



Do stream fish track climate change? Assessing distribution shifts in recent decades

Lise Comte and Gaël Grenouillet

L. Comte (lise.comte@univ-tlse3.fr) and G. Grenouillet, CNRS, UPS, ENFA, UMR5174 EDB (Laboratoire Évolution et Diversité Biologique), 118 route de Narbonne, FR-31062 Toulouse, France, and Univ. de Toulouse, UPS, UMR5174 EDB, FR-31062 Toulouse, France.

Understanding the ability of species to shift their distribution ranges in response to climate change is crucial for conservation biologists and resources managers. Although freshwater ecosystems include some of the most imperilled fauna worldwide, such range shifts have been poorly documented in streams and rivers and have never been compared to the current velocity of climate change. Based on national monitoring data, we examined the distributional changes of 32 stream fish species in France and quantified potential time lags in species responses, providing a unique opportunity to analyze range shifts over recent decades of warming in freshwater environments. A multi-faceted approach, based on several range measures along spatial gradients, allowed us to quantify range shifts of numerous species across the whole hydrographic network between an initial period (1980–1992) and a contemporary one (2003–2009), and to contrast them to the rates of isotherm shift in elevation and stream distance. Our results highlight systematic species shifts towards higher elevation and upstream, with mean shifts in range centre of $13.7 \text{ m decade}^{-1}$ and $0.6 \text{ km decade}^{-1}$, respectively. Fish species displayed dispersal-driven expansions along the altitudinal gradient at their upper range limit ($61.5 \text{ m decade}^{-1}$), while substantial range contractions at the lower limit ($6.3 \text{ km decade}^{-1}$) were documented for most species along the upstream–downstream gradient. Despite being consistent with the geographic variation in climate change velocities, these patterns reveal that the majority of stream fish have not shifted at a pace sufficient to track changing climate, in particular at their range centre where range shifts lag far behind expectation. Our study provides evidence that stream fish are currently responding to recent climate warming at a greater rate than many terrestrial organisms, although not as much as needed to cope with future climate modifications.

One of the main challenges for biodiversity conservation lies in understanding how species are responding to contemporary climate change, which is essential if we are to improve our ability to forecast changes and initiate management strategies (Dawson et al. 2011). Earth may face its sixth mass extinction if the current dramatic loss of species continues (Barnosky et al. 2011), and evidence is accumulating that many species are responding to recent climate change in a consistent way across ecosystems and regions (Parmesan 2006, Daufresne et al. 2009, Thomas 2010). One such response consists of distribution shifts poleward and upward in elevation (Hill et al. 1999, Parmesan and Yohe 2003, Hickling et al. 2006, Chen et al. 2011), as species attempt to track their favourable climate niche across space (Tingley et al. 2009, Crimmins et al. 2011). However, species have exhibited a wide diversity of range shifts, and recent evidence has suggested that many distributional shifts may not be enough to cope with the acceleration of climate change that has occurred in recent years (Devictor et al. 2008, Bertrand et al. 2011, La Sorte and Jetz 2012). As recently advocated, one approach to characterizing species vulnerability to climate change is

to compare the spread of distribution shifts with the rate which is required to keep pace with isotherm shifts (i.e. climate change velocity, Loarie et al. 2009, Isaak and Rieman 2013). Several studies have yet examined the rate of climate velocity both historically (Burrows et al. 2011, Dobrowski et al. 2013) and for the future (Loarie et al. 2009), but much less work has been devoted to quantifying time lag in species responses (but see Zhu et al. 2012).

To date, more climate-induced range expansions have been documented than range contractions (Parmesan et al. 1999, Moritz et al. 2008). However, individual species are likely to respond differently to climate change depending on their distribution ranges (Hill et al. 1999, Moritz et al. 2008). Indeed, low-elevation species may be able to expand their ranges, while physical barriers may affect the colonization of high-elevation species, leading them to decline (Hill et al. 2002, Chen et al. 2010). In addition, the determinants of species distribution could differ along environmental gradients, leading to asymmetric species responses (Hampe and Petit 2005). For instance, warm limits may be determined by complex temperature-mediated biotic interactions, whereas physiological climatic constraints

are more likely to be limiting at cold limits (Brown et al. 1996, Normand et al. 2009). Compensatory changes in demographic rates may also temporally buffer the extinction of local populations at the warm limit of their bioclimatic distribution (Doak and Morris 2010). Alternatively, physiological stress due to climate change may occur not only at range limits, but also among populations experiencing the greatest magnitudes of climate change even within the range of the species (Lenoir et al. 2008). Despite the relevance of using several descriptors to find out whether species are shifting across their entire distribution range, most of the studies available offer only a limited view of ecological responses to climate change, either geographically or with regards to the range parameters analyzed (Hampe and Petit 2005, Parmesan 2006).

Globally, rivers and streams are among the most threatened ecosystems, suffering from declines in biodiversity that are far greater than those in even the most severely affected terrestrial ecosystems (Dudgeon et al. 2006). In particular, climate change could be one of the main threats faced by aquatic ecosystems and freshwater biodiversity (Sala et al. 2000, Heino et al. 2009). Like many terrestrial species, the distribution of aquatic organisms could be significantly modified by climate change, as temperature has critical effects on ectotherms through its combined impacts on dissolved oxygen levels and metabolism (Pörtner and Knust 2007). Changes in stream flows due to increase in temperature can also be expected to further reduce the suitable habitat available for stream fish, even if total precipitation goes unchanged (Carpenter et al. 1992, Leith and Whitfield 1998). Recent findings have confirmed that changes in water temperatures could have significant effects, leading to alterations of fish growth and recruitment success (Schindler et al. 2005, Daufresne et al. 2009, Clews et al. 2010, Nunn et al. 2010). Furthermore, in contrast to their terrestrial counterparts, stream fish distributions are determined by biotic and abiotic factors that vary along the upstream–downstream gradient (i.e. downstream distance, stream order) (Matthews 1998, Buisson et al. 2008). Their ability to move in response to environmental change is thus constrained by the dendritic structure of drainage basins (Fausch et al. 2002, Brown and Swan 2010), although most of the previous studies exploring climate change impacts on freshwater fish have not explicitly considered the spatial structure of dispersal networks. Surprisingly, except for a documented general poleward and upward shift of British fish between 1965–1975 and 1990–2000 (Hickling et al. 2006), range shifts for stream fish have been poorly documented, and in most cases involve salmonids (Hari et al. 2006, Almodóvar et al. 2012). Therefore, for assessing species vulnerability to climate change in aquatic environments, the question of how fast stream fish are shifting compared to the speed required to keep pace with changing climate has yet to be resolved.

