



Inferring shifts in tree species distribution using asymmetric distribution curves: a case study in the Iberian mountains

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Nomenclature

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Introduction

Rapid anthropogenic global changes, such as climate change, land-use change, nitrogen deposition and invasive species introduction, interfere with many natural ecosystems. A critical issue is to understand how these global

Abstract

Questions: The objectives of this study were to examine altitudinal shifts in tree species distributions over one decade to quantify the potential for tree migration.

Location: Spain.

Methods: We analysed presence–absence data using two successive surveys of the Spanish Forest Inventory in five *Fagaceae* tree species (two temperate: *Fagus sylvatica* and *Quercus petraea*, one sub-Mediterranean: *Q. faginea* and two Mediterranean: *Q. suber* and *Q. ilex*) in two mountain ranges (the Pyrenees and the Iberian system). Half of the fitted altitudinal distributions were skewed and required use of an asymmetric model for unbiased estimates of optimum altitude and changes in the probability of presence along the altitudinal gradient. For each species and mountain range, shifts were considered to have occurred when the difference in optimum altitude was significant or when differences in probability of occurrence between the two surveys demonstrated the occurrence of colonization or extirpation events.

Results: Overall, depending on species and mountain range, shifts in optimum altitude ranged between -34 m and $+181$ m. The altitudinal distribution of the Mediterranean species at the core of their latitudinal distribution range presented no sign of change. For the temperate and sub-Mediterranean *Fagaceae* species, the patterns demonstrated the existence of distribution changes over a 10-yr period. The largest, although not statistically significant, upward shift in optimum altitude was observed for *Q. petraea* in the Iberian system. More interestingly, its distribution indicated colonization events at higher altitudes. For *Q. faginea* in the Pyrenees, the shift in optimum altitude was the second largest and statistically significant, and was associated with large extirpation events at the lower altitudes. No evidence of shifts was observed for *F. sylvatica*.

Conclusion: This work demonstrates that changes in altitudinal distribution could occur over a 10-yr time period for tree species located at the southern limit of their distribution, such as some temperate and sub-Mediterranean oaks, whereas no movement was detected for Mediterranean oaks in the core of their distribution area.

changes will impact biodiversity (e.g. Thomas et al. 2004), productivity (Hughes 2000) and species distributions (Bakkenes et al. 2002; Thuiller et al. 2005; Walther et al. 2005). Recent phylogeographic and genetic studies have described examples of tree migration during Quaternary climate changes. For instance, pollen data analysis

revealed that spruce (*Picea* spp.) shifted northwards in the eastern part of the USA as the climate warmed at the end of the last glacial period (Davis & Shaw 2001). Petit et al. (2005) analysed the variability of haplotype data in Holm oak (*Quercus ilex*) populations to make inferences about the existence of several migration routes from east to west and then towards northern latitudes around the Mediterranean Basin during the Holocene. However, the current temperature increase is occurring so rapidly that tree species might not be able to track these changes; for instance, Murphy et al. (2010) studied the whole latitudinal abundance distributions of 102 North American trees and showed that 31% of the species presented a distribution skewed towards the southern latitudes of their geographic range, suggesting difficulty in colonizing northern areas and in tracking climate change.

Still, because field monitoring and observations are not feasible at the spatial scale of species distributions and at the time scale of tree migrations, little data exist on tree species migrations. More generally, studies have focused on one of the boundaries rather than the whole species distribution. Many studies showed events of colonization at the altitudinal tree line of the species (Magee & Antos 1992; Meshinev et al. 2000; Danby & Hik 2007; Shiyatov et al. 2007; Devi et al. 2008) or at the northern limits of woody species distributions (Lescop-Sinclair & Payette 1995; Sturm et al. 2001; Johnstone & Chapin 2003; Walther et al. 2005). Re-analysis of surveys carried out during the last century is now increasingly used to assess species movements along altitudinal gradients (Kelly & Goulden 2008; Lenoir et al. 2008; Parolo & Rossi 2008; Feeley et al. 2011). To our knowledge, few studies using the same data sets (USDA Forest Service's Forest Inventory and Analysis data) have presented analyses over a whole tree species' range (Woodall et al. 2009, 2010; Zhu et al. 2012). Recently, national forest inventories, such as the Spanish inventory, have finally completed successive inventories on the same sites, providing access to data that allow analysis of species range dynamics.

