

## Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006)

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Spatial fingerprints of climate change on tree species distribution are usually detected at latitudinal or altitudinal extremes (arctic or alpine tree line), where temperatures play a key role in tree species distribution. However, early detection of recent climate change effects on tree species distribution across the overall temperature gradient remains poorly explored. Within French mountain forests, we investigated altitudinal distribution differences between seedling ( $\leq 50$  cm tall and  $> 1$  yr old) and adult ( $> 8$  m tall) life stages for 17 European tree taxa, encompassing the entire forest elevation range from lowlands to the subalpine vegetation belt (50–2250 m a.s.l.) and spanning the latitudinal gradient from northern temperate to southern Mediterranean forests. We simultaneously identified seedlings and adults within the same vegetation plots. These twin observations gave us the equivalent of exactly paired plots in space with seedlings reflecting a response to the studied warm period (1986–2006) and adults reflecting a response to a former and cooler period. For 13 out of 17 species, records of the mean altitude of presence at the seedling life stage are higher than that at the adult life stage. The low altitudinal distribution limit of occurrences at the seedling life stage is, on average, 29 m higher than that at the adult life stage which is significant. The high altitudinal distribution limit also shows a similar trend but which is not significant. Complementary analyses using modelling techniques and focusing on the optimum elevation (i.e. the central position inside distribution ranges) have confirmed differences between life stages altitudinal distribution. Seedlings optima are mostly higher than adults optimum, reaching, on average, a 69 m gap. This overall trend showing higher altitudinal distribution at the seedling life stage in comparison to the adult one suggests a main driver of change highly related to elevation, such as climate warming that occurs during the studied period. Other drivers of change that could play an important role across elevation or act at more specific scales are also discussed as potential contributors to explain our results.

Evidence is accumulating of changes on plant communities in relation to climate change (Walther 2004). Spatial fingerprints of climate change on plant species are usually associated with change in the distribution at latitudinal or altitudinal extremes (Sturm et al. 2001, Sanz-Elorza et al. 2003, Pauli et al. 2007). By focusing on the extremes, such information overlooks the overall latitudinal or altitudinal gradient. Detection of changes at only one point or within a truncated and narrow observation window of the geographic gradients, presents just one expression, albeit important, of the likely consequences of climate change. Changes along the overall latitudinal or altitudinal gradient and for multi-species distribution ranges remain poorly explored in plant species distribution despite existing evidence of a general pattern of shift towards newly suitable climatic conditions for herbaceous species (Lenoir et al. 2008).

Tree species distribution changes have been widely studied at their altitudinal extremes, namely the tree line ecotone (Cairns and Moen 2004, Gehrig-Fasel et al. 2007, Kullman 2007) as well as at the transition distribution margins between two tree species (Hattenschwiler and Körner 1995, Allen and Breshears 1998, Beckage et al. 2008). Nonetheless, it remains unclear whether climate change is the main driver of change. Disentangling all possible drivers of distribution changes is difficult since detection at one point or across a narrow range of elevation involves both large scale climatic variables (primary factors) and local scale biotic interactions (secondary factors) that control species altitudinal distribution. At high elevations, land-use change (Gehrig-Fasel et al. 2007), herbivory pressure (Cairns and Moen 2004) and species interactions such as facilitation of seedling establishment and survival (Akhalkatsi et al. 2006) are secondary drivers that have been

reported to act in concert with global warming and even overwhelmed it. Additionally, across truncated observation windows of elevation, secondary drivers of distribution changes have been reported to act in contrast with climate warming and even mask it (Hattenschwiler and Korner 1995). Detecting distribution changes at a larger scale, across a wide window of elevation in relation to recent warm conditions is complex for some plant species due to their long generation times (Lenoir et al. 2008). As of yet, no studies focusing on tree species distribution changes across their entire altitudinal distribution have reported changes at a multi-species scale. Only changes in the distribution of specific tree species have been related to climate change by spanning the whole range of their altitudinal distribution (Gworek et al. 2007, Penuelas et al. 2007). For species such as trees, which are both motionless and have long generation times, distribution changes are difficult to observe. The lack of historic field observations hampers the analysis of changes in tree species distribution along the overall altitudinal gradient.

Assuming niche conservatism over time (Peterson et al. 1999), we tested a multi-species (temperate and Mediterranean tree species) and a large-scale (from lowlands to the subalpine vegetation belt in western European mountains) climate-related response in tree species distribution. The observation of species at a young life stage (seedlings) depicts a response to recent climatic conditions. Presence/absence information of an older life stage (adults) of the same species at the same place reflects a response to former climatic conditions. We thus compared altitudinal distribution between seedling and adult life stages using paired observations of the same tree species in the same plot of ca 400 m<sup>2</sup> during a period of recent climate warming (1986–2006). Considering the entire altitudinal gradient covered by forests, climatic conditions are the most structuring factors to explain tree species distribution. Temperature conditions and water availability are the two main abiotic factors determining successful establishment and persistence of long-lived woody plants (Stephenson 1990). At high margins, extreme cold temperature may represent an absolute boundary for tree species survival (Vetaas 2002, Korner and Paulsen 2004) whereas at low margins of tree species distribution, warm temperatures also matter but in conjunction with water availability that has a strong effect (Stephenson 1990). Although increasing temperatures on their own probably do not limit seedling establishment in the ranges observed in our study area and even facilitate it at high margins, the related effects of water availability are likely to limit seedling establishment, especially at low margins. Hence, we hypothesised, in relation to climate warming, a distribution range at higher elevations for seedlings as compared to adults of the same species. We began with an exploratory data analysis of distribution records of the most common tree species along an altitudinal gradient spanning from lowlands to forest subalpine limits. This approach makes it possible to assess differences in species distribution between the two successional life stages, focusing on presence records from French floristic databases, without fitting any *a priori* distribution model. A modelling approach was then carried out to quantify distribution differences between seedlings and adults regardless of sampling intensity. We discuss our

results in relation to changes in abiotic and biotic conditions focusing on human-induced modifications such as climate warming, nitrogen deposition, land or pasture abandonment and game management as well as in relation to changes in species-environment relationships such as ontogenetic niche shift.

## Materials and methods

### Study area

We studied tree species from temperate and Mediterranean French forest communities between the lower collinean vegetation belt to the higher subalpine vegetation belt across the western Alps, the northern Pyrenees, the Massif Central, the western Jura, the Vosges and the Corsican range (Fig. 1a). Working over the entire altitudinal gradient covered by forest ecosystems makes it possible to browse a wide observation window of temperature conditions and thus to analyse distribution changes over the whole tree species range and especially in the most suitable part of it, namely the mean geographic location. The studied mountain ranges have undergone increases in mean annual temperature for the last 40 yr (Fig. 2a), including the 1990s as the warmest decade in France since the beginning of climate measurements (Moisselin et al. 2002). During the same period, the trend in rainfall has not exhibited any specific changes in French mountains (Fig. 2b).