Here, we documented range shifts of stream fish in France, based on comparatively diverse regions and species data, providing a unique opportunity to analyze range shifts over recent decades in freshwater ecosystems. Our description of range shifts considered changes that have occurred at the limits (i.e. range boundaries), as well as at

the centre of the species' distributions. These measurements have made it possible to characterize the patterns of range shift in two distinct survey periods along altitudinal and upstream–downstream (i.e. distance from source) gradients, both of which are strongly related to species distribution and climatic gradients (Cassie 2006). Moreover, we assessed whether range shifts along environmental gradients were related to climate tracking through the potential time lags between climate velocity and biological responses, expecting species to have responded to climate change by modifying their ranges to remain within their preexisting climatic niche (Tingley et al. 2009).

The specific aims of the study were to 1) characterize patterns of range shifts along altitudinal and upstream–downstream gradients for 32 fish species inhabiting French streams between an initial survey period (1980–1992) and a more recent 'contemporary' one (2003–2009), 2) compare these responses according to the distribution preferences of species along environmental gradients, and 3) find out whether changes in distribution were related to climate tracking by comparing species range shifts to the velocity of climate change.

Material and methods

Study area and species

The French monitoring programme of freshwater fish populations is ensured by the French National Agency for Water and Aquatic Environments (Onema), which aims to preserve water quality and good ecological status of aquatic systems. The electrofishing database of the Onema provides a spatially and temporally extensive survey of freshwater fish at the national scale, with the potential to assess long-term trends in fish populations (Poulet et al. 2011). From this database, we initially refined our selection to stream sites with reliable GIS data. We then extracted two well-balanced pools of sites sampled during 'cold' and 'warm' temperature regime periods relative to the average conditions between 1965 to 2008 (Supplementary material Appendix 1, Fig. A1). The first period included 3549 sites sampled from 1980 to 1992 (hereafter referred to as initial surveys). The second period included 3543 sites sampled from 2003 to 2009 (hereafter referred to as contemporary surveys). For both time periods, the sampling sites were distributed throughout France (Fig. 1A, B). Although only 7.5% of sites were common to both time periods, surveys were conducted in all the major hydrographic basins of France and covered the entire range of environmental conditions. Data on the presence–absence of fish species were recorded at each site from 1 to 19 times during the initial period, and from 1 to 14 times during the contemporary period, resulting in 4533 and 7548 sampling records, respectively. After correcting for taxonomic revisions that had occurred during the entire study period (i.e. pooling together existing species in the initial period that have been divided into two or more species in the contemporary period), we considered only species present on at least 75 sites in both periods, for a total of 32 species (Table 1).

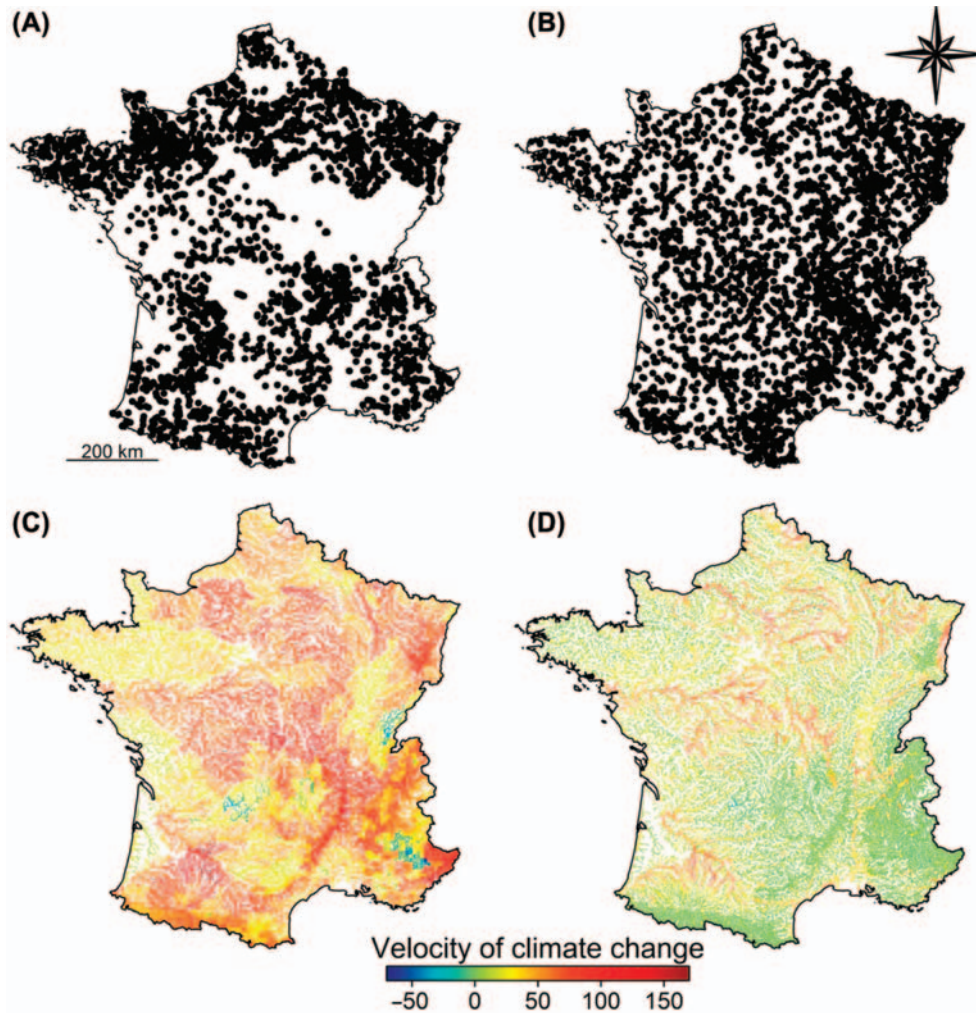


Figure 1. Study area showing the spatial position of (A) initial and (B) contemporary surveys. Velocity of climate change along the reaches of the hydrographic network expressed in (C) altitudinal distance (m decade^{-1}) and (D) upstream–downstream distance (km decade^{-1}). Positive velocities means isotherms shifts towards higher elevation or upstream, while negative means isotherms shifts towards lower elevation or downstream.

