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A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century

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Spatial fingerprints of climate change on biotic communities are usually associated with changes in the distribution of species at their latitudinal or altitudinal extremes. By comparing the altitudinal distribution of 171 forest plant species between 1905 and 1985 and 1986 and 2005 along the entire elevation range (0 to 2600 meters above sea level) in west Europe, we show that climate warming has resulted in a significant upward shift in species optimum elevation averaging 29 meters per decade. The shift is larger for species restricted to mountain habitats and for grassy species, which are characterized by faster population turnover. Our study shows that climate change affects the spatial core of the distributional range of plant species, in addition to their distributional margins, as previously reported.

Recent warming has induced biological and ecological responses from animals and plants throughout the world (*1*–*3*). Consistent responses to global warming or "fingerprints" are apparent in the phenology and distribution of species (*1*–*5*). For plants, invertebrates, and vertebrates, climate change has strongly influenced distribution and abundance at range margins both in latitude (polar margins) (*5*–*8*) and in elevation (upper margins) (*5*, *9*–*11*), and even in depth for marine fishes (*8*). Shifts at the upper edge of altitudinal range agree with the hypothesis of an upward trend to escape rising temperatures (*12*–*14*). Changes in range limits, however, are just one, albeit important, expression of the likely consequences of climate change. More subtle changes within the ranges of species are also likely and, although poorly explored as yet, might have important ecological and evolutionary consequences. Assuming niche conservatism over evolutionary time (*15*), we tested for large-scale (across temperate and Mediterranean mountain forests in west Europe), long-term (over the 20th century), and multispecies (through an assemblage of 171 species) climate-related responses in forest plant altitudinal distributions. We analyzed species responses by measuring shifts in the altitudinal position of species' maximum probability of presence within their distribution, instead of focusing on distributional extremes. Additionally, we tested for the effect of ecological and life history traits on the magnitude of the response to climate warming (*16*). In particular, we tested whether species restricted to mountain areas (*10*–*12*, *17*, *18*) and/or fast generation times (*19*) are particularly sensitive to temperature changes.

We studied species in forest communities found between lowland to the upper subalpine vegetation belt (0 to 2600 m above sea level) over six mountain ranges in west Europe (the Western Alps, the Northern Pyrenees, the Massif Central, the Western Jura, the Vosges, and the Corsican range). Climatic change in France has been characterized by increases in average temperature of far greater magnitude than increases in the world mean annual temperature, of about 0.6°C over the 20th century (*20*), reaching up to 0.9°C (*21*) and even close to 1°C in the alpine region since the early 1980s (*22*). From two large-scale floristic inventories (about 28,000 surveys) (*23*), we extracted two well-balanced subsamples, including 3991 surveys each, carried out across the studied mountain ranges (see fig. S1 for surveys location). The first subsample included surveys carried out before the mid-1980s (1905–1985), and the other one, after 1985 (1986–2005) (see fig. S2 for altitudinal distribution of surveys). We chose this temporal threshold because the analysis of yearly mean surface temperature anomalies between 1965 and 2005 shows that in 1986 the studied mountain ranges experienced a temperature regime shift (Fig. 1A), staying above the average baseline conditions. In contrast, analysis of annual precipitation anomalies between 1965