### Retrospective approach

The development of a tree from seed to its mature form can be divided into different successional life stages (seedling, sapling, young tree, adult and mature adult). While the youngest stages (pre-reproductive) reflect actual and recent environmental conditions, older and mature stages (potentially reproductive) depict former conditions that prevailed when they established. To distinguish between successional life stages, we used the age-size relationship. However, this relationship is not linear as it depends on site fertility and climatic conditions, especially for intermediate life stages (saplings and young trees). It is also not linear at the tree line ecotone where the tree age-size relation can vary. To limit this difficulty, we eliminated the intermediate life stages (from 50 cm to 8 m tall), focusing on the youngest and the oldest life stages. We thus distinguished between seedling ( $\leq 50$  cm tall) and adult ( $> 8$  m tall) tree species, observed simultaneously in the same plots of ca 400 m<sup>2</sup> each and during the 1986–2006 period, analogous to exactly paired plots in space. First year seedlings, also called germination that are hyper-sensitive to inter- or even intra-annual climatic variations are not included in our analyses. Examining the earliest and latest developmental stages identified simultaneously on the same plots during the studied period made it possible to compare adults established far before 1985 (during the first half of the 20th century) and seedlings established mostly after 1985 (during the second half of the 20th century) without any bias due to spatial variation since the plots for adults and seedlings were located in the same sites.

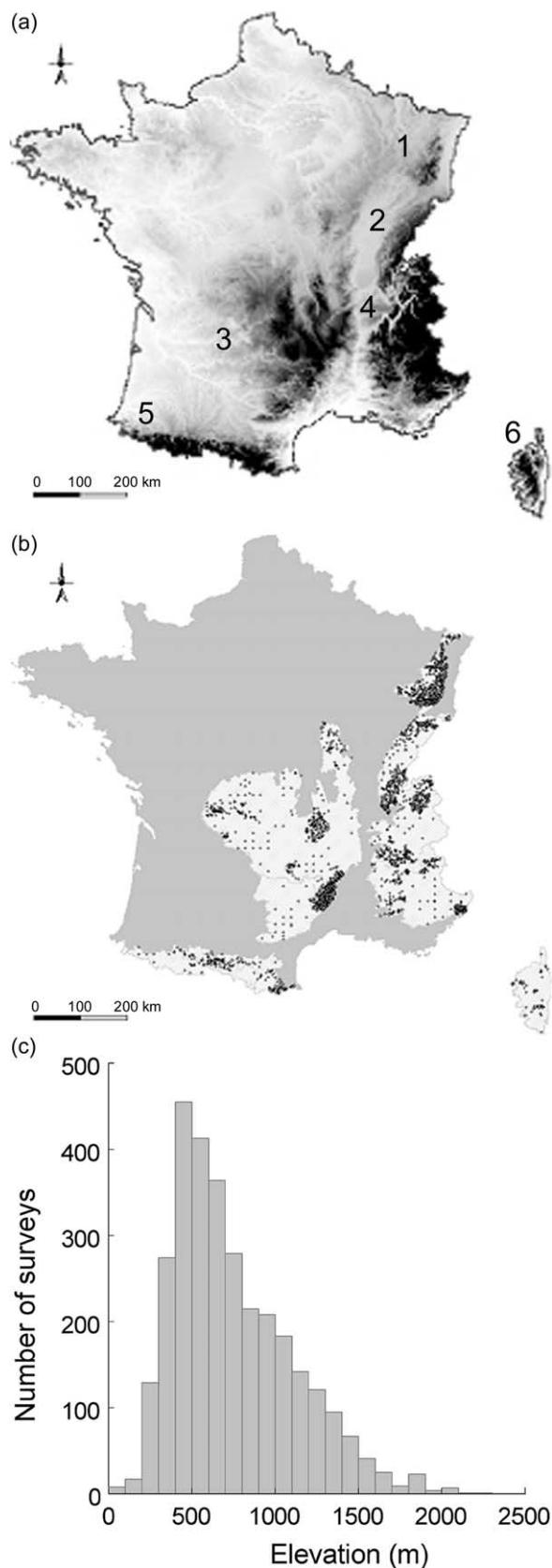


Figure 1. Location of mountain ranges in France: (a) 1–Vosges, 2–Jura, 3–Massif central, 4–Alpes, 5–Pyrenees, and 6–Corsica displaying the elevation gradient of (b) 3081 investigated forest sites during the 1986–2006 period from (c) 50 to 2250 m a.s.l. in elevation.

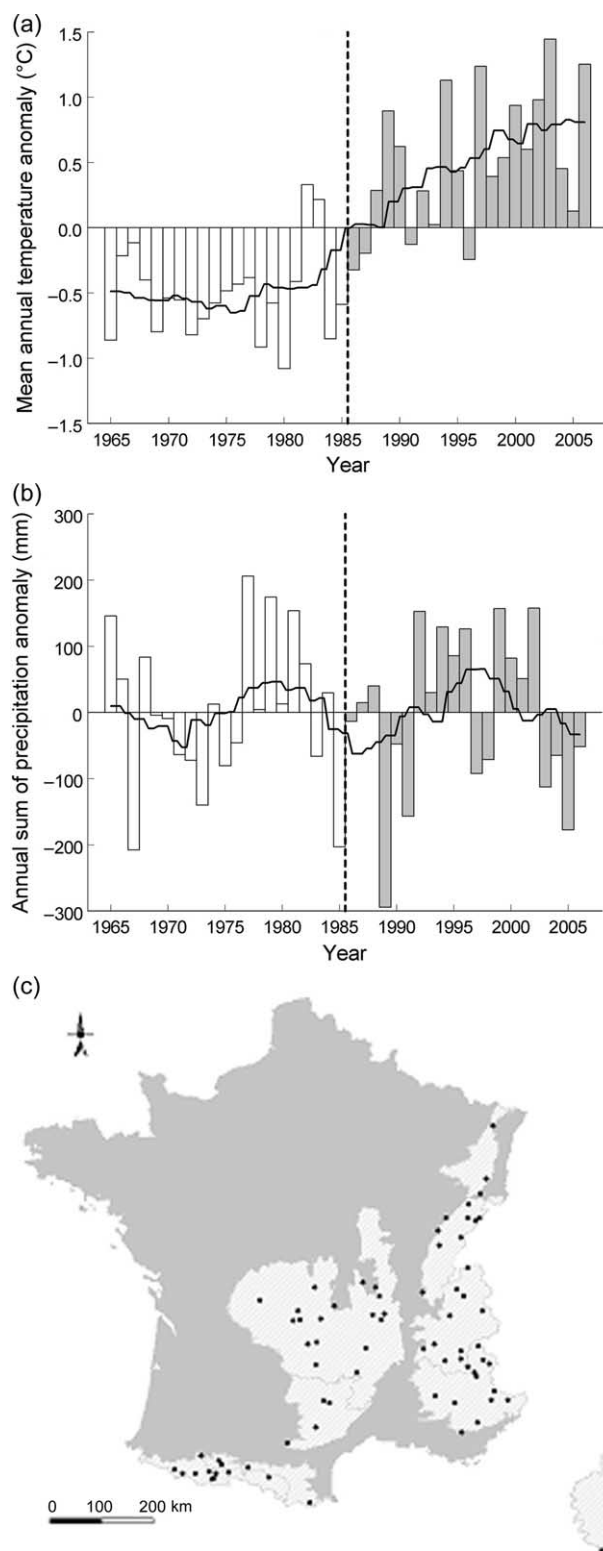


Figure 2. Trends in mean annual temperatures and precipitation sums from 1965 to 2006: (a) yearly-mean surface temperature anomalies (overall mean of temperature as baseline) and (b) annual sum of precipitation anomalies (overall mean of annual sum of precipitation as baseline) averaged for (c) 73 elevation sites in the French mountains ranging in altitude from 10 to 2010 m a.s.l. Filled grey bars refer to the sampled period. The dark curves have been smoothed with a ten year filter. Data were gathered from the French National Climatic Network (Météo-France).

