Disparity in elevational shifts of European trees in response to recent climate warming

SONIA G. RABASA*, ELENA GRANDA*, RAQUEL BENAVIDES*, GEORGES KUNSTLER†, JOSEP M. ESPELTA‡, ROMÁ OGAYA‡§, JOSEP PEÑUELAS‡§, MICHAEL SCHERER-LORENZEN¶, WOJCIECH GIL‖, WOJCIECH GRODZKI**, SLAWOMIR AMBROZY**, JOHAN BERGH††, JOSÉ A. HÓDAR‡‡, REGINO ZAMORA‡‡ and FERNANDO VALLADARES*

*Laboratorio Internacional de Cambio Global LINCGlobal, Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales (MNCN), CSIC, Serrano 115 dpdo, 28006 Madrid, Spain, †Cemagref – U.R. Ecosystèmes Montagnards, 2 rue de la Papeterie, BP 76 38402, St-Martin-d'Heres Cedex, France, ‡CREAF, Cerdanyola del Vallès, 08193 Spain, §CSIC, Global Ecology Unit CREAF-CEAB-UAB, Cerdanyola del Vallès, 08193 Spain, ¶Faculty of Biology, Department of Geobotany, University of Freiburg, Schaenzlestr. 1, D-79104 Freiburg, Germany, ‖Department of Silviculture and Genetics, Forest Research Institute, Braci Lesnej 3, 05-090 Raszyn, Poland, **Department of Mountain Forestry, Forest Research Institute, Fredry 39, 30-605 Krakow, Poland, ††Swedish Forest Research Center, Department of Southern Swedish Forest, Swedish University of Agricultural Sciences (SLU), Skogsmarksgränd, SE- 901 83 Umea, Sweden, ‡‡Department of Ecology, Universidad de Granada, Campus de Fuentenueva s/n, 18071 Granada, Spain

Abstract

Predicting climate-driven changes in plant distribution is crucial for biodiversity conservation and management under recent climate change. Climate warming is expected to induce movement of species upslope and towards higher latitudes. However, the mechanisms and physiological processes behind the altitudinal and latitudinal distribution range of a tree species are complex and depend on each tree species features and vary over ontogenetic stages. We investigated the altitudinal distribution differences between juvenile and adult individuals of seven major European tree species along elevational transects covering a wide latitudinal range from southern Spain (37°N) to northern Sweden (67°N). By comparing juvenile and adult distributions (shifts on the optimum position and the range limits) we assessed the response of species to present climate conditions in relation to previous conditions that prevailed when adults were established. Mean temperature increased by 0.86 °C on average at our sites during the last decade compared with previous 30-year period. Only one of the species studied, *Abies alba*, matched the expected predictions under the observed warming, with a maximum abundance of juveniles at higher altitudes than adults. Three species, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*, showed an opposite pattern while for other three species, such as *Quercus ilex*, *Acer pseudoplatanus* and *Q. petraea,* we were no able to detect changes in distribution. These findings are in contrast with theoretical predictions and show that tree responses to climate change are complex and are obscured not only by other environmental factors but also by internal processes related to ontogeny and demography.

Keywords: altitudinal gradient, climate change, forest, generalized additive models, species distribution

Received 25 October 2012 and accepted 4 March 2013

Introduction

Predicting species responses to climate change is a major challenge for ecology and biodiversity conservation. Evidence for climate change has been documented on many biological processes, such as phenology, physiology and species distribution, in both animal and plants (Peñuelas & Filella, 2001; Walther *et al.*, 2002; Parmesan, 2006; Rosenzweig *et al.*, 2007). For plants, analyses of long-term data sets have shown clear advances in budding, leafing and timing in flowering

with increasing temperature (Peñuelas *et al.*, 2002; Walther *et al.*, 2002; Menzel *et al.*, 2006). The biological responses to warming at the individual level affect the population responses and can lead to changes in the distributional ranges of species. Simulations, mainly elaborated from niche-based models over the last decade, have predicted that ranges of species will be shifted polewards and towards higher elevations in response to future climatic scenarios with elevated temperatures (Thuiller *et al.*, 2005; Hickler *et al.*, 2012). These expectations are supported by several studies and they have reported that global warming influences on species ranges (e.g. Parmesan & Yohe, 2003; Lenoir *et al.*, 2008). Despite that, evidence for range shifts in

Correspondence: Sonia G. Rabasa, tel. +34 91452500,
fax +34 915640800, e-mail: sonia.rabasa@mncn.csic.es

woody plants remains scarce, with most of them coming from local and single-species studies. In Spain, Peñuelas & Boada (2003) and Peñuelas *et al.* (2007) detected an upward shift of ca. 70 m in the altitudinal distribution of *Fagus sylvatica* in the last 55 years. Similarly in France, Lenoir *et al.* (2008) reported an average altitudinal shift of 29 m per decade in the optimum elevation of 171 forest plant species in relation with increasing temperature over the study period, although the shift in the optimum was smaller and nonstatistically significant when only woody species were considered (+9 m per decade, $n = 56$ woody species). Upward shifts in the distribution of woody plants have been also observed in the United States, in South Carolina (Kelly & Goulden, 2008) and in Green Mountains (Vermont) (Beckage *et al.*, 2008) consistent with changes in regional climate. Many studies have also evidenced the advance of treeline in response to climate change (e.g. Moiseev & Shiyatov, 2003; Danby & Hik, 2007; Kammer *et al.*, 2009).

