

# Illuminating geographical patterns in species' range shifts

GAËL GRENOUILLET<sup>1,2</sup> and LISE COMTE<sup>1,2</sup>

<sup>1</sup>CNRS, UPS, ENFA, UMR5174 EDB (Laboratoire Évolution et Diversité Biologique), 118 route de Narbonne, Toulouse F-31062, France, <sup>2</sup>Université de Toulouse, UPS, UMR5174 EDB, Toulouse F-31062, France

## Abstract

Species' range shifts in response to ongoing climate change have been widely documented, but although complex spatial patterns in species' responses are expected to be common, comprehensive comparisons of species' ranges over time have undergone little investigation. Here, we outline a modeling framework based on historical and current species distribution records for disentangling different drivers (i.e. climatic vs. nonclimatic) and assessing distinct facets (i.e. colonization, extirpation, persistence, and lags) of species' range shifts. We used extensive monitoring data for stream fish assemblages throughout France to assess range shifts for 32 fish species between an initial period (1980–1992) and a contemporary one (2003–2009). Our results provide strong evidence that the responses of individual species varied considerably and exhibited complex mosaics of spatial rearrangements. By dissociating range shifts in climatically suitable and unsuitable habitats, we demonstrated that patterns in climate-driven colonization and extirpation were less marked than those attributed to nonclimatic drivers, although this situation could rapidly shift in the near future. We also found evidence that range shifts could be related to some species' traits and that the traits involved varied depending on the facet of range shift considered. The persistence of populations in climatically unsuitable areas was greater for short-lived species, whereas the extent of the lag behind climate change was greater for long-lived, restricted-range, and low-elevation species. We further demonstrated that nonclimatic extirpations were primarily related to the size of the species' range, whereas climate-driven extirpations were better explained by thermal tolerance. Thus, the proposed framework demonstrated its potential for markedly improving our understanding of the key processes involved in range shifting and also offers a template for informing management decisions. Conservation strategies would greatly benefit from identifying both the geographical patterns and the species' traits associated with complex modifications of species' distributions in response to global changes.

**Keywords:** climate change, colonization, distribution shifts, drivers, extirpation, lag, range limits, stream fish

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## Introduction

Species' distribution shifts in response to contemporary climate change have been documented for many taxa (Root *et al.*, 2003; Parmesan, 2006; Chen *et al.*, 2011), and these distributional shifts can have important ecological implications at various levels of organization. Species' range shifts can elicit evolutionary responses with rapid life-history shifts (Phillips *et al.*, 2010) and changes in neutral evolution (McInerney *et al.*, 2009), species' genetic structure, and diversity patterns (Jezkova *et al.*, 2011; Espíndola *et al.*, 2012). Range shifts can also result in community reorganization (Le Roux & McGeoch, 2008) and lead to no-analog communities, in which species co-occur in previously unknown combinations (Williams & Jackson, 2007), which can have considerable impacts on species interactions and lead to profound alterations of ecosystem functioning and services (Lovejoy & Hannah, 2005; Walther, 2010).

Consequently, as it informs both species-specific extinction risks and future changes in ecosystem integrity, understanding the capacity of species to shift geographic ranges in the face of climate change is of crucial importance from a conservation perspective (Angert *et al.*, 2011). To date, although reported range shifts (poleward and upslope) have predominantly been in the direction expected from observed climate changes (Parmesan, 2006), there is also ample evidence of idiosyncratic responses, which limits our ability to predict distributional shifts across species and calls for a better understanding of the processes involved in range shifts (Angert *et al.*, 2011; Chen *et al.*, 2011; Tingley *et al.*, 2012). There is still little consensus about the ability of different species to track changing climates (Angert *et al.*, 2011), and whether species' range shifts are occurring fast enough remains hardly quantifiable. Thus, understanding species' abilities to shift range successfully is crucial for assessing species' vulnerability to climate change and remains one of the main challenges facing biodiversity conservation.

Correspondence: Gaël Grenouillet, tel. +33 561556911, fax +33 561557327, e-mail: gael.grenouillet@univ-tlse3.fr

Several factors are probably responsible for some aspects of the variation observed among the range shifts of individual species. Firstly, ecological responses to climate change may depend on complex patterns of microclimates (Tingley *et al.*, 2012; Bennie *et al.*, 2013), as interactions between several climatic variables and species-specific sensitivities to those variables shape the direction and magnitude of range shifts (Crimmins *et al.*, 2011; VanDerWal *et al.*, 2013). Moreover, patterns of climate change are often highly dynamic and spatially heterogeneous (Burrows *et al.*, 2011; Chen *et al.*, 2011). Geographical topography and variability in climate change can then create both microrefugia, where species might persist locally (Lenoir *et al.*, 2013), and gaps in climate paths that prevent range expansions and shifts (Lyons *et al.*, 2010; Early & Sax, 2011). Secondly, although it has been argued that range shifts are caused by climate change, nonclimatic influences of global change (e.g., regional anthropogenic drivers) or indirect effects (e.g., climate-mediated biological invasions and expansions of nonnative species) can also contribute to differential rates of range shifting (La Sorte & Thompson, 2007; Le Roux & McGeoch, 2008; D'Andrea *et al.*, 2009). Specifically, habitat fragmentation or degradation and land-use changes can both have a marked impact on the ability of species to cope with climate change (Hof *et al.*, 2011), while nonnative invasions may also vary in their importance across space and differently affect native species through competitive interactions (Walther *et al.*, 2009). Finally, individualistic traits (e.g., physiological tolerances, life-history strategies, habitat requirements) probably underlie the high level of variability in the degree of the response to climate in different species (Parmesan, 2006; Reif & Flousek, 2012). For instance, although the ability to disperse is acknowledged to be of major importance in enabling species to respond successfully to climate change (e.g., Anderson *et al.*, 2009; Hof *et al.*, 2012), recent work has shown that population persistence (i.e. the ability of populations to persist during periods of unfavorable climatic conditions) may in fact play a critical role in determining whether species are able to shift their range along a climate path (Early & Sax, 2011). Ecological specialization could also be an important cause of lags and species-specific rates of range shift, with habitat generalists expanding more rapidly in response to warming than habitat specialists (e.g., Warren *et al.*, 2001; Le Roux & McGeoch, 2008). Thus, the numerous mechanisms and physiological processes behind range shifting act in concert, and give rise to spatially complex and multi-faceted range shifts (Parmesan *et al.*, 2005; Rabasa *et al.*, 2013).