It's intuitively more likely for a seedling to be present in a plot with an adult tree of the same species than in one without an adult. However, we considered that the probability for a seedling to be present without an adult tree of the same species in a circular plot of ca 11 m radius (400 m<sup>2</sup>) is highly dependant on edge dispersal from adults occurring in close vicinity and excluded from the surveyed plot. Making distinction between seedlings with an adult tree of the same species in a plot and seedlings without an adult did not allow us to separate edging dispersal effects from long dispersal events due to an unfair representativeness between seedlings and adults in plots we used. Therefore, we did not distinguish between these two observations in our study.

## Data collection

From two large-scale/long-term/multi-species French databases called Sophy (Brise et al. 1995) and EcoPlant (Gégout et al. 2005), we extracted forest vegetation plots containing species life stage details gathered across the mountain ranges studied from 50 to 2250 m a.s.l. during the 1986–2006 period, regarded as a warm period (Fig. 2a). We then looked at plots in close proximity to one another. Plots considered too close in location (i.e. within a 750 m radius) were removed to minimize spatial correlation and overweighing effects (Diniz-Filho et al. 2003). Finally, we excluded plots in which seedlings are present and adult trees are absent, assuming that such plots are not representative of mature forests but constitute dynamic stages (early stages of secondary succession) highly dependent on issues of land or pasture abandonment. Removing these plots rendered us to remain in mature forest stands including a canopy cover and to limit land-use issues. On the basis of these temporal, spatial and biological conditions 3081 forest vegetation plots were selected (Fig. 1b).

## Species selection

We excluded tree species with high risks of human introduction across French mountains (*Abies grandis*, *Quercus rubra*, *Picea abies*, *Pinus nigra*, *Pinus pinaster*, *Pinus sylvestris*, *Pinus strobus*, *Pseudotsuga menziesii*, and *Robinia pseudacacia*) and included only tree species that naturally occur in our study area with a lower risk of human introduction (n = 48). We then focused on tree species displaying both seedling and adult life stages and represented in each life stage by at least 50 occurrences within the 3081 plots (n = 17). Following this procedure made it possible to select the most common western European tree species from temperate and Mediterranean forests (see Table 1 for a species list) and to use modelling techniques to fit ecological response curves (Coudun and Gégout 2006). This set of tree species displayed a wide range of ecological requirements along the main ecological gradients: 1) species requirements spanned the whole gradient of temperatures from cold non-tolerant (*Carpinus betulus*, *Castanea sativa* and *Fraxinus excelsior*) to cold-tolerant species (*Abies alba*, *Fagus sylvatica* and *Sorbus aucuparia*) (Rameau et al. 1993); 2) they encompassed the whole gradient of water supply from water-demanding (*Acer platanoides*, *Fagus sylvatica* and

*Fraxinus excelsior*) to water stress-tolerant species (*Quercus ilex*, *Quercus pubescens* and *Sorbus aria*) (Rameau et al. 1993). Selected species also included wind-dispersal (*Abies alba*, *Acer opalus* and *Fraxinus excelsior*) and vertebrate-dispersal species (*Quercus petraea*, *Castanea sativa* and *Prunus avium*) (Rameau et al. 1993).

## Exploring differences between distributions at central positions and edges

Firstly, we carried out an exploratory approach using a non parametric method with a description of altitudinal presence records of tree species at each studied life stage. For each tree species at both life stages, we selected plots with presence values, sorted them by altitudinal locations and computed the nine altitudinal values which divide this frequency distribution into ten groups of equal frequency, namely deciles. To highlight differences between seedling and adult life stages at low, median and high elevations, we compared the 1st, 5th and 9th deciles respectively. Using deciles makes it possible to analyse the overall range of species distribution with strong assumptions on the median position (5th decile) and provides more robust indices of range edges (i.e. 1st and 9th deciles) than extreme values of occurrence observed on an elevation gradient.

Additionally, we computed the mean position of presence distribution for seedling and adult life stages along the elevation gradient. The comparison between mean and median altitudinal positions gives us an indication of skewness in tree species distribution along the elevation gradient.

## Modelling distribution and computing differences between central positions

Secondly, we fitted the probability that the species occurs at a site as a function of site position along the elevation gradient. To fit the species elevation response curve for each life stage, generalised additive models (GAM) (Hastie and Tibshirani 1990) were used to determine the shape of the response. For each studied species and at both life stages we examined structures in the response curve to elevation with a restricted cubic spline smoother (DF = 4). If linear or hump-shaped structures were detected, parametric tests were made using logistic regression models (ter Braak and Looman 1986), a particular family of generalised linear models (GLM) (McCullagh and Nelder 1997) that display a logit link function computed with the log-likelihood expression of a Bernoulli distribution (presence/absence):

$$\log \left[ \frac{p(S_i|ALT)}{1 - p(S_i|ALT)} \right] = a_0 + a_1 ALT \quad (1)$$

$$\log \left[ \frac{p(S_i|ALT)}{1 - p(S_i|ALT)} \right] = a_0 + a_1 ALT + a_2 ALT^2 \quad (2)$$

where  $p(S_i|ALT)$  describes the probability that the species occurs as a function of elevation (ALT) for both seedling ( $S_2$ ) and adult ( $S_1$ ) life stages. The parameters  $a_0$ ,  $a_1$  and  $a_2$  are the estimated coefficients of the logit model. We tested unimodality (2) against linearity (1) using the significance

Table 1. Logistic regression models (GLM) relating tree species occupancy to elevation at both life stages over the 1986–2006 period (17 species). Np = number of presence records in the complete data set;  $\delta L_{-2LL}$  = chi-square test of the drop in residual deviance between linear (one order polynomial of altitude) and null (no terms) models;  $\delta UL_{-2LL}$  = chi-square test of the drop in residual deviance between unimodal (two order polynomial of altitude) and linear (one order polynomial of altitude) models. Coefficients of the logistic models are  $a_0$ ,  $a_1$  and  $a_2$ . Significance: \*\*\* =  $p < 0.001$ ; \*\* =  $p < 0.01$ ; \* =  $p < 0.05$ ; n.s. = not significant.

