting with climate and seriously affecting freshwater fish.

6. Finally, we suggest avenues of research required to address current gaps in what we know about the climate-induced effects on freshwater fish distribution, including (i) the need for more long-term data analyses, (ii) the assessment of climate-induced effects at higher levels of organisation (e.g. assemblages), (iii) methodological improvements (e.g. accounting for uncertainty among projections and species' dispersal abilities, combining both distributional and empirical approaches and including multiple non-climatic stressors) and (iv) systematic confrontation of observed versus predicted effects across multi-species assemblages and at several levels of biological organisation (i.e. populations and assemblages).

Keywords: empirical data, predictive modelling, range shift, species distribution

Introduction

Knowledge of the biodiversity of freshwater ecosystems is still very incomplete, but declines in biodiversity are thought to be far greater in fresh water than in the most affected terrestrial ecosystems (Dudgeon *et al.*, 2006). It is suggested that the most influential drivers are related to climate-induced stress (Sala *et al.*, 2000; Heino, Virkkala & Toivonen, 2009). Freshwater ecosystems may thus be those most threatened by the effect of future climate change (Millennium Ecosystem Assessment, 2005). Therefore, a better understanding, monitoring and ability to predict these effects on biodiversity are crucial for researchers, policy makers and biodiversity managers.

There is a long history of research addressing the effect of climate change on freshwater fish, with particular attention being devoted to changes in species distribution (Heino *et al.*, 2009). Indeed, forecasting potential distributional shifts in freshwater fish in response to projected climate scenarios has become a popular conservation tool, favoured by the recent development of many statistical methods that are now applied routinely (e.g. Thuiller, 2003). Changes in species distribution based on current and historical records have also been documented. As this literature has been accumulated recently, both the observed and predicted effects of climate change on fish species distribution have already been reviewed (e.g. Reist *et al.*, 2006; Heino *et al.*, 2009; Booth, Bond & Macreadie, 2011). However, most previous reviews could be biased towards restricted geographic locations or 'iconic' species of interest, thus limiting robust generalisations (Wilson *et al.*, 2007).

Over the last two decades, climate change scenarios have been continuously refined. In the meantime, ecological modelling techniques have diversified, and major methodological advances have improved our ability to forecast how species and assemblages could respond to climate change (Guisan & Zimmermann, 2000; Elith, Kearney & Phillips, 2010). However, previous reviews have rarely focussed on methodological considerations, and how research activities assessing the effects of climate change on freshwater fish have changed in recent decades still remains unanswered. In particular, although theoretical considerations about the causes and consequences of climate-induced effects at different levels of biological organisation have already been reviewed (e.g. Woodward, Perkins & Brown, 2010), the compilation of recent evidence of climate-induced effects on freshwater fish remains limited (e.g. Heino *et al.*, 2009; Jeppesen *et al.*, 2010). Moreover, comparisons between observed and predicted effects have never been investigated

thoroughly, and we argue here that (i) such comparisons could be a crucial component for supporting the reliability of these projections (Araújo *et al.*, 2005; Maclean & Wilson, 2011) and (ii) our ability to forecast more realistic future effects would greatly benefit from the knowledge of recent climate-induced effects on freshwater fish.

This article sets out to review our knowledge of climate-induced effects on freshwater fish species distribution. By providing a general synthesis of the literature reporting observed and predicted climate-induced changes, we investigate how our perception of climate change effects may have been biased towards specific geographic areas or families and related to the conservation status of species. We then used both qualitative and quantitative meta-analyses to find out whether observed taxonomic patterns of responses to climate change match the predictions for the future. We also explored how methodological considerations have evolved in climate change studies and which methodological advances could strengthen our ability to detect or predict the consequences of climate warming. We conclude by highlighting the areas of research needed to address current gaps and to further our scientific understanding of the effects of climate change on freshwater fish distribution.

Literature review

We used the ISI Web of Knowledge to search for published articles reporting observed (i.e. empirical evidence recently documented in the field) or predicted (i.e. projections under future climate change scenarios) effects of climate change on freshwater fish distributions. Our search terms included all combinations containing (1) freshwater or 'fresh water*' or stream* or river* or lake*, and (2) 'fish*', and (3) 'climat* change*' or warming (2 December 2011). From this initial search, we selected the articles related to changes in the distribution of fish species. We excluded studies that focussed on individual or population climate-induced stress (e.g. effect on growth, reproduction, feeding and abundance). In addition, reports from the 'grey' literature were obtained, and non-peer-reviewed studies were selected for inclusion only if similar data had not been published elsewhere. A total of 77 studies published between 1980 and 2011 were included in the review, of which 11 and 66 corresponded to effects observed recently or predicted, respectively.

We recorded the realm, biome and ecosystem type where the studies were conducted and assigned each of the freshwater fish species studied to its family. We also assigned all species to IUCN (2011b) threat categories [i.e. critically endangered (CR), endangered (EN), vulnerable

(VU), near threatened, least concern (LC) and data deficient]. In accordance with the IUCN Red List, species assessed as CR, EN or VU were assigned to the threatened species category (IUCN, 2011a).

We also listed all the drivers cited or used as predictors to identify the relative contribution of climate change to both observed and predicted changes. More specifically, for the studies dealing with recent climate-induced effects, we recorded whether statistical analyses were carried out to link climate trends with fish responses or whether the relationship with climate was only discussed or hypothesised. For predictive studies, we categorised the different methodological approaches used (Table 1) and described how the projections had been generated (e.g. the climate scenarios employed, the number of projections) to obtain an overview of the evolution of predictive methods.

Finally, we listed all the metrics used to quantify the potential effects of both recent and future climate change on fish distribution. Metrics that had been given different names, but in fact corresponded to the same effect measurement were pooled. A total of 21 metrics quantifying climate-induced effects were identified and assigned to two classes: habitat suitability (14) and range shift (seven) (Table 2). We collected a total of 88 observed effects for 68 different species belonging to 24 families, and 773 predicted effects for 161 different species belonging to 25 families.

Qualitative assessment of effects

To determine the global trends in how fish are responding to climate change, we first assigned the quantitative

values of the measured effects to a 'positive' (e.g. increase in habitat suitability) or 'negative' (e.g. decrease in habitat suitability) effect. Distributional shifts metrics were not included in the analysis if neither positive nor negative effects could unambiguously be assigned to these metrics (e.g. change in altitudinal optimum). The proportion of positive and negative effects was tested against the random expectation of an equal probability of observing changes in either direction using binomial tests ($H_0: P = 0.5$). Observed and predicted effects were analysed separately to make it possible to compare the different patterns of research activity. Within each family, binomial tests were also used to compare the proportion of each categorical effect (negative or positive) between observed and predicted effects ($H_0: P_{\text{obs}} = P_{\text{pred}}$).