Sampling strategies and sampling success

Both surveys were conducted according to standard electro-fishing procedures defined on the basis of river width and depth. Small streams were sampled by wading, mostly by two-pass removal, and large rivers by fractional sampling strategies of the different types of mesohabitat, or by partial sampling strategies in the river margins and delimited areas of habitat (Poulet et al. 2011). However, several different methods were used successively until the introduction of a unified surveillance monitoring protocol in 1995.

One difficulty that persists in documenting range shifts is reconciling differences between the sampling protocols used in historical and recent surveys (Patton et al. 1998, Shaffer et al. 1998, Shoo et al. 2006, Tingley and Beissinger 2009). Many factors can have an impact on the probability of detecting a species, and the degree of this impact can differ on temporal, geographic and taxonomic scales (Kéry and Schmid 2006, Kéry and Plattner 2007). As a result, real distribution changes may be confounded by changes in detectability, particularly if only two time periods are

considered. To tackle this issue, we conducted separated analyses on a restricted dataset in order to assess whether potential variation in the sampling success had in fact impaired our ability to detect range shifts. Following the general approach developed by Kéry and Plattner (2007), we evaluated if the mean proportion of species detected and the species-specific detectability had varied over the temporal scale of our study (details in Supplementary material Appendix 2).

We found that the mean proportion of species detected differed between the initial and contemporary surveys, depending on the sampling prospection method employed (Supplementary material Appendix 2, Table A2). In particular, samplings conducted by boat seemed to be more successful in the contemporary surveys. As a result, the mean proportion of species detected at low to mid upstream–downstream locations (i.e. >200 km from the source) was higher in the contemporary surveys, whereas no differences were observed either for upstream locations or along the altitudinal gradient (Supplementary material Appendix 2, Fig. A2). In addition, the species-specific

Table 1. Spatial distribution preferences of fish species along elevation and upstream–downstream gradients in the initial surveys defined following a hierarchical clustering based on the Ward’s method with the Euclidean distance, and species-specific estimates of detectability in the initial (I) and contemporary (C) surveys based on GLMM analysis (Supplementary material Appendix 2). Detectability could not be estimated in the initial surveys for *Parachondrostoma toxostoma* due to the limited set of capture history data available.

Species names	Code	Altitudinal	Upstream–downstream	Initial detectability (SD)	Contemporary detectability (SD)
<i>Abramis brama</i>	Abb	Low	Low	0.58 (0.11)	0.47 (0.11)
<i>Alburnoides bipunctatus</i>	Alb	Low	High	0.44 (0.12)	0.79 (0.07)
<i>Alburnus alburnus</i>	Ala	Low	Low	0.67 (0.11)	0.79 (0.08)
<i>Ameiurus melas</i>	Amm	Low	Low	0.38 (0.12)	0.5 (0.09)
<i>Anguilla anguilla</i>	Ana	Low	Mid	0.88 (0.06)	0.81 (0.07)
<i>Barbatula barbatula</i>	Bba	High	High	0.77 (0.09)	0.85 (0.06)
<i>Barbus barbus</i>	Bab	Mid	Mid	0.67 (0.11)	0.82 (0.06)
<i>Barbus meridionalis</i>	Bam	Mid	High	0.81 (0.06)	0.81 (0.12)
<i>Blicca bjoerkna</i>	Blb	Low	Low	0.5 (0.12)	0.61 (0.1)
<i>Chondrostoma nasus</i>	Chn	Mid	Low	0.54 (0.13)	0.67 (0.1)
<i>Cottus gobio</i>	Cog	High	High	0.85 (0.06)	0.84 (0.06)
<i>Cyprinus carpio</i>	Cyc	Low	Low	0.33 (0.11)	0.4 (0.11)
<i>Esox lucius</i>	Esl	Low	Mid	0.58 (0.11)	0.6 (0.1)
<i>Gasterosteus aculeatus</i>	Gaa	Low	High	0.44 (0.12)	0.53 (0.1)
<i>Gobio gobio</i>	Gog	Mid	High	0.78 (0.09)	0.89 (0.05)
<i>Gymnocephalus cernua</i>	Gyc	Low	Mid	0.44 (0.13)	0.55 (0.11)
<i>Lepomis gibbosus</i>	Leg	Low	Mid	0.46 (0.11)	0.68 (0.1)
<i>Leuciscus leuciscus</i>	Lel	Low	High	0.65 (0.12)	0.66 (0.1)
<i>Lota lota</i>	Lol	Low	Mid	0.5 (0.14)	0.51 (0.11)
<i>Parachondrostoma toxostoma</i>	Pat	Mid	High	–	0.57 (0.1)
<i>Perca fluviatilis</i>	Pef	Low	Mid	0.82 (0.07)	0.72 (0.09)
<i>Phoxinus phoxinus</i>	Php	High	High	0.83 (0.06)	0.85 (0.06)
<i>Pungitius pungitius</i>	Pup	Low	High	0.53 (0.11)	0.52 (0.1)
<i>Rutilus rutilus</i>	Rur	Low	Mid	0.86 (0.06)	0.83 (0.06)
<i>Salmo salar</i>	Sas	Low	High	0.81 (0.06)	0.77 (0.08)
<i>Salmo trutta</i>	Sat	High	High	0.88 (0.05)	0.85 (0.06)
<i>Sander lucioperca</i>	Sal	Low	Low	0.34 (0.09)	0.37 (0.11)
<i>Scardinius erythrophthalmus</i>	Sce	Low	Low	0.51 (0.11)	0.47 (0.1)
<i>Squalius cephalus</i>	Sqc	Mid	Mid	0.88 (0.06)	0.91 (0.04)
<i>Telestes souffia</i>	Tes	High	High	0.76 (0.1)	0.81 (0.08)
<i>Thymallus thymallus</i>	Tht	Mid	High	0.58 (0.07)	0.55 (0.11)
<i>Tinca tinca</i>	Tit	Low	Mid	0.48 (0.12)	0.53 (0.11)

estimates of detectability were found to slightly differ in the contemporary and initial surveys, with a mean difference in detectability of 0.05 (Table 1; see Supplementary material Appendix 2, Table A3, A4 for details on model’s results). Nevertheless, there was no link between variation in species detectability and distribution changes (see below) between time periods ($p > 0.05$).