Species name	Adult life-stage						Seedling life-stage					
	Np	$\delta L_{-2LL}$	$\delta UL_{-2LL}$	$a_0$	$a_1 (10^{-3})$	$a_2 (10^{-6})$	Np	$\delta L_{-2LL}$	$\delta UL_{-2LL}$	$a_0$	$a_1 (10^{-3})$	$a_2 (10^{-6})$
<i>Abies alba</i>	822	***	***	−4.4	7.0	−2.9	620	***	***	−4.8	6.7	−2.6
<i>Acer campestre</i>	187	***	***	−5.1	8.8	−6.9	170	*	***	−6.5	11.6	−7.9
<i>Acer opalus</i>	109	**	***	−7.3	9.5	−4.8	77	***	***	−7.5	7.9	−3.4
<i>Acer platanoides</i>	52	n.s.	**	−6.0	5.9	−3.7	64	n.s.	***	−7.4	10.3	−6.6
<i>Acer pseudoplatanus</i>	376	***	***	−4.2	4.7	−2.0	372	***	***	−4.3	5.4	−2.7
<i>Betula pendula</i>	192	n.s.	n.s.	−2.7	n.s.	n.s.	52	n.s.	**	−5.9	5.3	−3.2
<i>Carpinus betulus</i>	307	***	***	−2.8	7.2	−9.1	112	***	***	−7.6	20.3	−20.1
<i>Castanea sativa</i>	669	***	***	−2.4	8.2	−8.9	580	***	***	−3.1	9.4	−9.4
<i>Fagus sylvatica</i>	1 313	***	***	−3.2	6.5	−2.8	755	***	***	−4.6	7.6	−3.4
<i>Fraxinus excelsior</i>	434	***	***	−2.9	4.3	−3.3	478	n.s.	***	−3.7	5.8	−3.5
<i>Prunus avium</i>	204	***	***	−3.2	4.0	−4.0	146	***	***	−4.2	5.1	−4.2
<i>Quercus ilex</i>	154	***	n.s.	−1.3	−2.7	n.s.	228	***	***	−2.4	3.0	−4.5
<i>Quercus petraea</i>	532	***	***	−1.0	1.6	−3.2	216	***	***	−3.7	5.0	−4.2
<i>Quercus pubescens</i>	252	***	***	−3.8	5.5	−4.2	179	**	***	−3.8	3.8	−2.7
<i>Quercus robur</i>	284	***	n.s.	0.4	−4.6	n.s.	116	***	n.s.	−1.3	−3.3	n.s.
<i>Sorbus aria</i>	190	***	***	−6.6	8.5	−4.0	206	***	***	−5.5	6.2	−2.8
<i>Sorbus aucuparia</i>	120	***	***	−9.3	9.9	−3.2	373	***	***	−6.9	8.8	−3.1

of a residual deviance test based on a chi-squared distribution (Chambers and Hastie 1991).

Difference between seedling and adult central positions along the elevation gradient was computed solely for tree species displaying significant unimodal response curves at both life stages (i.e. if parameter  $a_2$  was significant according to the chi-square test of the drop in residual deviance). The central position, also called optimum “OPT” (3), was measured as the altitude position where the probability distribution reached the maximum. We computed differences between life stage central positions for both GAM and GLM techniques. Regarding GAM response curves, we extracted the mode of the probability distribution to estimate the central position, whereas for GLM models, the central position was calculated using parameters of the unimodal distribution model (ter Braak and Barendregt 1986):

$$\text{OPT} = -\frac{a_1}{2a_2} \quad (3)$$

Modelling techniques to fit ecological response curves are still under debate in the scientific community. Models fitted with second order polynomials are unimodal symmetric models and thus do not enable the production of asymmetry in a hump-shaped response curve. We thus assessed the validity of the symmetric assumption by testing the significance of unimodal parametric fits from GLM techniques (2) against smooth fits from GAM techniques using a residual deviance test based on a chi-squared distribution (Chambers and Hastie 1991). Fitting parametric models such as GLM renders possible the comparison and use of estimated parameters to better understand ecological processes, whereas non parametric methods like GAM do not provide parameters but are useful in tracking and testing assumptions about the shape of the final curves we will fit with parametric models.

### Analysing differences between distributions over the entire gradient

Thirdly, we used parametric models to compare probability of occupancy between seedlings and adults over the whole species elevation range to detect any contraction, expansion or translation processes. However, direct comparison of the probability of occupancy between life stages was not possible because the adult probability of occupancy reflected far more generations than that of seedlings. Thus, for each species life stage, probability of occupancy along the elevation gradient was first normalised relative to the maximum probability of occupancy within the studied elevation range (50–2250 m a.s.l.). We computed our own index that we called “PNORM” (4) for tree species displaying significant unimodal response curves at both life stages:

$$\text{PNORM} = \frac{\left[ \frac{1}{(1 + \exp(-(a_0 + a_1 \text{ALT} + a_2 \text{ALT}^2)))} \right]}{\left[ \frac{1}{(1 + \exp(-(a_0 + a_1 \text{OPT} + a_2 \text{OPT}^2)))} \right]} \quad (4)$$

Running PNORM over the elevation range (50–2250 m a.s.l.) also made it possible to compare life stages within the same species as well as between species. Next, we computed a function we called “PDIFF” (5) to assess a complete distribution difference between seedlings and adults:

$$\text{PDIFF} = \text{PNORM}(S_2|\text{ALT}) - \text{PNORM}(S_1|\text{ALT}) \quad (5)$$

where  $\text{PNORM}(S_2|\text{ALT})$  and  $\text{PNORM}(S_1|\text{ALT})$  represent normalised probability of presence along the elevation gradient for seedling ( $S_2$ ) and adult ( $S_1$ ) life stages respectively.

Once we had run the PDIFF function, the area under the PDIFF curve was computed using composite Simpson’s rule for integration, also known as the trapezoid method (Burden and Faires 2001). The integration altitudinal intervals were defined within the elevation range (50–2250 m a.s.l.) and delimited inside this range by altitudinal positions for which the PDIFF function displayed null values. We distinguished between altitudinal interval integration for which the PDIFF function was negative (contraction processes of the seedling distribution in comparison to the adult distribution “PDIFF.CON”) and altitudinal interval integration for which the PDIFF function was positive (expansion processes of the seedling distribution in comparison to the adult distribution “PDIFF.EXT”). The number of integration subintervals was chosen so as to obtain a relative precision of  $10^{-3}$ . Finally, we built a ratio of differences, that we called “RDIFF” (6), between seedling and adult distributions ranging from 0 to 1, meaning no differences and completely different distributions respectively. The RDIFF sign is given by the difference between optimum elevations at both life stages:

$$\text{RDIFF} = \frac{\text{OPT}.S_2 - \text{OPT}.S_1}{|\text{OPT}.S_2 - \text{OPT}.S_1|} \times \frac{\text{PDIFF.CON} + \text{PDIFF.EXT}}{\text{PNORM}.S_2 + \text{PNORM}.S_1} \quad (6)$$

where  $\text{OPT}.S_2$  and  $\text{OPT}.S_1$  describe optimum elevations at seedling ( $S_2$ ) and adult ( $S_1$ ) life stages.  $\text{PNORM}.S_2$  and  $\text{PNORM}.S_1$  designate areas under the PNORM curve at seedling ( $S_2$ ) and adult ( $S_1$ ) life stages. PDIFF.CON and PDIFF.EXT both refer to areas under the PDIFF curve for contraction ( $\text{PDIFF} < 0$ ) and expansion ( $\text{PDIFF} > 0$ ) processes respectively. Here, we summarised the ecological amplitude, taking into account all of the response curve information and giving a newer and more integrative vision to investigate possible niche differences between life stages: the “RDIFF” ratio. All computations were performed using the “S-Plus 2000 professional release 3” and the “R Development Core Team 2006” statistical packages.