The altitudinal pattern of abundance of shrubs and trees of California's mountains showed an increase in mean altitude over a 30-yr period, related to a decrease in plant cover at lower altitudes and an increase at higher altitudes (Kelly & Goulden 2008). In six mountains of Western Europe, 118 out of 171 forest species shifted upward between 1905–1985 and 1986–2005 (Lenoir et al. 2008), but among woody species only 11 out of 56 presented a shift. Conclusions regarding latitudinal shifts in tree species distribution in the USA are not as straightforward to interpret: by comparing mean seedling latitude to mean biomass (tree) latitude, Woodall et al. (2009, 2010) interpreted the differences as a signature of northward tree migration, while comparing latitudes of seedlings and trees and focus-

ing on the northern and southern boundaries of 92 species, Zhu et al. (2012) found no evidence for climate-driven migration. Although these studies demonstrated the reality of tree migrations in response to current global change, they also highlighted that the type and magnitude of the response varied from one species to another. Thus, empirical studies on tree species shifts are all the more necessary to increase our knowledge regarding tree species movements in response to global changes.

Furthermore, quantitative information on speed of tree migration rates is still lacking. Climatic envelope models indicated that the suitable climatic niche of the main terrestrial vegetation types would change between several hundred and several thousand meters per year in response to climate change (Malcolm et al. 2002; Kaplan & New 2006; Iverson et al. 2008). Rates inferred from fossil pollen records ranged between 100 and 500 m·yr⁻¹ during the Holocene (Clark et al. 1998; Aitken et al. 2008). In contrast, cpDNA-based studies have reported migration rates <100 m·yr⁻¹ for the same period (McLachlan & Clark 2004; Aitken et al. 2008). Very few studies provide estimates of current tree migration rates. Over an important latitudinal gradient, Woodall et al. (2009) presented migration speeds up to 1000 m·yr⁻¹. Studies on altitudinal tree distributions reported much lower rates, with upward shifts of 20–35 m·decade⁻¹ (Kelly & Goulden 2008; Lenoir et al. 2008; Feeley et al. 2011). Thus, actual tree migration rates seem too slow to successfully track the rates of change of the suitable habitats under current and future climate change.

The aim of our study was to analyse altitudinal tree species distributions in Spain (Pyrenees and Iberian system mountains) to detect evidence of rapid shifts over a single decade using repeated surveys of the Spanish National Forest Inventory. Comparing *Fagaceae* species located in the core of their distribution areas to species located at the southern limit of their ranges, we also aimed to quantify the magnitude of these shifts in order to assess the ability of trees to keep pace with the current changes.

Methods

Study area

Continental Spain (492 173 km²) lies between 36° N and 43.5° N, and 9° W and 3° E. It covers a large altitudinal gradient from sea level up to 3500 m. Mountains cover 51% of the national surface area, and more than 20% of these mountain areas are forest-covered (Inventario Forestal Nacional 2007). We focused on two mountain ranges in this study: the Pyrenees and the Iberian system. Other Spanish mountain areas were excluded because of methodological failures in the inventories (geolocalization uncertainties, tree planting programmes). Both mountain

ranges are located at the southern limit of the temperate climate area and in the core of the Mediterranean climate area. The Pyrenees, located in the northern part of the country, bordering France (42.7° N, 0.79° E), reach >3000 m a.s.l.; the elevations of our studied area were 4–2499 m a.s.l. The Iberian system is in central Spain (41.35° N, -1.62° E), reaching its highest point at 2313 m a.s.l.; our studied area ranged from 40 to 2026 m a.s.l. (Fig. 1).

Mean annual temperature for each mountain range from 1980 to 2000 was calculated as the average obtained from 89 and 98 weather stations for the Pyrenees and the Iberian system, respectively (www.aemet.es). Linear regressions were then fitted to the data (Statistica 8.0; StatSoft Inc, Tulsa, OK, USA).

