Diversity and Distributions, (Diversity Distrib.) (2015) 21, 1014–1026

BIODIVERSITY RESEARCH

Distribution shifts of freshwater fish under a variable climate: comparing climatic, bioclimatic and biotic velocities

Lise Comte[1,2*†] and Gaël Grenouillet[1,2†]

[1]UMR5174 EDB (Laboratoire Évolution et Diversité Biologique), CNRS, UPS, ENFA, 118 route de Narbonne, F-31062, Toulouse, France, [2]UPS, UMR5174 EDB, Université de Toulouse 3, F-31062, Toulouse, France

[†]Co first author

*Correspondence: Lise Comte, CNRS, UPS, ENFA; UMR5174 EDB (Laboratoire Évolution et Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France.
E-mail: lise.comte@univ-tlse3.fr

ABSTRACT

Aim We aimed to quantify how stream fish species have responded to short-term variability in climate across eight consecutive periods over the last 20 years by comparing biotic (velocities of observed species range shifts) to expected bioclimatic (velocities of climate-induced shift in the suitable habitat of species) velocities, a measure combining species-specific exposure and sensitivity to climate.

Location French streams.

Methods Occupancy models were developed to model the distribution of 14 species across eight consecutive time periods between 1992 and 2011 and to project climate-induced changes in the distribution of suitable area over time. Based on the projected changes in habitat suitability, we first estimated the bioclimatic velocities for each species and each transition between consecutive periods. We then applied the same approach to the observed changes in suitable habitat to estimate the observed biotic velocities. Finally, the velocities of range shifts were compared to those expected on the basis of climate changes for each reach of the hydrographic network and the consistency of distributional responses – and potential lags – across species and transitions were quantified.

Results We found that biotic velocities were overall consistent with expectations, with observed responses matching both the direction and magnitude of bioclimatic velocities. Nonetheless, we also show that species consistently lagged behind climate (mean = 4.64 m.year^{-1}). Lags in habitat gain were more pronounced than those in habitat loss and revealed differential vulnerability of local populations within species distributions.

Main conclusions These findings demonstrate that integrating species-specific sensitivities to climate into measures of climatic velocities (namely bioclimatic velocities) provide improved expectations for observed range shifts. They also suggest that stream fish may display both low ability to persist under short periods of unfavourable climate and limited capacity to disperse upstream towards newly suitable habitats.

Keywords
Climate variability, colonization, extinction, occupancy models, range limits, vulnerability.

INTRODUCTION

Species vulnerability to climate change is a function of both extrinsic and intrinsic factors that determine species exposure and sensitivity, mediated by their adaptive capacity to adjust to these changes (Williams *et al.*, 2008; Pacifici *et al.*, 2015). Species range shifts are expected to be one of the main responses of species to recent climate change and have now been documented for many taxa (Root *et al.*, 2003; Parmesan, 2006). However, quantifying whether those shifts are

DOI: 10.1111/ddi.12346
http://wileyonlinelibrary.com/journal/ddi
© 2015 John Wiley & Sons Ltd

Diversity and Distributions
A Journal of Conservation Biogeography

allowing species to keep pace with climate change and isolating unambiguous climatic effects remain two of the main challenges for assessing species vulnerability to climate change (Angert *et al.*, 2011; Hockey *et al.*, 2011).

Growing interest and research efforts have been focused on using the velocity of climate change (Loarie *et al.*, 2009; Burrows *et al.*, 2011) to infer shifts in species distributions (Burrows *et al.*, 2014). While palaeoecological evidence suggests that past climate velocities have left important legacies in contemporary range sizes through selective extirpations of small-ranged, weakly dispersing species (Sandel *et al.*, 2011), geographical variations in recent climate velocity has also been correlated to observed range shifts (Chen *et al.*, 2011a; Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013). However, many studies have suggested a lag between the velocity of climate change and both species distributional responses (Hiddink *et al.*, 2012; La Sorte & Jetz, 2012; Zhu *et al.*, 2012) and the resulting reshuffling of communities (Bertrand *et al.*, 2011), with several mechanisms potentially involved. First, complex patterns of microclimates and topography can create gaps in climate paths that prevent range shifts (Lyons *et al.*, 2010; Early & Sax, 2011), and microrefugia where species might persist locally (Lenoir *et al.*, 2013). Secondly, non-climatic drivers (e.g. habitat degradation or fragmentation) or indirect effects (e.g. competitive interactions through climate-related biological invasions) can affect the ability of species to cope with climate change (Walther *et al.*, 2009; Hof *et al.*, 2011). Finally, individualistic traits (e.g. ability to disperse, ecological specialization) can also be of major importance in enabling species to respond successfully to climate change (e.g. Anderson *et al.*, 2009; Hof *et al.*, 2012). These delayed distributional responses may have considerable impacts on species interactions, which remain to be studied to prefigure forecasted changes in ecosystem functioning and integrity (Walther, 2010; Devictor *et al.*, 2012).

To date, most previous studies have focused primarily on simple unidimensional climate description (mainly isotherm shifts) and implicitly disregarded idiosyncratic sensitivities to climate. However, the direction and magnitude of range shifts are shaped by interactions between several climatic variables (Crimmins *et al.*, 2011; VanDerWal *et al.*, 2013) and the species-specific sensitivity to climate changes (e.g. physiological tolerance, resilience and potential to adapt) (Deutsch *et al.*, 2008; Huey *et al.*, 2012). As climate velocity can demonstrate divergent climate vectors between climatic variables (Dobrowski *et al.*, 2013), considering the multidimensional nature and complex mosaic of local climate changes may be critical in understanding the variation observed among range shifts of individual species (Ackerly *et al.*, 2010; Tingley *et al.*, 2012; Pinsky *et al.*, 2013). Similarly, recent human-driven environmental changes have influenced species geographical ranges (Newbold *et al.*, 2014; Di Marco & Santini, 2015) and the importance of human impacts as drivers of range shifts may override the climate change signal (Hockey *et al.*, 2011). Accordingly, accounting for current anthropogenic pressures and describing changes in climatic suitability for individual species, rather than in a single, physical climate variable would provide a more biologically meaningful assessment of where species likely need to move to track their climatic niches (e.g. Lawler *et al.*, 2013).

Empirical evidence also supports the hypothesis that fine-scale variability in climate can drive species range dynamics (Early & Sax, 2011; Bennie *et al.*, 2013). Indeed, patterns of climate change are spatially heterogeneous and often highly dynamic (Burrows *et al.*, 2011; Chen *et al.*, 2011a), with considerable short-term fluctuations superimposed upon long-term climate trends (Karl *et al.*, 1995). As a result, species range shifts are typically characterized by intermittent episodes of expansion and contraction (Bennie *et al.*, 2013). Considering short-term variability in climate could thus be critical when characterizing range edges (Zimmermann *et al.*, 2009), determining species persistence through time (Bateman *et al.*, 2012) and understanding species responses to rapid climate change (Reside *et al.*, 2010; Beever *et al.*, 2011). To date, most studies assessing biotic velocities have only focused on range shifts between two periods. This has thus prevented the evaluation of possible changes in velocity across time (Beever *et al.*, 2011; Ordonez & Williams, 2013), or identifying the extent to which range shifts occur gradually or as abrupt changes when environmental thresholds are exceeded (Harley & Paine, 2009; Jackson *et al.*, 2009). Besides being intuitively essential for climate change impact assessments, as it informs about how fast species track shifting climate or accumulate a climatic debt over time, very little attention has been devoted to assessing range shifts between multiple time periods.