## Results

### Data exploration focusing on central positions: median and mean

For 13 out of 17 species, the seedling life stage showed higher median elevation (5th decile) than the adult life stage within

the distribution of altitudinal presence records (Fig. 3). Conversely, *Acer platanoides*, *Acer pseudoplatanus*, *Sorbus aria* and *Sorbus aucuparia* displayed lower median elevations at the seedling life stage (Fig. 3). The 5th decile displayed a non significant tendency to be located higher in elevation at the seedling life stage than at the adult one (confidence interval for the difference in the location parameters  $CI[95\%] = [-7.5; 57.5]$ , Wilcoxon signed-rank test,  $V = 106$ ,  $n = 17$ ,  $p = 0.16$ , considering independence between species distribution). Regarding the mean altitude of presence records, differences between tree species life stages showed similar trends with a statistically significant positive difference of 26 m (confidence interval for the difference in the location parameters  $CI[95\%] = [2.1; 46.4]$ , Wilcoxon signed-rank test,  $V = 118$ ,  $n = 17$ ,  $p = 0.05$ , same hypothesis). Moreover, exactly the same 4 species displayed lower mean elevations at the seedling life stage. We also found an overall right-skewed structure (mean higher than median) that remained steady-state from seedling to adult life stage without any significant difference between life stages (confidence interval for the difference in the location parameters  $CI[95\%] = [-10.9; 16.4]$ , Wilcoxon signed-rank test,  $V = 100$ ,  $n = 17$ ,  $p = 0.27$ , same hypothesis). Overall, most species had a central position of seedlings at higher altitudes than adults over a 20 yr period stretching from 1986 to 2006. However, it's not clear if this trend is significant, depending on the criterion we used to assess differences in central positions between seedling and adult altitudinal distributions.

## Data exploration focusing on edges: 1st and 9th deciles

For 17 species, the overall difference between life stage presence records at low and high elevations showed that at both the upper and lower range limits, the seedling life stage displayed higher locations than the adult life stage. Figure 3 shows this general pattern of positive differences between seedlings and adults at the low altitudinal distribution limit (1st decile) with more species displaying positive differences from adults to seedlings (4 decreases, 11 increases). This overall trend was rather similar (6 decreases, 10 increases) at the high altitudinal distribution limit (9th decile). Differences at high elevations were however not as obvious as differences at low elevations. The 1st decile rose significantly, by ca 29 m from adults to seedlings (confidence interval for the difference in the location parameters  $CI[95\%] = [9.0; 45.0]$ , Wilcoxon signed-rank test,  $V = 100$ ,  $n = 17$ ,  $p = 0.02$ , considering independence between species distribution), whereas at the 9th decile, the difference was not significant despite a rise of ca 23 m in elevation (confidence interval for the difference in the location parameters  $CI[95\%] = [-10.5; 60.5]$ , Wilcoxon signed-rank test,  $V = 91$ ,  $n = 17$ ,  $p = 0.23$ , same hypothesis). Indeed, the confidence interval for the difference in the location parameters at the 9th decile had a wider range than the one at the 1st decile due to less intensive sampling at high elevations. The general pattern of differences between life stages is not evenly accurate between low

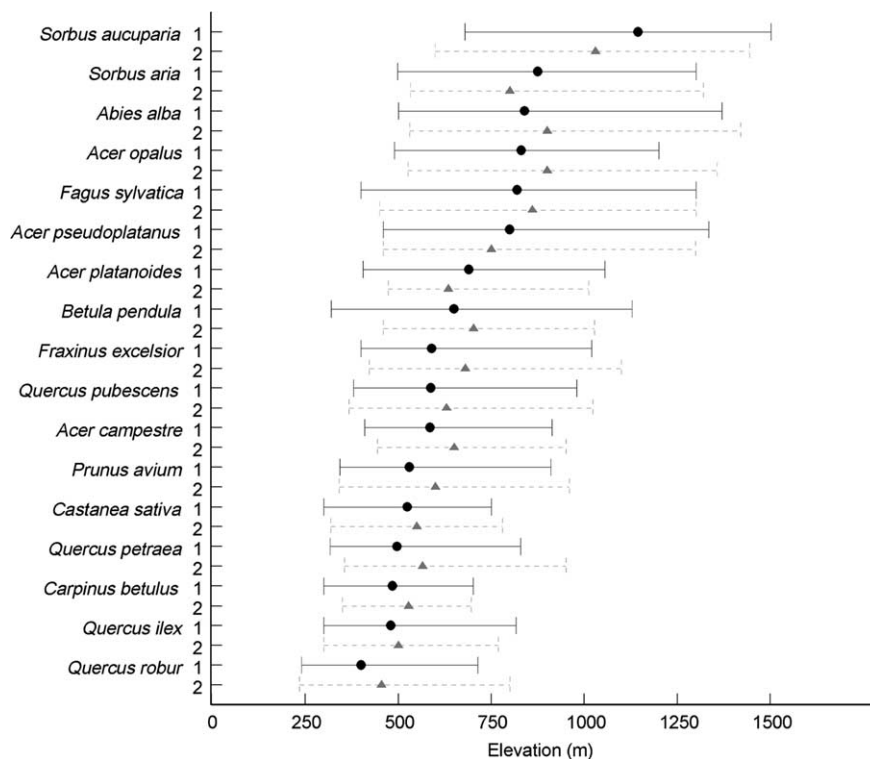


Figure 3. Comparison between seedling and adult presence records along the elevation gradient (17 species): 1st, 5th and 9th deciles of presence records for adult (1) and seedling (2) life stages. Symbols refer to the 5th decile and bars refer to lower (1st decile) and higher (9th decile) bounds.

(higher resolution) and high elevations (lower resolution) (Fig. 1c).

### Distribution models and differences between life stages at central positions

GAM mostly displayed hump-shaped structures in species presence records along the elevation gradient for both life stages. There was a strong uniform structure for *Betula pendula* at the adult life stage, signs of linear structure for *Quercus ilex* at the adult life stage and for *Quercus robur* at both life stages. A clear linear response was confirmed using GLM, with a highly significant one order polynomial and a non significant two order polynomial for *Quercus robur* at both life stages and for *Quercus ilex* at the adult life stage (Table 1). Similarly, GLM confirmed the absence of any relationship between altitude and *Betula pendula* presence records at the adult life stage (Table 1). All other species (14 species) had significant hump-shaped response curves against the linear model for both life stages according to elevation (Table 1). Among the 14 species (Table 2) whose optimum elevation “OPT” in both life stages fell within the available elevation range (from 50 to 2250 m a.s.l.), 4 species displayed lower OPT, whereas 10 species gave higher OPT at the seedling life stage than in the adult life stage (Fig. 4a). Globally, the difference in OPT between seedlings and adults was 69 m (confidence interval for the difference in the location parameters  $CI[95\%] = [-10.7; 131.6]$ , Wilcoxon signed-rank test,  $V=81$ ,  $n=14$ ,  $p=0.07$ , considering independence between species distribution). Similarly, the overall difference in mode between seedlings and adults using GAM was 68 m (confidence interval for the difference in the location parameters  $CI[95\%] = [-79.5; 204.5]$ , Wilcoxon signed-rank test,  $V=72$ ,  $n=14$ ,  $p=0.22$ , same hypothesis). Significant skewness (at the 0.001 level) appeared for *Abies alba* (at both life stages), *Castanea sativa* (at both life stages), *Fagus*

*sylvatica* (at the adult life stage), *Fraxinus excelsior* (at the seedling life stage), *Quercus petraea* (at the adult life stage) and *Sorbus aria* (at the seedling life stage). Thus, only 8 out of 28 hump-shaped response curves did not fit the symmetric assumption of second order polynomials. Here, we generalised the results we got from non parametric approaches independently from any sampling intensity, showing a similar pattern of differences for the optimum elevation between seedlings and adults.

