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Research

Highlighting declines of cold-demanding plant species in lowlands under climate warming

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High rates of species extinction have been predicted for the next century as a consequence of climate change. Although species range shifts have been widely reported, evidence of changes in species frequency linked to recent climate change is scarce. Moreover, studies have mainly focused on mountainous ecosystems and species. There is thus a clear lack of understanding of the recent changes in species frequencies linked to climate change across their whole range. Using a large forest vegetation-plot database, we investigated changes in cold and warm-demanding forest plant species frequencies between the periods 1914–1987 and 1997–2013 in French lowlands and highlands. Changes in frequencies were assessed for 185 lowland (warm-demanding), 135 sub-montane (intermediate) and 104 montane (cold-demanding) forest plant species. Observed changes were compared to predicted changes derived from species distribution model predictions. The frequency of montane and sub-montane species strongly declined, whereas the frequency of lowland species remained steady in lowland areas. In highlands, the frequency of lowland, sub-montane and montane species increased, remained steady and decreased, respectively. Predicted and observed trends of changes in the frequency of forest plant species were in agreement. These results clearly show that cold-demanding species are currently declining in lowlands that correspond to their warm range margins, whereas warm-demanding species are expanding in highlands that correspond to their cold range margins. These trends can be seen as early signs of future regional extinction and reshuffling of the spatial presence of species due to climate warming.

Keywords: climate change, vegetation, local extinction and colonisation

Introduction

It has been predicted that climate warming will drive species extinctions during the next century (Thomas et al. 2004), inducing a severe threat to biodiversity. These extinctions could result from a decrease in habitat availability as the climate warms (Shoo et al. 2005, Thuiller et al. 2005) and/or limits to species colonisation induced by low dispersal capability in contrast to the rate of climate change (Corlett and Westcott 2013). However, no direct links have yet been identified between the recent increase

in temperature and reported species extinctions (Cahill et al. 2013). Decreases in frequency or abundance at species warm range margins have been assessed for arctic, boreal, alpine and sub-montane plant species (Lesica and McCune 2004, Kopp and Cleland 2014, Hill and Preston 2015, Kuhn et al. 2016), which can be seen as early signs of potential future species extinctions. In contrast, increases in species richness and frequency linked to recent climate warming have been observed on mountain summits in Europe (Grabherr et al. 1994, Klanderud and Birks 2003, Pauli et al. 2012) as well as in the Arctic (Sturm et al. 2001, Tape et al. 2006), i.e. at species cold range margins. To our knowledge, only one study has reported both increases and decreases in species abundance, but at only one site in European mountains (Pauli et al. 2007). Changes in plant species frequencies have been studied separately at either cold or warm species range margins and have particularly focused on cold-demanding species and/or on cold areas. There is thus a lack of knowledge about changes in frequencies 1) across the whole range of a species (from its warm to its cold range margins), 2) for temperate and thermophilic species, and 3) in temperate lowland areas (Lenoir and Svenning 2015). In view of the predicted risk of future extinctions (Thomas et al. 2004, Thuiller et al. 2005), it is of primary importance to assess which species are currently declining and/or expanding, and where, in order to monitor and be able to mitigate future changes in the abundance of species populations.

Whereas studies reporting changes in species frequencies linked to recent climate warming are scarce, patterns of species range shifts have been assessed in most biomes and for a large number of taxa (Parmesan and Yohe 2003, Chen et al. 2011, Lenoir and Svenning 2015), indicating that species range shifts in response to recent climate change are currently widespread. These shifts result from the expansion and/or retraction of species range margins, reflecting increases and/or decreases in frequency across species ranges. Since range margin shifts have been widely reported, changes in species frequencies should be observable, not just for cold-demanding species. Species are expected to shift their ranges towards historically colder conditions. Therefore, increases and decreases in frequency are expected at their cold and warm range margins, respectively (Breshears et al. 2008). Since cold and warm margins are species-specific, changes in frequency in a given area will thus be species-specific. However, it can be assumed that across a given region, warm-demanding species should expand in highland (cold) areas, whereas cold-demanding species should decline in lowland (warm) areas.