Recently, bioclimatic models have been proposed to depict the velocity of changes in species climatic suitability (Serra-Diaz *et al.*, 2014). This approach has the potential to reveal species-specific exposure to shifting climatic habitats and makes it possible to compare the velocities of observed range shifts to those expected on the basis of spatially complex and multidimensional climate changes. While Serra-Diaz *et al.* (2014) have illustrated the usefulness of their approach to investigate the predicted velocities of species exposure to climate change under future scenarios, its application to observed range shifts offers a promising way to better understand how species are responding to ongoing climate change. Here, we assessed how species of stream fish shifted their ranges across multiple time periods over recent decades in France. Stream fishes provide particularly relevant model organisms for studying climate-induced distributional responses, as these ectotherms are likely to be strongly impacted by changes in thermal habitat and alteration of flow regimes and water availability (Crozier & Hutchings, 2014). By comparing species ranges modelled for eight consecutive periods, while accounting for imperfect species detection and potentially confounding non-climatic drivers, we analysed both species-specific exposure and species distributional responses to shifting climates. In particular, we aimed to (i) describe spatial patterns in species-specific paces

of climate change exposure and (ii) compare the velocities of observed range shifts to those expected on the basis of climate changes. As far as we are aware, this is the first time that velocities of observed range shifts have been compared to bioclimatic velocities, a measure of changes in climatic suitability likely to reflect both species-specific exposure and sensitivity to climate change.

METHODS

Approach

We used a dynamic modelling approach to model the observed distribution of species across eight consecutive periods over the last 20 years and to project climate-induced changes in the distribution of suitable areas over time (Fig. 1). Based on the observed changes in suitable habitat, we estimated the observed biotic velocities for each species and each transition between consecutive periods. We applied the same approach to the predicted changes in suitable habitat to estimate the expected bioclimatic velocities. In parallel, we calculated the climatic velocities between consecutive time periods using a multivariate measure of climate changes. We then compared the velocities of observed range shifts to those expected on the basis of climate changes (climatic and bioclimatic) and quantified the consistency of distributional responses to short-term climate variability – and potential lags – across species and transitions.

Environmental data

Climate data were derived from the French weather service model SAFRAN, a gauge-based analysis system computing daily data for various meteorological parameters. As fish are known to be sensitive to extreme conditions and climatic seasonality (Matthews, 1998), from this high-resolution (8 km x 8 km) database, we used daily data for temperature and precipitation to derive six climate variables that are relevant as regards their influence on stream fish distributions: mean temperature of the coldest quarter (*Tcold*, °C), mean temperature of the warmest quarter (*Twarm*, °C), temperature seasonality (*Tvar*, SD × 100), cumulated precipitation of the wettest quarter (*Pwet*, mm), cumulated precipitation of the driest quarter (*Pdry*, mm) and precipitation seasonality (*Pvar*, CV). Climate variables were calculated for each studied year and then averaged within each time period, with a shift in time window of one year. To avoid collinearity, these climate variables were reduced into two independent axes using principal component analyses (PCA) before being included in the models. PC1 represented a gradient from cooler, wetter areas to warmer, drier areas, whereas PC2 contrasted areas with relatively stable climatic conditions with

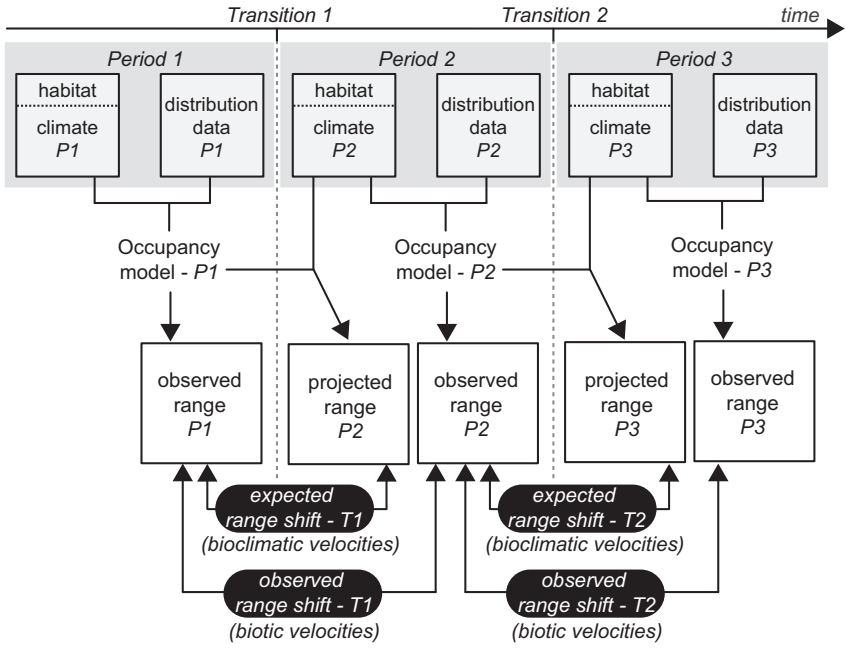

Figure 1 Dynamic modelling framework developed to assess species range shifts between consecutive time periods (depicted here for two transitions between three periods). For each period, occupancy models were developed to model the observed ranges of each species according to climate conditions of the considered period, as well as various static habitat descriptors over the study period (topography, upstream–downstream gradient, land use, degree of fragmentation and urbanization). Confronting these observed ranges to those projected onto the environmental conditions of the following period makes it possible to describe range shifts expected on the basis of climate changes (i.e. bioclimatic velocities reflecting both species-specific exposure and sensitivity to climate change), while these expected range shifts can be compared to observed ones (i.e. biotic velocities) to assess climate tracking for each transition.

areas showing greater variability (see Appendix S1 in Supporting Information).

Each stream reach of the hydrographical network (CCM2; Vogt *et al.*, 2007) was further described based on two topographic variables, elevation (m, extracted at the centre of each reach) and slope (‰, computed between both ends of each reach). A synthetic variable representative of the upstream–downstream gradient was obtained by the first axis of a PCA combining two variables, the full area drained by the upstream area (km²) and the cumulated length of the upstream flow network (m) (variability explained = 97.8%). To account for the potential effects of anthropogenic disturbances on freshwater fish distributions, we also included three anthropogenic-related variables. The degree of fragmentation was calculated as the number of high-size dams (> 15 m) within natural sub-basins based on Strahler level aggregates (Onema, 2010). Land use was described through the first axis of a PCA including two variables extracted from the second and third classes of the updated Corine Land Cover database (CLC 2000; Bossard *et al.*, 2000) and expressed as percentages of agricultural and forested lands of the sub-basin total areas (variability explained = 98.6%). The degree of urbanization was estimated through the first axis of a PCA including the percentage of urbanized land (i.e. first class of CLC 2000) and the mean density of human population (HYDE 3.0; Klein Goldewijk *et al.*, 2011) within natural sub-basins (variability explained = 87.6%).

