Drivers of freshwater fish colonisations and extirpations under climate change

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Climate change is expected to bring about profound rearrangement of ecological communities by affecting individual species distributions. The resulting communities arise from the idiosyncratic responses of species to future changes, which ultimately relate to both shrinking and expanding species ranges. While spatial patterns of colonisation and extirpation events have received great attention, the identification of specific drivers remains poorly explored. This study aims to investigate the relative contribution of species gain and loss to the turnover of fish assemblages in French rivers under future climate change, and to identify their principal drivers. Future projections of potential habitat suitability in 2080 derived from species distribution models for 40 fish species showed that colonisations and extirpations could play counterbalancing roles in the reshuffling of communities. Simultaneously, these two processes exhibited patchy spatial patterns, segregated along the longitudinal and altitudinal gradients, resulting in dramatic species turnover of ~60% of the current composition of species assemblages. Beyond the effect of topographic location, colonisations were found to be driven by temperature seasonality while extirpations were affected by modifications in both thermal and precipitation regimes.

These results generate the possibility of developing ecosystem-based management tools focused on the early identification of areas where particular species may be sensitive to climate changes. Disentangling the drivers of colonisation and extirpation processes provides ready-to-use information that may be easily integrated into conservation planning. This information could be used to identify potential hotspots of species gain and loss and to then compare these hotspots with newly favourable areas so as to consider their actual accessibility in order to facilitate future range shifts.

Climate change is widely recognised as having a profound impact on distribution of species (Pearson and Dawson 2003), modifying biodiversity patterns in terrestrial (Thuiller et al. 2005, Levinsky et al. 2007, Huntley et al. 2008, La Sorte and Jetz 2010), marine (Hiddink and ter Hofstede 2008, Cheung et al. 2009, Albouy et al. 2012) and freshwater (Buisson et al. 2008, Heino et al. 2009, Comte et al. 2013, Pace et al. 2013) ecosystems. On ecological timescales, species assemblages are the result of a synergic interplay between colonisation and extirpation, two spatial- and temporal-dependent processes influenced by regional and local drivers (He et al. 2005, Korhonen et al. 2010). At the continental scale, climate can be considered the dominant factor shaping species distribution, whilst at more local scales factors including topography and land-cover type become increasingly important (Pearson and Dawson 2003). For instance, a species might be buffered from the full magnitude of regional climate change by persisting in thermally sheltered microhabitats (Hampe and Jump 2011) or might be affected by local anthropogenic factors that interact synergistically or antagonistically with climate change (Le Roux and McGeoch 2008, D'Andrea et al. 2009, Hockey et al.

2011). In this context, species colonisations and extirpations result in so-called niche tracking (i.e. the process by which species follow favourable environmental conditions through geographical space, Graham et al. 1996, Tingley et al. 2009) fundamentally driven by the contraction and expansion of species ranges (Thomas 2010).

In order to quantify modifications of species assemblages along geographical or environmental gradients (i.e. beta diversity), species turnover is among the most common metrics used, as well as its temporal equivalent, to estimate compositional changes over time (Albouy et al. 2012). Numerically, species turnover considers the number of colonisation (species gain) and extirpation (species loss) events within each spatio-temporal unit and compares the net change with the baseline species richness (Peterson et al. 2002, Thuiller et al. 2005). A vast number of studies and meta-analyses have addressed the issue of spatial variability in species composition (see Heino 2011, Leprieur et al. 2011, Oberdorff et al. 2011 for a review on the freshwater realm), demonstrating that beta diversity could be driven by functional traits, geographical gradients and ecosystem properties (Soininen et al. 2007). By contrast, assessing temporal

turnover has been far less investigated, generally hindered by the lack of long-term data (Micheli et al. 1999, Korhonen et al. 2010). In particular, although the number of studies focusing on spatial and temporal patterns of species turnover (Buisson et al. 2008, Buisson and Grenouillet 2009, Villéger et al. 2013) is increasing, few attempts have been directed towards the identification of drivers and geographical patterns in the processes shaping local richness, namely colonisations and extirpations.

On ecological timescales, climate change may influence the congruence between species tolerance limits (i.e. species niche) and their current distribution in three principal ways: 1) presently occupied sites may remain within the climatic niche of the species, 2) the local environment may shift outside a species niche potentially leading to extirpation, or 3) currently unoccupied sites may become favourable by shifting inside a species niche potentially leading to colonisation (i.e. niche tracking; Tingley et al. 2009). When a new equilibrium is reached, the combined result of colonisation and extirpation events defines a species new geographical range, although both processes may have not been equivalent in their extent, geographical location and, more importantly, in the drivers producing them (Hampe and Petit 2005). Studies based on species distribution models (SDMs) often focus on the overlap between current and future favourable or unfavourable space units, in order to detect spatial patterns and local hotspots of potential increased or decreased species diversity. To date, the relative contribution of colonisations and extirpations to range shifts and local turnover of species has been investigated in a wide range of taxa and ecosystems (Peterson et al. 2002, Thuiller et al. 2005, Cheung et al. 2009). Nevertheless, few of these studies attempt to relate both shrinking and expanding ranges to specific drivers, typically focusing on range contractions (i.e. increased extinction risk) (Thomas et al. 2004, Thuiller et al. 2005, Brook et al. 2009). Among these, Thuiller et al. (2005) showed that plant species loss may be positively correlated to accumulated warmth and decreased moisture availability across Europe.

