LETTER

Changes in plant community composition lag behind climate warming in lowland forests

Romain Bertrand[1,2], Jonathan Lenoir[3], Christian Piedallu[1,2], Gabriela Riofrío-Dillon[1,2], Patrice de Ruffray[4], Claude Vidal[5], Jean-Claude Pierrat[1,2] & Jean-Claude Gégout[1,2]

Climate change is driving latitudinal and altitudinal shifts in species distribution worldwide[1,2], leading to novel species assemblages[3,4]. Lags between these biotic responses and contemporary climate changes have been reported for plants and animals[5]. Theoretically, the magnitude of these lags should be greatest in lowland areas, where the velocity of climate change is expected to be much greater than that in highland areas[6]. We compared temperature trends to temperatures reconstructed from plant assemblages (observed in 76,634 surveys) over a 44-year period in France (1965–2008). Here we report that forest plant communities had responded to 0.54 °C of the effective increase of 1.07 °C in highland areas (500–2,600 m above sea level), while they had responded to only 0.02 °C of the 1.11 °C warming trend in lowland areas. There was a larger temperature lag (by 3.1 times) between the climate and plant community composition in lowland forests than in highland forests. The explanation of such disparity lies in the following properties of lowland, as compared to highland, forests: the higher proportion of species with greater ability for local persistence as the climate warms[7], the reduced opportunity for short-distance escapes[8,9], and the greater habitat fragmentation. Although mountains are currently considered to be among the ecosystems most threatened by climate change (owing to mountaintop extinction), the current inertia of plant communities in lowland forests should also be noted, as it could lead to lowland biotic attrition[10].

Despite the general pattern of poleward and upward range shifts[1,2], the timing, magnitude and direction of these biotic responses vary greatly among species and geographic conditions[11–13]. This variation can prevent biotic communities from migrating as intact units in response to climate change[3]. Since the last interglacial, biotic communities have been reshuffled, leading to the formation of novel species assemblages linked to new climatic conditions[3,4]. Recent changes supporting this pattern have occurred within plant and animal communities in response to contemporary climate warming[14–18]. Even though these biotic signals are coherent with climate change[2], many studies suggest a lag between the magnitude of climate warming and the reshuffling observed in biotic communities[5,12,17–19]. However, comparisons between the extent of the observed biotic signals and that expected based on the intensity of climate warming are still scarce, especially for lowland areas, which offer no short-distance escapes for species facing climate change[8,9]. If biotic communities respond synchronously without lagging behind climate warming, current species compositions would reflect contemporary climatic conditions within both lowland and highland areas. However, the greater velocity of climate change in lowland areas compared to highland areas[6] suggests that reshuffling in biotic communities is more likely to lag behind climate warming in lowland areas compared to highland areas. However, this theory remains unverified.

Climate change in France has been characterized by increases in mean annual temperatures of far greater magnitude than the worldwide average, reaching up to about +1.05 °C on average during 1987–2008 (Supplementary Fig. 2), compared to about +0.35 °C for the worldwide average[20]. Assuming that species assemblages can be used to infer climatic conditions at a given location and time (an approach commonly used by paleoclimatologists[21], who refer to the relationship as a transfer function), we report a study monitoring plant communities across French forests over 44 years, 1965–2008 (totalling 76,634 surveys; Supplementary Figs 1, 3 and 4). Here we compare temperature trends reconstructed from observed reshuffling of plant assemblages ('floristically reconstructed' temperatures based on 760 species; Supplementary Table 1) with temperature trends reconstructed from instrumental records and climate models ('climatically reconstructed' temperatures based on 237 stations; Supplementary Fig. 5) in lowland (<500 m a.s.l.) and highland forests (500–2,600 m a.s.l.) (Supplementary Methods). Changes in floristically reconstructed temperatures involve reshuffling of plant community composition towards more heat- or cold-demanding species assemblages. Following the current climate warming, small differences between floristically and climatically reconstructed temperatures may indicate important reshuffling of plant community composition, close to the magnitude of climate change (that is, high recovery of the climate–flora equilibrium; Fig. 1). In contrast, large differences between floristically and climatically reconstructed temperatures may indicate that reshuffling in plant communities lags behind climate warming (that is, low recovery of the climate–flora equilibrium; Fig. 1).