A better understanding of the geographical patterns in species' range shifts could therefore help to refocus

strategies from protected areas toward landscape networks that include protected areas, connecting zones, and intermediate landscapes (Opdam & Wascher, 2004). For instance, species' range shifts could be enhanced by management measures intended to improve population persistence (e.g., by increasing habitat patch size and connectivity, Lawson *et al.*, 2012). In this context, disentangling population persistence in climatically suitable areas could be used to provide a better identification of refugia that are likely to sustain viable populations, whereas persistence in areas that are no longer suitable could be used to pinpoint the areas where the species are most at risk. Furthermore, identifying spatial patterns in species' lags behind climate change can also be particularly useful, as the availability and accessibility of colonizable habitats are key factors underpinning species' abilities to shift their ranges successfully (D'Andrea *et al.*, 2009). In the context of species' responses, strategies that encourage the colonization of newly suitable habitats (e.g., landscape management for habitat corridors or managed relocation) may facilitate range shifts in response to climate change (Ackerly *et al.*, 2010; Early & Sax, 2011).

Previous studies addressing contemporary species' range shifts have mainly used modeling approaches (i.e. correlative or physiologically based bioclimatic models, Guisan & Zimmerman, 2000) in which the ranges of species are modeled over periods of time to provide the basis for quantitatively assessing the changes in species distributions. In most of these studies, range shifts were assessed by contrasting species' distributions during two periods (i.e. historical vs. current), making it possible to determine whether particular species exhibit range expansion (i.e. colonization), range contraction (i.e. extirpation), or a stable range size. However, these studies often rely on rather simplistic descriptors of the geographical distribution of species (e.g., using the range center, or the upper/lower range limits along elevational/latitudinal gradients), which may provide only a limited biological indication of the impact of climate change on geographic ranges (La Sorte & Thompson, 2007). Moreover, so far, relatively few studies addressing contemporary species' range shifts have taken the entire ranges of species into account (Lehikoinen *et al.*, 2013) or attempted to detect shifts using several descriptors (e.g., leading and trailing edges, Maggini *et al.*, 2011; Zhu *et al.*, 2012; Ordonez & Williams, 2013). The comparison between species distribution models trained with historical data and projected over time, and independently constructed, current models has also been previously addressed (e.g., Kharouba *et al.*, 2009; Maiorano *et al.*, 2013). Nevertheless, most of these studies focused

primarily on the temporal transferability of the models (e.g., Araújo *et al.*, 2005a; Dobrowski *et al.*, 2011) or niche stability (e.g., Dudgeon & Stigall, 2010), while the assessment of geographical patterns in range shifts has remained mainly limited to identifying the locations where species are experiencing range expansion, contraction, or stability (e.g., Parra & Monahan, 2008). Therefore, although this would be of great benefit to our understanding of species' responses to recent climate change, comprehensive comparisons of spatial patterns in species' ranges over time remain poorly explored.

Here, we outline a modeling framework based on historical and current records of species distribution intended to disentangle the different drivers (i.e. climatic vs. nonclimatic) and the diverse facets (i.e. colonization, extirpation, range persistence, and lags) of species' range shifts. To demonstrate the potential usefulness of this approach, we used extensive monitoring data of stream fish assemblages obtained throughout France to describe changes in species' ranges for 32 fish species between an initial period (1980–1992) and a more recent one (2003–2009). Because of their ectothermic physiology and the facts that their movements are spatially constrained within hydrographic networks, stream fishes provide particularly relevant model organisms for studying species' range shifts. As many extrinsic and intrinsic factors are expected to be involved, we predict that species' range shifts are geographically complex and related to various combinations of species' traits, leading to idiosyncratic responses. Our main objectives were to (i) model species' ranges in both periods; (ii) quantify different facets of species' range shifts; (iii) describe spatial patterns in those range shifts; and (iv) test whether species' traits explained the variability in multi-faceted range shifts of individual species, providing a way toward a deeper understanding of the complex modifications of species' distribution observed in a context of changing climate.