Environmental data

Several variables, all of them strongly related to the spatial distribution of stream fish (Buisson et al. 2008), were used to describe climatic and habitat conditions over the French hydrographic network and subsequently used to model species distribution (see Supplementary material Appendix 1, Table A1 for details). Habitat characteristics consisted of elevation (ELE, m), slope (SLO, ‰), the entire area drained by the upstream area (km²) and the cumulated length of the upstream flow network (m) (CCM2, Vogt et al. 2007). To eliminate the colinearity between the last two variables which both reflect the upstream–downstream position, we used a principal component analysis (PCA) and the first axis of the PCA was kept as a synthetic variable describing the upstream–downstream gradient (G). High G values corresponded to the most

downstream sites and low G values to the most upstream sites. Bioclimatic variables were derived from the high resolution (8 km grid-data) SAFRAN atmospheric reanalysis over France (Le Moigne 2002): mean temperature of the coldest quarter (°C), mean temperature of the warmest quarter (°C), temperature seasonality (SD × 100), cumulated precipitation of the wettest quarter (mm), cumulated precipitation of the driest quarter (mm) and precipitation seasonality (CV). For both period, we obtained mean climatic conditions by averaging the climatic variables within each period plus the three preceding years, which correspond to the mean duration of the species life cycle.

Climate change velocity

Long-term temperature and precipitation trends were estimated using linear regressions on mean annual temperature and precipitation for each stream reach over the 1968–2008 period using the SAFRAN climate database. Air temperature was used as a surrogate of water temperature after applying a scaling factor of 0.8°C. To determine the rate of isotherm shifts in space (Loarie et al. 2009), we calculated the velocity of climate change along both the altitudinal and upstream–downstream gradients. Following Isaak and Rieman (2013), we first calculated climate velocity

using spatial temperature gradient expressed in elevation distance (m decade^{-1}) as the ratio of long-term temperature trends ($^{\circ}\text{C decade}^{-1}$) to the stream lapse rates ($^{\circ}\text{C m}^{-1}$). The stream lapse rates were estimated using linear regression between temperature and elevation within each of the 54 hydrographic units of the stream network. We then calculated climate velocity expressed in stream (i.e. longitudinal) distance (km decade^{-1}) as the ratio of the altitudinal velocities to stream slopes (SLO, $^{\circ}$).

Modelling species spatial distribution

To account for uncertainty in comparing observed range limits over time based on data sets not originally collected with the explicit purpose of detecting range shifts (Shoo et al. 2006, Tingley and Beissinger 2009), we modelled the spatial distribution of each species across the French hydrographic network as a function of several climatic and environmental variables using an ensemble modelling framework (Marmion et al. 2009). Modelling response curves of species along an environmental gradient is considered to be an effective way of carrying out ecological gradient analysis (Lenoir et al. 2008, Crimmins et al. 2011, Maggini et al. 2011), that is insensitive to irregularly-spaced sampling (Oksanen et al. 2001). Although Gaussian functions have usually been applied, combinative algorithms are known to increase the accuracy of an ensemble of model outputs (Marmion et al. 2009, Grenouillet et al. 2011). In addition, although a single gradient may act as suitable surrogate to model the spatial distribution of some animals (Maggini et al. 2011), species ranges are clearly influenced by multiple habitat and climatic factors, particularly in aquatic systems where environmental conditions vary along the dendritic network (Matthews 1998). Therefore, modelling fish species distribution by incorporating additional variables should provide more accurate estimates than single-gradient models (Oksanen et al. 2001).

The occurrence of each species was modelled independently for both time periods as a function of the habitat and climatic data extracted at all survey sites to avoid potential bias due to variation in the distribution of the sites over time. To take into account the variability introduced by the modelling method, we followed the procedure applied in Marmion et al. (2009) by averaging the probabilities of occurrence predicted by eight single-SDMs: generalized linear models, generalized additive models, multivariate adaptive regression splines, mixture discriminant analyses, classification and regression trees, random forest, generalized boosted trees and artificial neural networks. Datasets for each period were composed of one sampling record randomly chosen for each site, to avoid pseudoreplication. Models were calibrated on 70% of the sampling records, while the remaining 30% were used for evaluation and threshold optimisation. To take into account the variability induced by the threshold setting-method, three of the most common methods were applied to convert predicted occurrence probabilities into binary data (i.e. presence or absence, Liu et al. 2005). Specifically, we used threshold values maximizing the sum of sensitivity and specificity, sensitivity equalling specificity and maximizing

Kappa. Finally, the different steps of the modelling process were repeated 30 times with 30 different sampling record datasets to take into account the variability due to the quality of the calibration dataset.

We then predicted the probabilities of occurrence of the species on the reaches of the French hydrographic network for which environmental conditions did not differ from those of the calibration datasets. These probabilities were then transformed into binary predictions of presence and absence using the previously calculated thresholds. We thus obtained 90 final modelled species distributions for each period and species, resulting from 30 iterations and 3 thresholds.

Details on model performances are given in Supplementary material Appendix 3.

Estimating range descriptors

The thermal regime of a stream depends mainly on its altitudinal and upstream–downstream position within a river basin (Cassie 2006). Therefore, to test for a potential modification in the distribution of stream fish in response to climate change, shifts along the upstream–downstream gradient were assessed using the distance from source (km), and shifts along the altitudinal gradient using ELE, as these two gradients were uncorrelated when considering the whole French hydrographic network ($r_p = -0.21$). We defined the centre of species' distributions (hereafter referred to as 'range centre') along both the altitudinal and the upstream–downstream gradients in terms of the median values of the stream reaches where the species were predicted to be present (Zuckerberg et al. 2009). We also considered the lower and upper range limits as 2.5 and 97.5%, respectively, of the altitudinal and upstream–downstream values of all predicted presences in order to reduce the influence of outliers (Quinn et al. 1996). The overall extent was then defined as the absolute value of the upper minus the lower range limits along the above-mentioned gradients.

Analyzing range shifts

As threshold selection is known to strongly influence species distribution modelling (Nenzén and Araújo 2011), temporal changes in range centre, upper and lower range limits and overall range extent were evaluated by controlling for this effect. For each species, the shift (i.e. extension or contraction) in each range descriptor was assessed by fitting a linear regression through all the range descriptors obtained for each period with the threshold-setting method and the period as explanatory variables. This shift was then determined by the least-squares mean of the contemporary period-group effect.