Disentangling the relative importance of synoptic (i.e. occurring in the same spatio-temporal range) and often synergic (i.e. interacting) changes in environmental variables on geographical species responses is a major goal of current research (Brook et al. 2009). Nevertheless, identification of specific environmental and climatic features affecting either colonisation or extirpation events remains to date poorly explored. Filling this knowledge gap may be particularly important for the strategic development of conservation strategies of climate-sensitive species (Heller and Zavaleta 2009). From a management perspective, dealing with colonisations and extirpations does not represent simple antinomies, but may require different approaches. For instance, strategies to counteract species range contractions may focus on improving species abilities to cope with a less favourable habitat within their original range (e.g. enlarging patch size and number of dispersing individuals or improving the condition of key sites) (Pearce-Higgins et al. 2011). Alternatively, species range shifts towards new climatically favourable habitats can be facilitated by conservation measures improving landscape connectivity (Lawson et al. 2012). The selection of the most effective strategy to enact is case-based, depending on spatial scale, regional features, and the idiosyncratic response of species coping with a changing climate (Hoegh-Guldberg et al. 2008). Under a warming climate, species at their upper thermal limit may disappear rapidly after the loss of suitable habitat, while colonisation of new climatically favourable patches may not be straightforward (Jackson and Sax 2009). Range shifts may be hindered by species dispersal abilities, landscape fragmentation, physical barriers and population survival in the newly colonised patches, which all contribute to a delay in the expansion at the leading edge (Warren et al. 2001). This colonisation credit (i.e. the number of species committed to eventual immigration, Jackson and Sax 2009) represents a great challenge for conservation, which may be cashed more rapidly by enhancing population survival and facilitating range expansions through increased landscape-scale connectivity (e.g. corridors or matrix management, Lawson et al. 2012).

In the present study, we used SDMs to model climate-induced changes in freshwater fish distributions for French rivers into the 2080s in order to investigate the different pressures acting on species persistence. Starting from the assessment of the relative contribution of shrinking and expanding ranges to the species turnover, the main objectives were 1) to investigate spatial patterns in colonisation and extirpation events along the hydrographical network and 2) to relate both processes to topographic and climatic predictors, quantifying the effects of these different drivers of species range expansion and contraction.

Material and methods

Study area

This study was conducted at the scale of the French hydrographical network. Geo-referenced data for 103790 river segments within French borders were extracted from the Catchment Characterisation and Modelling [CCM2, ver. 2.0 (Vogt et al. 2007)] database, a coding system for European continental waters (i.e. coastlines, rivers, river branches, watersheds and islands).

Biotic and abiotic data

Fish data

Fish data were provided by the French National Agency for Water and Aquatic Environment (Onema), which is the national fisheries organisation in charge of the protection and conservation of freshwater ecosystems in France. The database of the Onema provides an extensive survey of freshwater fish at the national scale, with sites covering the entire range of environmental conditions found in French streams. At each site, a standardized electrofishing protocol during low-flow period (mainly May–October) was defined depending on river width and depth and a removal method was used to sample stream fish in one to three successive passes (Poulet et al. 2011). From this database, we extracted 1417 sites sampled at least three times from 2000 to 2010. We used presence and absence records of the 40 most common

species (i.e. occurring in at least 5% of the sites) belonging to 13 families, among which Cyprinidae represented by far the most diverse family with 22 species (Supplementary material Appendix 1). For each site, we pooled multiple sampling records into a single dataset and we computed inventory completeness (i.e. the proportion of species detected) as the ratio of observed species richness for a given site to estimated species richness for the corresponding site. Species richness was estimated using the maximum of two different non-parametric estimators, based on the frequencies of species in the collection of sampling occasions for a given site: Chao 2 and Jackknife 1 (Colwell and Coddington 1994). We hence retained well-sampled sites with inventory completeness higher than 0.8, providing a selection of 1038 sites for further analyses.

Climate data

Six climatic variables were extracted from the WORLDCLIM ver. 1.4 (Hijmans et al. 2005) database, at a 30 arc-second resolution grid: temperature seasonality (Tsea, standard deviation of the monthly mean temperatures × 100), mean temperature of the warmest quarter (Twar,°C), mean temperature of the coldest quarter (Tcol,°C), precipitation seasonality (Psea, coefficient of variation of the monthly precipitation), precipitation of the driest quarter (Pdry, mm) and precipitation of the wettest quarter (Pwet, mm). The quarterly parameters were not aligned to any calendar quarters. A quarter is any consecutive 3 months that are for example drier (or warmer/colder/wetter) than any other set of 3 consecutive months.

Future climate conditions for each of the selected climatic variables were extracted for the time period 2051–2080 (referred as the 2080s scenario) and derived from three General Circulation Models (GCMs): HadCM3 (Hadley Centre for Climate Prediction and Research's General Circulation Model), CGCM2 (Canadian Centre for Climate Modelling and Analysis), and CSIRO-MK2 (Australia's Commonwealth Scientific and Industrial Research Organisation). For each GCM, two greenhouse emissions scenarios (GES) from the Special Report on Emission Scenarios of the Intergovernmental Panel on Climate Change (IPCC SRES) were used, namely the A2A (high energy requirements-emissions) and the B2A (low energy requirements-emissions), for a total of six coupled GCM-GES scenarios for the 2080s scenario.