Species data

Species distribution data covering the period from 1992 to 2011 were taken from the French National Agency for Water and Aquatic Environments database, where 3627 sampling sites (mean sampled area = 813 $m^2 \pm 486$ SD) were monitored following a standard electrofishing protocol during low flow months. To study the distributional responses of species to short-term climate fluctuations, we then divided the data set into several consecutive short-time periods where sites were resurveyed repeatedly within each period. Due to the uneven sampling effort across the overall studied period, eight short-time periods of two to four years were defined to maximize the number of visits per site within each period, as well as to minimize the potential effects of spatial and environmental heterogeneity across periods (Fig. S1, Fig. S2 and Table S1 in Supporting Information Appendix S1): 1992–1995 (*P1*); 1996–1997 (*P2*); 1998–1999 (*P3*); 2000–2001 (*P4*); 2002–2003 (*P5*); 2004–2005 (*P6*); 2006–2008 (*P7*); 2009–2011 (*P8*). From the full set of species detected, we restricted our analyses to 14 of the most prevalent species.

Species distribution models

We modelled the distribution of species in each time period using single-season occupancy models explicitly accounting for species detectability (MacKenzie *et al.*, 2006). Following a model averaging procedure using different parameterizations for the probability of detection p (Julian day and the upstream–downstream position of the survey) and the probability of occurrence Ψ (aforementioned climatic, topographic and anthropogenic covariates), we obtained one composite model for each species and time period (see Table S2 and Table S3 in Supporting Information Appendix S1). Those models were subsequently used to reconstruct species distributions (i.e. observed ranges) in each time period and climate-induced shifts in suitable areas (i.e. expected range shifts) within time intervals across the French hydrographic network. For each species, the projected suitable habitats were forecast by projecting the models of each time period onto the environmental conditions of the following one.

Climate velocity

Climate velocity is usually expressed as the instantaneous horizontal (latitudinal) or vertical (altitudinal) velocity of climate change derived from the ratio of temporal (climatic changes per unit of time) and spatial (climatic changes per spatial unit) gradients (Loarie *et al.*, 2009; Burrows *et al.*, 2011). To characterize climatic changes over the last 20 years, we extended the climatic velocity approach developed by Loarie *et al.* (2009) to a multivariate measure of climatic velocity. We first calculated the climate velocities ($\vec{V}_i$) between consecutive time periods using a multidimensional representation of the climatic space based on a PCA including the six purely physical climatic variables as previously described.

$$\vec{V}_i = ((\delta c/\delta t)/(\delta c/\delta x), (\delta c/\delta t)/(\delta c/\delta y))$$

For each transition between two consecutive periods, the temporal gradient in climatic conditions ($\delta c/\delta t$) was computed as the mean difference in the coordinates of each stream reach along the two PCA axes expressed per unit of time (i.e. year). The spatial (i.e. altitudinal) gradient ($\delta c/\delta xy$) was computed as the ratio of the Euclidean distance within the two-dimensional PCA climatic space by the altitudinal distance between adjacent reaches using a neighbourhood weighting (Burrows *et al.*, 2011) (Fig. S4 in Supporting Information Appendix S1).

We also calculated the multivariate climate velocity across the eight consecutive time periods, associated with a measure of divergence in short-term climate velocities through time. To describe the climate velocity across all time periods, we calculated the net mean velocity ($\vec{V}_{\text{net}}$) of the velocity vectors defined for each transition between consecutive time periods as follows:

$$\vec{V}_{\text{net}} = \frac{\sum_{i=1}^{p} \vec{V}_i}{p}$$

where p is the number of transitions.

Then, we assessed divergence in the velocity vectors, defined as the mean scalar difference between the net mean velocity and the velocity vectors defined for each transition:

$$\nabla.F = \frac{\sum_{i=1}^{p} \left| \vec{V}_{\mathrm{i}} - \vec{V}_{\mathrm{net}} \right|}{p}$$

when $\nabla.F = 0$, the vectors share the same magnitude and directions (i.e. consistent climate changes among transitions), while large values of $\nabla.F$ indicate vectors that diverge in direction and magnitude (Dobrowski *et al.*, 2013).

Bioclimatic and biotic velocity

We used the approach introduced by Serra-Diaz *et al.* (2014) to calculate the bioclimatic velocities (i.e. velocities of climate-induced shift in the suitable habitat of species) and the biotic velocities (i.e. velocities of observed species range shifts) for each species and transition. Instead of using purely physical climatic variables, this approach allows to explicitly take into account the species-specific sensitivities to climate. In the equations for climate velocity calculation, changes in climate conditions are replaced by changes in habitat suitability obtained using the occurrence probabilities from species distribution models (SDMs). For the bioclimatic velocities, the temporal gradient was calculated as the differences in probabilities per unit of time between the observed distribution in a given time period, and the expected distribution in the following one, forecasted by projecting the model of the focal time period onto the climatic conditions of the consecutive one. Similarly to the climate velocities, the spatial gradient was calculated as the altitudinal differences in probabilities across the observed suitable habitat (see above).

Biotic velocities were calculated using the same equations, except that we used the differences in probabilities within consecutive observed distributions for the temporal gradient calculation. To avoid the influence of outliers, 5% of the velocities at both ends of the distribution for each species and transition were removed prior to analysis.

Comparing measures of velocity

To determine whether biotic velocities matched those expected based on climate changes, we first averaged velocities for each species and each transition between two consecutive periods. To account for the differences in suitability across space, the velocities were weighted by the probabilities of the presence at the beginning of the time interval within species range (i.e. more weight is given to reaches where the probabilities of presence were the highest). We then tested whether overall biotic velocities matched bioclimatic velocities using a Type-II linear model because both predictor and response variables have variability (Ordonez & Williams, 2013). Second, we fitted weighted linear regressions accounting for the differences in suitability within species range to the different measures of velocities (biotic versus bioclimatic) calculated for each reach of the hydrographic network. Based on the estimated slopes of the models, we determined whether the velocities were congruent (i.e. slope > 0, $P < 0.05$) or not for each species and time interval. The proportion of congruent directions p_{obs} was then tested against the random expectation of an equal probability of observing velocities in either direction using binomial tests (H_0: $p_{\mathrm{obs}} = 0.5$).

To determine whether observed velocities were higher or lower than those expected, for each species and transition, we calculated the mean relative difference in velocities (i.e. negative values indicated lag and positive values credit), weighted by the probabilities of species presence at the beginning of the time interval. We then tested whether the overall mean difference between biotic and bioclimatic velocities was different from zero (i.e. if species were lagging behind or leading ahead climate change) using a one-sample *t*-test. We then proceeded to the same tests but excluding responses for which the observed versus expected directions were different to avoid inflating the estimated rates of lag due to potential antagonist confounding effects (Poloczanska *et al.*, 2013). Finally, to find out whether the observed responses were consistent overall, climate tracking was separately assessed for the different species and transitions, while considering the direction of the expected velocities (i.e. gains versus losses of suitable habitat and upslope versus downslope changes).

Analyses were performed in R 3.1.2 (R Core Team, 2014) using the packages *unmarked* (Fiske & Chandler, 2011) for developing the models, *maptools* (Bivand & Lewin-Koh, 2014) for spatial analyses and *ade4* (Dray & Dufour, 2007) for PCA.

