Climate interacts with anthropogenic drivers to determine extirpation dynamics

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There is abundant evidence that species’ borders can fluctuate in time and space (Graham et al. 1996, Davis and Shaw 2001), and that the unusually large magnitude and speed of the fluctuations can occur quickly in response to human modifications of the environment (Parmesan and Yohe 2003, VanDerWal et al. 2013). Although global species extinctions due to recent climate change appear limited (Cahill et al. 2013), an increasing number of studies have documented a strong fingerprint of climate change on species distributions, driven by both range expansions and contractions (Parmesan and Yohe 2003, Poloczanska et al. 2013). However, there is also considerable variation in species’ responses, both among and within taxonomic groups (Chen et al. 2011). In turn, these idiosyncratic responses have the potential to alter community dynamics by driving the disaggregation of some species interactions and the emergence of others (Williams and Jackson 2007). A mechanistic understanding of climate-mediated fluctuations in species distribution is thus essential to predict the vulnerability of populations, species and communities under global change and to guide conservation efforts (Bates et al. 2014, Lenoir and Svenning 2015).

Climate change vulnerability can be defined as a combination of exposure to climatic changes, intrinsic sensitivity to that exposure, and capacity to buffer climatic alterations (Williams et al. 2008, Staudinger et al. 2013). In general, extirpation dynamics are expected to depend on both the distance from species’ physiological limits and the extent of population climatic exposure (Fig. 1a). The response of species may also be mediated by their ability to tolerate short-term exposure to temperature changes (i.e. acclimation ability) or their capacity to avoid acute exposures to thermal extremes by moving between microhabitats (i.e. behavioural thermoregulation) (Huey et al. 2012, Sunday et al. 2014).

Yet, these expectations assume that all populations display similar thermal tolerances regardless of their source population, thus disregarding the potential influence of local evolutionary processes in determining species’ vulnerability (Lavergne et al. 2010, Thuiller et al. 2013, Valladares et al. 2014). Current genetic diversity has been shaped by historical constraints, with a strong fingerprint of past climatic fluctuations (Davis and Shaw 2001, Razgour et al. 2013). For instance, trailing edge populations inhabiting past climatic refugia often harbour locally adapted phenotypes, consistently different to their leading edge counterparts (Hampe and Petit 2005). Hence, if populations contain only a subset of the tolerances found in the species’ range as a whole, extirpation dynamics may be expected to occur irrespective of the distance to the species’ niche centroid, driven by the magnitude of climate change impacts (Fig. 1b). Several biological traits, such as life-history strategies, ecological specialization and population size are also likely to influence genetic flow and redundancy, and the resulting degree of local adaptation.

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Theoretical studies suggest that the dynamics of a species’ range during a period of climate change depends upon the existence and interplay of various ecological and evolutionary processes. Here we tested how anthropogenic pressures contribute to climate-mediated extirpation patterns of 32 freshwater fish species over the last 20 yr. We contrasted two extreme cases to determine whether extirpations were governed by patterns of climate exposure, assuming full adaptation of species to local climate, or instead by the interplay between climate exposure and the distance from the centroid of species’ climatic niches, assuming a fixed niche, and asked whether anthropogenic disturbances interact with these climatic drivers. We found strong support for the fixed niche hypothesis, but showed that species-specific local adaptation to climate may also be important in determining extirpation dynamics. We also demonstrated that anthropogenic disturbance acted in concert with climate, ultimately determining population changes. Our results add novel evidence that unravelling the direct links between range dynamics and climate requires a multifaceted treatment, and that accounting for the cumulative effects of anthropogenic pressures deserves special attention in the context of climate change.
among populations (Aitken et al. 2008). Surprisingly, however, the consequences of local adaptation for extirpation dynamics under recent climate change have received little attention.

Despite the increasing importance of climate factors in explaining extirpation patterns (Beever et al. 2011), evidence also suggests that climate acts in concert with other anthropogenic factors (Brook et al. 2008). While extinction risk may not fundamentally differ as a result of climatic and non-climatic threats (Pearson et al. 2014), land-use practices or other human pressures may modify, hide or exacerbate the effects of warming in new and unanticipated ways (Warren et al. 2001, Clavero et al. 2011, Morelli et al. 2012). Therefore, understanding and predicting the biological consequences of climate change, including extirpations and distribution range shifts, require the analysis of the interplay of these processes (Opdam and Wascher 2004, Staudt et al. 2013). Although the direct effects of these stressors are often well-known, their potential interactions with climate are less well-understood and predicting the outcome of multiple stressors remains challenging (Crain et al. 2008).