Due to strong correlations between the six climatic variables (Supplementary material Appendix 4), a principal component analysis (PCA) was performed on the six climatic variables, which were pooled into a single dataset encompassing current climate conditions and the six future scenarios. The first three axes of the PCA (PCA1, PCA2, PCA3) were then used as individual predictors.

Topographic data

Four variables were used to describe the hydrographical network: surface area of the drainage basin above the sampling site (Sdb, km^2), cumulated length of the upstream flow network (Clf, m), river slope (Slo, ‰), and altitude (Alt, m). Among these, two predictors were synthesised into an individual variable describing the longitudinal gradient (G), derived from the first axis of a PCA on Sdb and

Clf. Generalised additive models (GAM) were then fitted between each of the three topographic (G, Alt, Slo) and climate (PCA1, PCA2, PCA3) variables in order to remove the strong correlations between them. Residuals of these three models were then used as individual predictors describing environmental variability, independent of climate (Buisson et al. 2008, 2010).

Ensemble modelling of species distribution

The dataset of 1038 sites was split into a calibration set (2/3 of the original data) and a validation set (1/3 of the original data), preserving a homogeneous number of sites belonging to different river basins within the two datasets. This splitting procedure was repeated 50 times. For each iteration, seven statistical methods were used to infer the distribution of the 40 selected species (step 1, Fig. 1): generalised
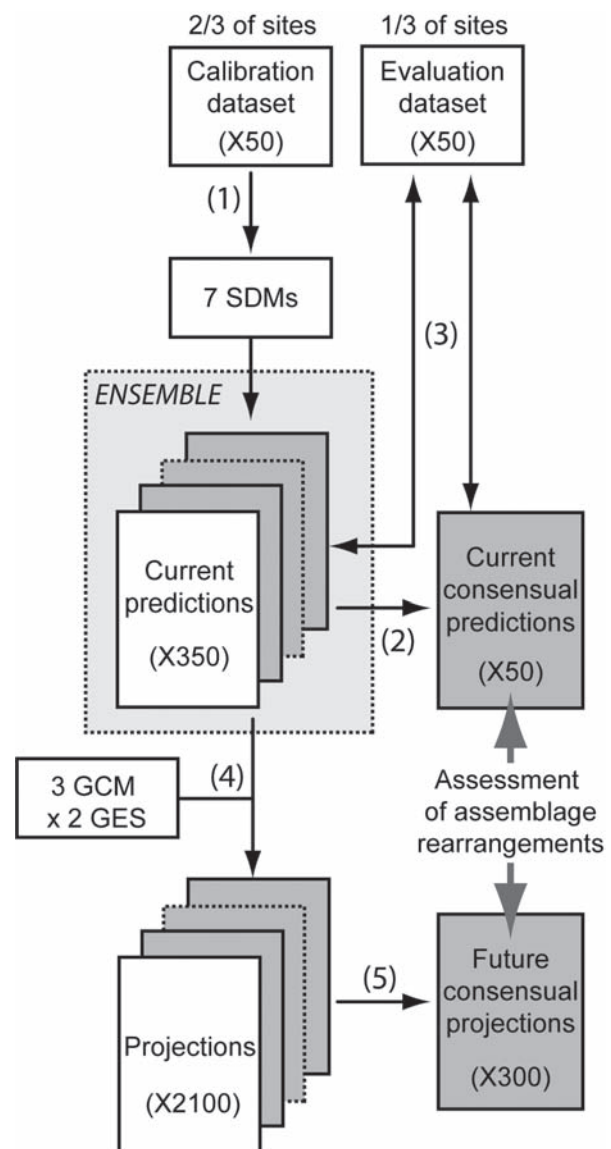

Figure 1. Schematic representation of the modelling design. See Methods for details. SDM: species distribution models; GCM: general circulation models; GES: greenhouse gas emission scenarios.

linear models (GLM), generalised additive models (GAM), multivariate adaptive regression spines (MARS), mixture discriminant analysis (MDA), random forests (RF), general boosted trees (GBM), and artificial neural networks (ANN), leading to 350 different statistical models calibrated for each species. Calibrated models were used to predict the current distribution of the 40 fish species at the scale of the French hydrographical network. We used a consensus method based on the average values of the ensemble modelling predictions across single-SDMs (step 2, Fig. 1), an attractive modelling framework as it reduces the predictive uncertainty of the single statistical models by combining their predictions (Araújo et al. 2005). For each river segment, the current averaged probabilities of occurrence of the 40 species were then transformed into presence–absence data using a threshold maximising the sum of sensitivity (i.e. percentage of presence correctly predicted) and specificity (i.e. percentage of absence correctly predicted) (Fielding and Bell 1997). The predictive performances of the seven statistical models and the 'consensus model' were evaluated on validation datasets (step 3, Fig. 1) using the area under the curve (AUC) of a receiver operating characteristic plot (Fielding and Bell 1997). Paired t-tests with correction for multiple testing were performed on AUC values (Benjamini and Hochberg 1995), showing that the consensus model outperformed single models (p < 0.001), with the exception of RF providing comparable predictions (Supplementary material Appendix 2). Information regarding the performance measures of the consensus model and the variability of the predictions obtained with each of the seven statistical methods are provided in the Supplementary material Appendix 1, 2.

Calibrated models were used to project future potential habitat suitability for the 40 fish species at the scale of the French hydrographical network (i.e. assuming an unconstrained dispersal) under the six coupled GCM-GES scenarios (step 4, Fig. 1). The predictions across the seven statistical modelling techniques were then averaged for each climate scenario and each iteration (step 5, Fig. 1), resulting in 300 future distributions projected for each species. Finally, the future averaged probabilities of occurrence were transformed into presence–absence values using the same threshold values as used for the current predictions.