Quantitative assessment of effects

Focussing on quantitative effects, our goal was to compare observed and predicted rates of climate-induced change. We first combined similar types of metrics that reported quantitative estimates of change over a specified time period or warming scenario. Only effects reported in terms of change per individual species were included. This meta-analysis was restricted to changes related to habitat suitability (Table 2), as the number of effects reported in this class made such a comparison possible, unlike range shift classes, which did not. We defined habitat suitability effects as any change in the distribution previously occupied by species (e.g. stream length, area). These changes were expressed as a percentage change per degree of warming ($\%^{\circ}\text{C}^{-1}$). This required converting

Table 1 Summary of the modelling approaches used in the freshwater fish literature for assessing climate-induced effects on fish distribution

Modelling approach	Aim	Biological input data	Output	References
Physiological ($N = 39$)	Delineation of suitable habitats from environmental information about known limiting factors	Physiological tolerance limits: Temperature Dissolved oxygen	Suitable habitat for fish species	Meisner (1990b), Fang <i>et al.</i> (1999)
Empirical ($N = 13$)	Mechanistic link between species distribution and environmental variables	Measurements of life history strategies and population dynamics: Life stage abundances Fecundity Growth rate Survival rate	Specific demographic parameters integrated in an overall model to assess species distribution	Mackenzie-Grieve & Post (2006), Williams <i>et al.</i> (2009)
Distributional ($N = 14$)	Correlative relationship between fish distribution and environmental variables	Species distribution: Abundance Presence-absence	Probability of presence Abundance	Buisson <i>et al.</i> (2008), Lassalle & Rochard (2009)

N : number of studies published between 1980 and 2012.

Table 2 Examples of climate-induced effects on fish species distribution in freshwater ecosystems

Climate-induced effects	Ecosystem type	Selected references
Habitat suitability (<i>N</i> = 4; 57)		
Number of suitable entities		
<i>stations</i>	S	Eaton & Scheller (1996), Nakano <i>et al.</i> (1996), Mohseni <i>et al.</i> (2003), Buisson <i>et al.</i> (2008)
<i>catchments</i>	S	Chu <i>et al.</i> (2005), Lassalle & Rochard (2009)
<i>streams</i>	S	Flebbe (1993)
<i>habitat patches</i>	S	Rieman <i>et al.</i> (2007), Isaak <i>et al.</i> (2010)
<i>lakes</i>	L	Stefan <i>et al.</i> (2001)
Size of suitable entities		
<i>stream length</i>	S	Keleher & Rahel (1996), Flebbe <i>et al.</i> (2006), Kennedy <i>et al.</i> (2009), Lyons <i>et al.</i> (2010)
<i>habitat volume</i>	L	Mackenzie-Grieve & Post (2006), Elliott & Bell (2011)
<i>distribution area</i>	S	Keleher & Rahel (1996), Rahel <i>et al.</i> (1996), Flebbe <i>et al.</i> (2006), Buisson <i>et al.</i> (2010)
<i>large habitat patches</i>	S	Flebbe <i>et al.</i> (2006), Rieman <i>et al.</i> (2007)
<i>thermal habitat</i>	S	Hari <i>et al.</i> (2006), Isaak <i>et al.</i> (2010), Almodóvar <i>et al.</i> (2012)
	L	Magnuson <i>et al.</i> (1990), Meisner (1990b), De Stasio <i>et al.</i> (1996)
<i>good growth habitat area</i>	S	Stefan & Sinokrot (1993)
	L	Fang <i>et al.</i> (1999)
<i>cold-water habitat</i>	S	Preston (2006)
Probability of presence	S	Buisson <i>et al.</i> (2008), Steen <i>et al.</i> (2010), Poulet <i>et al.</i> (2011)
Range shift (<i>N</i> = 6; 15)		
Altitudinal range	S	Hickling <i>et al.</i> (2006), Matulla <i>et al.</i> (2007), Kennedy <i>et al.</i> (2009)
Lower altitudinal limit	S	Meisner (1990a), Nakano <i>et al.</i> (1996), Hari <i>et al.</i> (2006)
Northern limit	S-L	Shuter <i>et al.</i> (1980), Minns & Moore (1992), Hickling <i>et al.</i> (2006)
Southern limit	S	Meisner (1990a)
	S-L	McCauley & Beitinger (1992)
Expansion	S	Gómez <i>et al.</i> (2004)
	S-L	Babaluk <i>et al.</i> (2000)
	L	Johnson & Evans (1990)
Fragmentation	S	Keleher & Rahel (1996), Rahel <i>et al.</i> (1996), Flebbe <i>et al.</i> (2006)
Harvest/yield capacity	L	Mackenzie-Grieve & Post (2006)
	W	Minns & Moore (1992)
Extinction	L	Trape (2009)

S: stream, L: lake, W: watershed.

N: number of studies published between 1980 and 2012 reporting observed and predicted effects. Values and references in bold indicate observed effects.

each change measured over a time period or under a warming scenario within each study to a rate of change that was assumed to be constant over the time covered by the study. If not explicitly reported in the study, the time span for observed effects was converted to an overall temperature increase according to the estimated rates of global mean temperature increase over the study period (IPCC, 2007). For predicted effects, warming was estimated according to the general circulation models (GCM) and greenhouse gas emission scenario used, as well as to the geographic areas where the study was conducted and the time horizon (IPCC, 2007).

We considered separate results within a single study as independent observations when they involved different species. In contrast, when different effects were reported for the same species in a given location, the mean change across different effects or warming scenarios was computed. In total, 50 observed and 277 predicted effects met the different criteria for the analysis, covering 16 and 22

families, respectively. As many studies did not report measures of variability, we attached the same weight to all effects, irrespective of either sample size or the number of species studied (Gurevitch & Hedges, 1999). Rates of observed change were compared with rates of predicted change using generalised linear mixed effect model (GLMM) with species nested within families specified as a random effect in the model (Sodhi *et al.*, 2008). Indeed, due to their common evolutionary histories, species are not in fact statistically independent units (Paradis & Claude, 2002), and as such, some variation of responses among families might be expected. Negative and positive rates of change were analysed separately, making it possible to compare effects among potential 'winners' and 'losers' of climate change (Rosset & Oertli, 2011). Lastly, to test for consistency between general trends among families, the mean observed and predicted rates of changes were calculated and compared (Spearman's rank correlation test).