Before the contemporary climate warming event (1965–86; Supplementary Fig. 2), we found no significant differences between floristically and climatically reconstructed temperatures in lowland and highland forests (Table 1), suggesting close equilibrium between species composition in biotic assemblages and temperature conditions. In contrast, during the current climate warming period (1987–2008), we found significant differences between floristically and climatically reconstructed temperatures in lowland and highland forests (Table 1), indicating a lag in the response of herbaceous forest species to climate change. In lowland forests, we found no significant increase in floristically reconstructed temperatures between 1965–86 and 1987–2008 (+0.02 °C on average), whereas climatically reconstructed temperatures increased by +1.11 °C on average (Table 1a). In contrast, the floristically reconstructed temperatures of highland forests increased by +0.54 °C, with climate warming reaching +1.07 °C over the same period (Table 1b). This discrepancy indicates an important lag in the response of herbaceous forest species to climate change, being 3.1 times larger in lowland forests (temperature lag = 1.29 °C on average) than in highland forests (temperature lag = 0.42 °C on average; Table 1). In 2008, the most recently investigated year, this lag decreased to an average of 0.28 °C in highland forests but was still 1.26 °C in lowland forests (Fig. 2).

Our results suggest that the recovery of forest plant communities facing climate warming is weak in lowland forests but strong and fast

[1]AgroParisTech, ENGREF, UMR1092 Laboratoire d'Étude des Ressources Forêt-Bois (LERFoB), 14 rue Girardet, F-54000 Nancy, France. [2]INRA, Centre de Nancy, UMR1092 Laboratoire d'Étude des Ressources Forêt-Bois (LERFoB), F-54280 Champenoux, France. [3]Ecoinformatics & Biodiversity Group, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark. [4]CNRS, Institut de Biologie Moléculaire des Plantes (IBMP), Université de Strasbourg (UDS), 12 rue du Général Zimmer, F-67084 Strasbourg Cedex, France. [5]Inventaire Forestier National, Château des Barres, F-45290 Nogent-sur-Vernisson, France.
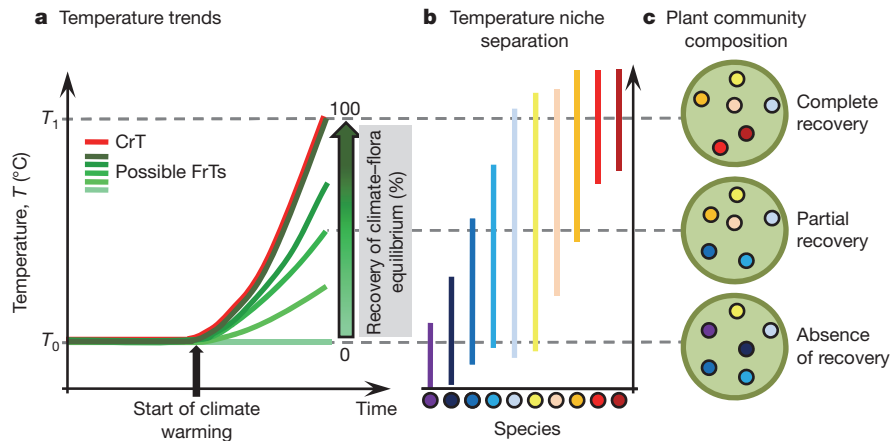
Figure 1 | Theoretical response of plant communities to climate warming.
a, Floristically (green scale; FrT) and climatically (red; CrT) reconstructed temperature trends over time. The green scale (0–100%) describes different hypothetical floristically reconstructed temperature trends corresponding to increasing intensity of the plant community responses and leading to increasing recovery of the climate–flora equilibrium (measured as the actual change in FrT over time relative to the effective change in CrT over the same time period; see Supplementary Methods for complete formula).
b, Temperature niche separation among 10 virtual species. The range of temperature requirements for each species is represented by a vertical line.
c, Three illustrative cases of increasing recovery of the climate–flora equilibrium in plant community composition (based on the 10 virtual species in

b). Bottom, absence of climate–flora equilibrium recovery, corresponding to plant communities composed mainly of cold-demanding species, reflecting temperature conditions before climate warming (T_0), and leading to an important temperature lag between FrT and CrT. Middle, partial recovery of the climate–flora equilibrium, corresponding to reshuffled plant communities, leading to a mixed assemblage of cold- and heat-demanding species and to reduced temperature lag between FrT and CrT. Top, complete recovery of the climate–flora equilibrium, corresponding to important reshuffling of the plant community, leading to an assemblage of heat-demanding species reflecting the effective temperature increase ($T_1 - T_0$) and to the absence of temperature lag between FrT and CrT. The small circles represent virtual plant species; the three large green disks each depict a community of plants.