Spatial patterns in species richness, turnover, colonisations and extirpations

To assess the potential impacts of climate change on fish assemblages, we first overlapped all the individual species distributions, following a 'predict first, assemble later' strategy (Ferrier and Guisan 2006). For each river segment, we defined current species richness (SR) by the sum of the predicted occurrences, and species turnover rate (ST) was computed as follows:

$$ST = 100 \times \frac{SG + SL}{SR + SG}$$

where SG is the species gain (number of colonising species) and SL is the species loss (number of extirpated species) (Peterson et al. 2002, Broennimann et al. 2006). Turnover

values range from 0 (i.e. current and future assemblages are identical) to 100 (i.e. current and future assemblages are completely different).

For each river segment, variability in current species richness was quantified by the coefficient of variation (CV) of SR values across the 50 iterations. To quantify variability in turnover, colonisations and extirpations was quantified by the CV of the values forecasted across the 50 iterations and the 6 climate scenarios (i.e. 300 values per segments). We assessed the spatial congruence of predictions by mapping these CVs at the scale of the French hydrographical network. Finally, we disentangled the variability among future projections due to iterations and climate scenarios by calculating the CVs across the modalities of one factor after averaging the projections resulting from the modalities of the other factors (Supplementary material Appendix 3).

Drivers of turnover, colonisation and extirpation

We performed RF to model species turnover (RF_{tur}), colonisations (RF_{col}) and extirpations (RF_{ext}). Based on its mathematical formulation, species turnover was modelled from three input variables (SR, SG and SL), while RF_{col} and RF_{ext} were calibrated using the whole set of topographic (G, Slo, Alt) and climatic predictors, the latter represented by climatic anomalies (i.e. the change between future and current conditions): ΔTsea, ΔTwar, ΔTcol, ΔPsea, ΔPdry, ΔPwet. More information about the relationships between current climatic conditions and climatic anomalies (Supplementary material Appendix 5) as well as maps of climatic anomalies (Supplementary material Appendix 6) are provided in the Supplementary material. Similarly to the SDM procedure described above, 2/3 of the dataset were used to calibrate the models, while the remaining 1/3 was used as the validation subset. The splitting procedure was repeated 10 times. The relative influence (i.e. importance) of individual predictor variables in the models was estimated by looking at the prediction error (mean squared error, MSE) on the out-of-bag (oob) portion of the data, after permuting the predictor variable while all other variables were left unchanged. The increase in oob error is proportional to the predictor variable importance (Peters et al. 2007). Relationships between topographical and climate anomalies are presented in the Supplementary material Appendix 7. Finally, because the predictor variables were correlated, partial dependence plots of responses to individual predictor variables, derived from the best RF model among the 10 iterations, were used to interpret the marginal effect of each variable in the model after accounting for the average effects of the other variables.

Results

Spatial patterns in climate change

Changes in climate predictors by 2080s emerged to be spatially structured for both temperature and precipitation (see scatter plots in Supplementary material Appendix 5 and climate anomalies maps in Supplementary material

Appendix 6). An increase in temperature variability ($\Delta Tsea = 536.03 \pm 236.84$) was predicted in southern France, and particularly for the sites that are currently experiencing a moderate thermal seasonality. Average temperatures in both warmest and coldest quarters showed a shift towards warmer values ($\Delta Twar = 4.34 \pm 0.81$, $\Delta Tcol = 3.05 \pm 0.73$) and negative correlations with current climate conditions (i.e. higher warming is expected at currently colder sites and at higher altitudes, Supplementary material Appendix 5–7).

Changes in precipitation showed a general trend towards higher variability ($\Delta Psea = 8.94 \pm 5.09$) due to a polarisation of dry and wet seasons, with more humid wettest quarters ($\Delta Pwet = 10.84 \pm 23.05$) and more arid driest quarters ($\Delta Pdry = -37.39 \pm 25.68$). These trends exhibited strong geographical patterns, with mountainous areas (e.g. Massif Central and Vosges) standing out for their stability in precipitation regimes for the three predictors.

Spatial patterns in species richness, turnover, colonisations and extirpations

Current species richness was highest in the main channels of large rivers (e.g. Garonne, Rhone, Loire and Seine rivers) while lower richness was observed along the English Channel coast, Brittany and in all the French mountainous areas (e.g. Pyrenees, Massif Central, Alps and Vosges mountains) (Fig. 2a). Predictions were generally congruent ($CV_{SR} = 0.34 \pm 0.19$), and particularly for those river segments hosting a large number of species. High species turnover rates were observed over the whole hydrographical network (mean ~60%) (Fig. 2b), although lower values were observed in the Alps, the Mediterranean coast, and in Brittany, as well as in high-order rivers. Similarly to species richness, projections of species turnover were generally congruent ($CV_{tur} = 0.33 \pm 0.23$) with higher variability of projections in mountainous areas (e.g. the Massif Central, the Alps and the Pyrenees). Colonisation and extirpation events displayed clearer spatial patterns compared to turnover (Fig. 2c–d). Colonisations showed three main hotspots at the base of the Pyrenees in southern France, the Massif Central and the Vosges mountains in north-eastern France, while extirpations showed higher values in the plains of western and north-western France. The degree of agreement among scenarios and iterations was also spatially heterogeneous ($CV_{col} = 0.56 \pm 0.29$, $CV_{ext} = 1.62 \pm 1.91$). Like species turnover, colonisation projections were less congruent in mountainous areas but extirpation projections showed higher discrepancies at intermediate altitudes and in two coastal areas in south-eastern and north-western France.