## Material and methods

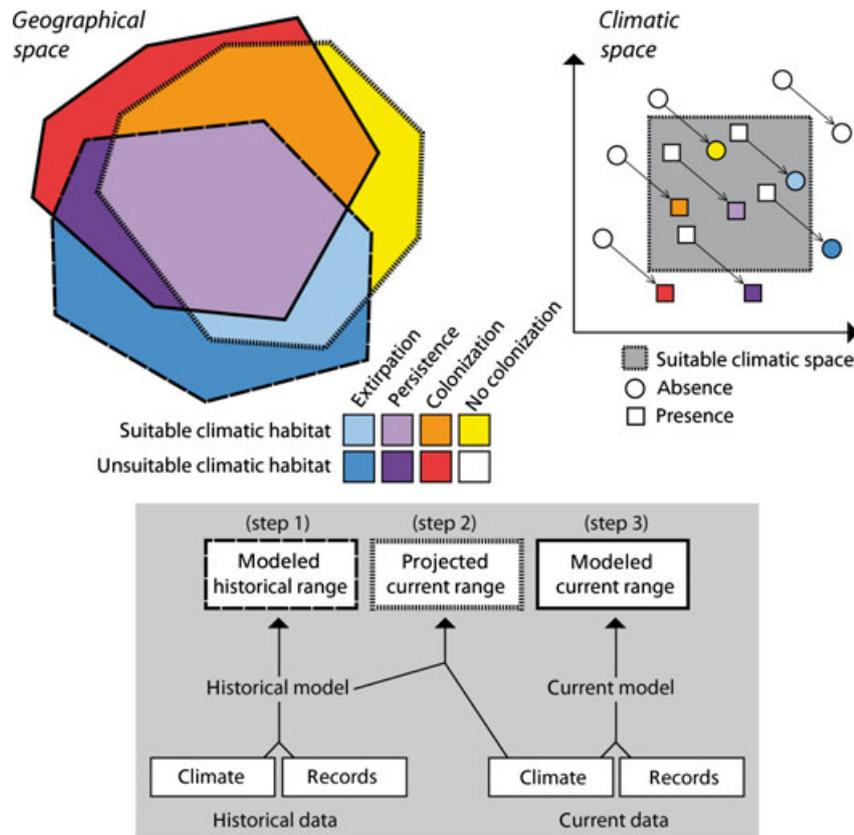
### Modeling framework

A modeling approach based on historical and current species distribution records was developed to describe species' range shifts. Our framework involved three steps (Fig. 1): (i) modeling historical species' range using historical environmental and distribution records (hereafter referred to as the 'historical model'); (ii) projecting the historical model onto the current climatic conditions (hereafter referred to as the 'projected model'); and (iii) modeling current species' range using current environmental and distribution records (hereafter referred to as the 'current model'). While historical and

current models predict the species' geographical ranges, the range predicted by the projected model should be interpreted as being the current climatically suitable range. Confronting these three geographical ranges makes it possible to distinguish geographical areas of population *persistence*, *colonization*, or *extirpation*, in both *climatically suitable* and *unsuitable* habitats, as well as *lag* corresponding to newly suitable habitats which have not so far been colonized (see Fig. 1). The distinction between climatically suitable and unsuitable habitats derives from the outputs of the projected model (e.g., climatically unsuitable if projected as being unoccupied). In both climatically suitable and unsuitable areas, persistence areas correspond to areas predicted to be occupied by both the historical and the current models, while colonization areas are predicted to be occupied only by the current model, and extirpation areas only by the historical model. Therefore, by dissociating range shifts in climatically suitable and unsuitable habitats, this framework proposes a way toward a better attribution of range shifts to climatic vs. nonclimatic drivers. For instance, a local extirpation can be attributed to nonclimatic drivers (e.g., anthropogenic habitat degradation, incursion by nonnative species) when this event is observed in an area yet still climatically suitable, while a colonization can be attributed to climatic drivers when it occurs in a historically unoccupied area which is predicted as being occupied by both the current and the projected models (see Table S1 in Appendix S1 for a comprehensive description of the distinct facets of species' range shifts).

### Species and environmental data

Stream fish data were provided by the French National Agency for Water and Aquatic Environments (Onema), the national fisheries organization in charge of protecting and conserving freshwater ecosystems in France. From this database, we extracted 3549 sites from 1980 to 1992 (referred to below as 'historical surveys'), and 3543 sites from 2003 to 2009 (referred to below as 'current surveys') (see Comte & Grenouillet, 2013). Both surveys were conducted during low-flow periods (mainly May–October), and sampling sites corresponded to stream reaches including several riffle and pool sequences (mean sampling area = 832 m<sup>2</sup> ± 395 SD). At each site, a standardized electrofishing protocol was defined depending on river width and depth. Small streams were sampled by wading, mostly by two-pass removal and a complete prospection of the stream reach, while large rivers were sampled by boat and by fractional sampling strategies of the different types of mesohabitat (Poulet *et al.*, 2011). For each period, the selected sites were distributed throughout France and covered the entire range of environmental conditions found in French streams (Figures S1 and S2 in Appendix S4). Similarly, no significant difference was observed in mean survey date (expressed in Julian days) between the two periods (*t*-test, *P* = 0.283; Figure S3 in Appendix S4). Data on the presence–absence of fish species were recorded at each site, and we considered only species that were adequately represented in both the historical and the current datasets (>75 presences), for a total of 32 species. Although the species-specific esti-



**Fig. 1** Modeling framework developed to assess how species have changed their geographical ranges and are lagging behind climate change. Comparisons between the modeled historical (dashed line) and current (solid line) ranges, and the projected current climatically suitable (dotted line) range are used to identify distinct facets of range shifts, here illustrated in both the geographical (top left) and the climatic (top right) space. In the climatic space, each arrow connects one site from its historical (start point) to its current (arrowhead) situation. Species persistence is shown in light violet (climate deemed to be suitable) and dark violet (climate deemed to be unsuitable, i.e. where the species is likely to be at risk). Extirpations are shown in dark blue (climate-related extirpations) and light blue (extirpations driven by nonclimatic factors). Colonizations are shown in orange for newly suitable habitats (i.e. climate tracking) and in red for climatically unsuitable habitats (e.g., human-assisted dispersal outside the species' climatic niche). Finally, newly suitable areas which have not been colonized (i.e. where the species is lagging behind climate change) are shown in yellow.

mates of detectability were found to slightly differ in the two periods (mean difference in detectability of 0.05), the sampling season did not influence species detectability, and there was no link between variation in species detectability and distribution changes between time periods (see Comte & Grenouillet, 2013 for further details).

Four habitat variables that were assumed to shape stream fish distributions were used to describe each site. These habitat characteristics consisted of elevation (m), river slope (‰), the entire area drained by the upstream area (km<sup>2</sup>), and the cumulated length of the upstream flow network (m) (CCM2, Vogt *et al.*, 2007). We then used a principal component analysis (PCA) to eliminate the colinearity between the last two catchment variables and the first axis of the PCA (accounting for 97.80% of the total variability) was kept as a synthetic variable representative of the position along the upstream–downstream gradient.