### Distribution models and differences between life stages over the entire gradient

Figure 4b depicts 4 kinds of complete distribution differences (PDIFF) between seedling and adult normalised response curves (PNORM). Upward translation, implying contraction of seedlings at the low altitudinal distribution limit and expansion of seedlings at the high altitudinal distribution limit, was the main kind of difference, with 8 species displaying upward translation (*Abies alba*, *Acer campestre*, *Acer opalus*, *Carpinus betulus*, *Castanea sativa*, *Fraxinus excelsior*, *Prunus avium*, and *Quercus petraea*). Only 2 species displayed downward translation, implying expansion of seedlings at the low altitudinal distribution limit and contraction of seedlings at the high altitudinal distribution limit (*Acer pseudoplatanus* and *Sorbus aucuparia*). *Acer platanoides* and *Fagus sylvatica* depicted contraction of seedlings at both margins, whereas *Quercus pubescens* and *Sorbus aria* illustrated expansion of seedlings at both margins. The average ratio of difference over the complete altitudinal distribution between seedling and adult life stages (RDIFF) was not significant (confidence interval for the difference in the location parameters  $CI[95\%] = [-0.015; 0.145]$ , Wilcoxon signed-rank test,  $V=77$ ,  $n=14$ ,  $p=0.12$ , considering independence between species distribution).

Table 2. Differences in central position and over the entire elevation range between seedling ( $S_2$ ) and adult ( $S_1$ ) life stages (14 species). OPT refers to the altitudinal position where the probability of presence reaches a maximum, namely optimum elevation. PNORM designs the area under the normalised hump-shaped response curve. PDIFF.CON and PDIFF.EXT describe the area under the PDIFF curve from 50 to 2250 m a.s.l. for PDIFF <0 (contraction processes) and for PDIFF >0 (expansion processes) respectively. RDIFF is a ratio of difference between seedling and adult normalised distribution along the elevation gradient, ranging from -1 (altitudinal distribution of the seedling life stage is completely below the one of the adult life stage) to 1 (conversely).

Species name	Optimum elevation (m)			Area under curves (m per prob. units)				
	OPT. $S_1$	OPT. $S_2$	OPT. $S_2$ – OPT. $S_1$	PNORM. $S_1$	PNORM. $S_2$	PDIFF.CON	PDIFF.EXT	RDIFF
<i>Abies alba</i>	1 212	1 310	99	1 233	1 257	82	106	0.08
<i>Acer campestre</i>	639	736	97	690	648	115	73	0.14
<i>Acer opalus</i>	983	1 173	190	821	981	108	268	0.21
<i>Acer platanoides</i>	797	783	-13	917	696	221	0	-0.14
<i>Acer pseudoplatanus</i>	1 170	1 007	-164	1 310	1 129	250	69	-0.13
<i>Carpinus betulus</i>	393	505	112	592	405	208	21	0.23
<i>Castanea sativa</i>	460	499	39	652	631	44	23	0.05
<i>Fagus sylvatica</i>	1 145	1 130	-14	1 352	1 122	230	0	-0.09
<i>Fraxinus excelsior</i>	654	819	165	980	993	139	152	0.15
<i>Prunus avium</i>	495	606	111	832	843	85	96	0.11
<i>Quercus petraea</i>	240	586	346	868	1 036	164	233	0.21
<i>Quercus pubescens</i>	652	694	42	777	846	2	170	0.11
<i>Sorbus aria</i>	1 079	1 109	30	923	1 088	1	166	0.08
<i>Sorbus aucuparia</i>	1 542	1 422	-120	1 021	1 122	66	167	-0.11



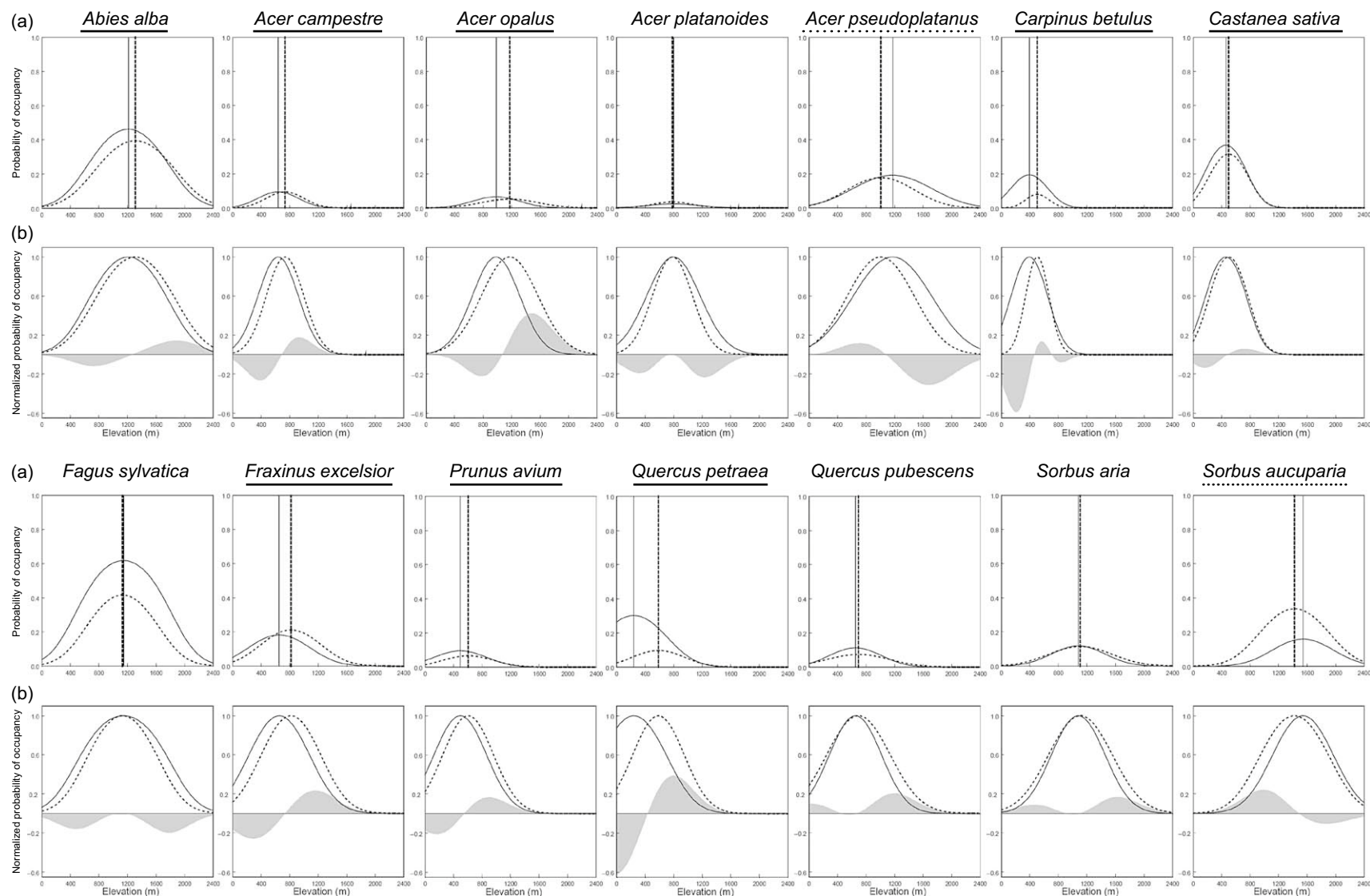


Figure 4. Elevational response curves derived with logistic regression models (14 species): (a) Probability of occupancy along the elevational gradient for adults (filled curve) and seedlings (dotted curve). Vertical lines show optimum elevation “OPT” with highest probability of occupancy for adults (filled line) and seedlings (dotted line). (b) Difference in normalised probability of occupancy (grey area curve) between adults (filled curve) and seedlings (dotted curve). Positive area under curve means expansion process (seedling colonisation), whereas negative area under curve means contraction process (seedling regression). Species with name underlined in filled black line translate upward, whereas species with name underlined in dotted black line translate downward.