Figure 1. Theoretical expectations of the dynamics of extirpation as mediated by climate change between two time periods for a hypothetical species characterized by (a–c) a fixed climatic niche where the climatic tolerance at the species level reflects the variation contained within individual populations or (b–d) local adaptations to climate where individual populations contain only a subset of the tolerances found in the species range as a whole. For simplicity, fitness (performance) curves (a–b) are illustrated only along one axis of the climatic niche which is defined by both temperature and precipitation (c–d). Circles represent the sites in the climatic space that can be either occupied (filled circles) or unoccupied (unfilled circle). Arrows illustrate the magnitude of changes in climate (Exp). (c) If the niche is fixed (grey ellipse with the centroid represented by the grey cross), a site can be extirpated if it shifts out of the climatic niche or stay occupied if it remains within the climatic niche. The extirpation events thus depend on both the distance from the site to the centroid of the climatic niche ($d_t$) and the extent to which the climatic conditions of the site shift (Exp), i.e. whether the site is pulled farther or pulled closer relative to the climatic niche centroid ($d_{t+1} - d_t$). In cases where the exposure to climate change is negligible compared to the distance from the centroid, one can expect the extirpation events to depend only on the distance from the centroid ($d_t$). (d) Alternatively, if the individual populations (illustrated by different colours) are locally adapted to climate, the extirpation events should not depend on the distance from the centroid (grey cross), but on the extent to which the site is pulled farther or pulled closer relative to the local suitable conditions, i.e. the magnitude of climate changes, independent from the position of the site within the species’ climatic niche (Exp).

Although laboratory studies allowed stressor effects to be carefully isolated, large gaps still exist in our understanding of the interactive effects, and context-dependence, of multiple stressors in nature (Crain et al. 2008). Yet, often studies conducted across two sampling periods are not extensive enough to permit the evaluation of the relative contributions of these different determinants to observed biological changes (Parmesan et al. 2005, Beever et al. 2011).

Focusing on birds in California, Tingley et al. (2009) developed a set of competing models to test how changes in occupancy related to the position of the sites relative to the climatic niche of a species. They considered a null model where all sites were equally likely to change in occupancy, a static model where changes in occupancy were a function of the distance from a site to a species’ climatic niche centroid, and a dynamic model where changes in occupancy were a function of both the distance from a site to a species’ climatic niche centroid and the degree of exposure of the site to climate changes. They provided strong support for the fixed niche hypothesis, suggesting that extirpations from areas that shift farther from a species’ climatic niche centroid may be a widespread, although not universal, response of species to climate change. Indeed, despite this overall pattern, their models failed to predict the fluctuations
in species distribution for several species, which the authors explained by a likely influence of anthropogenic landscape transformation.

Here, we expanded this hypothesis-testing framework to ask how climate fluctuations across several consecutive time periods governed extirpation dynamics and potentially interacted with and accelerated ongoing anthropogenic threats to biodiversity. We first introduced an alternative exposure model where climate change impacts were governed by the patterns of climate fluctuations alone, assuming full local adaptation of populations within the core of species distribution. We then supplemented this set of climate-related hypotheses by considering the additional or interacting effects of non-climatic anthropogenic stressors. Applied to 32 freshwater fish species inhabiting French streams, we quantified the relative contribution of climate fluctuations, the degree of fragmentation and urbanization and their interactions in determining extirpation patterns across eight consecutive time periods over the last 20 yr. Lastly, we assessed whether species response to these climatic and non-climatic drivers was related to common biological traits.