However, some of these studies have also found species range shifts in contrast with theoretical predictions (Lenoir *et al.*, 2010). Species-specific responses to climate change are likely to be much more complex than those simply predicted by the effects of warming temperatures and changing precipitations. For example, it remains largely unclear whether and how different responses to climate change in interacting species might influence future species distributions. A very recent study investigating how biotic interactions are affecting the elevational ranges of arctic-alpine species has concluded that dominant species appear to exert a strong influence on the elevational distribution of other species at high latitude environments regardless of abiotic variables (le Roux *et al.*, 2012). In addition, range shifts driven by climate change can only be achieved by organisms with a sufficient dispersal capacity, which may be a limiting factor for many tree species. Although the seeds of many trees can be dispersed over rather large distances, the bulk of the seeds are usually carried only tens of metres. Thus, factors like species interactions and dispersal and colonization capacities together with local environmental heterogeneity can profoundly influence the potential elevational or latitudinal shift in response to global warming.

In this study, we investigated the differences in altitudinal distribution between juvenile and adult individuals of seven major European tree species. Altitudinal gradients have been commonly used to study the impacts of climate change as changes in altitude reproduce the predicted climate changes in temperature. Due to inconsistencies in periodic forest inventories, detecting range shifts over time from long-term forest data sets across large regions becomes very difficult. As an alternative we compare juvenile distribution to distribution of adult trees. Assuming a lower temperature climate at the time when adult trees were established, we expect a higher elevational position of juveniles because they were established in a warmer climate. A limitation of this approach is that temperature sensitivity and response capacity differs between adults and juveniles of the same species. In fact, different responses to climate have been recorded between different ontogenetic stages (Donovan & Ehleringer, 1994; Cavender-Bares & Bazzaz, 2000). Nevertheless, the elevational distributions of the two contrasting cohorts represent a proxy for eventual demographic and distribution changes induced by climate as argued by other authors (e.g. Lenoir *et al.*, 2009; Woodall *et al.*, 2009; Vitasse *et al.*, 2012; Zhu *et al.*, 2012). Our main goal is to detect recent changes in the distribution of main dominant tree species in Europe and to contribute to the knowledge of how European forests are responding to recent global warming.

Materials and methods

Study area and data collection

The study was conducted at eight different sites located along a latitudinal gradient across Europe, from southern Spain to northern Sweden (Fig. 1). We selected an altitudinal gradient at each site. Table 1 provides a brief description of the study sites, including information about the elevational, temperature and precipitation ranges of each site, as well as tree species occurring there. According to the records from meteorological stations, the mean annual temperature of all sites increased on average by 0.86 °C in the last decade compared to the previous 30 years (except in Sweden where we were not able to detect any change due to the small data set; Table 2). We observed no consistent changes in precipitation between the two periods (Table 2).

Samplings were carried out between 2009 and 2011 (see Table 1 for more details). On each altitudinal gradient, we established a number of transects according to the altitudinal range, separated from each other by at least 100 m in altitude (50 m for Swedish transects, where the temperature decreases more rapidly with increasing altitude; Stone & Carlson, 1979). To minimize the effect of forest management we selected plots with no management evidences over the past 40 years.

For recording adult and juvenile abundances we established circular plots of 20 m radius along each transect on each site. The number of circular plots varied among 4 and 6 plots per altitude. We recorded the number of adult individuals (defined as individuals with a dbh > 10 cm) of all tree species that occurred in a plot. The abundance of juveniles (up to 50 cm in height) was recorded in 1 m^2 subplots in the centre of each plot. The number of these subplots varied among species, with four for species with high density (five or more individuals within the four central subplots), and increased to 16 for low density species (<5 individuals in the four central subplots, e.g. *Quercus*
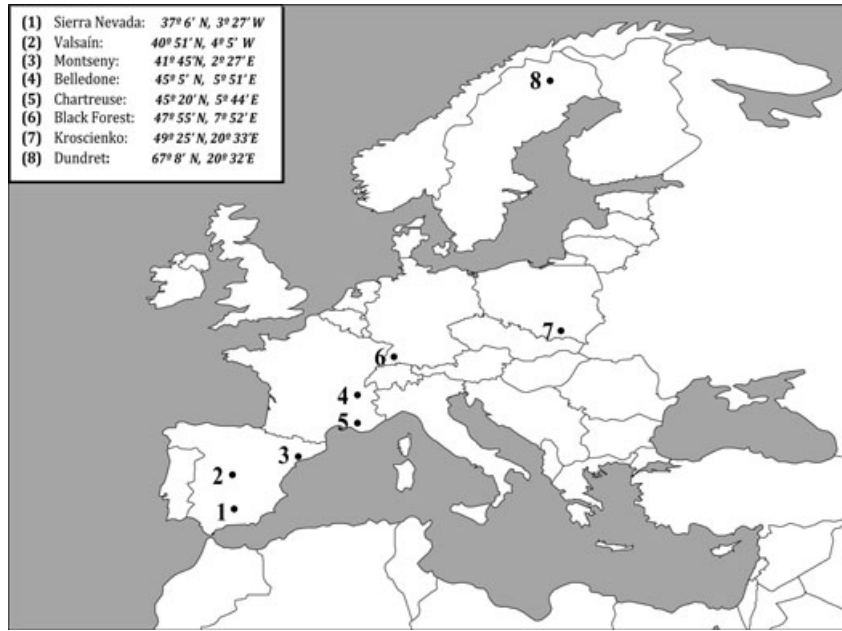
(1) Sierra Nevada: 37º 6' N, 3º 27' W
(2) Valsaín: 40º 51' N, 4º 5' W
(3) Montseny: 41º 45'N, 2º 27' E
(4) Belledone: 45º 5' N, 5º 51' E
(5) Chartreuse: 45º 20' N, 5º 44' E
(6) Black Forest: 47º 55' N, 7º 52' E
(7) Kroscienko: 49º 25' N, 20º 33'E
(8) Dundret: 67º 8' N, 20º 32'E