In lowland areas, topographic gradients are quite smooth and the temperature gradient observed is mainly related to the latitudinal gradient. A difference of 1°C thus corresponds to wide areas and, in this case, climate change is expected to deeply modify species distribution areas with displacements exceeding hundreds of kilometres (Guralnick 2007, Jump et al. 2009). However, apart from the work of Hill and Preston (2015), studies that have focused on lowland areas have reported either a weak response of plant species to

climate change (Bertrand et al. 2011) or a weak link between observed and expected species range shifts (Groom 2013). This weak response of plant species in lowlands could result from a lag between the expected and experienced local extinction (meaning a persistence) of species due either to their longevity (García and Zamora 2003) or to mechanisms of population dynamics (Dullinger et al. 2012) or to source-sink processes (Pulliam 1988) or to limitations in dispersal (Corlett and Westcott 2013). In highlands, plant species and community responses to climate warming have been widely reported (Grabherr et al. 1994, Pauli et al. 2007, 2012, Bertrand et al. 2011, Gottfried et al. 2012), and highland ecosystems could possibly be more responsive to recent climate change than lowlands (Bertrand et al. 2011), indicating that an increase in the frequency of warm-demanding species has probably already occurred. The smaller dispersal distance needed to recover from climate change in highlands than in lowlands may explain this apparent difference in species responses (Bertrand et al. 2011, Corlett and Westcott 2013).

In order to better understand the impact of climate warming on species distribution, we investigated the differential responses of warm and cold-demanding forest plant species to recent changes in climatic conditions in lowland and in highland areas. More specifically, we addressed the following question: has the frequency of cold-demanding species decreased in lowlands and the frequency of warm-demanding species increased in highlands?

Methods

Potential declines and expansions of forest plant species populations were investigated by analysing changes in their frequencies across France in highlands (above 500 m a.s.l.) and in lowlands (below 500 m a.s.l.) (Fig. 1a and 2) between the periods 1961–1987 (historical) and 1997–2013 (recent). Cold and warm-demanding species were divided into three categories: montane (the most cold-demanding), sub-montane (intermediate between cold and warm-demanding) and lowland (warm-demanding) species. Lowland, sub-montane and montane species were defined as species with an optimum in mean annual temperature above 10°C, between 10°C and 6°C and below 6°C, respectively (see Fig. 1b for examples). Optimums in temperature of species were defined from species response curves as the value of the gradient corresponding to the maximum probability of presence. Expected changes in species frequencies were modelled using species distribution models in order to compare observed changes in frequency to predicted ones.

Floristic data

Vegetation plots were extracted from three databases (Sophy, EcoPlant and the French Forest Inventory) to obtain both historical and recent floristic surveys. The Sophy database (Brisse et al. 1995) is a phyto-sociological database that
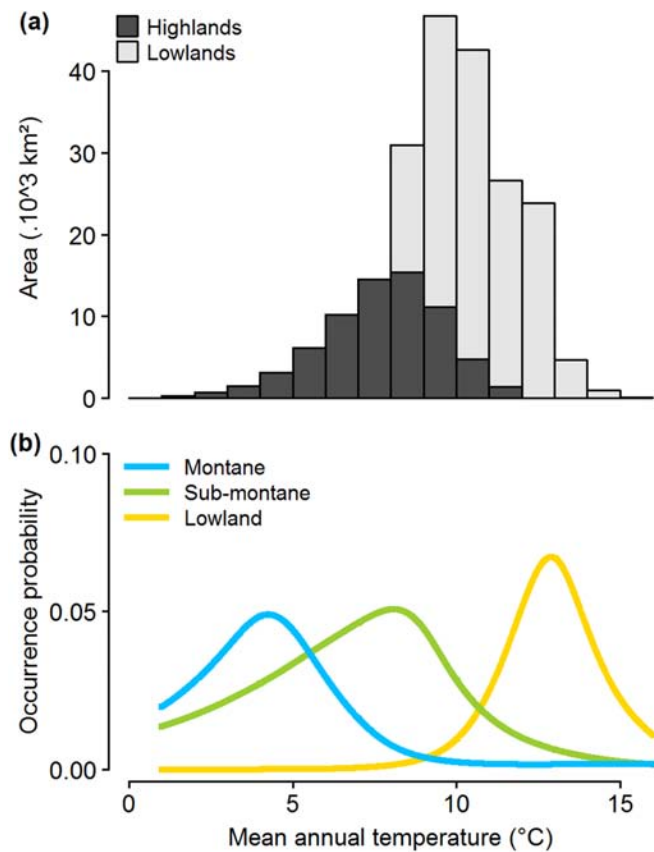
Figure 1. Distribution of forested areas in France and examples of species response curves along the temperature gradient. The decrease in forested areas with decreasing temperature (a) should result in differential changes in frequencies for montane (e.g. *Petasites albus*), sub-montane (e.g. *Carex digitata*) and lowland (e.g. *Arbutus unedo*) species (b) due to recent climate warming.