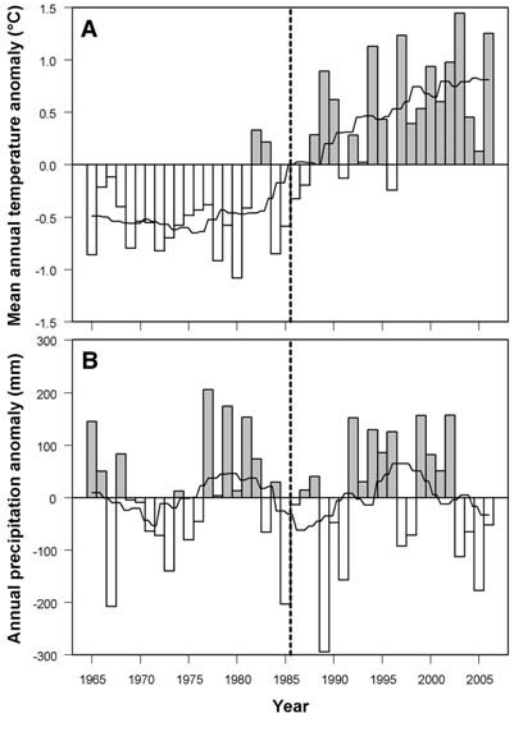

Fig. 1. Climatic trends from 1965 to 2006. (**A**) Yearly mean surface temperature anomalies (using overall mean temperature as baseline) and (**B**) annual precipitation anomalies (using overall mean annual precipitation as baseline) averaged for 73 elevation sites in the French mountains ranging in altitude from 10 to 2010 m above sea level. Solid gray bars refer to positive anomalies, whereas open bars refer to negative ones. The solid curve is the smoothed average with use of a 10-year filter. The vertical dotted lines mark the split between the two studied periods. Data have been gathered from the French National Climatic Network (Météo-France).

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and 2005 does not show any trend or precipitation regime shift (Fig. 1B). The subsampling method (*23*) was carried out in order to avoid a potential bias attributable to an uneven sampling effort between periods. In particular, we controlled for artificial warming (fig. S1) (*23*), which could be generated by the sampling of recent plots located in warmer conditions (i.e., southern latitude) regardless of climate warming. Our study was restricted to forest communities where long-term changes outweigh short-term tendencies because the forest canopy acts as a buffer zone, smoothing extreme interannual variation in temperature, in comparison with open areas that are far more influenced by both interannual climatic variation and agricultural practices. Changes in species distribution under the forest canopy can therefore be considered as fingerprints of regional trends rather than reflecting idiosyncratic trends in time or space.

Because we were more interested in the unexplored phenomenon of within-range shifts in plant species, we investigated changes in species optimum elevation over the study period instead of changes at the upper and lower boundaries of their distributions, which are more sensitive to sampling effort (*24*). By using simple logistic regression, we computed the altitude of maximum probability of presence, also called optimum elevation, within each period for 171 species (table S2) that were best described by unimodal bell-shaped models (*23*) and had more than 50 occurrences (*25*). In total, the studied species account for almost 62% of occurrences in our data set. The change in the altitudinal distribution of species was measured as the difference in their optimum elevation between 1905–1985 and 1986–2005.

The optimum elevation of forest plant species shifted mostly upward during the end of the 20th century (Fig. 2). The general upward trend between 1971 (mean year of surveys occurring from 1905 to 1985) and 1993 (mean year of surveys occurring from 1986 to 2005) is statistically highly significant [mean difference in optimum elevation 64.8 m, 95% confidence interval (95% CI) for mean = 40.8, 88.8; $n = 171$; Student's paired-sample t test, $t = 5.33$; df = 170; $P < 10^{-4}$], amounting to an average of 29.4 m per decade. As a test of the robustness of the observed trend, we confirmed that the potential existence of an artifact in optimum elevation estimations because of the use of unimodal symmetric curves (*26*) did not account for the observed pattern of positive shifts in altitudinal distributions. Indeed, such potential artifacts should affect optimum elevation estimations regardless of the period, and thus no trend should be expected. Interestingly, the size of the species altitudinal range around the optimum elevation (*27*) did not show a significant change between periods. The observed change in optimum elevation and lack of it in amplitude or range suggest that both the upper and the lower distributional margins may have shifted upward, implying the displacement of the whole altitudinal range.

Most species in the 1986–2005 period had higher optimum elevations than those in the 1905–1985 period (Fig. 2). More than two-thirds (118/171) of the species shifted their optima upward, whereas only one-third (53/171) shifted their optima downward. Change in optimum elevation of any individual species or taxon may have a number of possible explanations, but confounding factors decline with increasing numbers of species studied (*1*). This overall upward trend for an assemblage of 171 forest plant species in western European mountains is consistent with results focusing on the highest alpine and nival vegetation belts (*10*–*12*, *28*). We provide strong evidence that forest plant species, as many vertebrates and invertebrates species (*8*, *24*, *29*–*31*), have already followed the pace of climate change by shifting their distributions to higher altitudes and that these changes affect the core of their ranges or those areas where habitat suitability or maximum probability of presence is the highest. Thus, climate warming does not only affect species at their range boundaries, but its consequences ripple through the whole range of species.