Shift patterns were then plotted according to changes in range centre, and in the lower and upper limits along the gradient (see Fig. 2 for theoretical examples), making it possible to visualize directional consistency in species responses. To avoid dealing with shifts that we did not consider as ecologically meaningful (i.e. smaller than the resolution of the hydrographic network used), the average slope and length values of all stream reaches were computed,

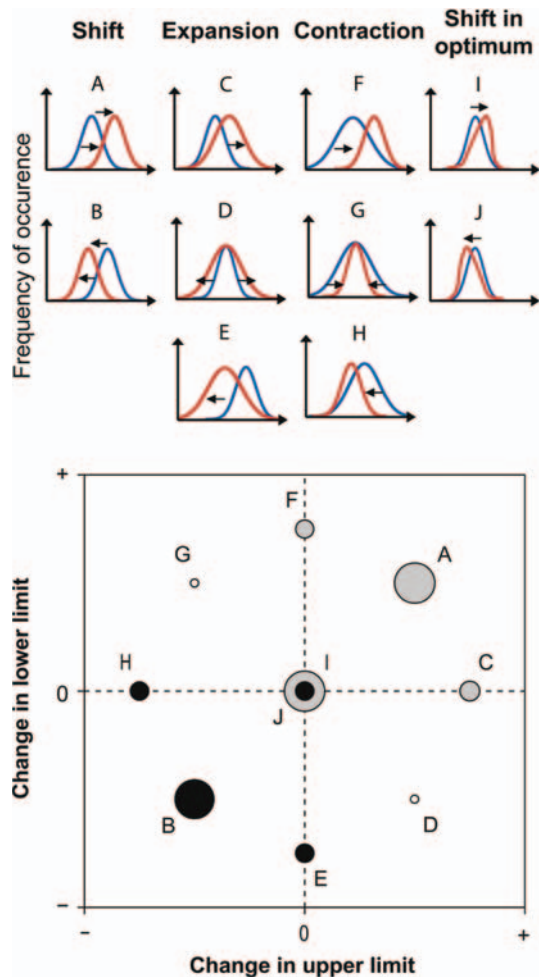


Figure 2. Theoretical plot and associated response curves depicting potential shift patterns (A–J) along an environmental (i.e. altitudinal or upstream–downstream) gradient as a function of the mean changes in range centre, and of the upper and lower range limits between the contemporary and initial periods. The size of the circle represents the absolute changes in range centre along the environmental gradient. Solid circles indicate significant ($p < 0.05$) shifts in range centre, with grey for positive (i.e. shift towards higher elevation or upstream) and black for negative (i.e. shift towards lower elevation or downstream). Blue line in response curves represents the initial distribution and red line the distribution during the contemporary period. Arrows indicate the direction of the shift patterns. Changes can either occur at the upper and lower range limits or at the range centre along this gradient and consist of either expansion or contraction. Patterns C, F and I depict positive shifts that may be considered as intermediate patterns towards the full distributional shift shown in A. Pattern I is a special case of a positive shift, where only the range centre along the gradient moved towards higher elevation or upstream. In contrast, patterns E, H and J depict negative shifts that may be considered as intermediate patterns towards the full negative shift illustrated in B. Patterns D and G depict contrasting changes in both range limits, which may indicate complex responses of species to multiple stressors and/or competitive interactions (Lenoir et al. 2010, Maggini et al. 2011).

and supplementary thresholds of 30 m and 2 km were then used to interpret the range shifts along the altitudinal and upstream–downstream gradients, respectively.

To test whether species exhibited differential patterns depending on their distribution along environmental gradients,

species were classified as having ‘low-’, ‘mid-’ or ‘high-’ elevation preferences and ‘upstream’, ‘midstream’ or ‘downstream’ preferences, respectively. Species preferences were defined following hierarchical clustering (Euclidean distance and Ward’s linkage criterion) based on the range centre and the upper and lower range limits of the initial survey dataset for each gradient (Table 1).

Finally, to find out whether habitat shifts were consistent with potential climate tracking, we compared the distribution shifts for each species with the velocity of climate change at its range centre along altitudinal and upstream–downstream gradients.

Models and analyses were developed using R environment software ver. 2.13.0 (R Development Core Team).

Results

Climate change velocity

Temporal trends in mean annual temperature and precipitation indicated that the area studied had become warmer (Supplementary material Appendix 1), whereas no trend in precipitation was apparent. On average, the mean annual temperature had increased by about $0.24^{\circ}\text{C decade}^{-1}$, although changes were not consistent across the hydrological network (Supplementary material Appendix 1, Fig. A1). Similarly, the velocity of climate change appeared spatially structured, and particularly along the upstream–downstream gradient where the major shifts were observed for downstream sections. Depending on the gradient considered, the velocity of climate change ranged from -65.2 to $169.5 \text{ m decade}^{-1}$ in elevation (mean: $57.3 \text{ m decade}^{-1}$), and from -28.6 to $162.6 \text{ km decade}^{-1}$ in stream distance (mean: $14.2 \text{ km decade}^{-1}$). Nevertheless, the majority of mean annual temperature shifts ranged from 40.6 to $74.3 \text{ m decade}^{-1}$ and 1.1 to $17.3 \text{ km decade}^{-1}$, respectively, indicating that isotherms moved towards higher elevation and upstream for most French streams and rivers.