Material and methods

Fish distribution data

We examined the presence–absence data of 32 stream fish in France using the Onema national monitoring data across eight consecutive time periods from 1992 to 2011 (Supplementary material Appendix 1, Fig. A1). Surveys were conducted using standardized electrofishing protocols where sites were sampled by wading (69.76% of the sites), mostly using two-pass removal of the entire stream section (mean area = 758.18 m\(^2\) ± 160.40 SD), by boat (24.60% of the sites) using point sampling, or mixed strategies (5.64% of the sites) in the river margins and delimited areas of habitat (see Poulet et al. 2011 for more details). We chose 1992 as a starting date because sampling effort became relatively consistent at approximately this time, although unevenly distributed through time. The eight periods were then defined so as to allow a sufficient spatio-temporal coverage of the sites both within and across time periods. We selected sites that were sampled at least twice within a single time period but only if they were sampled in two consecutive periods. Other sites were discarded if they were environmentally different from the full pool of sites (e.g. elevation > 1500 m), leaving a total of 794 sites. This approach provided a reliable picture of species occupancy within each time period and extirpation events between consecutive time periods. Considering several sampling events per site within each time period allowed to obtain a more realistic assessment of species presence or absence (see below for detectability issues), while the periods were short enough to capture fine-scale effects of climate fluctuations on population dynamics (e.g. recruitment, adult mortality). Finally, we restricted our analyses to the 32 most common species in France which represented 94.1% (± 0.97 SD) of the species sampled in each time period across the studied sites.

To avoid sampling bias due to species that were undetected but were present, presence–absence data were pooled within each period for each species and site, resulting in 3287 presence–absence data scattered across the eight periods. However, we cannot regard the possibility that in specific sites (e.g. high flow), species with low detection probabilities went undetected in all of these consecutive samplings, and thus were erroneously considered absent in this time period. Nonetheless, the sampling efficiency of the Onema national monitoring program has proven to be high (e.g. average detection probability of 0.95 using two-passes wading strategy, Bergerot et al. 2013), and relatively consistent through time (e.g. average difference in detection probability of 0.05 over the last three decades, Comte and Grenouillet 2013). We are therefore confident that our analyses did not suffer from a systematic bias which could have blurred the extirpation dynamics observed over the studied period. Sites were sampled on average in four consecutive periods (4.13 ± 2.33 SD) while 25.3% of them (i.e. about 200) were re-sampled in each successive period. The transition events for each species between two consecutive periods were then classified as follows: extirpated (1–0), colonized (0–1), persisted (1–1), and unoccupied (0–0).

Climate data

Climatic data were extracted from the SAFRAN climate database (monthly data on a 8 km grid; Le Moigne 2002): temperature of the coldest quarter (Tcold), temperature of the warmest quarter (Twarm), temperature seasonality (Tvar), cumulative precipitation of the driest quarter (Pdry), cumulative precipitation of the wettest quarter (Pwet), and precipitation seasonality (Pvar). For each period, the yearly climatic conditions for each site were extracted based on the exact coordinates and then averaged within a time-window shifted by one year (i.e. excluding the ending year and including the preceding one).

Species’ climatic niches

For each species, climatic niches were characterized using a temporally independent dataset composed of 3347 sites collected before major climatic changes (1980–1991) and spanning a large range of environmental conditions across the French hydrographic network (Supplementary material Appendix 1, Fig. A2). Occurrence records were extracted conjointly from the Onema database and the Global Biodiversity Information Facility (GBIF, <www.gbif.org/>). GBIF occurrences were included based on the accuracy of their coordinates (i.e. suspicious projections or rounded values were excluded) and the basis of records (i.e. fossil specimens were excluded). To finalize the reference dataset, we further removed spatial and temporal replicates by pooling the occurrences of each species based on the coordinates of the occurrence records.

We then constructed a multi-dimensional representation of the climatic conditions occurring in French streams using a principal component analysis (PCA) based on the six bioclimatic variables of the reference dataset (Supplementary
Climate change predictors

We projected into the PCA climatic space the conditions at the sampling sites in each of the successive periods (grey dots, Supplementary material Appendix 1, Fig. A3). Although the mean conditions at the sampling sites were overall warmer than in the reference period, they were also highly variable across time periods (arrows, inset Supplementary material Appendix 1, Fig. A3).