In general, our results show that species displayed different rates of movement, behaving in a seemingly idiosyncratic way in response to climate change (Fig. 2 inset). However, species that share the same ecological properties may show similar consistent patterns of changes (*32*). We tested the hypothesis that species geographically restricted to mountains and/or with a shorter life cycle show more pronounced changes in distribution than those not restricted to mountain habitats and/or long-lived (*23*). Figure 3A illustrates a larger shift in the optimum elevation for the mountainous (area of occupancy restricted to mountain ranges) *Orthilia secunda* than for the ubiquitous (area of occupancy that encompassed both mountain ranges and lowland areas) *Paris quadrifolia*, whereas Fig. 3B illustrates a larger shift for the small grassy (associated with a fast breeding rate) *Galium rotundifolium* than for the large woody (associated with a slow breeding rate) *Sorbus aria* (see also tables S1 and S2). Overall, species that shifted the most are mountainous species as compared with ubiquitous species (Fig. 4) [one-way analysis of variance (ANOVA), $F = 10.73$, $n = 171$, df = 1, $P < 10^{-4}$]. Similarly, most shifting species tend to have life forms (herbs, ferns, and mosses) involving faster life history traits (shorter life cycle, faster maturation, and smaller sizes at maturity) than do species showing a reduced shift (trees and shrubs) (Fig. 4) (one-way ANOVA, $F = 5.73$, $n = 171$, df = 1, $P = 0.02$). Larger distributional shifts for faster life cycle species are consistent with results already observed in vertebrate taxa (*8*). Similarly, larger shifts for

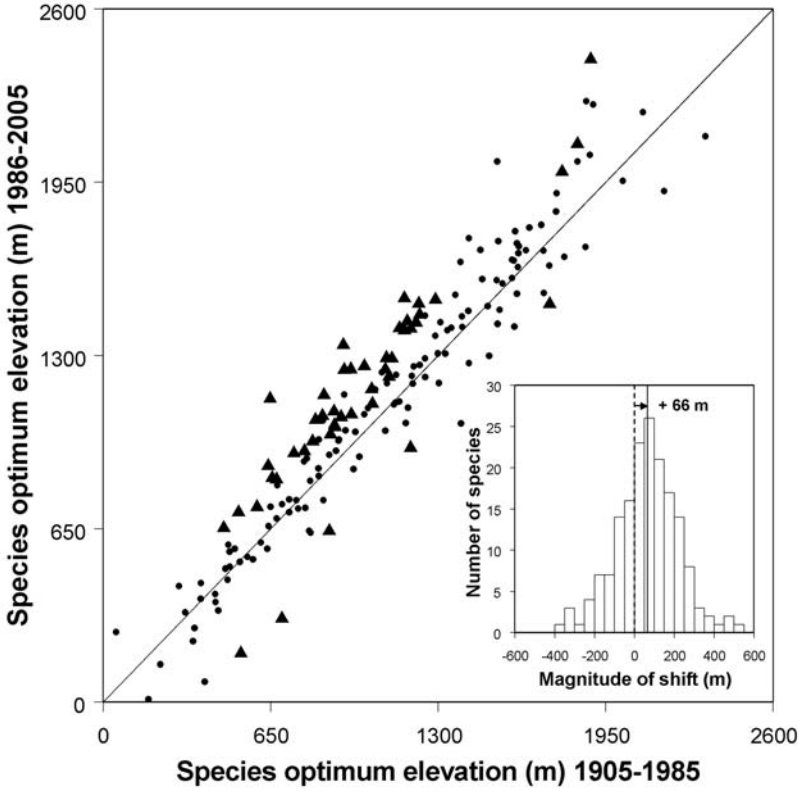

Fig. 2. Scatter diagram of forest plant species ($n = 171$) optimum elevation (i.e., altitude value at maximum probability of presence) for the periods 1905–1985 and 1986–2005. Each point represents one species: Species showing nonoverlapping 95% CIs around the optimum elevation between periods are displayed as solid triangles (▲) ($n = 46$), whereas species with overlapping 95% CIs are displayed as solid circles (●) ($n = 125$) (see tables S1 and S2 for details) (*23*). (**Inset**) The distribution of the species differences in optimum elevation between periods. The vertical dotted line marks zero shift, and the vertical solid line marks the median shift. The arrow describes the direction of the shift.