RESULTS

Patterns of climate velocities

We found considerable spatial and temporal variation in climate velocities (Fig. 2). This heterogeneity reflected short-term fluctuations (i.e. between consecutive periods, Fig. 2a) superimposed upon temporal climatic trends over the 20-year period showing patchy spatial patterns (Fig. 2b). Overall, long-term trends were directed towards increasing variability in temperature and precipitation and a warmer and drier climate in southern France. Likewise, divergence in climate velocities through time was spatially heterogeneous, with more diverging patterns in south-eastern France (Fig. 2c). As a result, averaged climate velocities within species ranges revealed varying patterns of exposure to shifting climates (Fig. 2a).

Comparing climate and bioclimatic velocities

Climate velocities and bioclimatic velocities were not significantly correlated when averaged across species ranges (Type-II regression, $P = 0.071$). Bioclimatic velocities varied significantly more ($F = 3.608$, $P < 0.001$) than climate

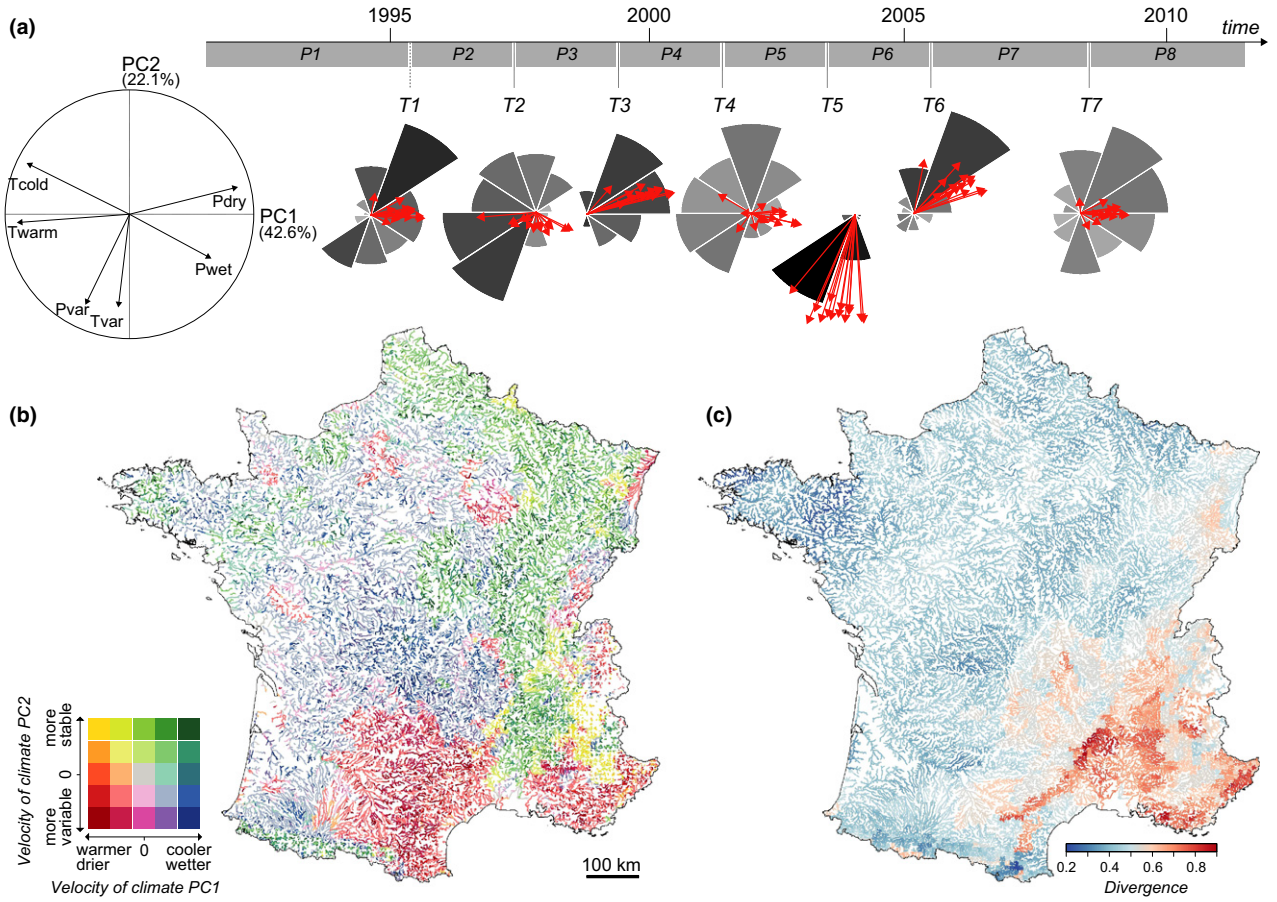

Figure 2 (a) Short-term climate fluctuations over the study period. The correlation circle shows projections of the six climatic variables onto the first two axes of a principal component analysis. In this bidimensional climatic space, changes in the position of each reach of the hydrographic network between two consecutive periods allowed the direction (i.e. angular coordinate) and magnitude (i.e. radial coordinate) of changes in climate to be measured. Polar diagrams show frequencies of occurrence and directions of climate change for each transition, with grey scale proportional to mean amplitude of changes. Red arrows portray climate velocity vectors (both directional and magnitude components) calculated for the 14 species within their respective distribution areas. (b) Temporal trend in climate velocities across all time periods of study. (c) Divergence between climate velocity vectors calculated for each transition.

velocities (Fig. 3) and showed contrasting (i.e. shrinking or expanding) patterns both between- and within-species ranges (Fig. 3b). Nonetheless, these predicted losses or gains in suitable habitat represented a substantial part of the hydrographic network for all species (mean = 84.8% ± 9.8 SD, Table S4 in Supporting Information Appendix S2).

Comparing bioclimatic and biotic velocities

Across all species and transitions, expected and observed velocities were of similar magnitude (paired *t*-test, $P = 0.370$) and showed consistent spatial patterns (Fig. 3b). When averaged across the whole hydrographic network, biotic and bioclimatic velocities showed a significant positive relationship (Type-II regression, $r = 0.25$, $P = 0.029$, Fig. 3c), suggesting that biotic velocities were overall paced by those expected based on climate changes. Moreover, the directions of the velocities where highly consistent when considering the observed:expected slopes for each species and each transition (70.4% of positive relationships, binomial test, $P < 0.001$). This agreement remained predominant when species with non-significant slopes were excluded (68.4%, binomial test, $P < 0.001$). At the stream reach scale, consistency between biotic and bioclimatic velocities varied between species but remained constant through time (Table S4 and Fig. S5 in Supporting Information Appendix S2). Overall, 54.4% and 56.8% of the observed velocities matched expectations towards gains and losses of suitable habitat, respectively. Proportions of observed velocities consistent with expectations were significantly non-random for all species (binomial tests, $P < 0.001$), demonstrating that species were tracking fine-scale shifting climates. Nevertheless, differences between observed and expected velocities were also apparent and showed strong geographical patterns where observed responses lead and lag expected responses (Fig. S6 in Supporting Information Appendix S2). By contrast, when expected velocities were null, most biotic velocities were also null (56.1%) or marginal, without any spatial pattern in those unexpected responses.