Fig. 1 Location of the eight field sites in Europe: (1)-Sierra Nevada (Spain); (2)-Valsaín (Spain); (3)-Montseny (Spain); (4)-Belledonne (France); (5)-Chartreuse (France); (6)-Black Forest (Germany); (7)-Kroscienko (Poland); and (8)-Dundret (Sweden).

ilex). We then computed the average abundance (number of seedlings per m²) over all subplots. We excluded current year seedlings because they are very sensitive to mast seeding.

We obtained the annual temperatures and precipitation time series for the last 40 years from the weather stations closest to our field sites.

Species selection

From all the species found, we selected those that occurred at least in two different locations and in more than 10 plots, for both adults and juveniles. This resulted in seven dominant tree species: Silver fir (*Abies alba* Mill.*),* Norway spruce (*Picea abies* (L.) H. Karst.), European beech (*F. sylvatica* L.), Holm oak *(Q. ilex* L.), sessile oak (*Q. petraea* (Matt) Leibl.), Scots pine (*Pinus sylvestris* L.) and sycamore maple (*Acer pseudoplatanus* L.) from a total of 37 woody species (Table 1). *A. alba*, *P. abies*, *P. sylvestris* and *A. pseudoplatanus* are anemochorous species, while *Q. ilex*, *Q. petraea* and *F. sylvatica* possess a zoochorous dispersal mode. In addition, *Q. ilex*, *Q. petraea* and *A. pseudoplatanus* are able to reproduce vegetatively. For these species, we recorded 13 040 adult individuals and 5322 juvenile individuals in total.

Statistical analysis

For each species, we modelled the abundance of a species as a function of elevation using Generalized Additive Mixed Models (GAMM; Hastie & Tibshirani, 1990). GAMs are nonparametric extension of Generalized Linear Models (GLM; McCullagh & Nelder, 1989) in which we fitted smooth curves to data using local smoothing functions instead of the parametric functions used in GLM. The strength of GAMs is their extremely high flexibility to deal with complex model

basing on the shape of data with no assumptions on the actual relationship between the response variable and the explanatory variables. The degree of smoothness was automatically selected by cross-validation. This approach allows the comparison of the distribution of juveniles and adults regardless of sampling intensity.

To test for differences between ontogenetic stages, we performed models separately for each stage, representing adults and juveniles. We assumed a Poisson distribution and a log link function for all models. Abundances at the transect sites of each location are likely more related to each other than abundances from transects on different sites. Thus, we used a mixed approach, with site as a random variable, to take into account the correlation between data within the same site. To test this approach we repeated all the models for each species on each site, by performing GAM's (without the random term). That resulted on 52 models. Because the main trends did not change these results are not shown (but see Fig. S2).

Nonparametric methods like GAMs do not provide parameters that allow an easy comparison of the range limits, but are useful in tracking and testing assumptions about the shape of the final curves. Because of this drawback, we used the presence/absence data and computed the deciles of the frequency distributions (the nine altitudinal values which divide the frequency distribution into 10 groups of equal frequency) to detect changes in the limits of the range. Using a bootstrap approach, we estimated the 1st, 5th and 9th deciles, and their 95% CI, of juveniles and adults for each species. 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.