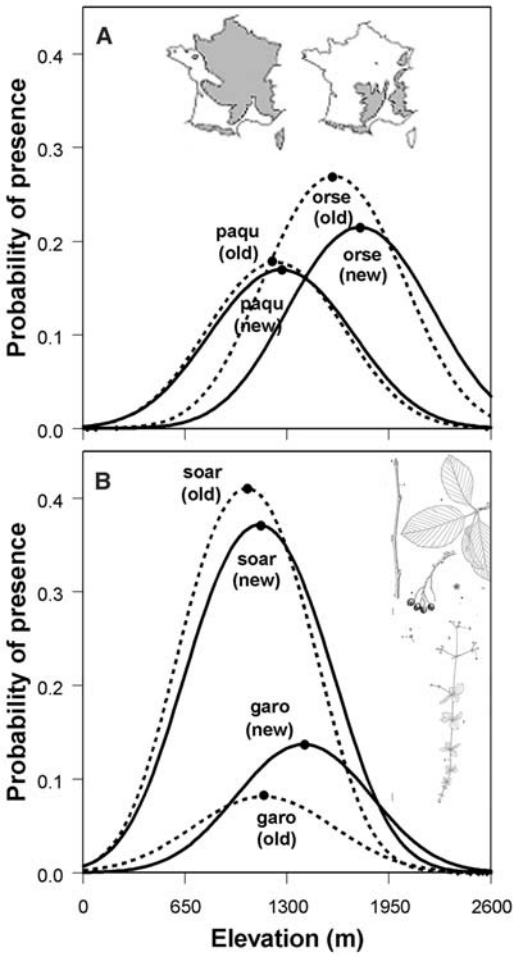

Fig. 3. Examples of western European plant distributions that have shifted upward. Elevational response curves derived with logistic regression models during 1905–1985 (dotted lines) and during 1986–2005 (solid lines) for two species according to geographic distribution pattern (**A**), ubiquitous *P. quadrifolia* (paqu) and mountainous *O. secunda* (orse), and also for two species according to life form (**B**), grassy *G. rotundifolium* (garo) and woody *S. aria* (soar). The solid circles (•) indicate the position of the optimum elevation. Maps and drawing pictures (D. Mansion) are from the Flore Forestière Française Sources (Institut pour le Développement Forestier).

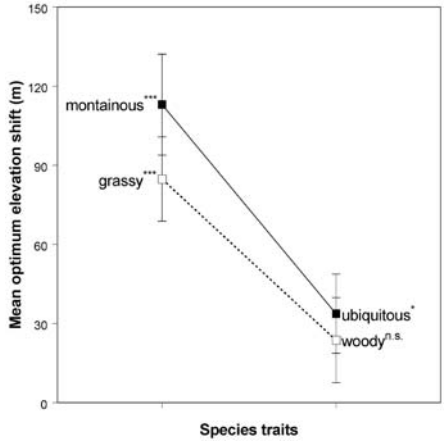

Fig. 4. Magnitude of optimum elevation shifts for plant species in relation to their ecological and life history traits (*23*). Shifts in mean optimum elevation according to geographic distribution pattern (solid line and symbols) correspond to ubiquitous (n = 104), and mountainous species (n = 67). Shifts in mean optimum elevation according to life form (dotted line and open symbols) correspond to woody (n = 56) and grassy species (n = 115). Means are shown with standard errors. Significance of the magnitude of mean shift from the null hypothesis of zero shift is displayed for each trait (n.s. indicates nonsignificant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; Student's paired sample t test).

mountainous species are in agreement with the suggestion that plant species would be more sensitive to climate change at high-altitude locations (*10*, *11*, *17*). There is no significant interaction between geographic distribution pattern and life form (two-way ANOVA, $F = 0.24$, $n = 171$, df = 1, $P = 0.63$), which rules out the possibility that forest plant species restricted to mountains show larger changes because most of them exhibit a grassy life form.