Range shifts

The distributional shifts showed directional trends towards higher elevation and upstream position for most species (Fig. 3A, B). Changes higher than 30 m were more common at the upper elevation limit (71.9%) than at the lower limit (3.1%), and only 1 species showed changes at both ends of their range. However, all shifts of the lower limit were relatively negligible compared to those of the upper limit, with mean shifts of 4.9 m and 116.9 m, respectively. All but 7 species exhibited a shift in elevation range centre towards higher elevation, with a mean elevation shift of 26.1 m. Only 4 species exhibited a shift in elevation range centre towards lower elevation, although the magnitude of the shifts toward lower elevation was relatively minor. As a result, when considering changes in range limits higher than 30 m, 78.1% of species actually showed a consistent altitudinal shift, with 17 patterns of range expansion to higher elevation (Fig. 2, pattern C), 1 pattern of full altitudinal shift (Fig. 2, pattern A), and 7 pattern of change in

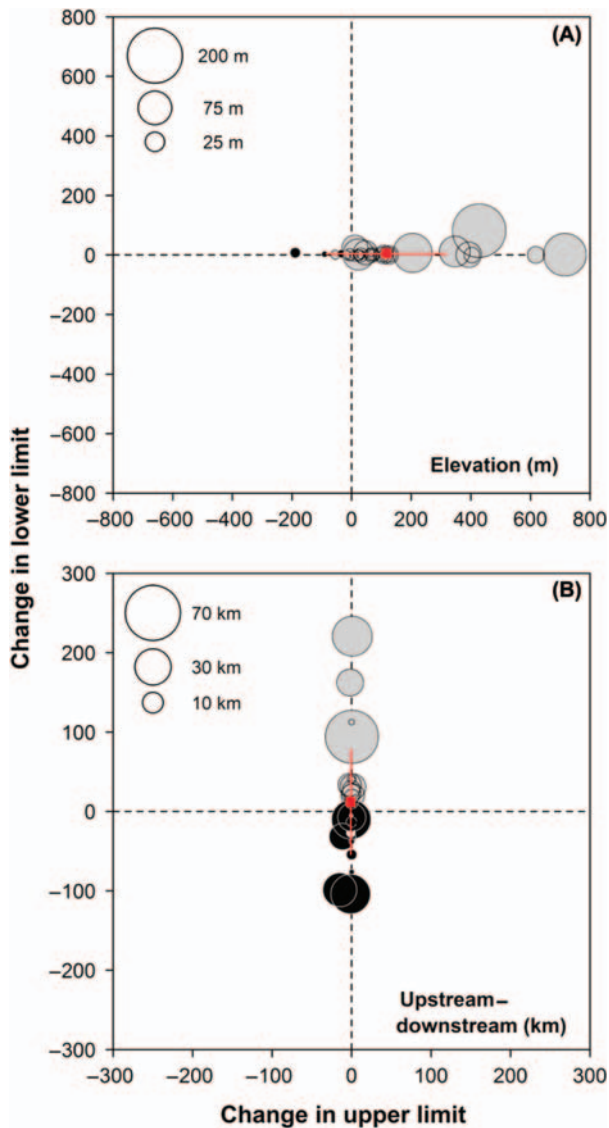


Figure 3. Changes in the upper and lower range limits between the initial and contemporary periods for (A) elevation and (B) upstream–downstream position. Upper limits correspond to high elevation and upstream position. Lower limits correspond to low elevation and downstream position. Each circle represents the value for a stream fish species. The size of the circles indicates differences in species range centre along the gradients. Significant ($p < 0.05$) differences in species range centre are coloured as in Fig. 2: grey for positive (i.e. shift towards higher elevation or upstream) and black for negative (i.e. shift towards lower elevation or downstream) shifts. Red squares and the associated error bars indicate the mean shifts (\pm SD) in lower and upper limits across all species. Values of range shifts for each species are given in Supplementary material Appendix 4, Table A7.

elevation range centre (Fig. 2, pattern I), while 3 species showed a contraction of their upper range limit (Fig. 2, pattern H).

In contrast, changes of > 2 km in the downstream limit were more common (84.4%) than those of the upstream limit (9.4%). Mean shifts in upstream and downstream limits were of 1.0 km downstream and 11.9 km upstream, respectively, and the shift in range centre along this gradient was of

1.2 km upstream. Overall, when considering changes in range limits of more than 2 km, 65.6% of species showed consistent patterns towards upstream positions. The pattern of range contraction (Fig. 2, pattern F) was the one most commonly observed (40.6%), with a mean contraction upstream of both the downstream limit and the range centre of 64.6 and 13.6 km, respectively. Nevertheless, 5 species exhibited a downstream shift with an expansion of the downstream limit towards a position further downstream (Fig. 2, pattern E), while 2 species showed a downstream shift in range centre (Fig. 2, pattern J).

By comparing range shifts of species according to their distribution along environmental gradients in the initial period, we found that the magnitude of range expansion at the upper elevation range limit was greater for low-elevation species (Fig. 4A). In contrast, contraction along this gradient at either the upper or lower range limits were mostly observed for mid- or high-elevation species. As a result, although most species extended their overall extent, about 30 and 20% of high- and mid-elevation species showed a contraction of their overall extent, respectively. No clear pattern of range shifts was apparent along the upstream–downstream gradient, although the magnitude of the contraction at the lower range limit was greater for few mid-stream and upstream species (Fig. 4B). A contraction of the overall extent was commonly observed for all species, although about 40 and 50% of upstream and midstream species showed an expansion related to a downstream shift at their lower range limit. However, about 20% of downstream species showed no changes in their overall extent along this gradient.

The patterns of range shifts were consistent with the expectations based on the velocity of climate change. At the downstream limit, in particular, climate change velocity suggested that species may need to shift at a much faster rate to track climate change than at the upstream limit (Fig. 1D). However, stream fish range shifts lagged far behind expectations along both the elevation and upstream–downstream gradients (Fig. 5). Overall, changes in the spatial distribution of species were directed towards colder conditions with respect to initial climate, but most species have shifted far less than necessary to track the rising annual temperature at their range centres. Indeed, only two species have shifted at a pace sufficient to track temperature change, resulting in mean lags across species of $46.8 \text{ m decade}^{-1}$ and $15.0 \text{ km decade}^{-1}$ along the altitudinal and upstream–downstream gradients, respectively. Nevertheless, the lag behind temperature-based expectations at the species range centre varied considerably among stream fish while no trends with the velocity of climate change was apparent.