consists of a compilation of botanical studies conducted from 1914 to 2000. EcoPlant (Gégout et al. 2005) is a phyto-ecological database focused on forest ecosystems and including plots surveyed from 1922 to 2011. The database provided by the French National Inventory (Robert et al. 2010) includes plots inventoried between 1991 and 2013 and uniformly distributed across French forests in a 1-km² grid. Only floristic inventories conducted between April and October and for which coordinates were available with a precision of less than 1 km were selected. A total of 116 760 floristic plots were extracted from these three databases.

Definition of the historical and recent periods

In order to study the effect of the recent climate warming on species frequencies across France, we defined two periods: one preceding the observed recent climate warming (the historical period), and the second one corresponding to the new environmental conditions (the recent period). Vegetation plots were thus allotted to these two periods depending on their date of survey. In France, recent climate warming is characterised by a strong increase in temperature from the
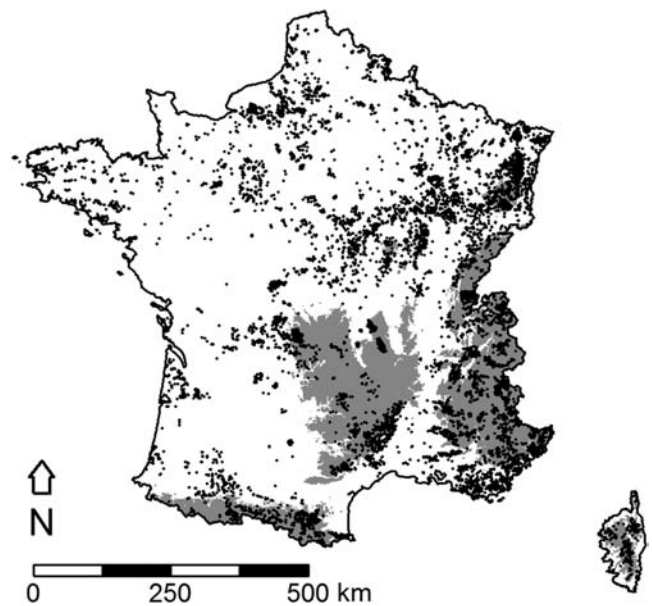

Figure 2. Location of plot pairs involved in the study. Dots correspond to the centroid of each plot pair (n = 11 505) and shaded areas represent highlands (areas where the elevation is higher than 500 m a.s.l.).

end of the 1980s until the end of the 1990s, followed by a period of relative stability. A close look at the annual averages reveals that 1987 is the year after which all mean annual temperatures were over the average mean annual temperature of the period 1961–1990, except for the year 1996. Finally, using the French meteorological network, we observed that there was no significant trend in temperature either from 1961 to 1987 (linear regression, p = 0.60) or from 1997 to 2012 (linear regression, p = 0.75). That is why 1987 was chosen as the last year of the historical period and that is also why 1997 was chosen as the first year of the recent period. The mean temperature warming between the historical and the recent periods as measured by the French meteorological network is 1.13°C.