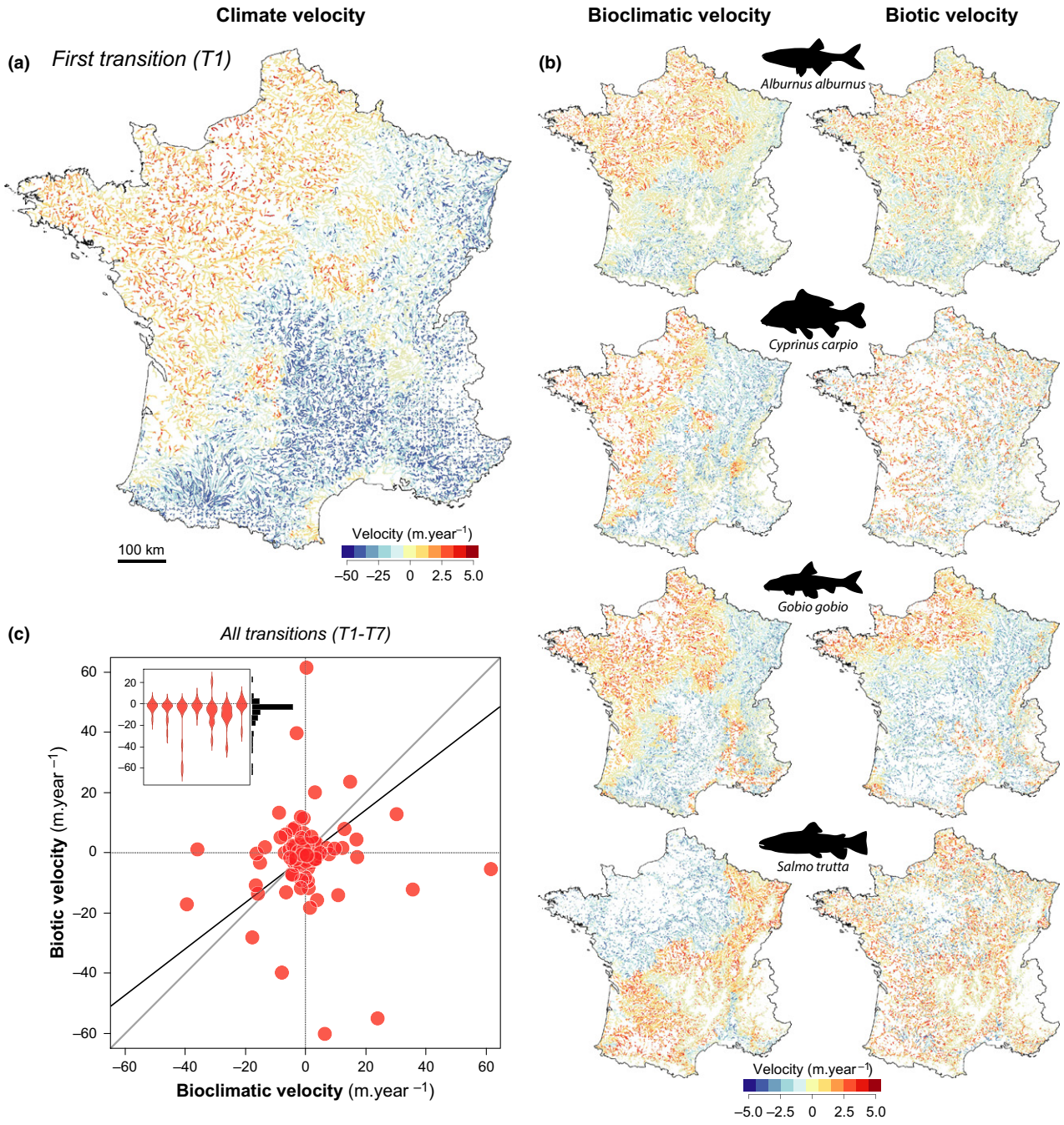

Figure 3 (a) Patterns in climate velocities illustrated for the first transition and (b) corresponding patterns in bioclimatic and biotic velocities for four exemplar species. (c) Relationship between biotic and bioclimatic velocities calculated for each species and each transition. Solid line indicates the best fit regression. Inset is the difference between biotic and bioclimatic velocities measured for each species and transition with the histogram of difference values across the seven transitions. Negative values indicate lags in observed species responses (i.e. gains or losses of suitable habitat) compared to those expected on the basis of changes in climatic suitability.

Lags in observed range shifts

We found that on average species lagged in their distributional responses (mean = 6.08 m.year^{-1}, one-sided *t*-test, $P < 0.001$, inset Fig. 3c). These lags remained significant when null responders were excluded (mean = 4.64 m.year^{-1}, one-sided *t*-test, $P = 0.001$). Lags in habitat gain appeared to be more pronounced than those in habitat loss (mean = 4.49 and 2.04 m.year^{-1}, respectively, Fig. 4a). Although bioclimatic velocities were of the same magnitude in both directions (paired *t*-test, $P = 0.558$), observed velocities were significantly lower (paired *t*-test, $P < 0.001$) for habitat gains. Nevertheless, lags in distributional responses varied considerably among species (Fig. 4b). Indeed, some species such as

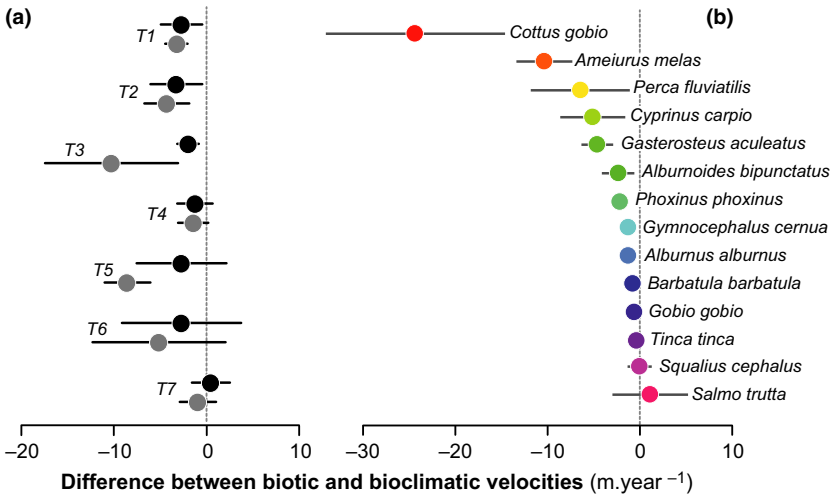

Figure 4 Mean differences (+SE) between biotic and bioclimatic velocities calculated for (a) each transition (from *T1* to *T7*) and (b) each species. Bioclimatic velocities correspond to expected velocities for habitat gains (i.e. positive velocities) or habitat losses (i.e. negative velocities). Differences between observed and expected velocities are calculated separately for habitat gains (in grey) and losses (in black), respectively, and indicate lags in observed distributional responses when negative (i.e. observed velocities lower than expected).

brown trout (*Salmo trutta*) and European chub (*Squalius cephalus*) appeared to have shifted at a pace sufficient to track climate fluctuations between periods. In contrast, bullhead (*Cottus gobio*) showed the highest expected velocities (mean = 29.37 m.year^{-1}), resulting in mean lag in distributional response of 24.09 m.year^{-1}. For this weakly dispersing species, lags in habitat gain were up to three times higher than those in habitat loss. Lags in habitat gain were also significantly more variable across species than those in habitat loss ($F = 3.886$, $P = 0.020$). While the magnitude of lags in habitat gain was positively correlated to expected velocities ($r = 0.79$, $P < 0.001$), no significant relationship was observed between expected velocities of habitat loss and the corresponding lags. Finally, lags were significantly ($P = 0.021$) higher when habitat gains were directed towards upper rather than lower elevation. Conversely, lags in habitat loss did not differ between lower- and upper-elevational boundaries of species distribution (Fig. 5).