Discussion

Our results highlight consistent shifts to higher elevation and upstream in the fish distribution ranges from 1980–1992 to 2003–2009. Increases in elevation range centre appeared to result from colonisations at higher elevations rather than extinctions at low elevations. The mean altitudinal shift ($13.7 \text{ m decade}^{-1}$) was consistent with the shifts measured by Hickling et al. (2006) for 15 fish species in

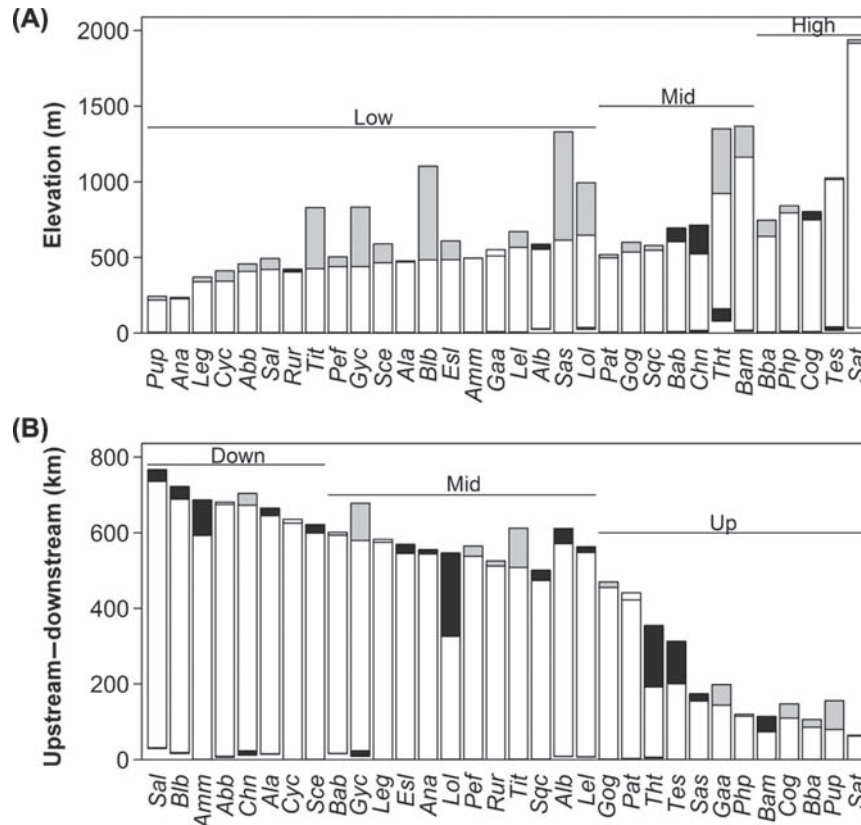


Figure 4. Summary of (A) altitudinal and (B) upstream–downstream range changes across all species in relation to their spatial distribution along these gradients in the initial period. White indicates sections where the initial and contemporary distributions overlapped. Significant ($p < 0.05$) shifts are coloured grey for range expansion and black for contraction. Species codes and spatial distribution preferences along these gradients as in Table 1.

Britain over a comparable period of time ($13.1 \text{ m decade}^{-1}$). Whereas this latter study focused on changes in species elevation range centre, shifts of the upper range limit by $6.1 \text{ m decade}^{-1}$ towards higher elevation were documented for 99 terrestrial species (Parmesan and Yohe 2003). We found that the shift rate was of greater magnitude ($61.5 \text{ m decade}^{-1}$), indicating that stream fish may be more sensitive to climate-induced impacts than other terrestrial organisms. In contrast, upstream movements were greater at the downstream limits ($6.3 \text{ km decade}^{-1}$) than at the upstream limits where a mean downstream shift across all species was observed ($0.5 \text{ km decade}^{-1}$). Such range contraction resulted in significant shifts in species range centre along this gradient ($0.6 \text{ km decade}^{-1}$), but, to the best of our knowledge, no comparable values have been reported in the literature. Similarly to North American streams (Isaak and Rieman 2013), climate change velocities in French streams indicated that isotherms shifted during the last decades about 40.6 to $74.3 \text{ m decade}^{-1}$ towards higher elevation, and about 1.1 to $17.3 \text{ km decade}^{-1}$ along the upstream–downstream gradient, as air temperature increased by $0.24^\circ\text{C decade}^{-1}$. Although the magnitude of species distribution shifts observed at range limits was coherent with these expected values, shifts at the centre of species' distributions were of lesser magnitude, particularly along the upstream–downstream gradient. Our findings therefore suggested that species are experiencing

greater changes at their range limits than within their range, where larger populations could be more stable and resistant to environmental changes (Brown et al. 1996), resulting in rarely complete but usually transient shifts along environmental gradients, especially over short periods (Maggini et al. 2011).

Under warming conditions, climate change has affected ecosystems in a non-linear way, and species in downstream or lowland (i.e. flat) areas have to cover longer distances to track their climate niche, compared to mountainous regions, where isotherms are highly packed (Loarie et al. 2009). Indeed, our findings provided evidence for such dispersal-driven expansion along the altitudinal gradient, where favourable new conditions at higher elevations prompted the species inhabiting lowland areas to move upward (Hill et al. 2002, Moritz et al. 2008). On the other hand, most species showed a contraction at their lower limit along the upstream–downstream gradient, indicating that climatic stress may be an important determinant of stream fish downstream limits. Given that downstream sections were also the areas where climate has changed most due to the concavity of stream profile (Isaak and Rieman 2013), geographic variation in the velocity of climate change may explain patterns of range shifts across species distributions. It is therefore likely that stream fish follow climate change through complex modifications of their geographical distributions.