Pairing historical and recent plots

In order to avoid biases due to differences in plot positions between the historical and the recent periods, plots were geographically paired. On the basis of the 21 473 historical and 65 742 recent plots available, an iterative procedure was used to set up plot pairs (each pair composed of one historical and one recent plot) by minimising the distance between historical and recent plots. The maximum allowed difference in elevation within each pair of plots was limited to 200 m, and the maximum distance allowed between two plots within a pair was 5 km. The procedure selected plot pairs from the closest plots to the furthest ones within the difference in elevation limit (200 m of difference), i.e. only the distance between two plots was optimised and the difference in elevation is almost random. It generated 11 505 plot pairs (Fig. 2) corresponding to a total of 23 010 plots: 11 505

plots with floristic information collected during the historical period and 11 505 plots collected during the recent period. On average, plots within pairs were 1535 m apart and the average difference in elevation was null (0 m).

Environmental data

Soil and climate data were used to predict species distribution according to the historical and the recent periods. The soil pH and C:N ratio were extracted for each plot from spatialised data at a resolution of 1 km² (Coudun et al. 2006). These soil data were produced by bio-indication: soil pH and C:N ratio (a surrogate of nitrogen availability) were calculated on forest vegetation plots spread across France from indices associated with each species present on the plots. These plots were independent from those used in this study. This information was then interpolated in order to estimate soil pH and C:N ratio across the entire French forested area. Mean annual temperature and the sum of precipitations during the growing season were extracted from spatialised average values for the periods 1961–1987 and 1997–2012 (corresponding to the historical and the recent periods, respectively) at a resolution of 1 km². Historical climatic data were spatialised by modelling values measured by meteorological stations. Values of mean annual temperature and the sum of precipitations during the growing season (from April to September included) were averaged from 202 and 862 meteorological stations distributed across the French territory from the year 1961 to the year 1987, respectively. The spatial climatic models combined topographical and geographical variables to predict average climatic values during the period considered (Ninyerola et al. 2000, modelled method). Recent climatic data (corresponding to the averages for the period 1997–2012) were obtained by summing historical values and interpolated differences between the two periods measured on meteorological stations (interpolated method). The inverse distance weighting method was used to interpolate measured differences. We use this method to obtain recent climatic data since it better predicted the spatial heterogeneity of climate change than using the same method as for historical data. Indeed, by using independent meteorological stations we found a R^2 of 0.296 and 0.39 between predicted and measured changes in temperature between the two periods for the modelled and the interpolated methods, respectively. The R^2 was of 0.892 and 0.890 between predicted and measured recent temperature for the modelled and the interpolated methods, respectively. Based on data from meteorological stations, average changes in temperature were +1.18°C and average changes in precipitation during the growing season were +14 mm across France between the historical and the recent periods.

Modelling species distributions

Species distributions were modelled according to environmental variables using generalized additive models (GAMs, Hastie and Tibshirani 1986). GAMs were chosen since they provide a good compromise between the flexibility of the

response curves and the theoretical response of species to environmental gradients (Heikkinen and Mäkipää 2010). Moreover, they have been proven to have a very good predictive capacity compared to other modelling methods (Araújo et al. 2005) and to prevent autocorrelation problems in multivariate models (Dormann et al. 2007). Models were calibrated using floristic data collected during the historical period (n = 11 505 plots) and response curves were fitted with smoothing regression splines limited to three freedom degrees. Model quality was assessed by measuring their area under the curve (AUC, Swets 1988) and their true skill statistic (TSS, Allouche et al. 2006). These indexes were calculated using a k-fold procedure (with $k = 10$): the calibration dataset was divided into 10 random subsets, models were iteratively calibrated by using nine of these subsamples, and AUC and TSS were then calculated with the 10th subsample. Finally, the 10 values of AUC and TSS obtained for each species were averaged.

The environmental variables included in the models were mean annual temperature, sum of precipitation during the growing season (from April to September), soil pH and soil C:N ratio. This set of environmental variables was considered as a proxy for the three main resources required by plant species: energy, water availability and mineral nutrition (Austin and Van Niel 2011). Moreover, these variables were selected after testing both complex models with many more variables and models specific to each species. The near absence of increases in model quality did not justify the use of more complex models. The average respective weights of mean annual temperature, precipitation during the growing season, soil pH and C:N ratio in models were 33, 10, 41 and 16%, respectively, of the explained deviance.