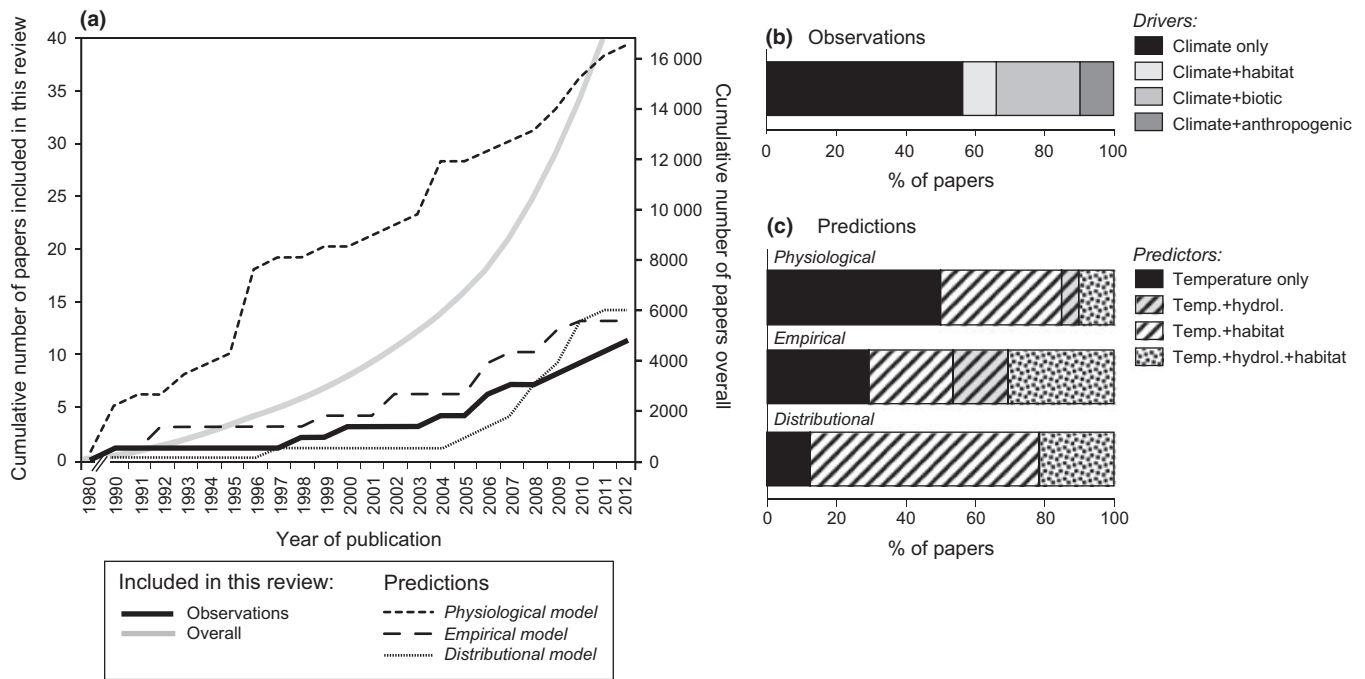


Fig. 1 (a) Cumulative number of published articles from 1980 to 2012 (i) included in this review that report climate-induced shifts in freshwater fish distribution (left axis, black lines), and (ii) resulting from a broader search of the ecological literature using species and ('climat* change*' or warming) as search terms (right axis, grey line). Articles reporting climate-induced shifts in freshwater fish distribution were divided into observations (continuous black line) and future predictions (dashed black lines). Those assessing potential future changes were classified according to the type of modelling approach used (see Table 1 for details); (b) proportion of published articles according to the categories of drivers presumed to be related to the observed effects. The categories of drivers consisted of climate only (e.g. precipitation, temperature), habitat, for habitat degradation (e.g. pollution, fragmentation, dewatering), biotic, for invasive species and biotic interactions (e.g. parasitism, predation) and anthropogenic, for human activities (e.g. fishing, stocking); (c) proportion of articles using the different kinds of environmental predictors according to the modelling approach performed to predict future effects.

All the statistical analyses were conducted using the R environment software v 2.13.0 (R Development Core Team, U., 2011).

Patterns in publication activity

The number of published studies has accelerated gradually over time, the first article dealing with predicted future climate-induced change in species distributions having been published in 1980 (Fig. 1a; see Table 1 for details). In contrast, the first article focussing on empirical evidence for the influence of climate change was published 10 years later. Given the recent intensity of climate alterations (IPCC, 2007), it is not surprising that studies reporting effects of climate change on freshwater organisms have increased rapidly during the last two decades. However, the number of articles reporting observed effects on freshwater fish hitherto still remains disproportionately low compared to the number of studies devoted to forecasted effects (Fig. 1a). Nevertheless, although the increasing trend in the publication of studies dealing with the influence of climate change on freshwater fish distribution

follows the overall trend of increasing publication activity, the number of studies included in this review still corresponds to only 0.5% of the papers in ecology dealing with climate change and biodiversity that have been published during the same period (Fig. 1a).

Assessment of potential geographic bias

Not surprisingly, publication activity appears to be geographically localised, with a strong bias towards the Northern hemisphere for both observed and predicted climate-induced changes (Fig. 2). We found that more than 90% of the studies reviewed were conducted in the Nearctic and Palaeartic realms, whereas only one paper per realm has been published for realms located in the Southern hemisphere (i.e. Australasian, Oriental and Neotropical realms; Fig. 2a). In addition, almost 50% of the studies were conducted in the temperate biome, whereas mountainous, Mediterranean and arid biomes have been poorly studied, even in the Northern hemisphere (Fig. 2b). Interestingly, many of the studies analysing recent climate-induced changes were located in the Palaeartic (45.5%)