Overall, we observed that model outputs were more congruent in those areas where more important biotic changes were predicted. This pattern derived from the combined effect of iterations and climate scenarios, which affected model output differently (Supplementary material Appendix 3).

The total number of colonisation and extirpation events was also unbalanced, with more species immigrating in newly favourable river segments (up to 31 among the 40 species analysed), compared to those extirpated from
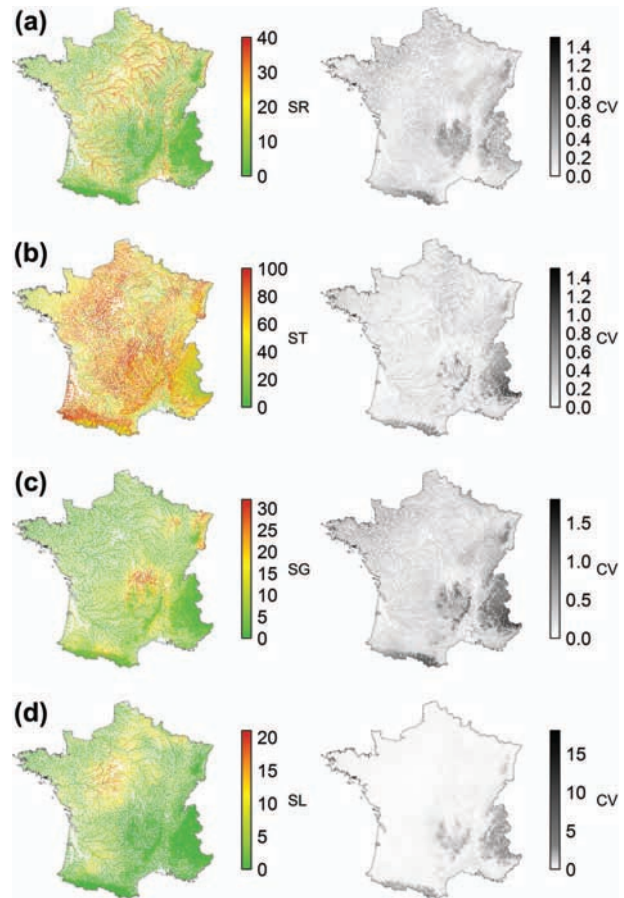

Figure 2. Maps of the average model outputs for the French hydrographical network (left) and spatial congruence among the projections (right). Spatial congruence was computed as the coefficient of variation (CV) among the 50 iteration outputs (for current species richness) or among the 6 GCM-GES scenario and the 50 iteration outputs (for 2080s, projections of turnover, colonisation and extirpation). (a) Current species richness (SR); (b) species turnover (ST, %); (c) number of colonisation events (species gain, SG) and (d) number of extirpation events (species loss, SL) by 2080s. Maps of the spatial congruence of the model outputs due to each of the two sources of variation (i.e. scenarios and iterations, respectively) are shown in Supplementary material Appendix 3.

currently occupied segments (maximum 20 species) (Fig. 3). Nevertheless, extremely high numbers of colonisations and extirpations were predicted only for a small fraction of the hydrographical network (i.e. only ~3% of river segments were predicted to be colonised by 20 or more species, or to be abandoned by 10 or more species).

Drivers of turnover, colonisations and extirpations

Performances of RF models predicting species turnover were good ($R^2_{tur} = 0.96 \pm 0.001$). Current species richness emerged as the most influential factor (Fig. 4a), showing a linear negative relationship with species turnover, with the highest taxonomic variation expected for the currently poorest communities (Fig. 4b). Colonisation and extirpation events showed similar effects on species turnover (Fig. 4a),
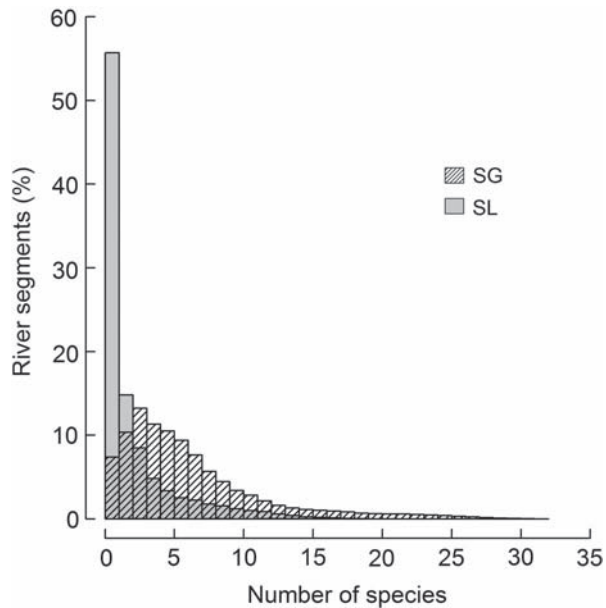
Figure 3. Frequency of colonisation (SG) and extirpation (SL) events in the French hydrographical network. Bars representing SL (grey) and SG (shaded black) are overlapping.
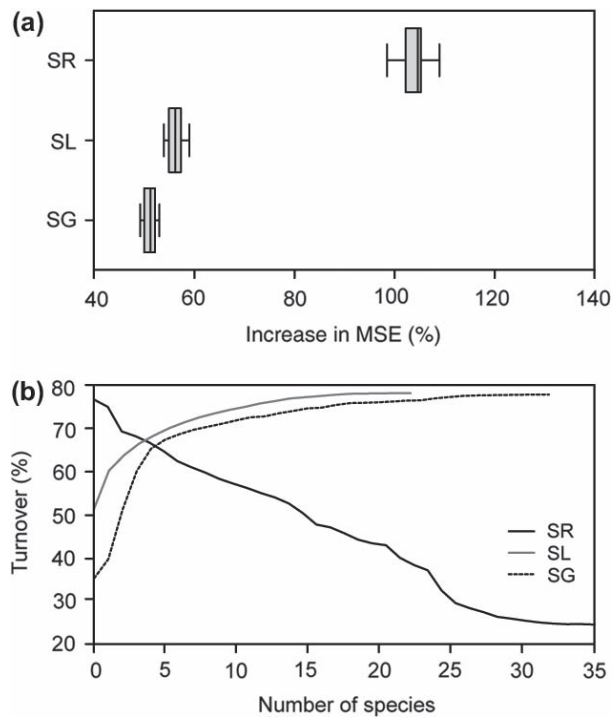