Predicting species occurrences during historical and recent periods

The calibrated models were used to predict species presence probability across France during both the historical (which corresponds equally to the calibration period) and the recent period. Historical and recent probabilities of occurrence were predicted using corresponding climatic data, while soil parameters (pH and C:N ratio) were considered stable over time. Since there was no trend in climatic data (mean temperature and precipitation during the growing season) for either the historical or the recent periods, average values for the two periods were used as predictors in the models.

Predicted presence probabilities were converted into modelled presences–absences in order to be compared to observed ones (extracted from floristic databases). Probabilities of occurrences predicted by models were available at a resolution of 1 km² and were retrieved on historical and recent plots. Predicted presences–absences were then generated by sampling the modelled probabilities of occurrence according to a binomial distribution (see Fig. 3c and d for an example). Since the random sampling of presences–absences from presence probabilities induced variability in the results, it was conducted 1000 times for each species, generating as
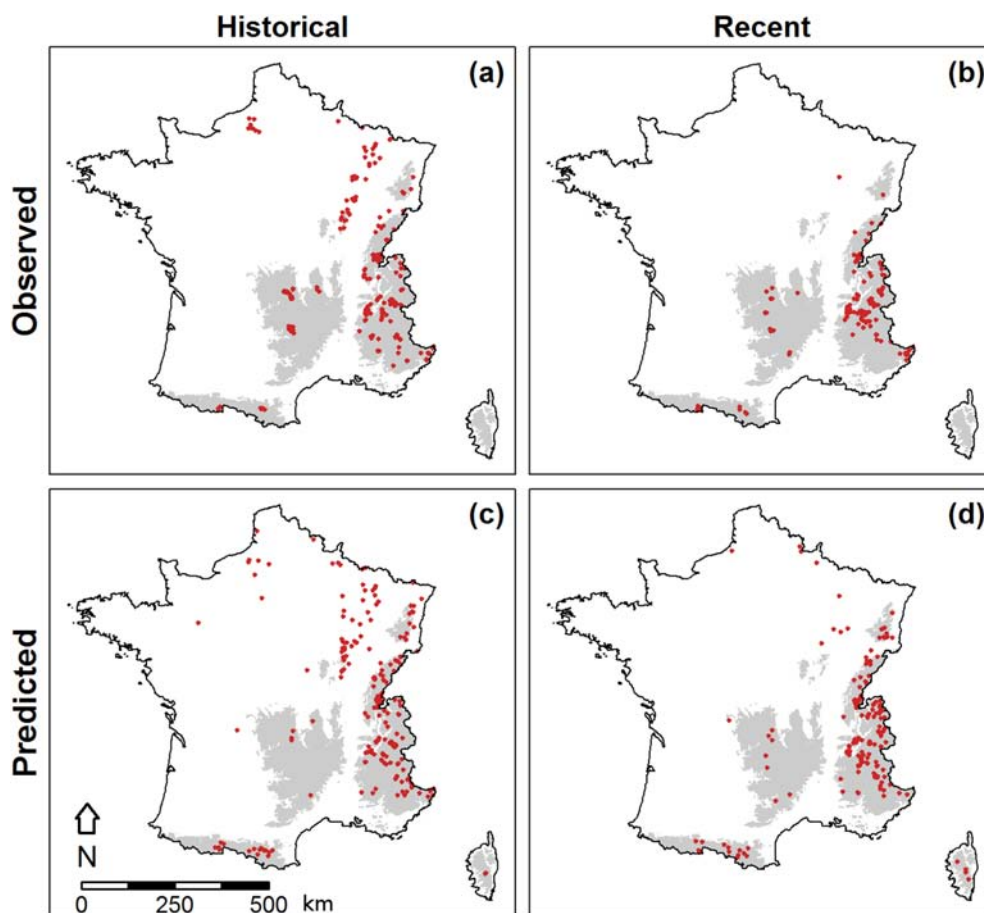
Figure 3. Example of predicted and observed changes in occurrence of *Actaea spicata*. Maps of observed (a, b) and predicted (c, d) occurrences of *Actaea spicata* (dots) during the periods 1961–1987 (historical) (a, c) and 1997–2013 (recent) (b, d). Shaded areas represent highlands (areas above 500 m a.s.l.).

many sets of presences–absences. We finally obtained one set of historical and observed presences–absences (extracted from floristic databases: observed data) and 1000 sets of predicted presences–absences (derived from model predictions: modelled data) for each studied species.