Table 1 Description of the eight field sites showed in Fig. 1. Climate variables for each plot location, annual mean temperature and precipitation, were obtained from Worldclim model (Hijmans *et al.*, 2005; http://WorldClim.org). Given in bold are species selected for this study

Country	Site	Sampling year	Altitudinal range (m a.s.l.)	Temperature range (°C)	Precipitation (mm)	N transects	N plot	Main woody species
Spain	Sierra Nevada	2011	1426–1990	8.6/11.5	573–731	5	30	*Acer opalus subsp granatense, Crataegus monogyna, Lonicera arborea, Pinus nigra, P. pinaster,* **P. sylvestris, Quercus ilex,** *Taxus baccata*
Spain	Valsaín	2010	1150–1800	6/10.5	455–640	6	42	**P. sylvestris, Q. ilex***, Q. pyrenaica*
Spain	Montseny	2010	716–1641	8/13	841–1022	6	36	**Abies alba,** *Arbutus unedo, Castanea sativa, C. monogyna, Erica arborea,* **Fagus sylvatica,** *Fraxinus excelsior, Ilex aquifolium, Juniperus communis,* **Q. ilex, Q. petraea,** *Sorbus aria, S. aucuparia, S. domestica*
France	Chartreuse	2011	614–1795	4/9	912–1190	5	19	*A. alba, A. platanoides,* **A. pseudoplatanus,** *Carpinus betulus, Corylus avellana,* **F. sylvatica,** *F. excelsior,* **Picea abies,** *P. uncinata, S. aria, S. aucuparia,, Tilia cordata*
France	Belledone	2009	550–2000	2.6/11	776–1294	7	40	**A. alba,** *A. platanoides,* **A. pseudoplatanus,** *C. betulus, C. sativa,* **F. sylvatica,** *F. excelsior, I. aquifolium,* **Q. petraea, P. abies,** *P. cembra, P. uncinata, Prunus avium, Populus tremula, S.aucuparia, T. platyphyllos*
Germany	Black Forest	2010	580–1240	5/8	976–1333	6	24	**A. alba, A. pseudoplatanus,** **F. sylvatica,** *F. excelsior, Larix decidua,* **P. abies,** *S.aucuparia*
Poland	Kroscienko	2010	500–1100	3.5/6.5	760–927	4	16	**A. alba,** *A. platanoides,* **A. pseudoplatanus,** *Betula pendula, C. avellana,* **F. sylvatica,** *F. excelsior,* **P. abies,** *P. avium, P. tremula, S. aucuparia, T. cordata*
Sweden	Dundret	2010	390–610	−3/−1.5	458–491	4	16	*Alnus incana, B. pubescens,* **P. abies, P. sylvestris,** *Salix sp*
TOTAL	8 sites	2009/10/11	390–2000	−3/13 °C	40.5–121.5	43	223	7 sp

In addition, because we expect that juveniles shift their optimum elevation towards colder conditions compared with adults, we checked the relationship between temperature and tree distribution by repeating all models using temperature as explanatory variable. We obtained mean annual temperature for each plot from the Worldclim model (Hijmans *et al.*, 2005).

All computations were carried out using the R environment (R Development Core Team, 2011), and the MGVC package (Wood & Augustin, 2002).

We tested for differences on annual mean temperature and precipitation between the last decade (2000–2010) and the previous 30 years (when available) with an unpaired two-tailed Student's *t*-test to detect recent changes in the climatic conditions.

Table 2 Annual mean temperatures and annual precipitation with standard errors (°C ± SE) from the Meteorological Stations nearest to study locations, during the last decade (2000–2010) (recent) and the previous 30 year period (previous) (except for Germany and Sweden, 25 and 5 year respectively). Statistical differences were assessed by two-tailed unpaired Student's t-test.

Site (Meteorological station name)	Mean annual temperature ± SE			Annual precipitation ± SE		
	Previous	Recent	Difference	Previous	Recent	Difference
Sierra Nevada (Granada)	15.25 ± 0.79	15.91 ± 0.27	+0.66 ***	363.99 ± 110.43	372.67 ± 101.76	−8.68 (ns)
Valsaín (Puerto de Navacerrada)	6.32 ± 0.83	7.23 ± 0.54	+0.91 ***	1330.50 ± 372.23	1277.77 ± 203.90	−52.73 (ns)
Montseny (Barcelona)	14.78 ± 0.68	15.92 ± 0.45	+1.13 ***	647.65 ± 173.48	587.32 ± 142.61	−60.33 (ns)
Chartreusse-Belledone (Grande-Chartreuse)	8.12 ± 0.62	8.56 ± 0.59	+0.44 ***	2099.39 ± 337.08	1908.12 ± 343.16	−191.28 (ns)
Black Forest (Schauinsland)	4.74 ± 2.27	6.32 ± 0.50	+1.59 **	NA	NA	NA
Kroscienko (Zakopane)	5.35 ± 0.66	6.08 ± 0.64	+0.73 **	1106.07 ± 148.66	1229.06 ± 204.49	+123.00 (ns)
Dundret (Gällivare)	−0.1 ± 0.94	0.02 ± 0.64	+0.12 (ns)	412.50 ± 191.38	607.88 ± 141.18	+195.38 (ns)
Mean difference			+0.86 °C			

Significance level: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns, not significant; NA, not available, incomplete time series.