DISCUSSION

Although growing evidence indicates that range shifts of many taxa follow the velocity of climate both in the ocean (Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013) and on land (Chen *et al.*, 2011a), considerable lags in responses or failure to detect the expected range shifts have also been documented (Devictor *et al.*, 2012; Zhu *et al.*, 2012). Here, our analyses reveal a complex mosaic of patterns in climate velocities characterized by considerable short-term fluctuations, along with climate shifts over the last 20 years. We show that, by depicting species-specific exposure to shifting climates, the velocities of changes in species climatic suitability provide improved expectations for observed range shifts. The comparison with observed velocities further reveals that although stream fish species were consistently lagging behind climate changes, the ability of species to track short-term fluctuations in their climatic niche over time may be much faster than previously thought.

We show large magnitude and rapid rates of change in bioclimatic velocities over time, with geographical areas displaying increases or decreases in species climatic suitability. These contrasted patterns resulted both from the combination of species exposure to climatic fluctuations and intrinsic climate sensitivity, ultimately defining species vulnerability (Moritz & Agudo, 2013). For instance, while bleak (*Alburnus alburnus*), a warm-water -adapted species, showed large areas of positive bioclimatic velocities in northern France and negative values in southern France between the first two time periods, the opposite pattern was identified for *Salmo trutta*, a cold-water species. The fact that bioclimatic velocities were not correlated to climate velocities reinforces the importance of taking species sensitivity into account and questions the assumption that climate velocities (even averaged across species range) provide sufficient estimates to infer the velocity of range shift required by species to track their climatic niche. Accordingly, by integrating complex interactions between multidirectional shifts in climatic space and species-specific sensitivities to climate, bioclimatic velocities may provide improved expectations for evaluating species vulnerability in a changing climate and reconcile current approaches based either on purely climatic patterns (e.g. Burrows *et al.*, 2014) or on species-specific attributes (e.g. Pearson *et al.*, 2014).

We demonstrate that observed velocities were overall consistent with expectations, with species range shifts matching both the direction and magnitude of bioclimatic velocities.

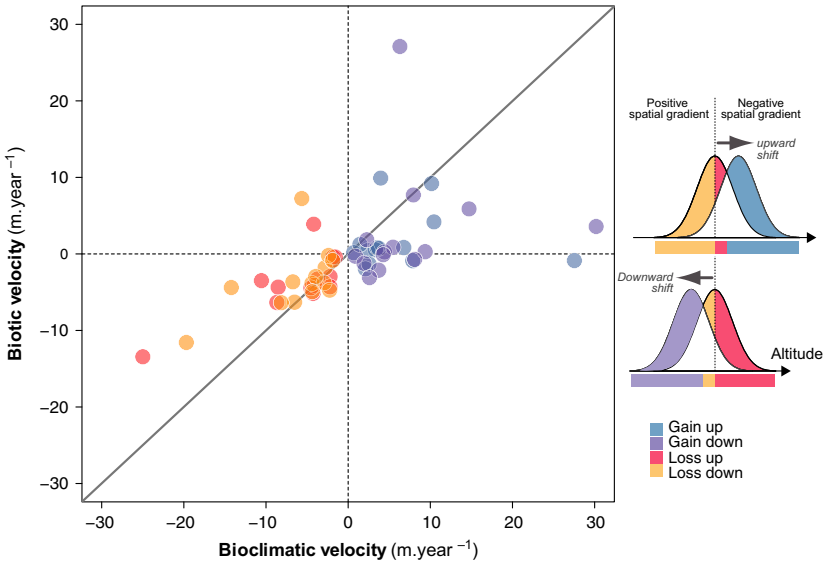

Figure 5 Relationship between biotic and bioclimatic velocities. Points represent mean responses of species for a given transition. According to the positive or negative spatial (i.e. altitudinal) gradient in species probability of the presence, positive velocities correspond to gains of suitable habitat towards lower or higher elevation, respectively, while negative velocities correspond to habitat losses at lower or higher elevation, respectively.

This result has several implications as understanding short-term species distributional responses is essential for quantifying species climatic limits and assessing species potential vulnerability to rapid climate changes (Reside *et al.*, 2010). Neglecting temporal variation in climate using long-term averages may overestimate species climatic suitability (Reside *et al.*, 2010) and underestimate the velocity of species responses by smoothing intermittent episodes of expansion and contraction (Bennie *et al.*, 2013). This may ultimately result in misleading assessments of the potential impacts of future climate changes (Beever *et al.*, 2011; Bateman *et al.*, 2012). Empirical studies have supported the hypothesis that fine-scale climatic variations influence species ranges (Beever *et al.*, 2011) and several approaches have begun to address the effects of climate variability to improve our ability to reveal species range dynamics (Early & Sax, 2011; Bennie *et al.*, 2013). By documenting rapid species responses to short-term climate fluctuations, our results suggest that the velocities of observed range shifts may be faster than previously thought (Comte & Grenouillet, 2013), evidencing species-specific expansion–contraction dynamics rather than gradual and directional shifts over time.

We also demonstrate that stream fish species are consistently lagging behind climate changes. This result adds to a growing body of evidence that many taxonomic groups will be unable to track ongoing climate change (e.g. Zhu *et al.*, 2012). Ectotherms are more likely to be more directly affected by climate warming, and taxonomic groups with short generation time, such as the species considered here, are expected to exhibit faster responses to climate-induced selective pressures (Devictor *et al.*, 2012). Aquatic organisms are also typically viewed as being limited in their dispersal capabilities because of the constraints imposed by the spatial structure of hydrographic networks, the presence of natural or anthropogenic barriers to dispersal and the directionality of asymmetric water flows (Sharma *et al.*, 2007; Sorte, 2013). Moreover, a wide range of traits may be involved in species distributional responses (Comte *et al.*, 2014) and within-taxon variation in those traits may preclude broader taxonomic generalizations (e.g. Hickling *et al.*, 2006). Thus, whether different taxonomic groups are tracking climate changes at the same rate is still unclear (Devictor *et al.*, 2012) and deserves more attention.