Figure 4. (a) Box-and-whiskers plot of the importance of individual predictor variables in predicting turnover of species assemblages (RF$_{tur}$, 10 iterations) i.e. percentage variation of mean squared error (MSE) on the oob portion of the data after permutation. The input variables are ranked according to their importance. (b) Partial dependence plot of the input variables: current species richness (SR, black solid line) and average number of extirpation events (SL, grey solid line) and average number of colonisation events (SG, black dashed line). Partial dependence is the dependence of the probability of presence on one predictor variable after averaging out the effects of the other predictor variables in the model (Cutler et al. 2007).

with both species loss and gain determining an increased turnover (Fig. 4b).

Performances of RF models predicting colonisation and extirpation were also good (R$^2_{col}$ = 0.95 ± 0.001, R$^2_{ext}$ = 0.93 ± 0.001). Topographic variables emerged as the most important predictors for modelling both species gain and loss (Fig. 5). In particular, longitudinal gradient outperformed any other input variable in predicting both colonisation and extirpation events, followed by altitude, while slope played a stronger role in driving colonisations compared to extirpations (Fig. 5a). Although colonisation events occurred along the whole range of altitudes (0–2600 m), the peaks in species gain and loss were segregated along longitudinal and altitudinal gradients, with colonisations occurring mainly upstream (lower G values) and at higher altitudes compared to extirpations (Fig. 6). In fact, colonisations showed a peak around 460 m a.s.l. (Fig. 6a), while the number of extirpation events sharply decreased at mid-altitudes, with the highest number of species disappearing from lowland river segments (< 80 m) (Fig. 6b).

Overall, climatic variables played a minor role compared to topographic variables (Fig. 5). Among them, changes in temperature seasonality showed the highest contribution to colonisation events, with strong increase in variability favouring species gain (Fig. 5a and 6a). In contrast, the number of extirpation events depended on both changes in temperature and precipitation (Fig. 5b). In particular, an increase in average temperature in the coldest quarter and stable precipitation in the driest quarter contributed to species loss (Fig. 6b).

Discussion

We found that future climate change might induce severe reorganisations of freshwater biodiversity patterns, resulting from spatially non-random species loss and gain, driven by both topography and climatic predictors. By deconstructing the mechanisms driving changes in the turnover of species assemblages, we observed that besides current species richness, both extirpation and colonisation events equally influenced the taxonomic rearrangement of communities.
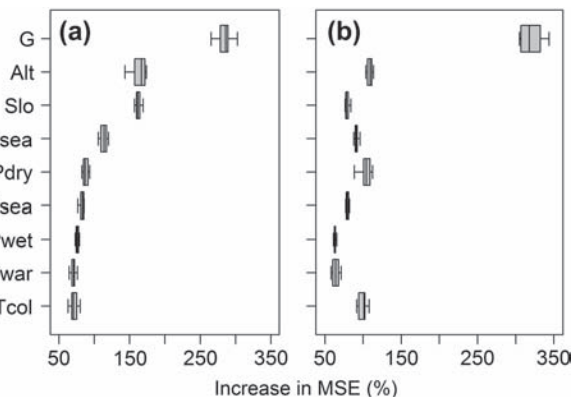