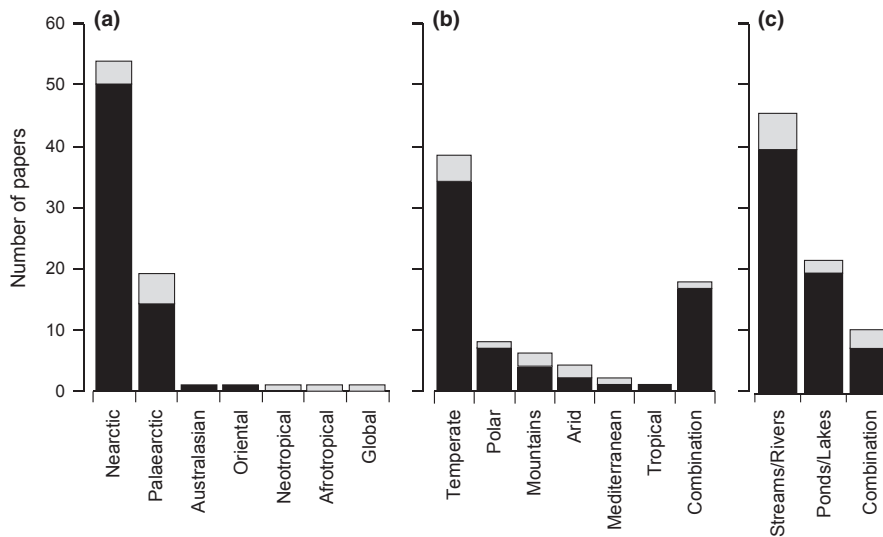


Fig. 2 Number of articles published according to (a) the realm, (b) the biome, and (c) the type of ecosystem where climate-induced shifts in freshwater fish were observed (in grey) or predicted (in black).

realm, while three quarters of the future predictions were for the Nearctic realm. This stemmed from the availability of historical or long-term surveys in these regions, often derived from fisheries data or interest in species with high commercial value. Lastly, streams and rivers are the most studied ecosystem types (58.4%), while studies focussing on ponds and lakes account for only around one quarter of the articles (Fig. 2c).

Assessment of potential taxonomic bias

Overall, a majority of the studies focussed on one or a small number of fish species, and importantly on a single family. Specifically, articles dealing with observed changes often focussed on at least one salmonid species (54%), while recent trends for 91% of the species studied

have been described only once. As a result, empirical evidence of the influence of climate change on freshwater fish distribution is still very patchy. A non-negligible proportion (24.2%) of predictive studies have forecasted the potential effects of climate change on fish thermal guilds (i.e. cold-, cool- or warm-water fish, *sensu* Magnuson, Crowder & Medvick, 1979) rather than on species.

Taxonomic bias in both observed and predicted climate-induced effects was also apparent when it comes to examining the level of threat to the fish species under investigation (Fig. 3). While most empirical studies reported observed climate-induced effects for species of LC, most of the predictive studies focussed on species of unknown threat levels. In the published articles as a whole, we found that threatened freshwater fish were

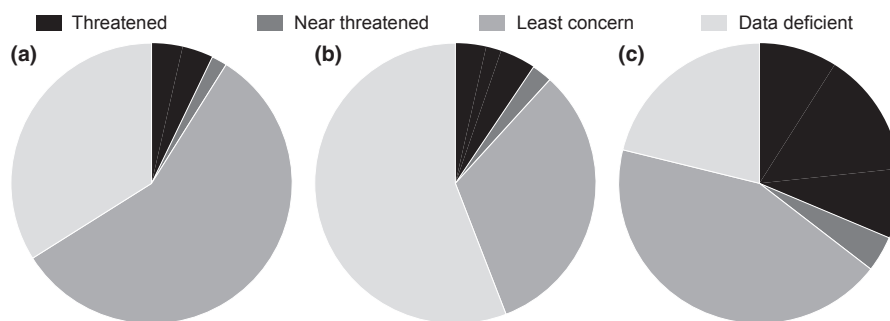


Fig. 3 Proportion of species classified according to the IUCN Red List assessment in published articles addressing (a) observed and (b) predicted climate-induced changes in freshwater fish distribution. (c) Proportion of the world's freshwater fish in each Red List category based on 3120 freshwater fish species according to the 2009 IUCN Red List (IUCN, 2009). Species assessed as critically endangered, endangered, or vulnerable are collectively classified here as 'threatened species'.

under-represented compared to their prevalence in the IUCN Red List (Fig. 3c). Indeed, although far from complete, categorisation of freshwater fish into IUCN classes revealed that 37% of the freshwater fish species assessed are threatened with extinction (IUCN, 2009). However, these species have been the topic of <10% of the studies devoted to climate-induced changes in freshwater fish distribution. Although Red List categories clearly need further refinement to identify the full suite of species at risk from climate change (Foden *et al.*, 2008), one can reasonably hypothesise that current threat status is likely to be related to climate change vulnerability of the species (e.g. with threatened species also being those that are the most vulnerable). The lack of studies reporting climate-induced effects on threatened species could, therefore, have severe implications, as these species may be precisely those that have been the most severely affected by recent climate change and for which conservation efforts could be needed most urgently.

Methods used to assess climate-induced changes

Observed changes

Sources of long-term data are diverse, including catch data derived from fisheries or recreational activities (e.g. Hari *et al.*, 2006), national monitoring surveys (e.g. Poulet, Beaulaton & Dembski, 2011), or compilations of all the available information on species distribution over large temporal (e.g. Van Damme *et al.*, 2007) and spatial (e.g. Parrish *et al.*, 1998) scales. The length of the data sets used to study the recent influence of climate change ranged from occasional reports outside of the well-established distribution area of species (e.g. Babaluk *et al.*, 2000) to more than seven centuries for a study using a combination of contemporary, historical and archaeological data (Van Damme *et al.*, 2007). Overall, 50% of studies covered a time span of between 11 and 35 years, with a median value of 21 years. Temperature warming has accelerated and intensified during the last 30 years (IPCC, 2007), and it has been demonstrated that the response of species often lags behind environmental change (Magnuson, 1995; Devictor *et al.*, 2008; Bertrand *et al.*, 2011). As a result, our ability to detect climate-induced range shifts is probably limited due to both the scarcity of available long-term data series and the recent unprecedented magnitude and speed of current climate change (Battarbee, 2010).

The link between observed biological changes and climate trends was tested statistically only occasionally (9%) and merely hypothesised or discussed in more than 60% of the articles. When tested, the effects of climate change were addressed mainly through mean tempera-

ture increase, and rarely considered hydrological descriptors or extreme events (but see Trape, 2009). The implications of recent climate change appeared to be difficult to establish, because of the existence of other drivers, as has already been noted for other organisms (Archaux, 2004). Biological effects were attributed to trends in climate alone in 55% of the articles, while interactions with other habitat, biotic and anthropogenic related factors such as damming, species introductions or fishing activities, were also frequently cited (Fig. 1b).