Further, we find higher observed velocities for habitat losses than for habitat gains, despite expectations of similar magnitude for both directions. While range expansions have been widely documented, evidence for range retractions at trailing margins remains comparatively weak (Thomas *et al.*, 2006). Asymmetric boundary shifts have been hypothesized, with leading margins likely to shift faster than trailing margins retreat (Chen *et al.*, 2011b) due to a greater importance of biotic constraints than climate in determining species limits at trailing margins. Our finding that observed velocities were significantly lower for habitat gains challenges this hypothesis as a generality, which might rather depend on species sensitivity and the capacity of populations to buffer climatic impacts (Ordonez & Williams, 2013). With lags in habitat gain more pronounced than those in habitat loss (in particular for habitat gain directed towards upper elevation), species of stream fish exhibit both low ability to persist under short periods of unfavourable climate and limited capacity to disperse upstream towards newly suitable habitats. These results confirm two key range-shift processes (i.e. population persistence and dispersal) likely to be critical

when evaluating species vulnerability (Anderson *et al.*, 2009; Early & Sax, 2011).

A better understanding of range-shift processes is still needed to develop a robust evaluation of species vulnerability to climate change (Angert *et al.*, 2011; Bates *et al.*, 2014). In this context, our framework may enhance the assessment of the capacity of species to respond to climate change and offer new insights for conservation planning. Numerous studies have assessed whether individualistic traits are linked to species range shifts (e.g. Angert *et al.*, 2011), but the weak relationship often reported has been suggested to result from different mechanisms acting at both range limits (Comte *et al.*, 2014). By quantifying lags in both habitat gain and loss, our framework may be used to test whether the intrinsic species characteristics (e.g. dispersal ability, life-history strategy) are involved in complex climate-induced distributional responses. Comparing observed range shifts to those expected under short-term climate tracking also makes it possible to identify geographical areas where species are lagging behind climate change. By disentangling the lags in habitat gains and losses, this framework can inform landscape permeability (i.e. accessibility of colonizable habitats) and local population persistence at spatial and temporal scales relevant to conservation interventions (Vos *et al.*, 2008). This can be particularly helpful to refocus strategies from protected areas towards landscape networks that also consider intermediate landscapes and connectivity (Opdam & Wascher, 2004). Such insights could thus help decision-making intended to facilitate species range shifts and improve population persistence (e.g. landscape management for habitat corridors, increasing habitat patch size) (Ackerly *et al.*, 2010; Early & Sax, 2011; Lawson *et al.*, 2012). Finally, as variations in climate change can create gaps in climate paths that prevent range shifts (Early & Sax, 2011), considering short-term fluctuations in climate can also be crucial when forecasting climate-driven movements, improving our ability to identify where species will likely need to move in response to future climate changes (Lawler *et al.*, 2013).

ACKNOWLEDGEMENTS

Financial support was provided by grant ANR-09-PEXT-008-01. We are indebted to the French National Agency for Water and Aquatic Environment (Onema) for providing fish data. EDB laboratory was supported by 'Investissement d'Avenir' grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41). We thank Joanna Gozlan for improving the English in editing of this article.

REFERENCES

Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R. & Kraft, N.J.B. (2010) The geography of climate change: implications for conservation biogeography. *Diversity and Distributions*, **16**, 476–487.

Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1415–1420.

Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677–689.

Bateman, B.L., VanDerWal, J. & Johnson, C.N. (2012) Nice weather for bettongs: using weather events, not climate means, in species distribution models. *Ecography*, **35**, 306–314.

Bates, A.E., Pecl, G.T., Frusher, S., Hobday, A.J., Wernberg, T., Smale, D.A., Sunday, J.M., Hill, N.A., Dulvy, N.K., Colwell, R.K., Holbrook, N.J., Fulton, E.A., Slawinski, D., Feng, M., Edgar, G.J., Radford, B.T., Thompson, P.A. & Watson, R.A. (2014) Defining and observing stages of climate-mediated range shifts in marine systems. *Global Environmental Change*, **26**, 27–38.

Beever, E.A., Ray, C., Wilkening, J.L., Brussard, P.F. & Mote, P.W. (2011) Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology*, **17**, 2054–2070.

Bennie, J., Hodgson, J.A., Lawson, C.R., Holloway, C.T.R., Roy, D.B., Brereton, T., Thomas, C.D. & Wilson, R.J. (2013) Range expansion through fragmented landscapes under a variable climate. *Ecology Letters*, **16**, 921–929.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C. & Gégout, J.-C. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, **479**, 517–520.

Bivand, R. & Lewin-Koh, N. (2014) *maptools*: tools for reading and handling spatial objects. R package version 0.8-30. http://CRAN.R-project.org/package=maptools.

Bossard, M., Feranec, J. & Otahel, J. (2000) *CORINE land cover technical guide – Addendum 2000*. European Environment Agency, Copenhagen.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J. & Richardson, A.J. (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.

Burrows, M.T., Schoeman, D.S., Richardson, A.J. *et al.* (2014) Geographical limits to species-range shifts are suggested by climate velocity. *Nature*, **507**, 492–495.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011a) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Chen, I.-C., Hill, J.K., Shiu, H.-J., Holloway, J.D., Benedick, S., Chey, V.K., Barlow, H.S. & Thomas, C.D. (2011b) Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography*, **20**, 34–45.

Comte, L. & Grenouillet, G. (2013) Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography*, **36**, 1236–1246.

Comte, L., Murienne, J. & Grenouillet, G. (2014) Species traits and phylogenetic conservatism of climate-induced range shifts in stream fishes. *Nature Communications*, **5**, 5053.

R Core Team (2014) *R: a language and environment for statistical computing*. R Core Team, Vienna, Austria.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, **331**, 324–327.

Crozier, L.G. & Hutchings, J.A. (2014) Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications*, **7**, 68–87.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA*, **105**, 6668–6672.

Devictor, V., van Swaay, C., Brereton, T. *et al.* (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.

Di Marco, M. & Santini, L. (2015) Human pressures predict species' geographic range size better than biological traits. *Global Change Biology*, **21**, 2169–2178.

Dobrowski, S.Z., Abatzoglou, J., Swanson, A.K., Greenberg, J.A., Mynsberge, A.R., Holden, Z.A. & Schwartz, M.K. (2013) The climate velocity of the contiguous United States during the 20th century. *Global Change Biology*, **19**, 241–251.

Dray, S. & Dufour, A.B. (2007) The *ade4* package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.

Early, R. & Sax, D.F. (2011) Analysis of climate paths reveals potential limitations on species range shifts. *Ecology Letters*, **14**, 1125–1133.

Fiske, I. & Chandler, R. (2011) *unmarked*: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, **43**, 1–23.

Harley, C.D.G. & Paine, R.T. (2009) Contingencies and compounded rare perturbations dictate sudden distributional shifts during periods of gradual climate change. *Proceedings of the National Academy of Sciences USA*, **106**, 11172–11176.

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

Hiddink, J.G., Ben Rais Lasram, F., Cantrill, J. & Davies, A.J. (2012) Keeping pace with climate change: what can we learn from the spread of Lessepsian migrants? *Global Change Biology*, **18**, 2161–2172.

Hockey, P.A.R., Sirami, C., Ridley, A.R., Midgley, G.F. & Babiker, H.A. (2011) Interrogating recent range changes in South African birds: confounding signals from land use and climate change present a challenge for attribution. *Diversity and Distributions*, **17**, 254–261.