Figure 5. Box-and-whiskers plots of the percentage variation in mean squared error (MSE) of (a) RF$_{col}$ and (b) RF$_{ext}$ outputs after permutations among the 10 iterations. The input variables are ranked according to their importance in predicting colonisation events.
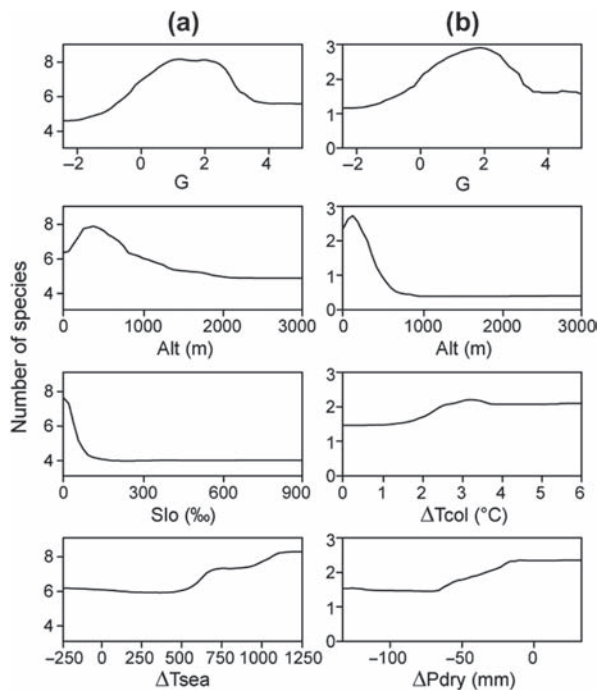
Figure 6. Partial dependence plots of the four most important input variables driving (a) colonisation and (b) extirpation. Species gain was mainly affected by the three topographical variables [longitudinal gradient (G), altitude (Alt) and slope (Slo)] and by changes in temperature seasonality (ΔTsea), while species loss was driven by altitudinal gradient, changes in average temperature in the coldest quarter (ΔTcol) and in average precipitation in the driest quarter (ΔPdry).

As observed in previous studies, species turnover rates in our system indicated that more than half of the current pool of species may be replaced over the whole hydrographical network (Buisson et al. 2010). Nevertheless, the greater number of colonisation events suggested that range expansions may be more common than range contractions, a pattern commonly observed as a result of ongoing climate change (Parmesan et al. 2005). Similar results were obtained by Cheung et al. (2009) in marine ecosystems, showing that the pattern of species turnover was generally dominated by species colonisations. Despite the observed difference in the number of colonisation and extirpation events, we showed that both processes played a comparable role in the turnover of species assemblages. This suggests that although changes in biodiversity patterns are expected to derive from the combined effect of both range expansions and contractions, extinction selectivity could have a greater influence on the rearrangement of community structure. As vulnerable species often have combinations of extinction-promoting traits (e.g. habitat specialisation and rarity; Davis et al. 2004), addressing the respective effects of colonisations and extirpations on other facets of biodiversity patterns (e.g. functional) could improve our understanding of the ecological consequences of climate-driven community reshuffling.

Species gain and loss displayed spatially structured (i.e. patchy) patterns, with colonisations concentrating along the major mountainous systems, while extirpations were principally predicted in the plains of western France. Species

loss was also predicted to be higher in lowland rivers, which generally host more diverse fish assemblages compared to upstream stretches (Horwitz 1978). Spatial segregation of colonisation and extirpation events along an altitudinal gradient has already been described across a wide range of taxonomic groups, both recently observed (Chen et al. 2011, Comte and Grenouillet 2013) and predicted for the future (Peterson et al. 2002, Thuiller 2004, Buisson and Grenouillet 2009). An exception to this general pattern was represented by the low occurrence of colonisations in the Alps. This discrepancy may be linked to a combination of different temperature and precipitation scenarios predicted for eastern France compared with the other mountainous systems.

Understanding multi-species patterns of colonisation and extirpation in the face of a changing climate requires to address the various environmental filters shaping species distributions. First, climate itself is a combination of spatially heterogeneous and often highly dynamic facets, each one displaying a different pattern of change in magnitude, velocity and direction (Burrows et al. 2011, Chen et al. 2011). Second, these climate vectors interact with regional topography, and generate a mosaic of heterogeneous microclimates (Tingley et al. 2012, Bennie et al. 2013). This fine-grained variability (i.e. also known as topoclimate; Geiger and Aron 2003) might buffer, amplify or modify the impact of changes on resident communities, by creating both micro-refugia where species might persist locally (Lenoir et al. 2013), or gaps in climate paths that might impede range expansions and shifts (Lyons et al. 2010, Early and Sax 2011). Finally, the interaction between these complex environmental filters and species-specific tolerances may ultimately define the magnitude and direction of species responses (Crimmins et al. 2011, Dobrowski et al. 2012, VanDerWal et al. 2013).

In this study, we identified topographic variables as the strongest drivers of both species gain and loss, with the longitudinal gradient being by far the most important predictor. However, no clear relationship was observed between this variable and climate anomalies, while comparable patterns of climate change emerged along both slope and altitude gradients. These patterns could partly arise from the spatial distribution of climate change exposure, but may also be explained by the rates of isotherm shift along the hydrographic network. Following this assumption, slope is expected to affect the velocity of thermal change to a lesser degree in steeper sloped streams (Isaak and Rieman 2013). The decreasing number of colonisations upslope could also reflect the hydrodynamic constraints acting as physical barriers to the dispersal of downstream (i.e. with slow-flow preferences) species. Upstream colonisations can also be strongly affected by natural connectivity (e.g. presence of vertical barriers such as waterfalls or bedrock chutes). Indeed, slope-dependent hydrodynamic features have been identified as effective natural barriers to the colonisation of upslope reaches by shifting species (Spens et al. 2007). This is of particular concern as the highest number of colonisations was projected to occur in mountainous areas, where hydrodynamic conditions are likely to hinder fish species dispersal. The observed patterns highlight the importance of considering slope as a predictive variable for modelling stream biota distributions, especially under the hypothesis of

unconstrained dispersal. Nevertheless, the co-occurrence of natural (e.g. slope-dependent) and non-natural (e.g. dams, weirs) barriers in high-elevation streams could suggest that the large number of predicted colonisations in those streams might be strongly reduced. Therefore, although not affecting extirpation patterns, overlooking the effects of non-natural barriers could lead to overestimate the number of potential vs realised colonisation events (Peterson 2003, Hein et al. 2011).