Predicted future changes

When the articles were grouped according to the modelling approach used to project future fish distribution in response to climate change (Table 1), we found that the physiological approach was the one most commonly used (59.1%), followed by the distributional (21.2%) and empirical (19.7%) models. The popularity of the physiological approach lies in its simplicity, as these models are usually restricted to the known thermal tolerance of the species (Fig. 1c). In contrast, distributional models frequently combine temperature and other habitat predictors, while empirical models intended to capture mechanisms are mainly based on complex combinations of predictors, including hydrology (Fig. 1c). It is worth noting that the number of studies using species distribution models has risen sharply since 2005 (Fig. 1a), focusing on large numbers of fish species (on average 15 species per paper, ranging from 1 to 50), probably driven by recent advances in species distribution modelling (Elith *et al.*, 2010). As empirical models require more detailed knowledge about the physiological and ecological constraints on species distribution, they have only been applied to a very limited number of well-studied species.

Although many of the methodological decisions taken during the forecasting process are known to have a major influence on the effects predicted, the inherent uncertainty in those remains rarely assessed (but see Buisson *et al.*, 2010). Overall, potential future shifts in the distribution of freshwater fish species are more often projected using climate scenarios from GCM (67%) rather than using uniform scenarios (e.g. predicted warming of +3 °C). However, most studies have projected these shifts using a single GCM and a single greenhouse gas emission scenario, and 49% of the studies rely on a single projection. Finally, only five of the 66 articles have accounted for the variability that results from using different kinds of models or climate scenarios. Thus, the variability between different projections undoubtedly deserves further attention.

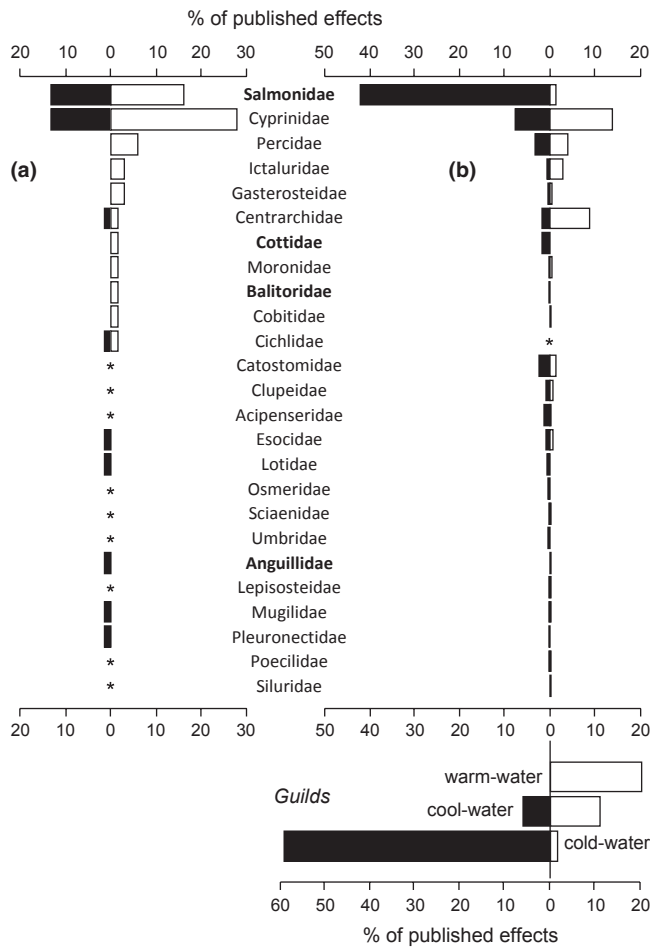


Fig. 4 Proportion of negative (black bars) and positive (white bars) effects reported: (a) observed effects and (b) predicted effects according to the level of biological organisation for which predictions have been made (thermal guilds versus species). Asterisks indicate families of which no species has been studied. Bold indicates families for which the proportion of categorical effects differed between the observed and predicted effects, according to binomial tests ($P < 0.05$).

The influence of climate change on fish distribution

Global trends: qualitative assessment of effects

When global trends on how fish are responding to climate change were analysed, we first noted that the responses of the Salmonidae, Cyprinidae, Centrarchidae and Percidae families have been particularly thoroughly investigated. In contrast, there have been only a limited number of published effects for other fish families (Fig. 4). The overall patterns of observed and predicted effects were similar for most families (binomial test, $P > 0.05$), and it is worth noting that the responses of most families were not unidirectional (Fig. 4). Indeed, both positive and negative effects have already been observed or predicted for almost all the families included in our analysis. However,

although the observed effects showed a higher proportion of positive effects (66%; binomial test, $P < 0.01$), most predicted influences were negative (65%; binomial test, $P < 0.001$). Observed positive effects were mainly reported for Cyprinidae, Percidae, Ictaluridae and Salmonidae, although negative effects were also reported frequently for this family (Fig. 4a). The higher proportion of predicted negative effects can be explained by the large number of studies focussing on cold-water species (Fig. 4b). Indeed, we found that 59.7% of the effects derived from published studies addressing fish thermal guilds focussed on cold-water fish, and 42.5% of future species-specific effects were devoted to salmonids (Fig. 4b).

Although no overall directional trend is yet apparent for the Salmonidae, it seems likely that cold-water species could be negatively affected by future climate changes. In contrast, warm-water species (e.g. Centrarchidae and Cyprinidae) could benefit from them. The response of cool-water species could be more variable, with 12 and 6% of the total predicted effects being reported as positive and negative, respectively (Fig. 4b).

A quantitative assessment of effects

When quantitative effects on species habitat suitability were estimated (i.e. the rate of change per degree of warming), we found that the magnitude of the observed effects was almost eight times higher than those predicted

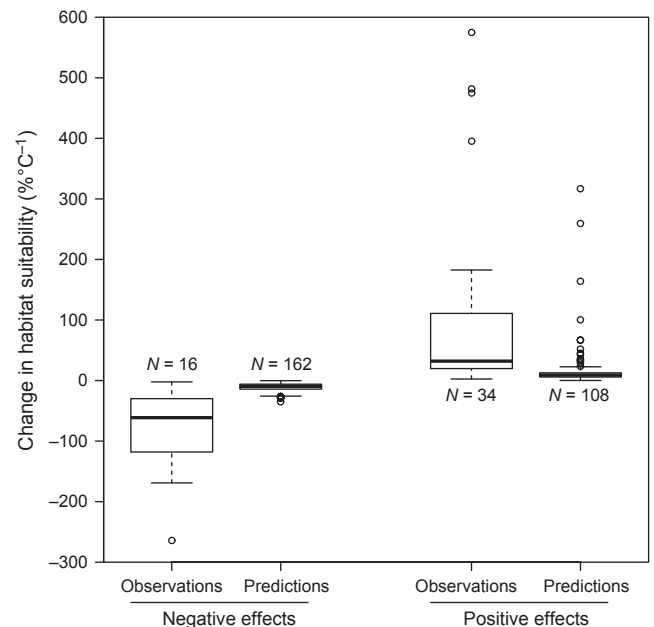


Fig. 5 Changes in habitat suitability observed and predicted according to the direction of the effect (i.e. negative or positive). N indicates the number of species \times location included in the analysis.