Six climatic variables were derived from the SAFRAN atmospheric reanalysis over France (8 km grid-data, Le Moigne, 2002): the mean temperature of the coldest (Tcold) and

warmest (Twarm) quarters (°C), temperature variability (Tvar, CV of the monthly average temperature), cumulated precipitation of the wettest (Pwet) and driest (Pdri) quarters (mm), and precipitation variability (Pvar). Climatic conditions were averaged across each period, including the three preceding years (e.g., Rowe *et al.*, 2010). Air temperatures were used as a surrogate of water temperatures because water temperatures are currently not available for all French streams. However, streams are well-mixed water bodies that easily exchange heat with the atmosphere, and air temperatures show a strong positive correlation with water temperatures (e.g., 86–96% of the water temperature variability explained using only air temperature and simple linear regression models, Crisp & Howson, 1982; Caissie, 2006).

### Changes in climate

To assess changes in climate between the two periods, we performed a PCA on the six climatic variables. Changes in climate

were quantified by assessing the changes in the position of each reach of the hydrographic network in the climatic space defined by the first two axes (accounting for 81.9% of the total variance). Specifically, we measured the direction (i.e. angular coordinate) and the magnitude (i.e. radial coordinate) of changes in climate for each reach of the network. Beyond global warming, this approach made it possible to identify consistent trends across the reaches, showing more frequent and greater changes toward warmer and thermally more variable conditions (polar diagram, Fig. 3).

### *Ensemble modeling of species' ranges*

For each period and each species, presence–absence data were related to the environmental variables using an ensemble modeling approach (Araújo *et al.*, 2005b) based on eight different species distribution models (SDMs): generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), mixture discriminant analyses (MDA), classification and regression trees (CART), random forest (RF), generalized boosted trees (GBT), and artificial neural networks (ANN). SDMs were built using a random subset of data containing 70% of the sites (i.e. the training dataset), and the remaining 30% of the data (i.e. the testing dataset) were used to evaluate the predictive performance of the models. Datasets for each period were composed of one sampling record randomly chosen for each site, to avoid pseudoreplication. This split-sample procedure was reiterated 30 times.

For each iteration, we combined the single-SDM predictions by computing the mean value of this ensemble (i.e. 'average model', Marmion *et al.*, 2009). Following Hijmans (2012), the predictive performances of average models were then evaluated using a threshold-independent measure, the calibrated area under the receiver operating curve (cAUC), which controlled for the effect of spatial sorting bias (i.e. inflation of cross-validation results due to spatial autocorrelation).

Finally, the predictions of the average model were computed for the reaches throughout the whole hydrographic network (CCM2, Vogt *et al.*, 2007) and converted into binary values (i.e. presence–absence) using a threshold maximizing the sum of sensitivity and specificity (Liu *et al.*, 2005). Individual species ranges were then mapped, resulting in 30 species ranges modeled for both the historical and the current periods.

The same methodology was used to project the historical models onto the current climatic conditions. For each species, we forecasted current suitable habitats (i.e. potential current ranges) based on the historical models combined with current climate data. The eight single-SDM projections were then averaged, evaluated using cAUC, and converted into binary data by using the same threshold values as for the historical predictions, thus resulting in 30 projected species ranges.

### *Changes in species' ranges*

First, to compare the modeled species' ranges between the two periods, we computed two commonly used measures of

the overall change: (i) the difference between the current and historical spatial extents (range sizes) of the species defined as the length of the hydrographic network occupied by the species (Fagan *et al.*, 2002) and expressed as a percentage of the historical spatial extent; and (ii) the dissimilarity between spatial distributions predicted by the historical and current models. This dissimilarity between the two spatial distributions (presence–absence data of the species predicted for the reaches throughout the whole hydrographic network) was computed using the pairwise Jaccard's dissimilarity index (Gower & Legendre, 1986), ranging from 0 (i.e. no change in spatial distributions) to 1 (i.e. no overlap between the two distributions).

For each species and each iteration, we then contrasted the two species' ranges modeled (historical and current), and the projected current range, allowing us to quantify the different facets of species' ranges as described in Fig. 1. We computed the length of the hydrographic network corresponding to each of these facets, and we expressed them as a percentage of the historical spatial extent. In addition, we further analyzed changes in species' ranges by mapping them on both geographical and climatic space to provide a better visual assessment of spatial patterns. Finally, we assessed uncertainty in spatial patterns arising from our modeling framework (i.e. 30 SDM iterations). For each facet of species' ranges, we mapped the sum of the 30 predictions (i.e. presence–absence data). This enabled us to visualize geographical areas of agreement for both absence (i.e. sum equals 0) and presence (i.e. sum equals 30) of each facet, and areas of high disagreement (i.e. intermediate sum values) among SDM iterations.

### *Species trait effects and phylogenetic relatedness*

All species were characterized using five traits expected to affect species' range shifts: dispersal ability, life-history strategy, thermal tolerance (i.e. the upper temperature limit), geographical range size, and elevational distribution preference (see Table S2 in Appendix S2 for details of these traits). We tested whether these traits explained the observed variability in range shifts after accounting for the phylogenetic relatedness among species.

First, the phylogeny of the 32 species studied was built on the basis of molecular data obtained from Genbank for three mitochondrial genes (Grenouillet *et al.*, 2011). Sequence data consisted of 1124, 651, and 459 base pairs for cytochrome *b*, cytochrome oxidase I, and ribosomal 16S subunit, respectively. Phylogenetic relationships among species were reconstructed using the Bayesian method under the TVM\_I\_G substitution model, and the phylogeny estimation implemented with MRBAYES and PAUP softwares.

Then, we related species' traits to distinct facets of species' range using phylogenetic generalized least-squares (PGLS) models (Freckleton *et al.*, 2002). These models accounted for the nonindependence of data by adjusting the variance/covariance matrix to the phylogenetic relatedness among species using Pagel's  $\lambda$  (i.e. the degree of phylogenetic autocorrelation). More specifically, we focused on

four descriptors of range shift: (i) climate-related extirpations; (ii) extirpations due to nonclimatic drivers; (iii) persistence in climatically unsuitable areas; and (iv) lags behind climate change. All the predictors were transformed into z-scores to standardize the slope coefficients ( $\beta$ ) for comparison across traits.