Species selection

Subsequent analyses were conducted on a subset of the total available species in the dataset. Only species with more than 50 occurrences in both historical and recent data were selected. This ensured that models could be calibrated with sufficient species presence and that changes in species frequencies were sufficiently relevant. In addition, two criteria concerning model quality were applied to select species: a significant response to mean annual temperature ($p < 0.001$) and a value of AUC greater than 0.7. In the dataset, 525 species had more than 50 historical and recent occurrences, but ten species were removed due to infinite values of relative changes in frequency in lowlands or in mountains since they were not sufficiently abundant in one of these areas. Selection criteria based on the significance of temperature in

models and AUC values resulted in a selection of 424 species. Among these species, 185 were considered as lowland species (optimum in mean annual temperature above 10°C), 135 as sub-montane species (optimum in mean annual temperature comprised between 10°C and 6°C) and 104 as montane species (optimum in mean annual temperature below 6°C). AUCs of models for selected species ranged from 0.70 to 0.99, with an average value of 0.87, and TSSs ranged from 0.33 to 0.98, with an average value of 0.66.

Analysis of species frequencies and their changes

Species frequencies were calculated as the ratio of species occurrences to the number of plots. They were calculated for each species from historical and recent plots, in highlands (n = 4731 plots) and in lowlands (n = 6774 plots). Absolute changes in frequency were computed as the difference between recent and historical frequency. In order to scale changes to the historical frequencies of species, relative changes in frequencies were computed as the ratio of absolute changes divided by the historical frequencies of species. Species frequencies and their changes between the historical

and the recent periods were calculated from both observed and modelled occurrence data (see Fig. 3 for an example). Since modelled occurrence data was composed of 1000 sets of predicted presences–absences for each species, corresponding frequencies were calculated 1000 times and then averaged. For each studied species, we finally obtained the historical and the recent frequency, as well as the difference between the two across France and in lowlands and in highlands separately for both the observed and the modelled data. The Wilcoxon signed-rank test was used to assess the significance of these changes.

Results

The average absolute frequency of montane and sub-montane species was lower in lowlands (0.02 and 0.05, respectively) than in highlands (0.06 and 0.07, respectively), whereas the average frequency of lowland species was higher in lowlands (0.05) than in highlands (0.02). During the historical period, lowlands, sub-montane and montane species constituted 53, 39 and 9% of total occurrences in lowland areas and 22, 45 and 33% in highland areas, respectively.

The relative changes in frequency across France (according to the historical frequencies) of montane and sub-montane species decreased by an average of 6 and 3% (Wilcoxon signed-rank test: $p < 0.01$), respectively. On the contrary, the relative changes in frequencies of lowland species increased by an average of 18% ($p < 0.001$) (Fig. 4).

As illustrated by the changes in the spatial distribution of the occurrences of *Actaea spicata* (Fig. 3), the change of species frequencies differed between lowlands and highlands. Predictions and observations of the frequency of this sub-montane species showed a strong decrease in lowlands
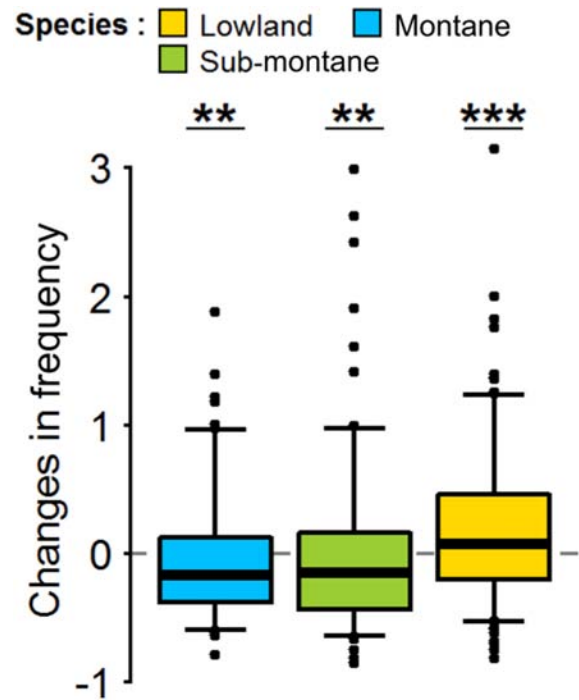
Figure 4. Global changes in frequencies of lowland, sub-montane and montane species with respect to their historical frequency. n = 185 lowland, 135 sub-montane and 104 montane species.

between the historical and the recent periods, whereas it remained stable in highlands.