The magnitude of exposure to climate change (Exp) was first assessed for each sampling site as the Euclidean distance between the coordinates of the site in the two consecutive periods along all the PCA axes. For each period ($t$), we then calculated the position of the site from the species’ climatic niche centroid ($d_t$) as the Euclidean distance between the coordinates of the site in a given period and the climatic niche centroid along all the PCA axes. Finally, to quantify the extent to which the climatic conditions of the sites shifted between two consecutive periods within a species’ climatic niche, we calculated the difference between the distances from the centroid in the two given periods as $d_{t+1} - d_t$. Negative values indicate sites that have been pulled farther relative to the centroid of the species’ climatic niche, and positive values sites that have been pulled closer relative to the centroid of the species’ climatic niche. As opposed to $d_{t+1} - d_t$, Exp is independent from the position of the sites within species’ climatic niches (i.e. values for a given site are equal for the different species), and only depicts the intensity of climatic changes.

Anthropogenic predictors

To account for the potential influence of human-induced stresses in determining the dynamics of extirpation, we considered two additional variables describing the degree of fragmentation of the streams and the degree of urbanization around the stream reaches. Because temporal changes for these variables were not available over the time scale of our study and most human-induced stresses preceded the studied period, especially concerning the degree of fragmentation, we used static estimates of the degree of anthropogenic disturbance at each site. The degree of fragmentation was calculated from the ROE database (<www.sandre.eaufrance.fr/atlas catalogue>), which provides an inventory of flow continuity barriers at the national scale. We used the number of high dams (>15 m) per kilometre of stream distance within natural sub-basins (i.e. SSHYD from BD CARTHAGE®) (frag). The degree of urbanisation was estimated using two variables. First, we calculated the percentage of urbanized land within a natural sub-basin total area, extracted from the first class of the updated Corine Land Cover database (CLC2000; Bossard et al. 2000). Second, we calculated the mean density of human population within each natural sub-basin, extracted from the HYDE 3.0 database for the period 2000 (Klein Goldewijk et al. 2011). We then used a PCA of these two variables to obtain a synthetic variable (pop) accounting for 87.6% of the total variability.

Model comparison

For each species, we modelled the dynamics of extirpation using logistic linear mixed models (Pinheiro and Bates 2000). The site ID nested within the hydrographic basin (i.e. with six levels corresponding to the major French basins) and the initial time period were specified as random factors to account for the clustering of responses within both spatial and temporal replications. In these models, we considered whether species was either extirpated ($y = 1$) or persisted ($y = 0$) between consecutive periods at each site. We constructed four types of models to test different theoretical expectations about the way that climate fluctuations mediated extirpation events, and whether they interacted with other anthropogenic factors. First, we ran models with a constant effect of exposure and climatic niche parameter but also a constant effect of anthropogenic disturbance (null model with no climate or anthropogenic covariate).

$$
\logit (y) = \beta_0
$$

Second, we considered models where extirpations were dependent on the position of the sites relative to the climatic niche centroid (static model), assuming a fixed niche but no direct effect of climate exposure. In this case, the climatic niche was expected to impact extirpation dynamics such as populations at the periphery of the species’ climatic niche would show a higher probability of extirpation than populations located within the core, independent of any directional change in climate.

$$
\logit (y) = \beta_0 + \beta_1 d_t
$$

Third, we considered models where extirpations were dependent on whether the site has been pulled farther or pulled closer relative to the climatic niche centroid (dynamic model), assuming that species track their climatic niche. In this case, extirpations were expected to be directional relative to the species’ climatic niche. They depended upon both the position of the sites from the climatic centroid and the magnitude of climate changes, with the probability of extirpation was higher when a site was pulled farther from the species’ climatic centroid.

$$
\logit (y) = \beta_0 + \beta_2 (d_{t+1} - d_t)
$$

Then, we ran models where extirpations were determined by the extent to which the species’ climatic habitat had shifted relative to local suitable conditions (exposure model), assuming full local adaptation of individual populations to climate. In this case, extirpations were expected to be independent from the species’ climatic niche and to occur only according to the magnitude of changes in climate between the consecutive periods, with the probability of extirpation higher for the sites experiencing a higher magnitude of climatic changes.

$$
\logit (y) = \beta_0 + \beta_3 \text{Exp}
$$
Finally, we also added to each of these models the additional or interacting effects of human-induced fragmentation (frag) and urbanization (pop), together (effect of both fragmentation and urbanization) or in isolation (effect of either fragmentation or urbanization), for a total of 31 competing models (see Supplementary material Appendix 1, Table A1 for the list of all models). The models including only anthropogenic factors are hereafter referred to as anthropogenic-only models. Although they were only moderately correlated (i.e. r ranged from −0.53 to 0.40), the climate variables are not independent (e.g. \( d_{t+1} - d_t \) depends on both the distance of the site to the climatic niche centroid and the exposure to climatic change), and thus their effects were modeled separately.