All models and analyses were developed using R environment software v 2.14.2 (R Development Core Team, 2012).

## Results

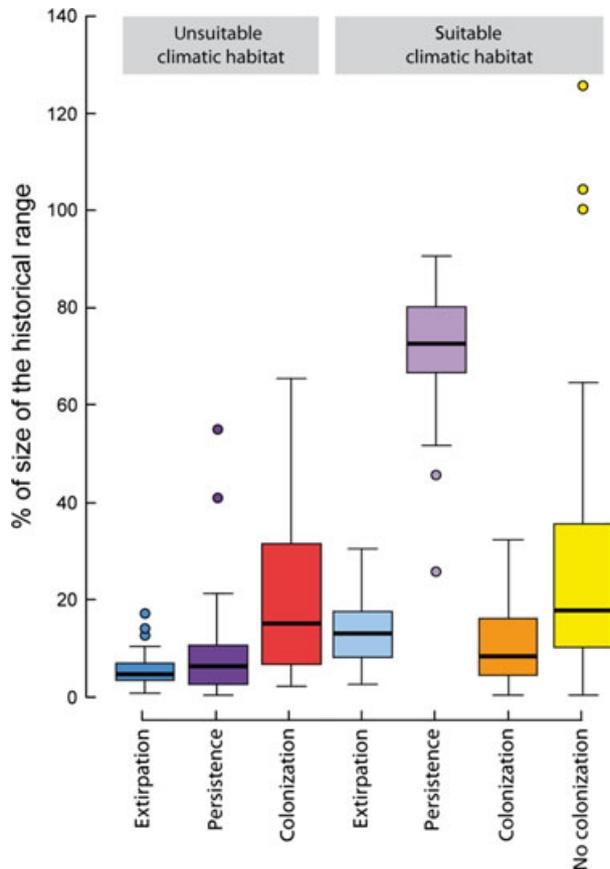
### Model performances between periods

Overall, both the historical and the current models showed a good ability to predict the observed species' ranges, with cAUC values among the 32 species ranging from 0.76 to 0.95 (mean =  $0.85 \pm 0.04$ ), and from 0.78 to 0.93 (mean =  $0.85 \pm 0.04$ ), respectively (Table S3 in Appendix S3). No significant difference was observed in predictive performances between the two periods (paired *t*-test,  $P = 0.354$ ). Compared to the current model, the projected model performed significantly worse (paired *t*-test,  $P < 0.001$ ), but showed good predictive performance, with cAUC values ranging from 0.73 to 0.90 (mean =  $0.83 \pm 0.05$ ).

### Changes in species' ranges

Among the 32 species, 12 species had undergone range contraction while 20 species had experienced range expansion (Table S3 in Appendix S3). In general, fish species exhibited a gain of area compared to their historic range, with changes in range size ranging from  $-28.2\%$  to  $+58.1\%$  (mean =  $+10.4\% \pm 0.19$ ). Similarity between the historical and current species' ranges also revealed clear differences between the modeled distributions, which ranged from 0.32 to 0.89 (mean =  $0.64 \pm 0.12$ ). While changes in species' range were unrelated to differences in model performances for the two periods ( $R^2 = 0.018$ ,  $P = 0.459$ ), dissimilarities between the modeled species' distributions increased with differences in model performance over time ( $R^2 = 0.261$ ,  $P = 0.003$ ). Although no effect of species status (i.e. native vs. nonnative) was detected for changes in range size, nonnative species showed significantly higher dissimilarities in spatial distributions between the two periods (Wilcoxon tests,  $P = 0.154$  and  $0.037$ , respectively).

When the distinct facets of species' range shifts were quantified, we observed contrasted responses among species (Fig. 2). While persistence was the predominant pattern for nearly all of the species (mean = 80.0% of the historical species' range), persistence in climatically



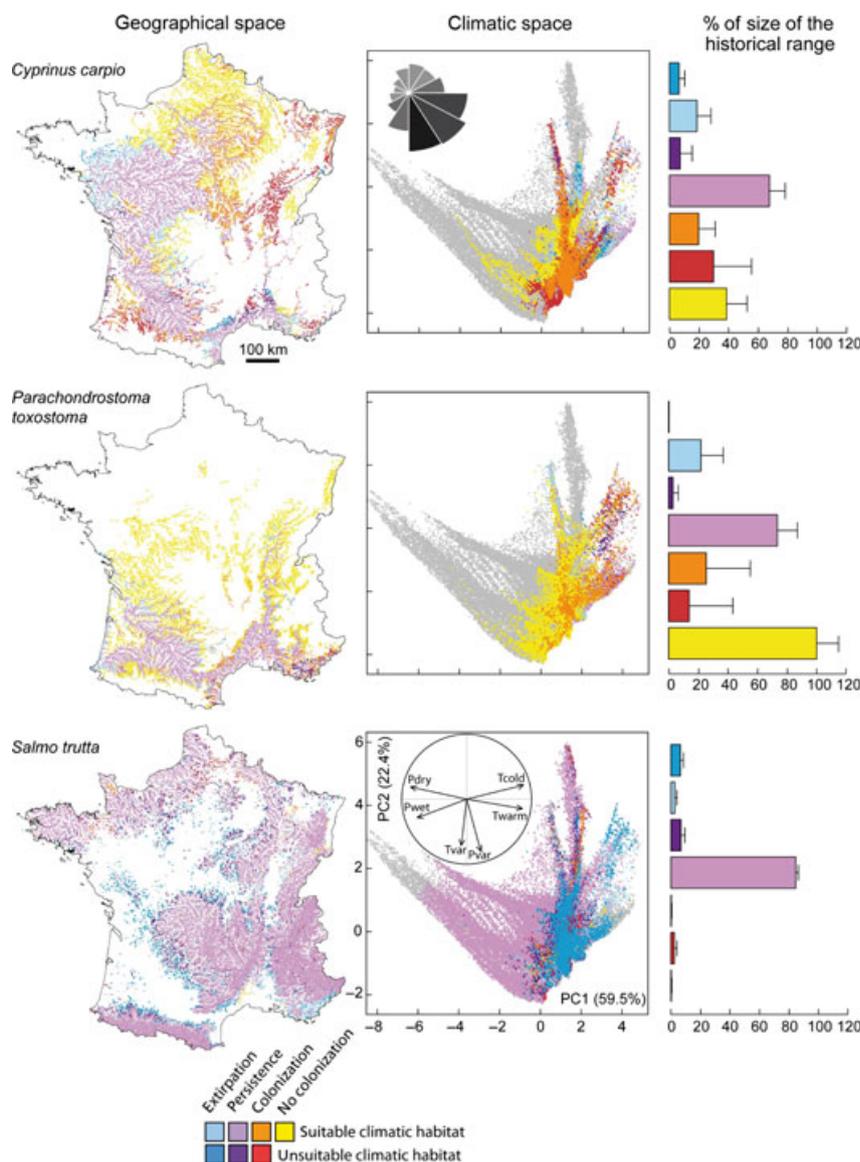
**Fig. 2** Distinct facets of geographical range shifts between historical and current periods for the 32 fish species studied. For each species, contrasting the two species' ranges modeled (historical and current) and the projected current range allowed to quantify the different facets of species' ranges as described in Fig. 1. Each facet was quantified by computing the length of the corresponding hydrographic network, and expressed as a percentage of the historical range of the species. Color legend as in Fig. 1.