Studied species

In order to investigate natural dynamics in species distribution, we selected five hardwood tree species of the Fagaceae and avoided e.g. Pine species, which have been extensively planted. Two of the five were deciduous

temperate species, *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Lielb.; *Quercus faginea* Lam. is a marcescent sub-Mediterranean species; finally we selected two evergreen Mediterranean oaks, *Quercus suber* L. and *Quercus ilex* L. *F. sylvatica* and *Q. petraea* are distributed throughout Europe and in Spain, both species are located at the southwestern limit (rear edge) of their distribution (Benito Garzon et al. 2008). *Q. faginea* is restricted to the Iberian Peninsula and Maghreb (Alia et al. 2009). Sub-Mediterranean areas are considered transitions between Mediterranean and temperate zones in term of climate, and present a specific vegetation type characterized by the abundance of marcescent species (Sanchez de Dios et al. 2009). The distribution area of *Q. suber* is from the Balkans, through southern France to the Iberian Peninsula and Maghreb (Alia et al. 2009). In Spain, it is abundant in the southwest and at lower altitudes in east, such as the Pyrenees and the Iberian system. *Q. ilex* is a typical Mediterranean species expanding around the Mediterranean Basin and is present throughout Iberia (Alia et al. 2009). Thus both *Q. ilex* and *Q. suber* are located at the core of their distribution areas.

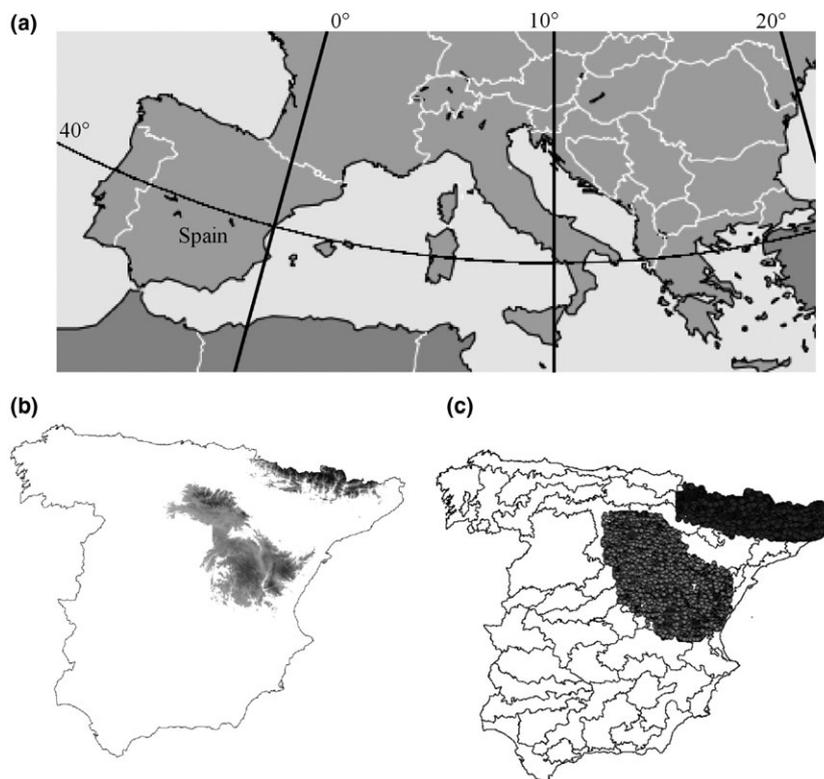


Fig. 1. Maps of the studied areas. (a) General map of southern Europe (extracted from Ssolbergj under CC licence BY-SA 3.0) (b) Map of Spain presenting the Pyrenees Mountains and the Iberian System, corresponding to the Spanish mountain ranges used in this study. (c) Map of Spain presenting the location of the plots of the Spanish National Forest Inventory that were used in this study.