We used the Akaike information criterion (AIC) to rank competing models and estimated their relative support by the AIC weights. To compare directly among the competing hypotheses, we calculated the cumulative weights of evidence for each of the four types of models with and without anthropogenic factors. We then estimated the relative importance of the predictors and their interactions by summing the AIC weights over all the top models (cumulative weight > 0.95) containing this given factor (Johnson and Omland 2004).

Lastly, we performed a complete-linkage hierarchical clustering based on the cumulative weights of evidence to identify groups of species displaying similar responses to both climatic and non-climatic factors. To test whether these groups differed in terms of biological traits, we fitted a one-way ANOVA for each of the following trait: mean body length, trophic position and log-transformed fecundity. For each of the three traits tested, the analysis of the residuals indicated that assumptions of normality and homoscedasticity were met (Shapiro–Wilk and Bartlett tests, respectively).

All analyses were conducted using R ver. 3.1.2 (R Development Core Team).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.55758> (Comte et al. 2015).

### Results

The site-specific percentage of extirpations was 4.47% on average across all the species and transitions between two consecutive periods (± 0.44 SD) but showed no overall temporal trend \((p = 0.36\) using a linear-mixed model with the initial time period as a continuous fixed effect and the site ID nested within the hydrographic basin as a random factor). Nonetheless, extirpations were not evenly distributed across geographical space (Supplementary material Appendix 1, Fig. A4). Some sites tended to display consistently higher or lower rates of extirpation but variations across time was also commonly observed. Similarly, although persistence between two consecutive time periods was the most commonly observed response, the extirpation percentage varied across species from 3.43% for *Squalius cephalus* to 39.95% for *Sander lucioperca* (Supplementary material Appendix 1, Table A2).

Models of extirpation dynamics that incorporated climatic or anthropogenic components showed better support than the null model overall (Table 1) and for the majority of species (Supplementary material Appendix 1, Table A3). The highest cumulative AIC weights were found for the static models, with an average value of 0.37. Exposure and dynamic models also showed strong support for several species with average cumulative values of 0.26 and 0.19, respectively. Nevertheless, a great variability in the strength of evidence among the three major climate-related models was the most commonly observed response, with the number of top models (i.e. cumulative AIC weights ≥ 0.95) varying between five and 26. Of these, the models that included anthropogenic factors showed the greatest support (Table 1). In particular, when focusing on the relative importance of the different climatic and non-climatic factors to the dynamics of extirpation, we found that the degrees of urbanization and fragmentation showed the greatest importance through additive effects with the climate-related factors (Fig. 2).

![Figure 2](http://example.com/fig2.png)

**Figure 2.** Relative importance of the predictors across the competing models linking the extirpation dynamics to different climatic- and anthropogenic-related factors and their interactions. The grey area indicates models including only climatic components. \(d_t\) refers to the distance from the climatic niche centroid. \((d_{t+1} - d_t)\) refers to whether the climatic conditions at a given site have been pulled farther or pulled closer relative to the climatic niche centroid. \(Exp\) refers to whether the climatic conditions at a given site shifted relative to the local species suitable conditions. pop is the degree of urbanization and frag the degree of fragmentation (see Methods for details).
Discussion

It is now recognised that many mechanisms may participate to determine species' responses to climate change or with the need for an integrative modelling framework for biodiversity distribution (Thuiller et al. 2013). Our results add to a small but growing body of evidence that unravelling the direct links between range dynamics and climatic fluctuations requires a multifaceted treatment (Chevin et al. 2010, Bates et al. 2014, Lenoir and Svenning 2015).