unsuitable areas corresponded, on average, to 8.9% of the historical range and ranged from 0.1% to 54.9% among the 32 species. Lags behind climate change (i.e. newly climatically suitable areas that remained unoccupied) varied considerably among species, ranging from 0.1% to 125.7% of the historical species' range. Climate tracking (i.e. colonizing newly climatically suitable areas) had allowed species to expand their historical range by 10.6% on average (range: 0.1–32.4%), whereas climate-related extirpations resulted in range contractions of 5.8% on average (range: 0.0–17.1%). For both the colonization and the extirpation patterns, the magnitude of the changes in species' range due to nonclimatic drivers was significantly greater (paired *t*-tests,  $P < 0.001$ ) than climate-related changes (i.e. 3.2 and 3.7 times higher, respectively).

*Spatial patterns in species' range shifts*

Following hierarchical clustering based on distinct measures of species' range shifts (Table S3 in Appendix S3), three species were used to illustrate the spatial

patterns in species' responses typical of most of the other species (Fig. 3). *Cyprinus carpio*, a downstream species, showed complex patterns in range shifts. All the distinct facets of species' range shift were represented (by areas of population persistence,

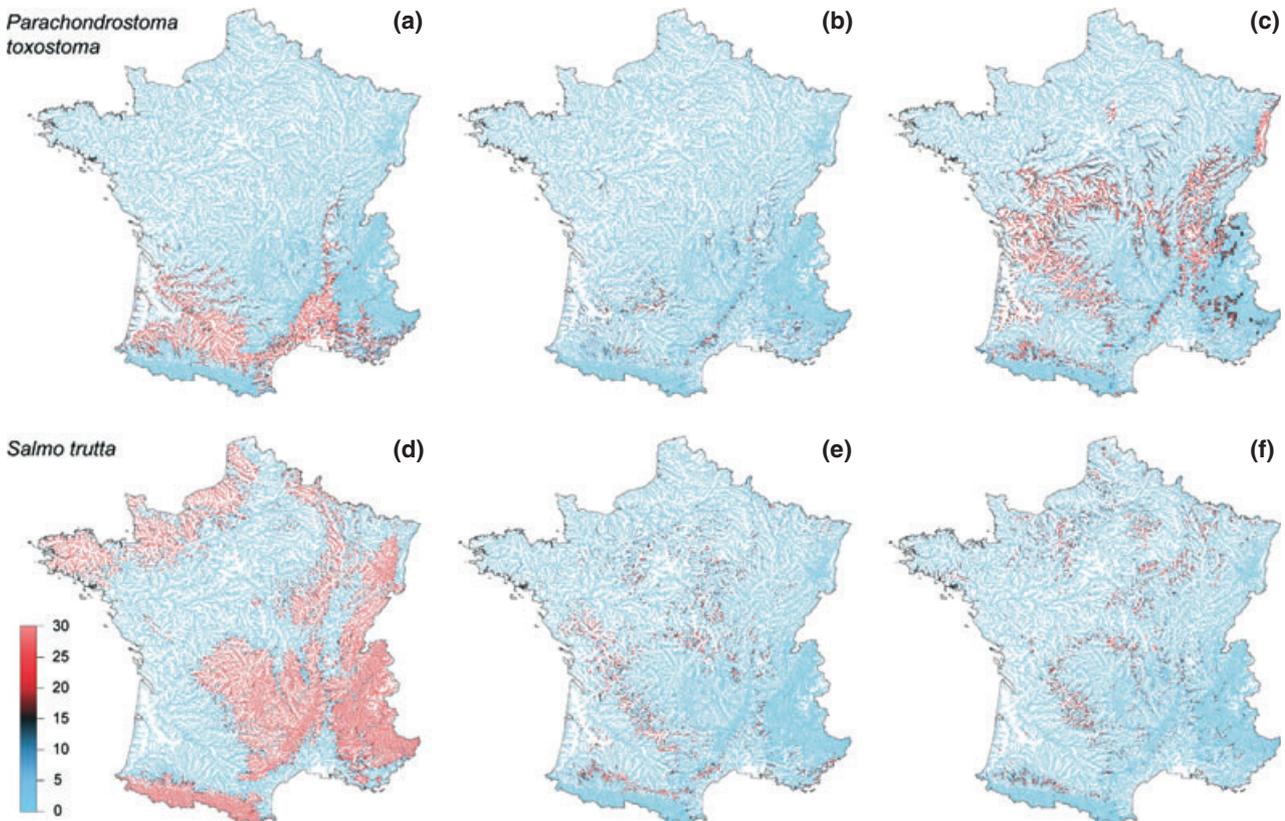


**Fig. 3** Patterns in species' range shifts over time for three fish species, mapped in both geographical and climatic space. Climatic space was defined by the first two axes (accounting for 81.9% of the total variance) of a principal component analysis performed on the six climatic variables. The correlation circle plot shows the projections of the climatic variables onto the first two principal components. PC1 represents a gradient from warmer, drier areas (positive loadings) to cooler, wetter areas (negative loadings), whereas PC2 was more strongly associated with temperature variability and contrasted areas with relatively stable conditions (positive loadings) with areas showing greater variation in temperatures (negative loadings). Changes in the position of each reach of the hydrographic network in the climatic space defined by the first two axes allowed to measure the direction (i.e. angular coordinate) and the magnitude (i.e. radial coordinate) of changes in climate between the two periods. The polar diagram shows the frequencies of occurrence and the directions of climate change, with the gray scale proportional to the mean amplitude of the changes for each direction. The percentage of the size of the historical range of the species was quantified for the distinct facets of species' range shifts. Error bars indicate standard deviations across the 30 modeling iterations (see methods). Color legend as in Fig. 1.

colonization, extirpation, and lag), and each of these facets displayed clear geographical patterns (i.e. a patchy spatial structure). For instance, large areas of lag behind climate change (characterized by cooler conditions compared to historical distribution) were identified in northern France, while colonizations and extirpations due to nonclimatic drivers were more often observed in northeastern France and northwestern France, respectively. Climate tracking was observed for reaches characterized by similar conditions in mean temperature (i.e. low dispersion in climatic space along the first axis, Fig. 3), and for a wide range of conditions in climate variability. *Parachondrostoma toxostoma*, a species restricted to southern France, persisted in warm reaches of the hydrographical network. This species exhibited lags behind climate change in many reaches located north of its historical distribution, while the species expanded its range in newly climatically suitable reaches at the edge of its historical distribution. No climate-related extirpations were observed for this species, but a loss of range attributed to nonclimatic factors

had contracted its historical range by 21.6%. Finally, *Salmo trutta*, a cold water species, showed large areas of persistence in cold reaches of the hydrographic network. This species exhibited climate-related extirpations and persistence in climatically unsuitable habitats in the warmest reaches at the edge of its historical distribution, while the few colonization events observed were mainly driven by nonclimatic factors.