## Discussion

### A general pattern with differences at a specific level

In accordance with our initial hypothesis, both modelling and exploring approaches have pointed out coherent evidence of a general pattern of positive differences between seedling and adult spatial distribution along the entire altitudinal gradient (50–2250 m a.s.l.) for 17 European tree taxa (temperate and Mediterranean species).

GAM and GLM analyses highlight an overall positive difference at the spatial core of altitudinal distribution ranges between seedling and adult optimum elevations with seedlings, on average, at 69 m higher elevation. This observation is similar to a former result showing a highly significant upward shift in forest plant species optimum elevation of 65 m during the 20th century (Lenoir et al. 2008). However, there are too few studies reporting altitudinal distribution differences between tree life stages to allow for comparison. In the Montseny mountains of north-east Spain, European beech forest replacement by holm oak forest has been described at medium altitudes within the central forest area (Penuelas et al. 2007). Additionally, one study has assessed a rapidly expanding population of Jeffrey pine *Pinus jeffreyi* at mid-elevation of its range, showing low adult tree mortality and high young tree recruitment in the semi-arid Carson Range of western Nevada (Gworek et al. 2007). These scattered observations on the mean altitudinal location of tree species distribution concerns only specific tree species without supplying any information at a multi-species scale.

Regarding our exploratory analyses at high elevation edges of tree species (9th decile), 10 European tree taxa have shown positive differences (Fig. 3), with seedlings at ca 23 m higher elevation. This result implies slowly expanding populations at high elevations but not significantly, similar to range expansions of alpine pioneer species at their leading edge in the high Alps (Pauli et al. 2007). However, as we remained within mature forest stands, differences we observed between the two life stages might be more important considering seedling establishment through secondary succession at the forest-grassland ecotone. Indeed, several and similar positive distribution differences between young and old life stages have been documented at the alpine tree line ecotone (Wardle and Coleman 1992, Akhalkatsi et al. 2006, Kullman 2007, Penuelas et al. 2007, Truong et al. 2007). Most alpine and arctic tree lines of the world show numerous seedlings above the forest limit. Many form krummholtz that may fluctuate over time (Lavoie and Payette 1994), since krummholtz represents a structural transition between forest and tundra where seedlings can grow but not adults for aerodynamic reasons. Concurrently, there are also studies that found no obvious positive differences between life stages, such as the absence of *Pinus sylvestris* seedlings above the adult high altitudinal distribution limit and within the *Pinus sylvestris*-*Pinus cembra* ecocline, suggesting stabilisation (Hattenschwiler and Korner 1995).

At low elevation edges of tree species (1st decile), exploratory analyses have shown that 11 European tree taxa displayed positive differences (Fig. 3), with seedlings at ca 29 m higher elevation. This significant result represents a

contracting population at low elevations through low frequency of recruits under adults, which is rather similar to an ongoing range contraction of subnival to nival species at their rear edge in the high Alps (Pauli et al. 2007). Concerning trees, species specific case studies show that low recruitment has already been reported for *Pinus jeffreyi* (Gworek et al. 2007) and *Fagus sylvatica* (Penuelas et al. 2007) at their low altitudinal distribution limit. Although there has been evidence for contractions at low elevations (Allen and Breshears 1998), there are also case studies that show static positions at the low tree line of *Quercus emoryi* (Germaine and McPherson 1999) or expansions of *Pinus cembra* young individuals below the low altitudinal distribution limit of adult trees (Hattenschwiler and Korner 1995).

Overall, there is a wide range of heterogeneous responses in the scientific literature in regard to altitudinal distribution differences between tree life stages, some of which are more coherent to our general pattern of differences along the elevation gradient (Gworek et al. 2007, Penuelas et al. 2007) and some of which are less (Hattenschwiler and Korner 1995, Germaine and McPherson 1999). However, at a species specific level, we also provide a wide range of heterogeneous responses (Fig. 4), distinguishing between the most frequent case of seedlings found at higher elevation (*Abies alba*, *Acer campestre*, *Acer opalus*, *Carpinus betulus*, *Castanea sativa*, *Fraxinus excelsior*, *Prunus avium*, and *Quercus petraea*) and the less frequent case of seedlings found at lower elevations (*Acer pseudoplatanus* and *Sorbus aucuparia*) with some intermediate cases showing no obvious differences (*Acer platanoides*, *Fagus sylvatica*, *Quercus pubescens*, and *Sorbus aria*). We thus conclude to a general pattern, which is significant at low elevation edges of tree species, but not to a systematic one.

### Change in abiotic and biotic conditions: human-induced modifications

Current adult life stage have been established long before current seedling establishment, reflecting abiotic and biotic conditions that prevailed long before the studied period. It is now widely agreed that recent human-induced modifications have major consequences on abiotic and biotic conditions (Vitousek et al. 1997). To identify the underlying cause of differences between seedling and adult altitudinal distribution, it is necessary to consider all possible abiotic and biotic drivers of change, including global warming, nitrogen deposition, land-use change and game management.

Climatic change in France has been characterized by increases in average temperature of great amplitude reaching 0.9°C (Moisselin et al. 2002) and even close to 1°C in the alpine region (Beniston et al. 1997). If each rise of 100 m in altitude corresponds to a 0.6°C drop in mean temperature (Woodward 1987), the 69 m difference we observed between seedlings and adults optimum elevation will imply a 0.4°C increase which is less than half the observed warming trend in France. To be coherent with the observed warming trend in France, we would have expected a 150 m difference between seedling and adult altitudinal distributions. This gap between observation and expectation

suggests dispersal limitations in European tree species (Svenning and Skov 2004). Beyond this potential disruption between the pace of climate warming and tree species dispersal abilities, quasi-systematic positive differences we observed between seedling and adult distributions along the entire altitudinal gradient suggest a wide-acting and consistent explanatory factor highly connected to elevation, such as climate. It supports the hypothesis that climate is the main driving force for the observed patterns (Lenoir et al. 2008). At high elevation, seedling establishment above the current limit of adults for a majority of European tree taxa (Fig. 3) suggests a temperature increase that slightly relieves the absolute boundary represented by extreme cold temperature. In northern Sweden, recent expansion of young recruits above the tree line has been related to climate warming using genetic and ecological analyses (Truong et al. 2007). Climate change has been considered a major driver of change at the alpine tree line by several studies focusing on seedling recruitment above this ecotone (Wardle and Coleman 1992, Sanz-Elorza et al. 2003, Kullman 2007, Penuelas et al. 2007), deemed to be one of the areas most sensitive to increasing temperature. At lower elevations, low frequency of recruits does not suggest a direct impact of temperature increase, assuming that tree species are more tolerant to warm temperatures (Vetaas 2002). However, in French mountains, the trend of increasing temperature in addition to the absence of change in precipitation (Fig. 2) may potentially change the evapotranspiration rate that could decrease the plant water availability at the low limit of species altitudinal distribution. Indeed, a long summer dry season and heat stress can limit seedling establishment at low elevations (Gworek et al. 2007), sometimes implying drought-induced shift of lower forest ecotones (Allen and Breshears 1998). Temperature and water availability are two potential drivers to explain our results at low elevations, but it is difficult to figure out which one of these two drivers here is the main one since water availability is highly connected to temperature.