Results

The smoothing function of elevation was statistically significant at 5% level in all models, except for adults of *A. pseudoplatanus* and juveniles of *Q. petraea*, indicating that, except for those, the abundance of individuals was related to the altitudinal gradient. Most of the estimated response curves showed an asymmetrical and nonparametric shape supporting the use of GAM models (Figs 2 and 3). *Q. ilex* showed a decreasing linear trend with elevation (degrees of freedom close to 1 evidenced this trend) both in juveniles and adults (Fig. 3). These patterns were consistent with those found when we modelled the abundance as a function of temperature: almost all species showed a significant relationship with the annual mean temperature, both in juveniles and adults (see Fig. S1). Only for adults of *P. abies* and juveniles of *A. pseudoplatanus*, the abundance was not related to temperature.

We found a high level of disparity in the response to elevation of juveniles and adults between species. For four out of seven species, we found differences between adults and juveniles in the mean elevation distribution (Fig. 2). For *A. alba* we found an upward shift of the optimum elevation with a maximum abundance of adults around 1350 m and around 1600 m for juveniles. However, for three species, *F. sylvatica*, *P. abies* and *P. sylvestris*, we detected changes opposite to predictions, with a peak of juveniles at lower elevations than adults. The difference in optimum elevation between juveniles and adults was 150, 620 and 550 m for *F. sylvatica*, *P. abies* and *P. sylvestris* respectively.

Quercus ilex showed similar patterns for juveniles and adults (Fig. 3), whereas in *A. pseudoplatanus* and *Q. petraea* we found no relationship between density and elevation in adult and juvenile life stages respectively.

When we analysed the presence/absence information to detect changes in the range limits we observed changes in the opposite direction to that expected for most of the species. Only for *Q. ilex* we found an upward movement both in lower and upper range limits of juveniles. *P. abies*, *F. sylvatica*, *P. sylvestris* and *Q. petraea* showed a negative difference on the upper limit of juveniles vs. adults (Fig. 4). We also observed a descending lower limit of juveniles in *A. alba*, *P. abies* and *A. pseudoplatanus*. However, most of these differences were not statistically significant. Only for *Q. ilex* the difference in the 5th and 9th deciles between adults and juveniles was significant [CI for the differences in 5th and 9th deciles respectively, (CI 95%) = (4; 349) and (CI 95%) = (43.5; 528.8)].

Discussion

Although species are expected to move upwards in elevation in response to climate warming (Hughes, 2000; IPCC, 2007), evidence for recent range shifts is not consistent. Most studies have focused on changes occurring at the edges of the ranges, and they have frequently reported advancements on treeline towards higher altitudes (e.g. Pauli *et al.*, 1996, 2012; Peñuelas & Boada, 2003; Gottfried *et al.*, 2012; Jump *et al.*, 2012), but less attention has been paid to changes in density of individuals within the species range (but see Lenoir *et al.*, 2009).

In the context of this study, we expected for each species a higher elevational maximum of density in
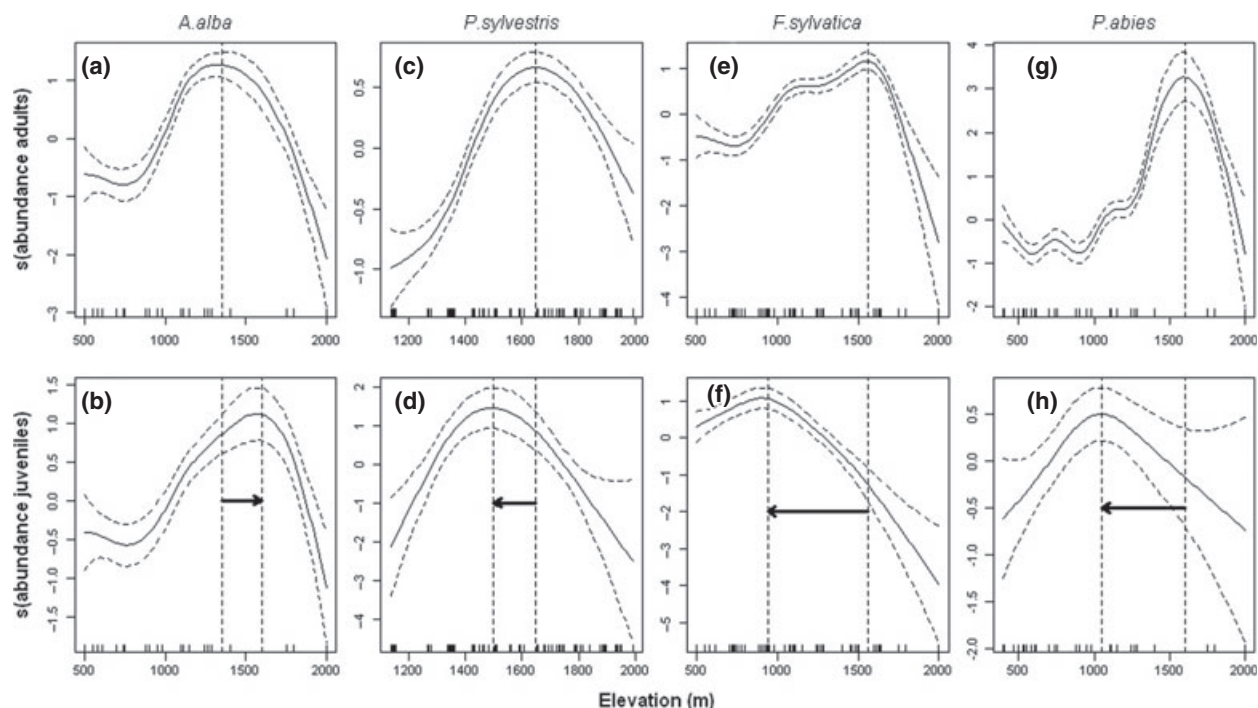
Fig. 2 Smoothing curves (solid) fitted for density of adults (upper part), and juveniles (lower part), for *Abies alba* (a, b), *Pinus sylvestris* (c, d), *Fagus sylvatica* (e, f), and *Picea abies* (g, h), along elevation gradients. The dashed lines indicate the upper and lower 95% CI around the smooth function. Vertical lines show the elevation with maximum density and arrows indicate changes between adults and juveniles. Ticks at the *x*-axis (elevation) show the specific sampling points across all transects where the species occurred.