Altitudinal distribution of the species

We used tree presence–absence data from two successive forest surveys consisting of a systematic sampling of permanent plots from all Spanish forests; the second survey of the Spanish Forest Inventory (Inventario Forestal Nacional 1995) took place between 1986 and 1996, and the third between 1997 and 2007 (Inventario Forestal Nacional 2007). Return to the same plot between inventories occurred after a 10-yr interval. For the purpose of this paper, we will use the decade of the mean year of the inventory time period in the 1990s and 2000s to refer to the 1986–96 and 1997–2007 inventories, respectively. The same plots were censused in both inventories (A1 plots, Inventario Forestal Nacional 2007) and change in plot number between the second and third inventory corresponds to new plots as well as plots that were removed from the database due to a localization problems (Table S1). Plots (25-m radius) were distributed systematically every 1 km at the intersection of the Universal Transverse Mercator (UTM) coordinates, over all forested areas in Spain. Altitude was extracted from a digital elevation model under GIS (ArcMap 9.2; ESRI, Redlands, CA, USA). We constituted one sample data set per species, mountain range and forest survey (20 data sets). For each data set, we counted the total number of plots (N_{alt}) per altitudinal class (25 classes, from 0 to 2500 m) and the number of plots per altitudinal class where the species was present (n_{alt}). The probability of occurrence of the species per class of altitude (p_{alt}) was then calculated as:

$$p_{alt} = \frac{n_{alt}}{N_{alt}} \quad (1)$$

Model fit and parameter estimate

In this study, we used three models to fit the altitudinal distribution of species probability of occurrence: the logistic regression, and modalities IV and V of the HOF model (Huisman et al. 1993). For each sample data set, we chose the best model considering goodness-of-fit in terms of (1) ability to represent the symmetry or the skewness of the distribution of probability of occurrence and (2) minimum Akaike criterion. The parameters of the models were estimated by maximizing the likelihood of a Bernoulli distribution (proc NLMIXED, SAS v. 9.2; SAS Institute, Cary NC, USA).

Logistic regression is a classical model used to fit symmetric distribution of species probabilities of occurrence (Coudun & Gegout 2006; Lenoir et al. 2008). With this regression, the probability of occurrence is related to the

altitudinal class through the following quadratic function using a logit link:

$$\ln\left(\frac{p_{alt}}{1 - p_{alt}}\right) = a1 + a2 \cdot alt + a3 \cdot alt^2 \quad (2)$$

where $a1$, $a2$ and $a3$ are parameters of the logistic regression, p_{alt} is probability of occurrence per altitudinal class and alt is altitudinal class (m).

For the logistic regression, the optimum altitude ($alt_{opt,t}$) at time t was then calculated as:

$$alt_{opt,t} = \frac{-a2}{2 \cdot a3} \quad (3)$$

The IV and V modalities of the HOF distribution models (Huisman et al. 1993) permitted fitting of a symmetrical and skewed distribution, respectively:

$$\text{HOF IV} : p_{alt} = M \frac{1}{1 + e^{b1+b2 \cdot alt}} \frac{1}{1 + e^{b3-b2 \cdot alt}} \quad (4)$$

$$\text{HOF ; V} : p_{alt} = M \frac{1}{1 + e^{c1+c2 \cdot alt}} \frac{1}{1 + e^{c3+c4 \cdot alt}} \quad (5)$$

where $b1$, $b2$, $b3$, $c1$, $c2$, $c3$ and $c4$ are parameters of the distributions; M is a constant equal to the maximum value that can be attained (Huisman et al. 1993), thus $M = 1$ since p_{alt} is a probability. For the HOF IV model, the altitude of the optimum was calculated as:

$$alt_{opt,t} = \frac{b3 - b1}{2 \cdot b2} \quad (6)$$

For the HOF V model, no analytical solution exists to calculate the optimum altitude; knowing the numerical values of the parameters of the HOF V model (Eq. 5), it was thus determined by solving Eq. 7 using optimization methods (proc MODEL, SAS v. 9.2):

$$c2 \cdot e^{(c1+c2 \cdot alt_{opt,t})} \cdot \left(1 + e^{(c3+c4 \cdot alt_{opt,t})}\right) + c4 \cdot e^{(c3+c4 \cdot alt_{opt,t})} \cdot \left(1 + e^{(c1+c2 \cdot alt_{opt,t})}\right) = 0 \quad (7)$$

The confidence interval on the supplementary parameter corresponding to the optimum altitude, i.e. the altitude of the optimum of probability of occurrence ($alt_{opt,t}$ m), was estimated using the delta method (Serfling 1980; Billingsley 1986; Couallier et al. 2011).