Table 3 Observed and predicted changes in habitat suitability among freshwater fish families

	Habitat suitability change (% °C ⁻¹)			
	N	Observations	N	Predictions
Acipenseridae	–	–	6	–5.5 (–16.6; –0.6)
Anguillidae	1	–53.5	2	3.1 (3.0;3.2)
Balitoridae	1	23.9	1	–1.1
Blenniidae	1	–89.6	–	–
Catostomidae	–	–	16	–2.8 (–18.2;52.1)
Centrarchidae	2	29.9 (–2.2;62.0)	37	12.8 (–15.1;316.7)
Clupeidae	–	–	6	–1.2 (–9.0;9.0)
Cobitidae	1	86.8	0	–
Cottidae	1	28.8	5	–13.3 (–20.2; –4.9)
Cyprinidae	23	70.2 (–159.2;575.0)	74	4.4 (–27.0;259.6)
Esocidae	1	–29.7	6	–3.9 (–12.4;3.1)
Gasterosteidae	2	21.2 (13.1;29.2)	3	3.6 (–6.1;10.6)
Ictaluridae	2	245.2 (8.5;481.9)	12	21.2 (–13.4;164.1)
Lepisosteidae	–	–	2	–0.5 (–9.7;8.7)
Lotidae	1	–36.5	1	–28.1
Moronidae	–	–	4	0.5 (–10.8;8.4)
Mugilidae	1	–169.0	1	2.1
Osmeridae	–	–	1	–14.5
Percidae	4	46.2 (9.4;110.9)	23	3.6 (–20.3;100.0)
Pleuronectidae	1	–264.2	1	–9.4
Poeciliidae	1	26.3	–	–
Poeciliidae	–	–	2	3.9 (–1.2;9.0)
Salmonidae	7	27.2 (–65.7;155.7)	71	–8.8 (–35.0;66.7)
Sciaenidae	–	–	2	0.8 (–7.4;9.0)
Umbridae	–	–	1	–9.6

N indicates the number of species × location included in the analysis. Numbers in parentheses correspond to the minimum and maximum values of effects. Dashes indicate families for which no quantitative effects were reported.

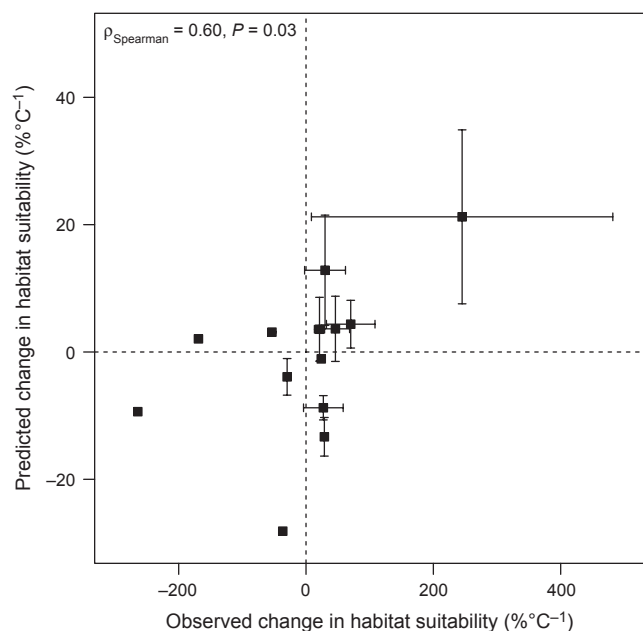


Fig. 6 Predicted versus observed changes in habitat suitability per family. Squares represent average values and bars the standard errors.

(GLMM, $P < 0.001$; Fig. 5). Across all studies reporting a decline in habitat suitability, the mean rate of change was -81.00 and $-10.66\% \text{ °C}^{-1}$ for observations and future predictions, respectively. For positive changes, these values were 100.06 and $18.82\% \text{ °C}^{-1}$, respectively. The degree of variability in habitat change was also much higher for observations than for predictions (Fig. 5), indicating stronger species-specific responses to climate change than predicted by models.

When changes were quantified for each family (Table 3), there was evidence that directional trends were not independent, thus supporting the proposal that there are some potential ‘winners’ (e.g. Ictaluridae, Centrarchidae, Cyprinidae) and some potential ‘losers’ (e.g. Lotidae) of climate change. This finding was also highlighted by the high degree of correlation between observed and predicted trends in family-specific effects ($\rho_{\text{Spearman}} = 0.60$; Fig. 6). Most of the families observed to have been positively affected by recent climate change were also predicted as likely to benefit in the future, although the consistency of negative effects was less consistent (e.g. Salmonidae). However, the taxonomic imbalance (i.e. high differences in the number of species per family) may introduce an artificial variability in the direction and magnitude of the effects for families composed of many species sharing different ecological features (e.g. Cyprinidae), thus leading to more ambiguous trends than for families composed of only few species (e.g. Siluridae). Nevertheless, we confirmed that rates of both positive and negative observed changes exceeded those of the predicted changes within each family. This may in part be triggered by a positive result bias, although previous studies have clearly confirmed that the evident signal of climate-induced biological changes was not driven by publication bias (Menzel *et al.*, 2006). In addition, the fact that species can respond to climate alterations in a nonlinear way (e.g. threshold effect) might lead to under- or over-estimated rates of changes. The influence of other additional drivers of change may also explain these differences, as these factors are usually neglected in predictive models (but see Steen, Wiley & Schaeffer, 2010). Therefore, although our results suggested that predictions can be supported by empirical evidence (Maclean & Wilson, 2011), the synergism between climate change and non-climatic stressors could also drive an unpredictable variability in how species respond to climate change (Heino *et al.*, 2009).

Some illustrations

Changes in habitat suitability. Changes in fish habitat suitability in response to climate change have been quite

well documented. In particular, many studies have focussed on species of commercial or recreational interest. As a result, because of their ecological, economic and cultural importance, salmonid species have been the focus of numerous studies. In addition, the preference of salmonid species for cold waters makes them a good model for studying climate change effects, especially in the early decades of climate alteration as they might be more prone to respond than other tolerant species.