Beside topography, colonisation and extirpation appeared to be affected by different facets of climate change. Expanding ranges were more influenced by changes in temperature seasonality and shrinking ranges by changes in both temperature and precipitation patterns. As already discussed above, species might track shifts in thermal or precipitation isotherms or a combination of these two climate features (VanDerWal et al. 2013). However, the responses of species depend not only on their sensitivity to those climatic variables, but are also locally influenced by current climate patterns. In fact, changes in temperature and precipitation were not evenly distributed among sites, but showed correlations with the actual conditions experienced by the species. For example, the highest amounts of warming in averaged temperatures was expected to occur in the currently coldest sites and at higher altitudes, providing more opportunities of colonisation in species-poor river stretches located at high altitudes. Under these complex conditions, the positive effect of increased thermal variability on colonisation processes may derive from the combination of wider temperature oscillations and the general warming trend expected under the different climate scenarios. In fact, species at the leading edge are expected to experience more variable temperature extremes, potentially disrupting the thermal barrier that hinders upstream colonisations and opening new opportunities for warm- and cool-water species range expansions (i.e. most species analysed in this study). Nevertheless, the highly dynamic nature of the thermal regimes might affect the rate of realised colonisations, depending on the species ability to survive seasonal extremes. Shifts in precipitation patterns may be expected to have an even greater impact on ecosystem dynamics than temperature (Weltzin et al. 2003, Crimmins et al. 2011), as suggested by the importance of precipitation anomalies in the driest quarter in explaining extirpation patterns (Fig. 6b). This is especially true in freshwater ecosystems where precipitation determines the hydrological regimes, having direct and indirect effects on the biota (Poff 1992). Indeed, water availability represents the most critical environmental filter for the survival of fish species, and the observed trend towards a more arid dry season could thus represent a threshold for the local persistence of numerous species (Xenopoulos et al. 2005).

In this study, climate change was taken as the principal driving force of species distribution, without consideration of the potential effects of biotic interactions. Nevertheless, it has been demonstrated that such interactions can influence the way climate change affects species (Gilman et al. 2010), not only at the local or landscape scale (He et al. 2005), but also at regional to global scales (Wisz et al. 2013). Previous studies on freshwater ecosystems support the idea that stream fish communities are not fully saturated, suggesting that

biotic interactions are unlikely to prevent colonisation and biotic homogenisation at some spatial scale (Oberdorff et al. 1998, Olden and Rooney 2006). However, inter-specific relationships may play a crucial role in the transition between the availability of a new climatically favourable patch and the realised colonisation (Wisz et al. 2013). Beside the ecosystem intrinsic obstacles to the climate-tracking of species distributions (e.g. topographical features, species-specific dispersal abilities and biotic interactions), further impacts on landscape permeability originate from the high levels of anthropogenic fragmentation of favourable habitats (Fagan 2002) and from other point source perturbations such as pollution, urbanisation and water development. These factors may add to the global warming trend, magnifying thermal threats on already affected populations, especially in lowland river stretches (Isaak and Rieman 2013). For instance, we might underestimate species extirpations by overlooking habitat loss and degradation originating from different sources of perturbation other than thermal suitability, but acting in synergy with climatic change. Amplified feedbacks among these stressors might affect the stochastic processes of populations coping with a changing environment, ultimately leading to their extinction (Brook et al. 2009).

Numerous studies have already demonstrated that the range of possible geographical responses to a changing environment is hardly classifiable into simple categories and that shifts may occur in any direction, at different paces, and along different gradients (Burrows et al. 2011). Given this complexity, there is a pressing need to advance methods to explore the additional influence of species characteristics on their vulnerability to future climate changes (Thuiller et al. 2005). Incorporating the dynamics and complexity of biotic interactions, as well as the spatial location of dispersal barriers into future predictions is another challenge of species distribution modelling (Lyons et al. 2010, Wisz et al. 2013).

Disentangling the drivers of colonisation and extirpation processes helps to overcome the difficulty of dealing with idiosyncratic responses of species to changed climate conditions, which represent a major issue for ecosystem management plans (Ackerly et al. 2010). Our findings reveal that topographic and climatic predictors both influence species range shifts, driving potential modifications of their geographical distribution. Nevertheless, species tracking favourable conditions must pass through a human dominated world, where ecosystems are highly fragmented and modified (Lawler et al. 2013). In this context, the identification of focal areas of greater expected changes, driving either species gain or loss, could represent ready-to-use information that could be easily integrated into conservation planning. Maps of future scenarios depicting those topographic and climatic components favouring colonisation may support an early evaluation of the extrinsic limitations on the species ability to reach newly favourable habitats. This information could represent the starting point for the identifications of climate-gradient corridors connecting reaches with suitable topographic conditions along which the species might shift as climate changes (Nuñez et al. 2013). Once the ability of habitat networks to support range shifts is assessed, conservation efforts such as assisted colonisation schemes or retaining landscape structures (e.g. protection of suitable

microclimates) might be enacted at the regional scale (Bennie et al. 2013).

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Supplementary material (Appendix ECOG-00753 at <www.ecography.org/readers/appendix>). Appendix 1–7.