Recent meta-analyses have conclusively showed the response of species to climate change (*1*, *3*, *5*). However, little is known regarding how climate change interplay with other regional- to global-scale drivers of changes in affecting species distributions such as variation in precipitation regime, nitrogen (N) deposition, land-use changes, invasive species, and CO_2 increases. Decadal-scale variation in precipitation has remained the same before and after the slicing of our studied period (Fig. 1B); thus, it cannot directly affect the distributional changes we observed. Atmospheric N deposition are important at high elevations, with rates ranging from 6 to 30 kg ha^{-1} $year^{-1}$ in western European mountains (*33*). However, we found a slightly lesser but not significant N demand (*23*) for upward-shifting species as compared with those shifting downward (mean N demands for upward and downward species were 4.38 and 4.97, respectively; Student's two-sample t test, $t = 1.72$; $n = 127$; df = 125; $P = 0.09$); hence, N deposition did not explain the general upward shift. The effect of land-use changes can also be ruled out because we paid particular attention to restricting our analysis to mature forests (*23*), where land-use changes are of reduced magnitude. Lastly, neither invasive species introduction nor changing concentration of atmospheric CO_2 seem to be important in determining the observed regional pattern of positive shifts in altitudinal distributions; if present, no significant trend in altitudinal shift would be expected because these drivers are nondirectional regarding species responses and would affect as many increases as decreases.

The average magnitude of change in forest plant species optimum elevation across the entire altitudinal gradient [29.4 ± 10.9 m per decade (*23*)] closely matches the figure observed for the shift of alpine plants above the tree line [27.8 ± 14.6 m per decade (*12*)] and even improves the precision. Further, if we assume a temperature lapse rate of 0.6°C, our results imply a 0.39°C increase in 22 years, which is coherent with the observed warming trend, supporting the hypothesis that climate warming is the main driving force for the observed patterns. The wide variability in the magnitude of optimum elevation shifts among species within assemblages may likely result in the disruption of biotic interactions and the ecological networks wherein these species are embedded. Further studies aimed at disentangling the magnitude and consequences of these changes, and their impact on species persistence and ecosystem functioning, are urgently needed.

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27. The ecological amplitude is a proxy for the size of the species altitudinal range around the optimum elevation (*23*). We found no significant differences between 1905–1985 and 1986–2005 (mean difference in ecological amplitude 2.3 m, 95% CI = −11.9, 16.6; n = 171; Student's paired-sample t test, t = 0.32; df = 170; P = 0.75).
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Polarization of the *C. elegans* Embryo by RhoGAP-Mediated Exclusion of PAR-6 from Cell Contacts

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Early embryos of some metazoans polarize radially to facilitate critical patterning events such as gastrulation and asymmetric cell division; however, little is known about how radial polarity is established. Early embryos of *Caenorhabditis elegans* polarize radially when cell contacts restrict the polarity protein PAR-6 to contact-free cell surfaces, where PAR-6 regulates gastrulation movements. We have identified a Rho guanosine triphosphatase activating protein (RhoGAP), PAC-1, which mediates *C. elegans* radial polarity and gastrulation by excluding PAR-6 from contacted cell surfaces. We show that PAC-1 is recruited to cell contacts, and we suggest that PAC-1 controls radial polarity by restricting active CDC-42 to contact-free surfaces, where CDC-42 binds and recruits PAR-6. Thus, PAC-1 provides a dynamic molecular link between cell contacts and PAR proteins that polarizes embryos radially.