Hof, C., Levinsky, I., Araújo, M.B. & Rahbek, C. (2011) Rethinking species' ability to cope with rapid climate change. *Global Change Biology*, **17**, 2987–2990.

Hof, C., Brandle, M., Dehling, D.M., Munguia, M., Brandl, R., Araújo, M.B. & Rahbek, C. (2012) Habitat stability affects dispersal and the ability to track climate change. *Biology Letters*, **8**, 639–643.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 1665–1679.

Jackson, S.T., Betancourt, J.L., Booth, R.K. & Gray, S.T. (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences USA*, **106**, 19685–19692.

Karl, T.R., Knight, R.W. & Plummer, N. (1995) Trends in high-frequency climate variability in the twentieth century. *Nature*, **377**, 217–220.

Klein Goldewijk, K., Beusen, A., van Drecht, G. & de Vos, M. (2011) The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography*, **20**, 73–86.

La Sorte, F.A. & Jetz, W. (2012) Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology*, **81**, 914–925.

Lawler, J.J., Ruesch, A.S., Olden, J.D. & McRae, B.H. (2013) Projected climate-driven faunal movement routes. *Ecology Letters*, **16**, 1014–1022.

Lawson, C.R., Bennie, J.J., Thomas, C.D., Hodgson, J.A. & Wilson, R.J. (2012) Local and landscape management of an expanding range margin under climate change. *Journal of Applied Ecology*, **49**, 552–561.

Lenoir, J., Graae, B.J., Aarrestad, P.A. *et al.* (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, **19**, 1470–1481.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

Lyons, S.K., Wagner, P.J. & Dzikiewicz, K. (2010) Ecological correlates of range shifts of Late Pleistocene mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3681–3693.

MacKenzie, D., Nichols, J., Royle, J., Pollock, K., Bailey, L. & Hines, J. (2006) *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier, New York.

Matthews, W.J. (1998) *Patterns in freshwater fish ecology*. Chapman and Hall, New York.

Moritz, C. & Agudo, R. (2013) The future of species under climate change: resilience or decline? *Science*, **341**, 504–508.

Newbold, T., Hudson, L.N., Phillips, H.R.P., Hill, S.L.L., Contu, S., Lysenko, I., Blandon, A., Butchart, S.H.M., Booth, H.L., Day, J., De Palma, A., Harrison, M.L.K., Kirkpatrick, L., Pynegar, E., Robinson, A., Simpson, J., Mace, G.M., Scharlemann, J.P.W. & Purvis, A. (2014) A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20141371.

Onema (2010) *Référentiel des obstacles à l'écoulement: un inventaire national des obstacles sur les cours d'eau*. Onema, Paris.

Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285–297.

Ordonez, A. & Williams, J.W. (2013) Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecology Letters*, **16**, 773–781.

Pacifici, M., Foden, W.B., Visconti, P. *et al.* (2015) Assessing species vulnerability to climate change. *Nature Climate Change*, **5**, 215–224.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., Mcnees, J. & Akçakaya, H.R. (2014) Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, **4**, 217–221.

Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L. & Levin, S.A. (2013) Marine taxa track local climate velocities. *Science*, **341**, 1239–1242.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A. & Richardson, A.J. (2013) Global imprint of climate change on marine life. *Nature Climate Change*, **3**, 919–925.

Reside, A.E., VanDerWal, J.J., Kutt, A.S. & Perkins, G.C. (2010) Weather, not climate, defines distributions of vagile bird species. *PLoS One*, **5**, e13569.

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

Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. (2011) The influence of late quaternary climate-change velocity on species endemism. *Science*, **334**, 660–664.

Serra-Diaz, J.M., Franklin, J., Ninyerola, M., Davis, F.W., Syphard, A.D., Regan, H.M. & Ikegami, M. (2014) Bioclimatic velocity: the pace of species exposure to climate change. *Diversity and Distributions*, **20**, 169–180.

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

Sorte, C.J.B. (2013) Predicting persistence in a changing climate: flow direction and limitations to redistribution. *Oikos*, **122**, 161–170.

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

Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C. & Beissinger, S.R. (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology*, **18**, 3279–3290.

VanDerWal, J., Murphy, H.T., Kutt, A.S., Perkins, G.C., Bateman, B.L., Perry, J.J. & Reside, A.E. (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, **3**, 239–243.

Vogt, J.V., Soille, P., de Jager, A., Rimaviciute, E., Mehl, W., Foisneau, S., Bodis, K., Dusart, J., Paracchini, M.L., Haastrup, P. & Bamps, C. (2007) *A pan-European river and catchment database*, European Commission - Joint Research Centre, Luxembourg.

Vos, C.C., Berry, P., Opdam, P., Baveco, H., Nijhof, B., O'Hanley, J., Bell, C. & Kuipers, H. (2008) Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *Journal of Applied Ecology*, **45**, 1722–1731.

Walther, G.-R. (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **365**, 2019–2024.

Walther, G.-R., Roques, A., Hulme, P.E. *et al.* (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*, **24**, 686–693.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. & Langham, G. (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, **6**, e325.

Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, **18**, 1042–1052.

Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A., Schmatz, D.R. & Pearman, P.B. (2009) Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences USA*, **106**, 19723–19728.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supporting methods.

Table S1 Characteristics of the sampling design across the eight time periods.

Figure S1 Spatial distribution of the sampling sites in France and along the altitudinal gradient (histogram) across the eight time periods.

Figure S2 Correlation circle (left) and coordinates of the sites within the bi-dimensional space of a principal component analysis performed on the environmental conditions of the sites (G = upstream-downstream gradient; Frag. = degree of fragmentation; Elev. = elevation) sampled across the eight time periods.

Figure S3 Inter-annual variability in climatic conditions over the study period.

Figure S4 Weightings used to calculate the average altitudinal gradient between a given reach (in red) and upstream and downstream reaches depending on the structure of the hydrographic network: (a) without or (b) with upstream tributaries.

Table S2 Variable importance for the occupancy component for each species expressed as the percentage of times the variables were selected within the best set of models across the eight time periods.

Table S3 Average regression coefficients for the occupancy component for each species across the eight time periods based on scaled and centered variables.

Appendix S2 Consistency between bioclimatic and biotic velocities.

Table S4 Percentages of hydrographic network for which positive, negative or null bioclimatic velocities are expected, and corresponding consistencies (% of hydrographic network) with biotic velocities for each fish species.

Figure S5 Consistency (% of hydrographic network) between bioclimatic and biotic velocities across species for the different transitions (*T1* to *T7*).

Figure S6 Spatial patterns in differences between biotic and bioclimatic velocities.

BIOSKETCHES

Lise Comte is a Postdoctoral Research Fellow in the laboratory 'Evolution et Diversité Biologique' (University of Toulouse, France). Her research interests mainly focus on how anthropogenic disturbances affect biodiversity patterns in freshwater ecosystems, with a special attention on the impact of climate change on species distribution.

Gaël Grenouillet is an associate professor in the laboratory 'Evolution et Diversité Biologique' (University of Toulouse, France). He has experience in species distribution modelling and stream ecology, and his work mainly focuses on the potential impacts of global changes on fish assemblages.

Author contributions: LC and GG contributed equally to the manuscript.

Editor: Risto Heikkinen