Observed data showed considerable trends in frequency changes (Fig. 5a). In lowlands, the relative change in the frequency of montane and sub-montane species was an average decrease of 49% ($p < 0.001$) and 25% ($p < 0.001$),
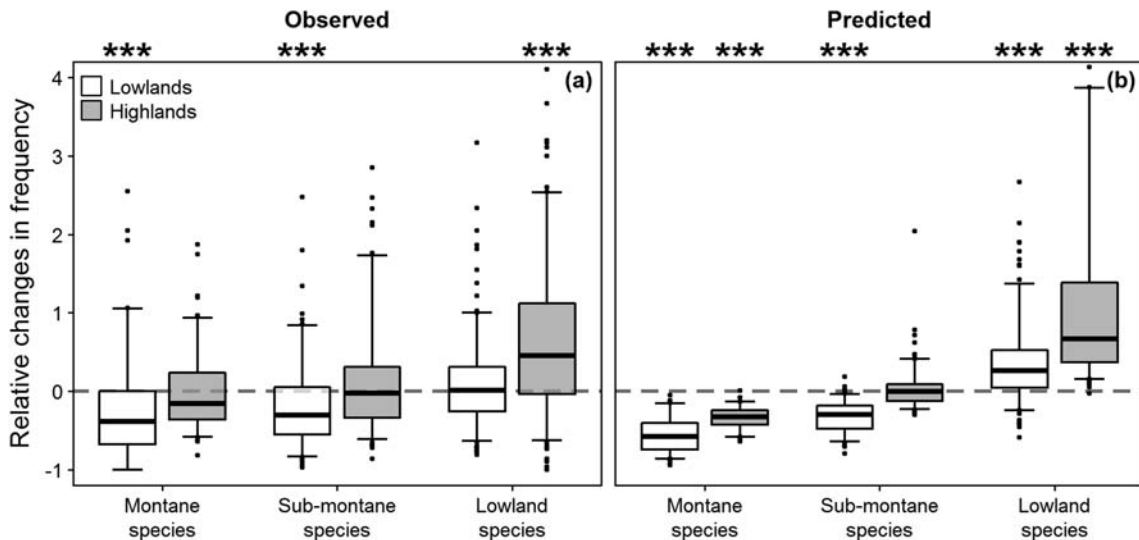

Figure 5. Relative changes in species frequencies. Observed (a) and predicted (b) relative changes in frequency of montane (n = 104), sub-montane (n = 135) and lowland (n = 185) forest plant species in lowlands and in highlands between the historical (1961–1987) and the recent (1997–2012) periods.

respectively. The relative change in frequency of lowland species was a non-significant increase of 4% (p = 0.25). In highlands, the relative change in frequency of montane species was an average non-significant decline of 6% (p = 0.17), that of sub-montane species remained stable (0%; p = 0.95), and the relative change in frequency of lowland species was an average increase of 55% (p < 0.001). Model predictions were in accordance with most of the observed changes, but showed a higher change rate (Fig. 5b). In lowlands, model predictions showed an average decrease in frequency of 56% (Wilcoxon signed-rank test: p < 0.001) and 31% (p < 0.001) for montane and sub-montane species, respectively. These decreases are relative changes in frequencies and correspond to decreases from 2.3 to 1.4% and from 7.4 to 5.6% for montane and sub-montane species, respectively. The frequencies of lowland species were predicted to increase by an average of 29% (p < 0.001) in relation to their historical frequencies. In highlands, the frequency of montane species was predicted to decrease by an average of 33% (p < 0.001), that of sub-montane species was predicted to remain almost stable (+ 0%; p = 0.90), and the frequency of lowland species was predicted to increase by an average of 86% (p < 0.001).