juveniles than in adult trees, in response to the recent observed climate warming (mean temperature increased 0.86 °C on average in our site studies, with a range between +0.12 and 1.56 °C). However, only one species, *A. alba*, was consistent with this expected upward shift. We observed an upslope movement of the optimum elevation of juveniles against adults, which did not translate into an expansion of the range limits to higher elevations. In line with this result, Kelly & Goulden (2008) have demonstrated that the actual boundaries of plant species ranges stayed the same, but the central tendencies of the plant population moved upslope over a period of 30 years, following a process that Breshears *et al.* (2008) defined as upslope 'leaning'. By focusing on the range limits of a species instead of optimum elevation the response of species to climate change could be neglected. We observed a shift in the optimum elevation of *A. alba* that is probably attributable to increases in temperature, although we acknowledge that many other biotic and abiotic factors may be also driving this change. According with our observations on this species, Vitasse *et al.* (2012) detected an upward shift in the elevational distribution of *A. alba* in synchrony with the current warming in the Alps. Nevertheless, they found a similar pattern for *Q. petraea*, *F. sylvatica* and *A. pseudoplatanus* in contrast to our

results. Similar results were found by Lenoir *et al.* (2009) with seedlings not only found at higher elevation than adults for *A. alba* and *Q. petraea* but also cases of seedlings found at lower elevations or showing no obvious differences with adults (e.g. *A. pseudoplatanus* and *F. sylvatica*). Also, in contrast to our results, Kullman & Öberg (2009) detected a substantial treeline upshift for *P. abies*, *P. sylvestris* and *B. pubescens* over the period 1917–2007 in the Swedish Scandes.