Consistent with the findings of Tingley et al. (2009), we found that extirpation patterns of freshwater fish over the last 20 yr were strongly influenced by the position of the sites relative to species' niche centroid. We also showed that fluctuations in species' range limits were more likely to occur at the periphery of the species' climatic niche rather than at the boundaries of changing environmental conditions. Our results suggested that, at a fine temporal scale, an important lag exists between exposure and climate change impacts (Devictor et al. 2012). Such transient phenomena represent a considerable challenge when seeking to generalize and anticipate species' responses to conserve biological diversity (Jackson and Sax 2013). As such, one would expect species that display the greatest dispersal ability and

Using hierarchical clustering based on the cumulative weights of evidence, we identified five groups of species showing contrasting patterns of extirpation dynamics (Fig. 3). These groups also differed in term of biological traits, although not significantly regarding fecundity (Fig. 4). Groups one, four and five showed higher support for the fixed niche hypothesis, while groups two and three showed higher support for the hypothesis of full local adaptation of populations within the core of species distribution. Among them, the first group, composed of medium-bodied species with relatively high trophic position, showed a particularly high level of support for the static + anthrop models. For instance, the extirpation dynamics of European perch Perca fluviatilis seemed highly dependent on the interaction between the distances from the centroid of its climatic niche and the degree of urbanization of the stream reaches. Group three showed strong support for the exposure + anthrop models, and was characterized by medium-bodied species with relatively low trophic position and a non-significant trend toward low fecundity, such as Mediterranean barbel Barbus meridionalis and black bullhead Ameiurus melas. Group five, characterized by large-bodied species and comparatively higher fecundity, such as European eel Anguilla anguilla and common dace Leuciscus leuciscus, was differentiated by the high level of support for the dynamic + anthrop models. Lastly, groups four and especially two, represented by gudgeon Gobio gobio and European bleak Alburnus alburnus showed the highest levels of uncertainty among the competing models, and also intermediate traits values between groups three and five.
population changes of three waterbird species were driven by the prevailing thermal conditions rather than by differences in temperature between consecutive years, as did Beever et al. (2011) for a small mammal species for several time periods over the past century. A possible explanation for the apparent discrepancy with previous work is that in this study we found that the importance of local adaptation for range dynamics was related to particular combinations of biological traits. Species displaying relatively small body size, low fecundity and trophic position were more likely to respond to direct climate exposure, perhaps as a result of limited gene flow among populations. Our results thus support the assertion that, as the suitable climatic space of species shifts along with climate change, some populations previously well-adapted to the local historical climate may no longer be well-adapted to their sites of origin, potentially facing an increased probability of extinction and range collapse at the trailing edge (Aitken et al. 2008, Atkins and Travis 2010). Whether evolutionary responses might rescue these populations by allowing them to keep pace with the predicted velocities of climate change is still a matter of debate (Schiffers et al. 2013, Valladares et al. 2014, Wilczek et al. 2014). Although the overall effect size of local adaptation was far from negligible, there was a high uncertainty in species’ responses. Nonetheless, by considering only the extreme case of full local adaptation to climate, we might disregard spatially structured adaptation patterns within species’ core (e.g. regional), and thus under-estimate their true influence.

Importantly, we found little evidence that climate alone was responsible for the observed population changes, which supports studies indicating that climate change may interact with, and accelerate, ongoing threats to biodiversity (Brook et al. 2008, Staudinger et al. 2013). The degree of urbanization appeared especially important in explaining population changes, acting cumulatively with climatic fluctuations. Such effects of anthropogenic activities on population persistence have already been reported, by either buffering (Warren et al. 2001, Morelli et al. 2012) or increasing climate change impacts (Hill et al. 1999). We therefore argue that ignoring the effect of anthropogenic threats may limit our ability to understand species’ vulnerability and biodiversity changes under climate change in human-modified ecosystems (Brook et al. 2008). This more detailed understanding will be essential for the implementation of efficient climate change adaptation strategies. Increasing the resilience of species may only be attained by explicitly considering the multifaceted context in which climate change occurs (Staudt et al. 2013). While reducing the impact of non-climatic stressors and increasing the connectivity of fragmented landscapes are integral parts of many restoration actions, such efforts may, for instance, be targeted in areas where climate changes are expected to influence species distributions. Taken together, and bearing in mind the potential shortcomings of our approach, we hope that these results will inspire more detailed examinations of the importance and implications of population structure and biological traits for understanding complex biogeographic responses to climate change.

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