Early embryos can polarize radially when cell contacts differentiate the contacted (inner) and contact-free (outer) surfaces of each cell. Radial polarity, called compaction in mammals, provides a foundation for executing critical patterning events such as cell fate specification and gastrulation (*1*, *2*). For example, radial polarity in *Caenorhabditis elegans* allows gastrulating cells to enrich myosin at their outer surfaces; myosin constricts these surfaces to help drive gastrulating cells into the embryo (*2*, *3*). The *C. elegans* embryo polarizes radially when cell contacts restrict the polarity proteins PAR-6 [PSD-95/DLG/ZO-1 (PDZ) and semi-Cdc42/Rac-interactive-binding (semi-CRIB) domain protein], PAR-3 (PDZ domain protein), and PKC-3 (atypical protein kinase C) to the outer surfaces of early embryonic somatic cells (EES cells) (*2*, *4*–*6*). This "inner-outer" PAR asymmetry begins at the four-cell stage and persists through early embryogenesis (*6*). The molecular link between cell contacts and the inner-outer PAR asymmetries they induce to polarize embryos is not known.

To learn how radial polarity is established, we screened for mutations preventing the inner-outer asymmetry of green fluorescent protein (GFP)–tagged PAR-6 (PAR-6-GFP). Two mutations (*xn1* and *xn6*) in a gene we named *pac-1* (PAR-6-at-contacts) caused PAR-6-GFP to associate with both inner and outer surfaces of EES cells (Fig. 1, A and B). *pac-1* mutations are maternal-effect, and hereafter we refer to embryos produced by *pac-1(xn6)* mutant mothers as *pac-1* embryos.

We immunostained *pac-1* embryos to examine the localization of endogenous PAR proteins. PAR-6, PAR-3, and PKC-3 are restricted to outer surfaces of wild-type EES cells, but each protein showed a symmetric cortical localization in *pac-1* EES cells (Fig. 1, C to H, and table S2). PAR proteins within the zygote and germline precursor cell of wild-type early embryos develop anterior-posterior (A/P) asymmetries that are not patterned strictly by cell contacts. These PAR asymmetries appeared normal in *pac-1* embryos (fig. S1). *pac-1* mutations also did not disrupt PAR-6 asymmetry in epithelial cells, which are born at later stages and localize PAR-6 apically (*7*). Thus, *pac-1* is essential for contact-mediated PAR asymmetries that develop during radial polarization but appears dispensable for other types of PAR asymmetries.

Depleting PAR-6 or PAR-3 specifically from EES cells causes slowed gastrulation (*2*). In wild-type embryos, gastrulation begins when the two endodermal precursor cells (EPCs) ingress into the interior. We filmed *pac-1* embryos to determine whether loss of inner-outer PAR asymmetry also disrupts gastrulation. EPCs ingressed significantly more slowly in *pac-1* embryos (*8*) and were often present on the surface at a time that they would be internalized in wild type (Fig. 2, A and B, movies S1 and S2). Similar to embryos lacking PAR-3 or PAR-6 in EES cells (*2*), the slowed cell ingressions in *pac-1* embryos did not prevent EPC descendants from ultimately internalizing, and embryos were viable.

PAR-3 is required for nonmuscle myosin to concentrate at and constrict the EPC outer surfaces (*2*, *3*). To determine whether the gastrulation defects we detected might be explained by altered myosin localization or activity, we immunostained embryos for activated myosin regulatory light chain (p-rMLC) (*9*). In wild type, p-rMLC concentrated at outer surfaces of ingressing EPCs, similar to published reports (Fig. 2C) (*9*). By contrast, levels of p-rMLC at outer surfaces of *pac-1* EPCs were reduced significantly (Fig. 2D and fig. S2). These data suggest that PAC-1 regulates gastrulation by restricting PAR-3 to the outer cortex, where PAR-3 is needed to concentrate active myosin.

We cloned the *pac-1* gene (*8*), which encodes a protein containing a pleckstrin homology (PH) and a RhoGAP domain (Fig. 3A and fig. S3A). RhoGAP domains inhibit Rho guanosine triphosphatase (GTPase) signaling by converting active guanosine triphosphate–bound Rho proteins to inactive guanosine diphosphate–bound forms (*10*).

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