Discussion

On average, predicted and observed changes in species frequency were in agreement with each other and showed a strong decline of montane and sub-montane species in lowlands as well as an expansion of lowland species in highlands. The comparison between modelled and observed changes in species frequency due to recent climate change has already been done for birds in protected areas (Johnston et al. 2013), but it has never been reported for plant species and, especially, across large parts of species ranges. Despite changes in species frequency that may result from factors other than climate change, such as habitat loss (Hill and Preston 2015), the agreement between predicted and observed trends of changes in species frequency reported here supports the role of recent climate warming in observed trends. It confirms that climate warming is currently driving declines and expansions of plant populations that are underlying processes behind species range shifts (Lenoir and Svenning 2015) and changes in community composition (Walther 2010) already assessed.

While species range expansions on mountain tops have been among the first reported signs of the impact of climate warming on species ranges (Grabherr et al. 1994), evidence of range retractions have remained scarce (Thomas et al. 2006), especially in lowlands where latitudinal shifts are expected (Jump et al. 2009). The decline of montane and sub-montane forest plant species in lowlands reported here confirms previously observed decreases in frequency and abundance of some cold-demanding plant species at their warm margins (Lesica and McCune 2004, Kopp and Cleland 2014, Hill and Preston 2015, Kuhn et al. 2016). It is also in agreement with early observations of local extinctions driven – at least

partially – by recent climate warming (Franco et al. 2006, Beever et al. 2011). Whereas montane plant species have only a small part of their ranges in lowlands, sub-montane species have a substantial part of their distribution in lowlands. This difference explains the stronger regression of montane species at low elevations and suggests a high risk of extinction of these species in lowlands. In addition, the decline of montane species in highlands highlights the current decrease in available habitat for these species. The declines in range areas of montane species predicted for the next century (Engler et al. 2011) seem to have already begun, and this observation suggests that species extinctions (Thomas et al. 2004) and biodiversity loss (Thuiller et al. 2005) predicted for the next century are likely to occur for cold-demanding species.

In contrast, the frequency of lowland species has remained stable in lowlands and has increased in highlands, indicating that they are colonising new areas at their cold margins. In accordance with the predictions of Skov and Svenning (2004), this demonstrates that not all species would decline in response to climate warming and that some species are currently benefiting from more favourable climatic conditions. This result clearly shows that colonisation is not only occurring at the tops of mountains, as has already been demonstrated (Gottfried et al. 2012), but along the whole elevational gradient in highlands as well. On the other hand, expansion of lowland species was also expected in lowlands, but has not yet been observed. This indicates a lack of colonisation in lowlands that may be due to the large distance of dispersal required to compensate for changes in climate (Jump et al. 2009) and to the higher fragmentation of the forest ecosystem in French lowlands than in highlands (Bertrand et al. 2011).

Apart from the declines of sub-montane and montane species in lowlands, observed changes in species frequency were weaker than those predicted. This was predictable since lags in colonisation are expected due to the limited dispersal capacity of plant species (Corlett and Westcott 2013), as well as lags in local extinction due to the capacity of species to persist under unfavourable conditions (Dullinger et al. 2012). This difference between theoretical and observed changes in vegetation is called disequilibrium (see Svenning and Sandel 2013 for a review) and our results confirm that this phenomenon exists already. This is in agreement with most of the studies that have reported species responses to recent climate change (Chen et al. 2011) and, especially, with species range shifts in French mountains (Lenoir et al. 2008) and the reshuffling of forest plant species communities across France (Bertrand et al. 2011) already reported.

These results show that partitioning the geographical space between lowlands and highlands as well as between warm and cold-demanding species made it possible to predict declines and expansions, two important consequences of recent climate warming for species populations. Indeed, since the proportion of cold-demanding species in lowlands is very low, changes in frequencies are observable mainly by focusing on these species and, inversely, for warm-demanding species

in highlands. This is of particular interest for monitoring bio-diversity response to climate warming. We show here that if highlands seem to be the most responsive areas, lowlands are also responding to recent climate change, particularly by declines in cold-demanding (montane and sub-montane) plant species. Due to their responsiveness to recent climate change and potential future retractions of their ranges, cold-demanding species could be considered in lowland areas as sentinels for species range retraction and local extinctions in response to climate warming.

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