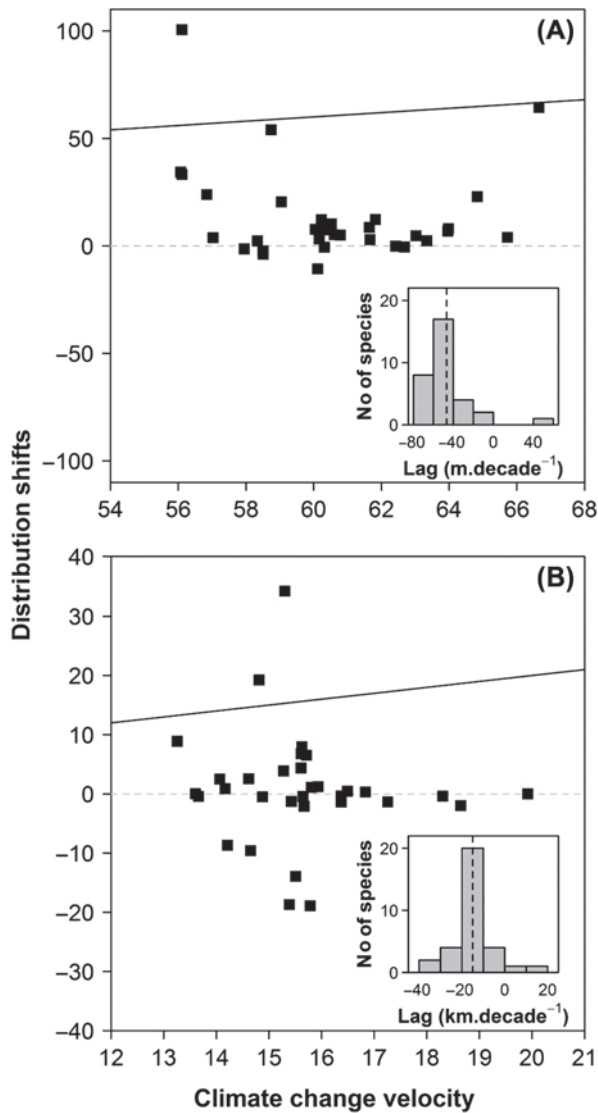


Figure 5. Comparison of distribution shifts with climate change velocity at the species range centre along (A) altitudinal (m decade^{-1}) and (B) upstream–downstream (km decade^{-1}) gradients. Positive distribution shifts indicate shifts towards higher elevation or upstream and negative shifts towards lower elevation or downstream. The solid line corresponds to cases where species track perfectly climate change. The histograms show the time lags between shifts in species range centre and the velocity of climate change (i.e. negative values indicate that species are lagging behind climate change).

However, although most species shifted in the expected direction, spread rates appeared insufficient to keep pace with changing climate conditions. The velocity of climate change at the species range centre was much greater than the observed distribution shifts, indicating that the response of stream fish actually lags behind climate warming (Devictor et al. 2008, Bertrand et al. 2011, La Sorte and Jetz 2012). Indeed, mean lags in species response (elevation: $46.8 \text{ m decade}^{-1}$; upstream: $15.0 \text{ km decade}^{-1}$) were beyond several order of magnitude the distance already moved by species along the altitudinal and upstream–downstream gradients, respectively. As the

velocity of climate change probably already exceeds the rates that species can achieve in colonizing newly suitable habitat, the accumulating delay may have profound consequences on the ability of species to cope with future climate modifications. As the temperature would shift upstream of $> 100 \text{ km}$ during the next decades (Isaak and Rieman 2013), our results provided strong empirical support that climate change is now a major threat to freshwater biodiversity (Sala et al. 2000, Heino et al. 2009). Nevertheless, this effect varied considerably among species, such as two species are already experiencing colder temperatures than expected based on isotherms shifts in mean annual temperature, while several species have moved to an unexpected direction. Changes in multiple climatic factors, in addition to mean temperature, may help to explain these conflicting observations (Burrows et al. 2011, Dobrowski et al. 2013). In particular, the impact of thermal stress may be particularly important for aquatic species such as stream fish because, as ectothermic animals, they are known to be sensitive to extreme temperature conditions (Elliott 1981, Matthews 1998). Future studies should therefore assess if shifts in the geographical space of species are related to changes in specific climatic conditions rather than to mean temperature increases.

However, the consistency between directional trends in climate and changing distribution may not be sufficient to demonstrate causation, particularly when there are potential confounding interactions with other drivers of change (Thomas 2010, Hockey et al. 2011). As a result, movements toward higher elevation and upstream cannot be unambiguously interpreted as a consequence of climate warming, particularly in aquatic systems where dispersal is limited by the structure of the river network. Hence, anthropogenic pressures and climate change may simultaneously influence species range shifts, given the large overlap between ‘climate-change-susceptible’ and threatened species (Foden et al. 2008). For instance, range retractions might be a consequence of drivers others than climate, as those species are more prone to react to changes in habitat suitability than more generalist species. Alternatively, directions towards previously warmer conditions might be explained by improvement in water quality that occurs over the course of the study period (Glennie et al. 2002, Poulet et al. 2011), especially in downstream sections. In addition, susceptibility of species to diseases or shifting competitive or predator–prey relationships have also been evoked to explain range retractions (Hari et al. 2006, Thomas 2010), while competition release (Lenoir et al. 2010, Maggini et al. 2011) may have benefited high-range species, allowing them to recolonise the lower periphery of their niche.

Expansion of the upper limit may also be easier to detect than contraction of the lower limit because extinction may be missed or underestimated as a result of the temporary persistence of local populations (Thomas et al. 2006, Doak and Morris 2010). In this study, we found that sampling success had increased in down to mid upstream–downstream bands over the study period. As a result, the fraction of lower range limits showing either a contraction or an expansion may have been overestimated. Nevertheless, although temporal trends in detectability may simulate range shifts or indeed hide real shifts (Kéry and Plattner

2007, Tingley and Beissinger 2009), two pieces of evidence suggested that the patterns observed were more likely to reflect changes in distribution rather than temporal changes in detectability. First, the differences in the mean proportion of species detected appeared to be limited to the downstream areas rather than occurring in the upper areas, where an increase in detection success might artificially suggest downstream shifts but in any case upstream shifts. Second, changes in species-specific detectability were relatively minor, and not related to shifts measured along environmental gradients. They may thus only reflect the increase in the number and abundance of species documented in large rivers over the last decades (Daufresne and Boët 2007, Poulet et al. 2011).

Freshwater ecosystems contain some of the most imperilled faunas worldwide and advancing our knowledge of the effect of climate change is a key challenge for conservation (Olden et al. 2010). Our approach, which integrates distinct facets of species ranges along environmental gradients, provides evidence that complex modifications of stream fish distribution have occurred over recent decades in France, that were consistent with the geographical variation in the velocity of climate change. However, we found that the degree of climate change exposure alone could not explain much of the differences across species range shifts. Indeed, responses of individual species may not be isolated phenomena, but determined by an array of interacting biological and environmental factors, that are sometimes difficult to predict (Walther 2010). Moreover, individualistic traits (e.g. dispersal capacity, trophic level) may induce high variability in the consistency of climate response across species (Parmesan 2006). Although species sharing similar characteristics should be expected to show similar patterns in range shift (Pöyry et al. 2009), recent work has not strongly supported this assertion (Angert et al. 2011). Additional work is thus needed to further elucidate the mechanisms underlying species responses to a changing climate and to understand the nature of multiple-stressor effects on species populations and local assemblages.

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Supplementary material (Appendix ECOG-00282 at < www.oikosoffice.lu.se/appendix >). Appendix 1–4.