To illustrate geographical areas of uncertainty in species' range shifts, we produced maps summing the predictions from the 30 modeling iterations for two species and three facets of range shifts (Fig. 4). For both species, visual inspection of these maps revealed that population persistence in climatically suitable areas was consensually predicted by all modeling iterations, with the most notable disagreement between iterations occurring at the edge of these persistence areas (Fig. 4a and d). For *Parachondrostoma toxostoma*, the observations of range expansion (i.e. colonization of newly climatically suitable reaches at the edge of the historical distribution) appeared less consensual among modeling



**Fig. 4** Maps showing the sum of the 30 model predictions of presence vs. absence of three facets of range shifts for two fish species. (a and d) persistence in climatically suitable areas, (b) climate-related colonizations, (c) lags behind climate shifts, (e) climate-related extirpations, and (f) persistence in climatically unsuitable areas. Agreement among predictions is shown as a slope from light blue (all modeling iterations predict absence) to light red (all modeling iterations predict presence), while areas of high disagreement among iterations appear in dark.

**Table 1** Phylogenetic generalized least-squares (PGLS) models testing the relationships between range shifts and species' traits. Changes in species' range included climate-related extirpations, extirpations due to nonclimatic drivers, persistence in climatically unsuitable areas, and lags behind climate change. Species' traits included dispersal ability, life-history strategy (i.e. life cycle duration), thermal tolerance (i.e. upper temperature limit), geographical range size, and elevational distribution preference. Slope coefficients ( $\beta$ ) and associated  $P$ -values (NS, not significant) are given. See Table S2 in Appendix S2, for details on traits

Species' trait	Climate-related extirpations		Nonclimatic extirpations		Persistence		Lags	
	$\beta$	$P$	$\beta$	$P$	$\beta$	$P$	$\beta$	$P$
Dispersal	-0.012	NS	-0.007	NS	-0.014	NS	0.023	NS
Life cycle duration	-0.015	0.019	0.030	NS	-0.095	0.003	0.063	0.012
Thermal tolerance	-0.016	0.026	-0.040	0.016	0.046	NS	-0.022	NS
Range size	-0.002	NS	-0.050	0.002	0.059	NS	-0.070	0.003
Elevational distribution preference	0.003	NS	-0.029	NS	0.067	NS	-0.076	0.002

iterations (Fig. 4b), while this consensus was more pronounced for areas of lags behind climate change located north of its historical distribution (Fig. 4c). For *Salmo trutta*, climate-related extirpations were more consensually predicted at the edge of its southern historical distribution (Fig. 4e), while many areas of persistence in climatically unsuitable habitats were consistently predicted in northern France (Fig. 4f).

#### Species' traits

When accounting for the effect of phylogenetic relatedness among fish species, the magnitude of climate-related extirpations was negatively related to life cycle duration and the species' upper temperature limit ( $P = 0.019$  and  $0.026$ , respectively), revealing that extirpations due to loss in climatic habitat suitability were greater for short-lived and cold-adapted species (Table 1). Extirpations driven by nonclimatic factors were negatively related to the species' thermal tolerance and geographical range size ( $P = 0.016$  and  $0.002$ , respectively), resulting in more pronounced range contractions for cold-adapted and restricted-range species. Persistence in climatically unsuitable areas was significantly ( $P = 0.003$ ) related to life cycle duration (persistence was greater for short-lived species). Finally, the magnitude of the lags behind climate change was related to life cycle duration and the two geographical attributes of the species (range size and elevational distribution preference), with significantly greater lags being observed for long-lived, restricted-range, and low-elevation species ( $P = 0.012$ ,  $0.003$ , and  $0.002$ , respectively).