More surprisingly, six out of the seven tree species in this study showed no change or changed in the opposite direction to that expected from warming. This kind of counterintuitive result not matching the predicted impacts of increasing temperatures on the distribution of species has been already reported in other studies. Parmesan & Yohe (2003) in their meta-analyses found that ca. 20% of the studied species have moved their ranges towards lower elevations and/or southern latitudes. Similarly, Lenoir *et al.* (2010) reported that 65% of the studied species shifted their mid-range positions upslope, 10% experienced no change and 25% shifted downslope. Also Crimmins *et al.* (2011) showed that climate changes have resulted in a significant downward shift in species' optimum elevations due to water deficit at higher elevations, by comparing the altitudinal distributions of 64 plant species between the 1930s
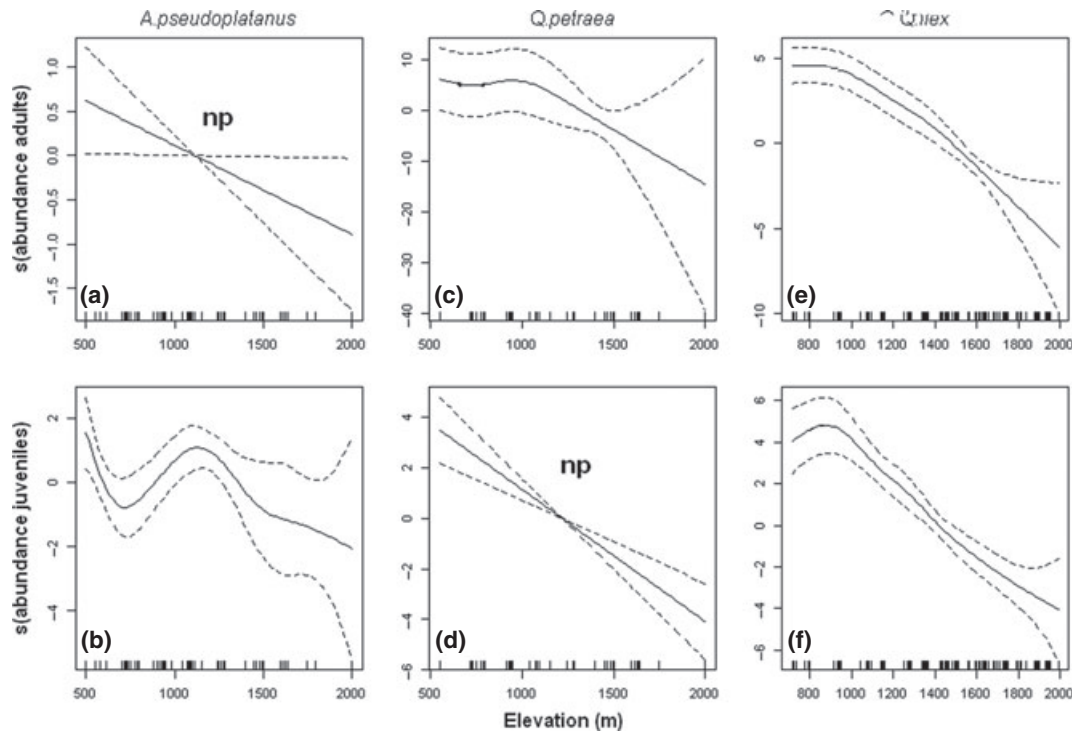
Fig. 3 Smoothing curves (solid) fitted for density of adults (upper part), and juveniles (lower part), for *Acer pseudoplatanus* (a, b), *Quercus petraea* (c, d) *and Q.ilex* (e, f), along elevation gradients. The dashed lines indicate the upper and lower 95% CI around the smooth function. np indicates no relationship between density and elevation. Ticks at the *x*-axis (elevation) show the specific sampling points across all transects where the species occurred.
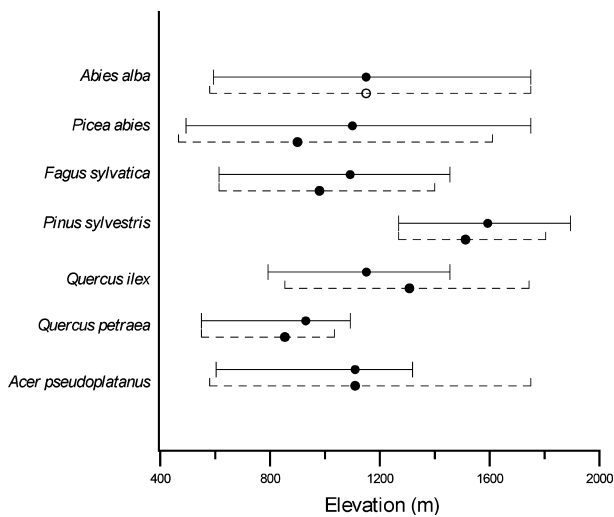

Fig. 4 Comparison between the presence of adults (solid lines) and juveniles (dashed lines) of the study species along the elevation gradients. Circles refer to the 5th decile and bars refer to lower (1st decile) and higher (9th decile) limits.

and the present within California. Recently, Zhu *et al.* (2012) have examined the latitudinal difference between offspring and adults of trees at both northern and southern range limits across the eastern United States and shown a lack of tree latitudinal range expansion in response to climate change for most of the species. There are several potential mechanisms that could explain these unexpected trends. Firstly, the lack of evidence for range shifts might reflect the mismatch in a temporal scale between changes in distribution and the rapid change in climate for long-lived organisms such as trees, or simply reflect the result of random population fluctuations (García & Zamora, 2003). Moreover, local variation in topography, microclimate, soils and hydrology can enable the local persistence of populations even where regional climatic conditions are unfavourable, as reported by Scherrer & Körner (2011) in an alpine landscape in the Alps. They demonstrated that the topographic variability in these landscapes creates a multitude of microclimatic conditions offering refugia for some species instead of forcing them to move upslope in response to climate warming. This idea is also supported by the findings of Lenoir *et al.* (2013), which suggest that fine-grained thermal variability over tens or hundreds of metres exceeds much of the climate warming expected for the coming decades, allowing the persistence of local species in microrefugia within regionally unsuitable climatic conditions.

Secondly, climate warming may not only affect species distribution by altering abiotic conditions but also by changing the importance and intensity of their interaction with other species (Hughes, 2000; Tylianakis *et al.*, 2008; Lenoir *et al.*, 2010). It is well known that species interactions have a profound influence on their distributions. Interactions in plants include interspecific competition for resources with other plant species, which causes shifts in the relative dominance of coexisting plants, and also mutualistic interactions among plants and with animals (pollination and dispersal) and the negative interactions with their natural enemies (pathogens and herbivores) have been shown to profoundly affect performance and population dynamics and distribution. Species distribution could in fact be limited as a consequence of the disruption of species interactions due to climate change (Van der Putten *et al.*, 2010). Different response times to climate change in interacting species could lead to a spatial mismatch between suitable climate niche and the presence of the associated species, especially between woody plants with long generation times and their mutualistic insects (Araújo & Luoto, 2007). Recent reviews have indicated that knowledge of the effects of climate warming on mutualistic interactions is still limited (Walther *et al.*, 2002). For example, speculations on the disruptions of plant-pollinator interactions due to climate change are often brought forward (e.g. Parmesan, 2006; Hegland *et al.*, 2009), but few empirical studies exist to verify whether such disruptions do occur. Because the effects of climate change on biotic interactions are species-specific, their impacts in range shifting become complex and unpredictable. For example, if climate warming reduces the competition at lower altitudes we would expect a downslope shift of species towards areas with more favourable conditions. In this line Hättenschwiler & Körner (1995)observed no shifts in the range limits of *P. sylvestris*, whereas the lower limit of seedlings distribution for *P. cembra* was even below than the limit of adult plants. They concluded that the current altitudinal range of *P. sylvestris* is primarily controlled by competition of seedlings with other species rather than by temperature. Also, Woodall *et al.* (2009) found that some tree species in the United States shifted southwards as result of filling niches that may be vacated by other species moving northwards.