First, the thermal habitats of several native salmonids have already been reported to have been affected by the recent rise in temperature (Hari *et al.*, 2006; Isaak *et al.*, 2010; Almodóvar *et al.*, 2012). Isaak *et al.* (2010) estimated a potential loss of 11–22% of suitable headwater stream length in central Idaho (U.S.A.) for the bull trout (*Salvelinus confluentus*), and small gains in the number of suitable patches of habitat for the rainbow trout. In addition, estimated changes in the thermal habitat of the brown trout in Switzerland and Spain were consistent with long-term population decreases, thus supporting the evidence of negative climate-induced effects (Hari *et al.*, 2006; Almodóvar *et al.*, 2012). However, differential effects can also occur at smaller spatial scales (e.g. along environmental gradients; Hari *et al.*, 2006), and some other salmonids displayed strong increases in their probability of presence over recent decades (Poulet *et al.*, 2011).

Future local extinctions and distribution contractions are also projected as a result of the decline in the number and size of areas of suitable habitat for most cold-water fish species (e.g. Flebbe, 1993; Keleher & Rahel, 1996; Chu, Mandrak & Minns, 2005; Rieman *et al.*, 2007). The potential effects of climate change on the habitat of cold-water species have also been widely studied in lakes, where both the number of lakes and habitat area per lake suitable for fish species were predicted to decrease (Stefan, Fang & Eaton, 2001; Mackenzie-Grieve & Post, 2006). However, some studies have also argued that in some North American lakes, climate change could result in an increase in suitable thermal habitats for all thermal guilds, including cold-water species (Magnuson, Meisner & Hill, 1990; De Stasio *et al.*, 1996; Fang, Stefan & Alam, 1999).

In addition, a large discrepancy was found between the negative effects identified by studies that focussed solely on cold-water species (i.e. salmonids), and the more patchy results of those that analysed climate-induced changes in habitat for the entire fish fauna of a region. In particular, the potential responses of cool- and warm-water species to future climate change show greater variation and often depend on the location and the climate change scenario used. It appears that cool-water species are likely to follow the same general trend as cold-water

species (i.e. a decline in the range and amount of suitable habitat, contraction of the distribution) but to a lesser degree (Stefan *et al.*, 2001; Mohseni, Stefan & Eaton, 2003; Lyons, Stewart & Mitro, 2010). Nevertheless, some studies have also suggested that some cool-water species could increase their probability of presence in some streams (Buisson *et al.*, 2008; Steen *et al.*, 2010) or could experience an increase in the area of suitable lake habitat (Magnuson *et al.*, 1990; De Stasio *et al.*, 1996).

Lastly, most studies are consistent in finding that warm-water species may stand to benefit from future climate warming. These species, which often constitute the greatest number of species in the fish fauna, could experience an increase in their suitable thermal habitat and their distribution (Stefan *et al.*, 2001; Mohseni *et al.*, 2003; Chu *et al.*, 2005). The observed increase in the probability of presence of 20 of 47 stream fish species in France over the two last decades (Poulet *et al.*, 2011) is consistent with the predicted increase in species richness under climate warming scenarios (Buisson & Grenouillet, 2009).

Changes in distributional range. As a result of changes in habitat suitability, the spatial position or altitudinal and/or latitudinal limits of fish species are expected to change. The most likely response is a shift in fish distribution to higher altitude or latitudes (i.e. northward in the Northern hemisphere), especially for cold-water species.

To date, the work of Hickling *et al.* (2006) remains one of the key studies quantifying recent shifts in the spatial distribution of freshwater fish. Using long-term data covering 25 years in Great Britain for 15 stream fish species, they have documented mean poleward shifts in northern range margin and altitudinal shifts in optimum by up to 51 km and 32.7 m, respectively. This pattern has also been reported for salmonid species in different parts of the northern hemisphere. For instance, population decline in the brown trout (*Salmo trutta*) at the vulnerable southern periphery of its range has recently been related to the loss of its thermal habitat (Almodóvar *et al.*, 2012), whereas Hari *et al.* (2006) have documented an upward habitat shift of about 130 m for this species in Switzerland. They also demonstrated that the contraction at the lower boundary of the distribution was linked not only with climate, but also with the interacting effects of the increase in the incidence of temperature-dependent Proliferative Kidney Disease since the early 1980s. There have also been several recent reports of pacific salmon (*Oncorhynchus* spp.) located outside their previously known distribution area which parallel an observed increase in water temperature (Babaluk *et al.*, 2000). Changes in precipita-

tion regime have also been reported to explain recent population threats. For instance, Trape (2009) showed that the tropical fish populations of Central Sahara have experienced an increased extirpation risk following an unprecedented period of drought.

Future shifts to higher altitudes, or shifts in northern and southern limits have also been predicted for a large number of species. For instance, Matulla *et al.* (2007) predicted a displacement to an upper altitude of 70 m for the entire fish community of a river in Austria. Other studies that have quantified the potential altitudinal shift of several trout species under climate change scenarios found that they could either increase their distributions to upper altitudes (+269 to 286 m, Kennedy, Gutzler & Leung, 2009) or increase the altitude of their lower habitat boundary (Meisner, 1990a: up to 714 m; Nakano, Kitano & Maekawa, 1996: up to 640–720 m depending on species). Meisner (1990a) also predicted that, in response to a 3.8 °C increase in water temperature, brook trout may disappear from the most southern states of its native range in the north-eastern United States.

However, these latitudinal shifts may not be restricted to cold-water fish, as populations of smallmouth bass (*Micropterus dolomieu*), walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*) and channel catfish (*Ictalurus lacustris*) are also predicted to move northwards (Shuter *et al.*, 1980; McCauley & Beitinger, 1992; Minns & Moore, 1992). In fact, expansions beyond the currently known spatial distribution of several fish species have already been reported, potentially promoting the colonisation or establishment of non-native species. Johnson & Evans (1990) suggest that climate warming has permitted an invasive species, the white perch (*Morone americana*), to invade the Great Lakes, thus potentially endangering native populations. Similarly, the spatial distribution of the European bitterling (*Rhodeus amarus*) appears to have recently expanded in Eastern Europe, probably due to a combination of factors including a rise in ambient temperature (Van Damme *et al.*, 2007). Finally, whereas evidence of recent effects of climate change on stream fish has mostly been documented in the Northern hemisphere, Gómez, Trenti & Menni (2004) demonstrated that species located in the Southern hemisphere could also be affected. Specifically, they showed that water bodies located in dry areas of the Pampa regions were colonised by 10 fish species after a 30% increase in rainfall over the last half century; this area was previously known as being fishless.