#### Discussion

The novel framework presented here demonstrates how dissociating different drivers (i.e. climatic vs.

nonclimatic) and assessing distinct facets (i.e. colonization, extirpation, persistence and lags) of species' range shifts can capture the complex mosaics of species' responses and could markedly improve our understanding of key processes involved in range shifts. Although such an approach has already been partially tackled (e.g., Warren *et al.*, 2001), we are not aware of any study that has actually proposed a similar framework.

Our findings provide strong evidence that the responses of individual species varied considerably and they exhibited complex mosaics of range shifts. Such individualistic and spatially complex range shifts have already been reported in response to changing climates in the past (Graham *et al.*, 1996), and evidence from paleoecology suggests that climatic microrefugia have been important in shaping current species' geographical ranges (Sublette Mosblech *et al.*, 2011). Similarly, geographical variation in ongoing climate change is critical in explaining the contemporary differences in the range shifts of individual species (e.g., Ackerly *et al.*, 2010; Chen *et al.*, 2011; Isaak & Rieman, 2013). As both climate change and topographic heterogeneity influence how species modify their distribution (Lyons *et al.*, 2010; Lenoir *et al.*, 2013), we propose that complex geographical patterns in species' responses should be expected to be common.

By confronting historical and current modeled ranges and projected current ranges, we have shown in both climatically suitable and unsuitable habitats geographical areas of range stability, colonization, extirpation, and lags behind climate change. Notably, both colonization and extirpation patterns that may be linked to climate were of lower magnitude than those likely to be linked to nonclimatic drivers. This finding is consistent with a recent meta-analysis of range shifts documented for freshwater fish, which compared both observed and predicted climate-induced changes in fish species'

ranges (Comte *et al.*, 2013). These authors showed that the current rates of change were of greater magnitude than those forecasted to occur under future climate conditions, thus indicating that other drivers of change may be interacting with climate and affecting freshwater fish species. Among these drivers, Alofs *et al.* (2014) recently noted that human-mediated dispersal could be influencing range shifts in fish species. Previous studies have also suggested that synergetic effects between ongoing climate change and regional anthropogenic drivers (e.g., habitat destruction and fragmentation concomitant with land-use changes) could have a marked impact on population trends (Eglington & Pearce-Higgins, 2012) and species' abilities to shift their ranges (La Sorte & Thompson, 2007; Hof *et al.*, 2011). In stream ecosystems, while land-use changes can result in hydrologic alteration, habitat degradation and declines in water quality, regulation of water flows (by water retention and diversion) is considered to be the most critical change and has led to substantial range contractions for many freshwater fish (Booth *et al.*, 2011; Pratchett *et al.*, 2011). This is of particular interest as it means that range shift forecasts based solely on climate variables may profoundly underestimate future changes in species' distribution (e.g., Wenger *et al.*, 2011). However, few studies have quantitatively assessed how human influence and species' range shifts are correlated (Laliberte & Ripple, 2004), and we recommend that further research be carried out to investigate the combined effects of climate change and other regional drivers on species' ranges.

After accounting for phylogenetic relatedness among species, we also found evidence that range shifts could be related to some particular traits of species and that the traits involved varied depending on the facet of range shifts considered. We showed that population persistence and lags behind climate change were related to life cycle duration, whereas lags also appeared to be related to the geographical attributes of the species. Numerous empirical studies have assessed whether species' traits are linked to recent shifts in geographical ranges (e.g., Perry *et al.*, 2005; Lenoir *et al.*, 2008; Pöyry *et al.*, 2009), but these studies have often reported weak or nonexistent relationships (Angert *et al.*, 2011; Crimmins *et al.*, 2011). For instance, Angert *et al.* (2011) failed to identify any consistent effect of geographic range size on recent range shifts, although this trait is the one most often correlated with extinction risk (Cardillo *et al.*, 2008). In contrast, when dissociating climatic and nonclimatic drivers of extirpations, we demonstrated that nonclimatic extirpations were primarily related to species' range size, while climate-driven extirpations were better explained by species' ther-

mal tolerance. Counter intuitively, we also showed that life cycle duration had antagonist effects on climate-related extirpations and persistence in climatically unsuitable areas. This result could indicate that extirpations are more difficult to detect for long-lived species (i.e. more likely to have an extinction debt, Kuussaari *et al.*, 2009), while short-lived species may better compensate for local extirpations through metapopulation dynamics (Opdam & Wascher, 2004; Early & Sax, 2011). These findings suggest that the weak relationships reported so far could partly result from the fact that (i) these traits are expected to differ fundamentally depending on which threatening processes predominate (e.g., Isaac & Cowlshaw, 2004; Bromham *et al.*, 2012); and (ii) most of the documented range shifts cannot unambiguously be attributed to climate change, because of possible confounding effects (e.g., Popy *et al.*, 2010). However, climate change is already beginning to exacerbate other extrinsic threats (Brook *et al.*, 2008), and species' vulnerability is likely to shift from anthropogenic effects in the near term to climate change in the near future (Zhu *et al.*, 2012). In addition, our results caution against overoptimistic conclusions about the vulnerability of species to climate change as lags in extinction and immigration could lead to more severe long-term effects as a result of extinction debts and immigration credits (Jackson & Sax, 2010). We therefore argue that the framework proposed here offers a promising way to better describe, understand, and predict complex modifications of species' distribution in response to global changes, and a template for informing management decisions with awareness of the inherent uncertainty in those changes.

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### Supporting Information

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

**Appendix S1.** Distinct facets of geographical range shifts between historical and current periods.

**Appendix S2.** Species' traits expected to affect range shifts.

**Appendix S3.** Model performances and changes in species' range between the historical and current periods.

**Appendix S4.** Characteristics of the sampling sites between the historical and current periods.