in highland forests, reaching +0.26 °C per decade (Fig. 2). This rate of increase in floristically reconstructed temperatures confirms the results of a previous study, which reported a similar trend of +0.25 °C per decade for herbaceous forest plants in the French mountains, despite the use of a completely different approach based on the comparison of species' optimum elevation between 1905–85 and 1986–2005[19]. In a Mediterranean forest, the flora turnover observed over the last decade was half that expected from temperature changes[22], whereas we found that reshuffling of forest plant communities recovered 0% and 60.7% (up to 68.2% in 2008) of the effective temperature increase between 1965–86 and 1987–2008 in lowland and highland areas, respectively. In highland forests, plant communities even completely recovered the effective change in temperature (that is, no significant differences between floristically and climatically reconstructed temperatures) for the years 1991, 1999, 2002, 2004 and 2005 (Fig. 2). Thus, lowland areas seem to be one of the least reactive terrestrial ecosystems to climate warming with respect to forest plant communities.

Several possible factors may explain the lower recovery of forest plant communities in response to climate warming in lowland versus highland areas. First, the larger proportion of cosmopolitan and thermophilous species (Supplementary Methods) in lowland communities (75.2% and 15.3% on average) compared to highland communities (67.2% and 8.8% on average) may result in a greater tolerance of lowland communities to climate warming throughout local persistence[7]. We did not find any significant changes in the composition of lowland

plant communities between 1965–86 and 1987–2008 (Fig. 3), whereas the proportion of mountainous and alpine species in highland plant communities decreased significantly (−4.6% on average), to the benefit of cosmopolitan species (+5.1% on average). In addition, we suggest that compensatory changes in demographic rates may buffer population dynamics against the negative effects of climate warming, causing a temporary delay in species turnover, especially in lowland plant communities (for example, a higher growth of individuals can compensate for the lower survival and recruitment rates, allowing persistence of threatened populations)[12]. Second, highland forests offer shorter-distance escapes for species facing climate warming compared to lowland forests[8,9], especially for forest plants that have strongly limited dispersal abilities[23]. Thus, species distributions are expected to migrate +1.1 km (median value; 5th to 95th percentile range $(PR_{5;95}) = [0.4; 15]$) upward in French highland forests, but +35.6 km (median value; $PR_{5;95} = [2.1; 137.6]$) northward in French lowland forests to track their climatic niches according to the contemporary climate warming event (1987–2008; Supplementary Fig. 9). Third, the migration rate of plant species may be delayed by the level of habitat fragmentation[8,23]. Forest patches exceeding 5 km² cover a larger proportion of highland areas (67.3%) than lowland areas (29.1%; Supplementary Fig. 10a). Moreover, forest patches are closer in highland areas (median proximity index (PI) = 3,813.7; $PR_{5;95} = [15.3; 122,034.3]$; see Supplementary Methods for details) than in lowland areas (median PI = 31.6; $PR_{5;95} = [1.3; 14,644.2]$; Supplementary Fig. 10b). All of these factors are not mutually exclusive and may,

Table 1 | Comparison of floristically and climatically reconstructed temperatures.

a Lowland				b Highland			
Reconstruction	Period			Reconstruction	Period		
	1965–1986 (P_1)	1987–2008 (P_2)	$P_2 - P_1$		1965–1986 (P_1)	1987–2008 (P_2)	$P_2 - P_1$
CrT	10.54 (1.2)	11.66 (1.23)	1.11 (0.02)**	CrT	7.98 (1.8)	9.05 (1.8)	1.07 (0.03)**
FrT	10.35 (1.23)	10.37 (1.22)	0.02 (0.02)	FrT	8.09 (1.77)	8.63 (1.61)	0.54 (0.03)**
FrT − CrT	−0.19 (0.87)	1.29 (0.99)**		FrT − CrT	0.11 (1.12)	0.42 (1.23)*	