Atmospheric nitrogen throughfall deposition has become one of the most important agents of vegetation change in densely populated regions. Nitrogen throughfall deposition rates have been reported to be from 6 to 30 kg ha<sup>-1</sup> yr<sup>-1</sup> in French mountain range ecosystems (Dambrine et al. 1994). These important deposition rates at high elevations suggest a potential pattern of increase nitrogen depositions with increasing altitude, which might contribute to increase seedling establishment above the upper limit of their adult altitudinal distribution by improving nutrient conditions at high elevations where nutrition is a more limiting factor. It cannot, however, be involved in explaining low seedling recruitment at the lower limit of their adult altitudinal distribution.

Land or pasture abandonment and forest cover change have been widely studied in European countries (Lepart and Debussche 1992, Debussche et al. 1999, Gehrig-Fasel et al. 2007). Besides temperature effects, the tree line ecotone in the Alps is assumed to have been largely determined by land-use management (Dirnbock et al. 2003). In the Swiss Alps, 96% of upper montane cover change in recent years has been explained by filling of gaps due to land-use change (Gehrig-Fasel et al. 2007). However, we paid particular attention in remaining within mature forest stands exclud-

ing early stages of secondary succession so as to avoid land-use change issues. To check this condition, we looked at the adult tree species composition above each species at the seedling life stage. Since it concerns issues of successions and replacement, we only focused on seedlings presence in a plot without an adult tree of the same species. For example *Abies alba*, *Acer campestre*, *Acer opalus*, *Acer platanoides*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Quercus petraea*, and *Sorbus aria* seedlings were mostly found under *Fagus sylvatica* stands. Additionally, *Fagus sylvatica*, *Quercus robur* and *Sorbus aucuparia* seedlings were mostly found under *Abies alba* stands and *Carpinus betulus* under *Quercus petraea* stands. Overall, seedlings that shifted outside their respective adult life stage are thus replacing stands of *Abies alba*, *Fagus sylvatica* and *Quercus petraea* that are species of late successional stages characteristic of mature forests. However, *Prunus avium*, *Quercus pubescens* and *Quercus ilex* seedlings were mostly found under *Castanea sativa* stands which is not a species characteristic of mature forests. *Betula pendula* and *Castanea sativa* were mostly found under adult tree species not included in our analyses. Only for these 5 species, seedlings that shifted outside their respective adult life stage distribution may potentially result in replacement of stands at early successional stages following pasture abandonment. Hence, our analysis does not involve the role of land or pasture abandonment as the most important general driver of the differences we observed.

Forestry practices including game management to control the recruitment rate of young trees is another possible cause of differences between seedling and adult distributions. It is common knowledge that hunting practices can control population size and browsing behaviour. It is also well documented that herbivorous mammals may change succession patterns of trees by slowing down the recruitment rate. For example, lower herbivory pressure in conjunction with climate change has been associated with increasing numbers of small trees above the current tree line in northern Sweden, suggesting that herbivory needs to be considered as a potentially significant driver of change (Cairns and Moen 2004). In 2005, red deer populations density in French mountains (the western Alps, the northern Pyrenees and the Massif Central) has been reported to be nine times more important than in 1985 (Pfaff et al. 2008), which implies an important browsing pressure for seedlings in mountain area during our studied period. Nonetheless, this increasing trend has been far greater at high elevations with area occupied by red deer increasing from 8 to 44% above 1500 m in comparison to area occupied by red deer below 600 m that increased from 13 to 22% (Pfaff et al. 2008). It suggests a potential increase browsing with increasing altitude from 1985 to 2005, which is in contradiction with our results showing that seedlings are located higher in elevation than adults during the same period. As a result, even if ungulates could act generating a general pattern along the elevation gradient, it cannot be comprehensively involved here to explain our results.

At a specific scale, change in any individual species at any location may have a number of possible explanations, but the overall effects of most confounding factors decline with an increasing number of species studied and zooming out of

the spatial scale involved (Parmesan and Yohe 2003). Indeed, all drivers of change in abiotic and/or biotic conditions that we reviewed above may potentially explain differences we observed between seedling and adult distribution if we consider each species separately and/or each part of the altitudinal gradient separately. However, the general pattern pointed out for 17 European tree taxa along the entire altitudinal gradient covered by forests can only be attributed to primary factors that affect species distribution and are globally coherent with such a pattern. Thus, among drivers modifying abiotic and biotic conditions and explaining altitudinal distribution differences between life stages, climate warming can be considered as the main driver, modulated and/or facilitated by other secondary drivers.

### Change in species–environment relationships: ontogenetic niche shift

It is generally accepted that plants change their abiotic requirements during their lives (Putwain and Harper 1970, Grubb 1977, Parrish and Bazzaz 1985). Individual species autecology from seedling to adult involves changes in species–environment relationships (abiotic requirements and/or biotic interactions) during the life span of species, namely ontogenetic niche shifts (Parrish and Bazzaz 1985, Eriksson 2002, Miriti 2006).

In our study, *Quercus ilex* displayed a negative linear relationship with altitude at the adult life stage and a hump-shaped response curve at the seedling life stage (Table 1), which perhaps best illustrates that thermophilous species adapted to warm conditions can also tolerate frost damage at a juvenile stage. Indeed plant species admit several stress tolerance strategies to cope with shortages of resources from seedling to adult life stage (Grubb 1998). Moreover, positive spatial associations between seedlings of one species and sheltering adults of another species through facilitation are common, especially at ecotones (Callaway and Walker 1997, Akhalkatsi et al. 2006). Ontogenetic niche shift may thus also explain differences we observed between seedling and adult life stages. Previous studies have already demonstrated that seedling and adult life stages present different spatial distribution patterns (Stohlgren et al. 1998, Battaglia et al. 2000, Collins and Carson 2004, Tsujino and Yumoto 2007), but none have demonstrated such a general pattern observed for temperate and Mediterranean tree species. However, there is no comprehensive reason that seedling stress tolerance to increasing harsh conditions along the altitudinal gradient would systematically be higher than that of adults, nor that facilitation of seedlings would systematically occur only at the high altitudinal distribution limit of adults and not at the low altitudinal distribution of adults. Ontogenetic niche shift cannot easily explain the observed pattern of positive differences between seedling and adult life stages along the altitudinal gradient, especially at low elevations. At low elevations positive differences are difficult to relate to ontogenetic niche shift since the future distribution of current seedlings would not match current distribution of adults in a stable environment.

## Conclusion

We provide results showing an overall positive difference between seedling and adult altitudinal distributions with seedling, on average, at 69 m higher elevation. This general pattern for 17 European tree taxa over the entire altitudinal gradient covered by forest ecosystems may involve a multi-species and/or a large-scale comprehensive driver of change. Climate warming is the most reliable driver of change capable of acting at a multi-species scale along a wide altitudinal range and in agreement with our results, whereas nitrogen deposition, game management and ontogenetic niche shift might be considered as secondary and/or modulating drivers acting at a species specific level and/or a regional specific scale.

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