The lower elevational optimum of juveniles vs. adults for *P. sylvestis*, *F. sylvatica* and *P. abies* found in this study might indicate that the current climate conditions constitute a limitation for reproduction or seedling establishment at higher elevations. Moreover, some studies have demonstrated that the niche requirements may change during the life of individuals giving different spatial distributions of seedlings and adults (Collins & Carson, 2004; Bertrand *et al.*, 2011). This may explain our results on *A. pseudoplatanus* and *Q. petraea*, for which the distribution of adults was not determined by altitude, whereas corresponding juveniles showed a distribution pattern significantly related to the elevation gradient in *A. pseudoplatanus*, and the opposite (no relationship with elevation for juveniles but for adults) in *Q. petraea*. However, recruitment limitation is only one side of the history. Sprouting ability may be an important, but widely neglected, issue under climate change allowing the persistence of sprouting species in regions where conditions have become too inhospitable (Bond & Midgley, 2001). In this line, we found that the three sprouting species in this study, *Q.ilex*, *Q. petraea* and *A. pseudoplatanus,* experienced no changes in distribution, likely due to persistence capacity of established plants. Dispersal mode may also affect the ability of species to colonize new areas. However, we have not found a clear pattern in relation with the dispersal syndrome, with both anemochorous and zoochorous species showing different distributional shifts.

Plant species are able to respond to changes in environment through a combination of phenotypic plasticity and genetic adaptation (Nicotra *et al.*, 2010). Because trees are both sessile and long-lived their ability to migrate to suitable areas is limited compared with other organisms such as animals, and therefore phenotypic plasticity becomes a key mechanism to adapt to rapid climate change. Although some studies have presented evidence of an inadequate ability of tree species to adapt to climate change (e.g. some studies on *F. sylvatica*, Jump *et al.*, 2006; Peñuelas *et al.*, 2011), some others have shown that trees possess enough phenotypic plasticity to cope with unfavourable climatic conditions. For example, Savolainen *et al.* (2007) through extensive experimental plantations showed that several tree species (including *P.sylvestris* and *Q. petraea*) were capable of surviving outside their natural range by adapting to contrasting environmental conditions.

Lastly, and besides the effects of climate, other components of global change such as habitat modification and land use changes may influence the distribution of species. Changes in land use may act in concert with climate warming to cause upslope range shifts due to recolonization of trees into abandoned grassland. For instance, in the Swiss Alps Gehrig-Fasel *et al.* (2007) reported that land abandonment was the main driver for 90% of the detected upward shifts on treeline and only a small fraction of upward shifts was attributable to climate warming. Bodin *et al.* (2013) have also found that changes in the successional stages of stands appear as the main cause of the apparent upslope movement of forest species in the mountain of south-east France. In addition, silvicultural interventions, such as thinning,

harvesting, or planting, may drive observed distribution patterns away from the expected ones. This might be especially true in European forests, which are all under some sort of forest management. However, we have no specific information whether some species might have been planted at lower or higher elevations or whether thinning or harvests would have favoured regeneration at certain elevations across all sites in the past.

In conclusion, this study highlights the fact that climate-change impacts on the distribution of tree species are far from homogeneous and do not always match the expectations based on earlier theories. The commonly accepted assumption that future climate warming will result in upward shifts in species elevation range remains unclear due to the complexity of drivers shaping the species' distribution. Despite that most of the observational studies published so far have shown directional changes according to predictions, several studies have also reported no changes or patterns as opposed to expectations. In addition to the publication bias towards positive results, recent theoretical studies modelling the distribution of species are already highlighting the importance of taking into account both climate and non climate drivers (information on species interactions and other factors limiting the species range)., There is increasing evidence showing that models based only on climate may lead to erroneous predictions of range shifts of species (e.g. Araújo & Luoto, 2007; Thuiller *et al.*, 2008). Hence, this study provides empirical evidence that counterintuitive responses to warming are occurring, and emphasizes the need of more multi-species studies covering large geographical areas that evaluate mechanisms underlying range-shifting dynamics.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Temperature–response curves estimated for density of adults (upper part), and juveniles (lower part) for each species.
Figure S2. Response curves estimated for density of adults (upper part), and juveniles (lower part) using GAMs for each species and location separately.