Shown are mean temperatures with standard deviations (in brackets) computed from the 1,000 floristically (FrT) and climatically (CrT) reconstructed temperature trends. P_1, Value for 1965–86; P_2, value for 1987–2008. **a**, Comparison for French lowland forests (<500 m a.s.l.). **b**, Comparison for French highland forests (500–2,600 m a.s.l.). Significance of temperature differences between periods (Student's t test) and between modelling approaches (Student's paired t test) are indicated: *$P < 0.01$, **$P < 0.001$ for more than 95% of the 1,000 reconstructed temperatures.
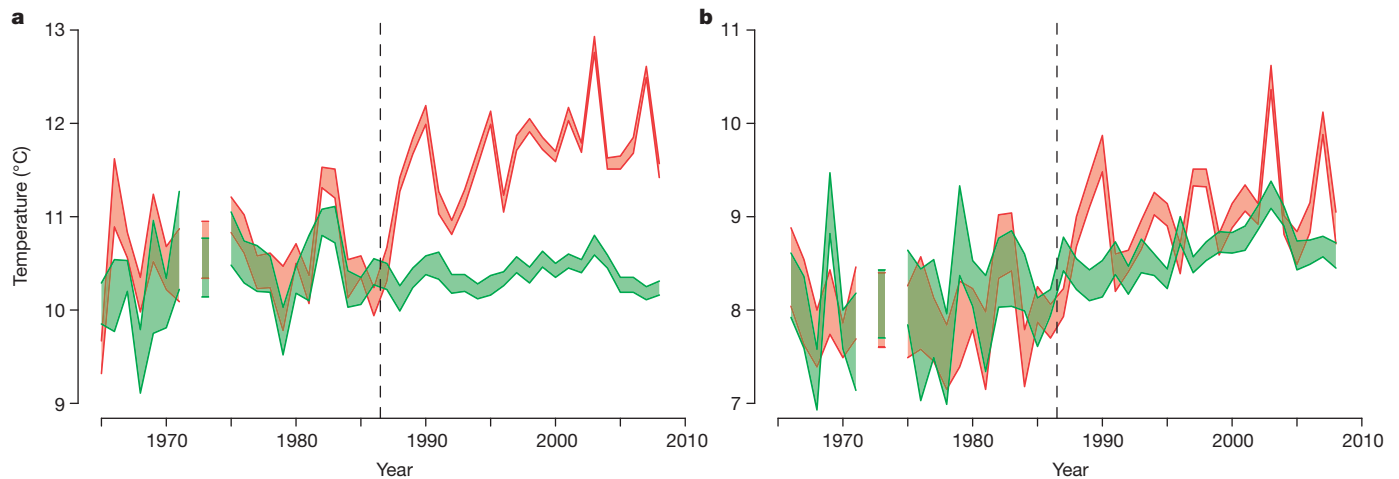
Figure 2 | Comparison of floristically (green) and climatically (red) reconstructed temperature trends between 1965 and 2008. a, Trends in lowland forest plant communities (<500 m a.s.l.). **b**, Trends in highland forest plant communities (500–2,600 m a.s.l.). The thickness of lines shows the range of reconstructed temperature trends ($n = 1,000$ trends). Dashed lines indicate the start of the contemporary climate warming period (1987–2008). Breaks in trends are due to no sample convergence for the years 1965 (in highland areas), 1972 and 1974 (in both lowland and highland areas).

independently or combined, explain our results showing that re-shuffling of plant communities in lowland forests strongly lag behind climate warming.
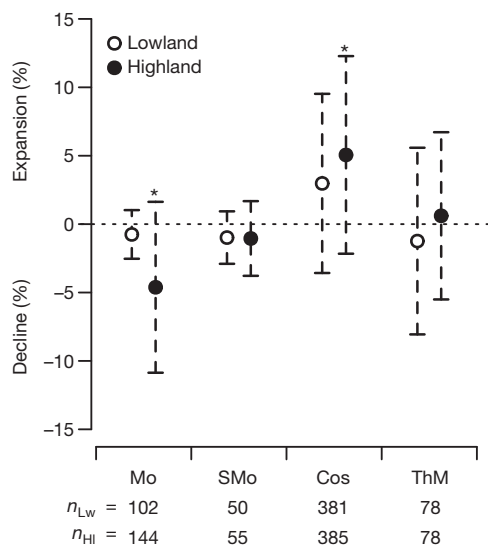
In this study, we linked reshuffling observed in plant assemblages in French forests to temperature changes between 1965 and 2008. However, water stress may also drive species range shifts[11,22]. In California, the core of the altitudinal range of 46 out of 64 forest plant species shifted downward in response to regional changes in climatic water balance between 1935 and 2005[11]. In contrast, no significant changes in the level of annual precipitation was observed throughout the French territory between 1965–86 and 1987–2008 (mean value of

precipitation changes [s.d.] = +1.04 mm [48.56] in lowland areas, $P = 0.35$, Student's t test for paired samples; −0.93 mm [60.09] in highland areas, $P = 0.44$, Student's t test for paired samples; Supplementary Fig. 2). Thus, the absence of changes in precipitation patterns over the 44-year study period is unlikely to explain the differences of reshuffling between lowland and highland forest plant communities. Similarly, acclimation or adaptation processes may also explain the differences we observed between floristically and climatically reconstructed temperatures. The large difference in temperature recovery between highland and lowland forest plant communities may indicate distinct interchanges between migration and adaptation, with migration being more prevalent in highland forests and adaptation more prevalent in lowland forests. Nevertheless, such processes are probably insufficient to mitigate completely the effects of the high temperature increase in just 22 years, especially at the scale of a large pool of perennial species in a fragmented landscape[24,25].