Differences in optimum altitude

For each species and mountain range, the shift (m) in altitude of the optimum of the probability of occur-

rence between $t = 1990s$ and $t = 2000s$ was calculated as:

$$\text{shift} = alt_{opt,2000} - alt_{opt,1990} \quad (8)$$

where $alt_{opt,1990}$ and $alt_{opt,2000}$ are the altitude of the optimum of probability of species occurrence for the 1990s and the 2000s forest surveys, respectively.

A bootstrapped t -test is usually used with models of species distribution along an environmental gradient (e.g. Maggini et al. 2011) in order to assess significance of the shifts. However, the resampling of binary data (presence-absence) during the bootstrap increases the variability within the bootstrapped samples compared to that in the original data set (Davison & Hinkley 1997); thus these tests are not suitable for analysing small amplitude shifts such as those we have been investigating. Therefore we abandoned similar permutation tests (data not shown) and simply considered that non-overlapping 95% confidence intervals between the two surveys indicated significant differences in optimum altitude.

Differences in probability of occurrence

We determined the altitudinal distribution of difference in probability of occurrence between the two surveys $pdiff_{alt}$ as:

$$pdiff_{alt} = p_{alt,2000} - p_{alt,1990} \quad (9)$$

where $p_{alt,1990}$ and $p_{alt,2000}$ are probability of occurrence per altitudinal class for the 1990s and the 2000s forest surveys, respectively, and $pdiff_{alt}$ is difference in probability of occurrence between the surveys per altitudinal class. We calculated $pdiff_{alt}$ for each of 1000 altitudinal classes inside the altitudinal range 0–2500 m using the model that best fitted our data (Eqs. 2, 4 or 5).

The area under the curve associated with the $pdiff_{alt}$ function was calculated applying the rectangle method as the sum of the $pdiff_{alt}$ multiplied by the altitudinal class interval (2.5 m). Integration of the $pdiff_{alt}$ values was performed separating the negative values to quantify extirpation events ($pdiff_{ext}$) and the positive values to quantify colonization events ($pdiff_{col}$) (Lenoir et al. 2009). Linear regressions were fitted to the plots of the 2000s probabilities of occurrence vs. the 1990s probabilities of occurrence: a linear regression differing from the 1:1 line indicated significant differences in colonization or extirpation events.

Shifts in tree altitudinal distribution were assessed by the occurrence of a significant shift in optimum altitude and/or occurrence of colonization or extirpation events.

Results

Model fitting and parameter estimates

We fitted 20 distributions of probability of occurrence along an altitudinal gradient, covering five tree species, two mountain ranges and two time periods, using two data sets: A1 plots only and all available plots, in order to make sure that the change in some sampling plots between the inventories did not induce bias (Table S1). The fittings and conclusions were the same (average absolute variation in optimum estimate of 14.8 ± 8.6 m, \pm SD), therefore we chose to present fittings using all the sampled plots. Overall, the goodness-of-fit was good regardless of the data set, as can be assessed with the Akaike criterion (Table S2) and comparing data and models, as illustrated for five altitudinal distributions in the Pyrenees in 1990 (Fig. 2). Ten distributions out of the 20 were symmetric and could be fitted using a classic logistic regression, although sometimes a best fit was obtained using the HOF IV symmetric model (Table 1). However, the other ten distributions were asymmetric (see e.g. *Q. petraea* and *Q. faginea*, Figs 2b,c and 3) and required use of the asymmetric HOF V model (Huisman et al. 1993). When the distributions were skewed, as for *F. sylvatica* and *Q. ilex* in the Iberian system and *Q. petraea* and *Q. faginea* in the Pyrenees, the optimum altitudes of the species were poorly estimated using the classic logistic model, with differences ranging between 10 and 233 m, corresponding to errors of up to 19% (data not shown).

Altitudinal shift in tree species distribution

Analysis of the altitudinal distribution of five tree species over a 10-yr period (1986–1996 and 1997–2007) demonstrated that a shift occurred in the distribution towards higher altitudes for two species, *Q. petraea* and *Q. faginea*, whereas the others showed no changes.