These shifts in spatial distribution may result in an increase in fragmentation, as populations are expected to become restricted to isolated patches at high altitudes or latitudes, and isolated from other appropriate habitat

areas (Keleher & Rahel, 1996; Flebbe, Roghair & Bruggink, 2006; Hari *et al.*, 2006). This potential increase in fragmentation has been mainly addressed for salmonid populations in North America, but patterns are congruent across studies. For instance, Rahel, Keleher & Anderson (1996) have demonstrated that, for cold-water species of the North Platte River Basin in the Rocky Mountains, single large enclaves of suitable habitat could be fragmented into numerous smaller ones and experience a 47–90% decline in size depending on the warming scenario. This could considerably increase the vulnerability of isolated populations to future extinction. However, the lack of observations makes it impossible to support the predicted risk, even though similar assertions have already gained strong empirical support for many other taxa (Maclean & Wilson, 2011).

Concluding remarks and future research

This global overview and meta-analyses of the literature reporting observed and predicted climate-induced effects on freshwater fish distribution confirm that freshwater fish species could be severely affected by contemporary climate change. Observations and predictions are quite correlated, thus supporting the reliability of future projections. Nevertheless, the magnitude and variability of changes actually observed in habitat suitability in response to recent climate warming exceeded those predicted under future climate scenarios, suggesting the influence of other non-climatic stressors. However, this synthesis also highlights the fact that current knowledge is still incomplete, notably because of geographic and taxonomic biases.

The geographic bias towards the Northern hemisphere and the temperate regions of the Nearctic and Palaearctic realms is not surprising, as this pattern largely mirrors the intensity of ecological research (Wilson *et al.*, 2007; Pyšek *et al.*, 2008). This geographic bias could have important implications when scientific findings are translated into conservation measures. Indeed, the ongoing regional and global freshwater assessment programmes are accumulating evidence that threatened or 'climate change susceptible' species show clear geographic patterns, with high concentrations of species at risk in the Southern hemisphere (e.g. Foden *et al.*, 2008). As these regions account for a major proportion of freshwater fish endemism (Oberdorff *et al.*, 2011), our overall understanding of climate-induced effects on freshwater fish distribution would greatly benefit from further research in so far poorly studied regions.

By meticulously reporting each targeted fish species and its representative family across all published articles, our study provides the first quantitative evidence of a serious

taxonomic bias in studies assessing climate-induced changes in freshwater fish distribution. The list of reported fish species ($n = 183$) represents only a tiny proportion of the global freshwater fish fauna that probably comprises around 13 000 species. More surprisingly, the bias against threatened species and towards a small number of thoroughly studied species persists in regions with high research intensity, reflecting human interest in some particular fish species. Undoubtedly, this taxonomic bias towards salmonids and cold-water species is problematic, as it affects our perception of the influence of climate on freshwater fish overall. Indeed, the general impression emerging from the literature is that freshwater fish may respond negatively to climate change. However, the dramatic effects predicted for most cold-water fish species do not hold for all fish species, and many others have already responded in a more mitigated (or even contrary) manner. In particular, despite their important role in ecosystem processes (Vanni, 2002), fish species with no commercial or recreational interest have been poorly studied. We suggest that broadening the range of studied species is critical in depicting the potential effects of climate change more effectively, thus providing more reliable assessments of freshwater fish vulnerability that will make it possible to identify the appropriate conservation measures.

More importantly, the threats facing freshwater fish are not limited to habitat loss, as species-specific shifts in distributions may result in novel species assemblages displaying changes in competition, predation or other biotic interactions (e.g. Williams & Jackson, 2007; Stralberg *et al.*, 2009). Because future climate-induced changes in assemblage composition have rarely been addressed for freshwater fish (but see Buisson & Grenouillet, 2009), the consequences of such novel species assemblages remain unexplored and deserve more attention. Empirical studies could also greatly benefit from community ecology, as the analysis of assemblage responses through functional diversity (i.e. the composition of biological traits) provides a promising area for future research (Olden *et al.*, 2010). Taking into account the ecological characteristics of species should be helpful for investigating the functional consequences of climate change, identifying similar responses across contrasting assemblages and thus enhancing our understanding of climate-induced changes across a broad level of organisation.

From a methodological point of view, the empirical evidence of climate-induced changes in freshwater fish distribution need to be related statistically to trends in climate using appropriate approaches (reviewed in Brown *et al.*, 2011), as sufficiently robust approaches have rarely been used so far. One of the critical challenges facing long-

term analyses is to enhance our ability to disentangle the relative effects of climate change and those of other stressors that affect freshwater fish distribution, especially as they may interact with one another (Olden *et al.*, 2010). In the case of predictive studies, a number of criticisms about distributional models have called their validity into question (reviewed in Pearson & Dawson, 2003; Elith & Leathwick, 2009). Although these acknowledged drawbacks fall outside the scope of this review, we claim that accounting for most of the recent advances in predictive modelling will reinforce our ability to refine projections of future freshwater fish distribution. Among these ongoing and future improvements, we suggest that particular attention should be paid to the inherent uncertainty in projections, the need to include the biological characteristics (i.e. dispersal abilities) of the species, and the promising combination of both distributional and empirical approaches (Kearney & Porter, 2009; Dormann *et al.*, 2012) to provide more robust and detailed projections. Given that predictions of future effects limited to changes in climate appear to be underestimated relative to recently measured changes, including other non-climatic stressors (e.g. change in land-use, invasive species, habitat destruction) would also enhance our ability to assess the potential influence of global change in the future.

Finally, our study has revealed that further empirical evidence of recent climate-induced changes in freshwater fish distribution is needed to allow a comprehensive comparison with predicted changes under climate change scenarios. Our encouraging results comparing observed and predicted changes in habitat suitability for a limited subset of freshwater fish families lead us to believe that this research topic deserves further attention. As national monitoring programmes are growing in number in response to the environmental policies being implemented in several countries for protecting and managing water bodies over the last decade (e.g. the Water Framework Directive in Europe), it is likely that long-term data will accumulate in the coming years. These data will provide a baseline guide allowing future methodological advances and better anticipation of future changes to be achieved. Observed and predicted trends would then provide more comprehensive knowledge to enhance the reliability of projections, thus reinforcing our ability to assess climate-induced effects on freshwater fish.

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