Although a potential lag between the magnitude of climate warming and the extent of changes within biotic communities has already been suggested[5,12,17–19], we provide the first (to our knowledge) assessment of such a lag and show that it is more important in lowland areas. This finding has important implications in terms of conservation issues. To date, a strong focus has been placed on mountaintop extinctions for species facing climate warming[10]. However, mountaintop extinctions are just one example, although important, of the likely consequences of contemporary species range shifts in highland areas. Highland areas offer short-distance escapes for species facing climate change[8,9] and provide ideal refuges for plant species to track their climatic requirements[10], which could lead to the formation of novel species assemblages. In lowland areas, the current inertia of forest plant communities suggests delayed extinction and immigration in the face of climate warming[26] due to species tolerance and low migration rate. Considering the velocity of predicted future climate change[6], the low dispersal abilities of forest plants[23] and the low opportunity for short-distance escape to track climate changes in lowland areas[8,9], the current inertia of forest plant communities will not be indefinite. Consequently, abrupt reshuffling of these plant communities may occur in the future, possibly leading to lowland biotic attrition[10] with important changes expected in ecosystem functioning[27]. Therefore, we recommend that research efforts be focused on understanding the implications of climate change in lowland areas.

Figure 3 | Compositional changes in the plant communities of lowland and highland forests according to four different biogeographic groups. Mean shifts in the proportions of plant communities are shown (data points) with standard deviations (error bars) estimated from 1,000 floristic samples used to reconstruct temperatures. The significance of changes from the null hypothesis of zero shift is displayed (*$P < 0.05$ for more than 95% of the floristic samples; Wilcoxon paired signed-rank test). The number of species analysed in lowland (n_{Lw}) and highland (n_{Hl}) plant communities are displayed below the figure. Mo, mountainous to alpine species; SMo, sub-mountainous to lowland species; Cos, cosmopolitan species; ThM, thermophilous to Mediterranean species. See Supplementary Methods and Supplementary Table 1 for more details about the different biogeographic groups.

METHODS SUMMARY

To achieve our aim, we compiled a complete species list including the year and location of 79,621 floristic surveys (44,509 and 35,112 in lowland and highland

areas, respectively) that were recorded across the French forest territory between 1965 and 2008. We computed a 1-km^2 grid of the mean annual temperature across the French territory for each year between 1965 and 2008 using a modelling approach based on 237 non-interrupted meteorological stations ($R^2 = 0.93$ for 13,620 independent temperature observations; Supplementary Figs 5 and 6)[28]. These climatically reconstructed temperatures were extracted at the location and year of each of the 79,621 floristic surveys. We then subsampled a training data set of 2,987 floristic surveys before the recent climate warming event (1975–85) to calibrate a transfer function using a combination of weighted averaging partial least squares[29] and Breiman's random forest[30] to infer temperatures from the plant assemblages ($R^2 = 0.83$ in a validation data set; Supplementary Fig. 7). These floristically reconstructed temperatures were then predicted across the French territory between 1965 and 2008 using the 76,634 floristic surveys. This predictive data set was bootstrapped separately in lowland and highland areas for each year to control for artificial temperature variations associated with inter-annual variations in floristic survey locations (Supplementary Fig. 8). We reconstructed 1,000 pairs of floristically and climatically reconstructed mean annual temperature trends separately for lowland and highland areas. We tested temperature differences in each pair of trends between 1965–86 and 1987–2008, as well as annually. To discuss our results, we assessed changes in plant community composition in four biogeographic groups of species. We then computed the mean distance separating equal isotherms between periods, in addition to performing independent spatial analysis of the degree of habitat fragmentation in lowland and highland forest areas (see Supplementary Methods for more details).

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Author Contributions R.B. designed the study, methodology and modelling approach, performed all the statistical analysis and wrote the paper; P.d.R. provided the Sophy database; C.V. provided the NFI database; J.-C.G. provided the EcoPlant database, helped to design the methodology and supervised the work; R.B. and G.R. contributed equally to format the floristic database; J.-C.P. advised the use of the Breiman's random forest regression to infer temperatures from the plant assemblages; R.B. and C.P. contributed equally to compute the climate model of historic temperature prediction; J.L. contributed actively to improve the clarity of the paper. All authors discussed and commented on the results.

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