Overall, the altitudinal range (maximum – minimum altitude) of the species distributions did not change during the 10-yr period, regardless of species and mountain range (Fig. 3). However, changes in terms of the optimum altitude of species occurrence or probability of occurrence across the altitudinal gradient presented some differences according to species and mountain range. The temperate species did not present the same trend in response. Indeed in the Iberian system, no shift in optimum altitude was observed for *F. sylvatica* (–1 m; Table 1) and nor any change in probability of occurrence (net gain of +2 m over the whole distribution area; Table 2); in the Pyrenees a small non-significant downward shift in optimum altitude was estimated (–34 m), together with a net increase in probability of occurrence at altitudes close to or slightly

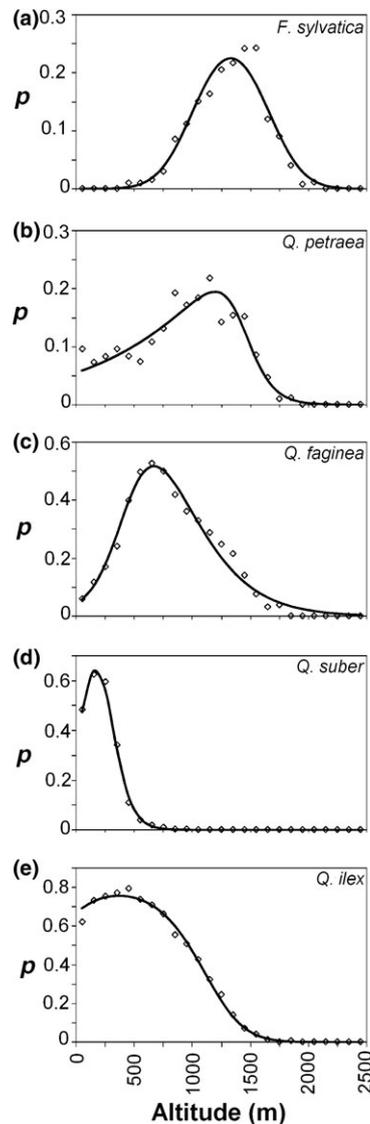


Fig. 2. Examples of altitudinal distribution of probability of occurrence (p) in the Pyrenees Mountains for the 1990 forest inventory. Data are represented by open diamonds and fitted models by full lines. (a) *F. sylvatica*, (b) *Q. petraea*, (c) *Q. faginea*, (d) *Q. suber* and (e) *Q. ilex*.

lower than the optimum ($pdiff.ext + pdiff.col = +21$ m; Table 2). For *Q. petraea*, the observed patterns demonstrated no significant upward shifts in optimum altitude in both mountain ranges; there was a 36-m shift in the Pyrenees and a substantial but statistically non-significant 181 m upward shift in the Iberian system (Table 1); the altitude of the optimum rising from 1393 m in 1986–1996 to 1574 m in 1997–2007 (Table 1, Fig. 3b). More strikingly, the altitudinal distribution of *Q. petraea* demonstrated a large drop in probability of occurrence at the lowest altitudes during the analysed period in the Pyrenees, as indicated by the magnitude of extirpation events

(Fig. 3b, Table 2; $pdiff.ext = -85$ m vs. $pdiff.col = +1$ m). Meanwhile in the Iberian system, the maximum probability of occurrence of this species was more than ten-fold lower than in the Pyrenees, indicating much lower abundance in the southern mountain area where colonization events occurred at the highest altitudes (Fig. 3b, Table 2; $pdiff.col = +5$ m).

For *Q. faginea*, the sub-Mediterranean species (Fig. 3c), our analysis demonstrated a significant upward shift in optimum altitude in the Pyrenees (93 m; Table 1), the optimum varying from 670 to 763 m (Table 1). Moreover, the probabilities of occurrence demonstrated large drops between the two surveys throughout the altitudinal gradient, with a maximum decreasing from 0.5 to 0.3 (Fig. 3c). These drops resulted in many extirpation events ($pdiff.ext = -204$; Table 2) in the Pyrenees. A moderate non-significant upward shift in optimum altitude was also observed in the Iberian system (25 m; Table 1) and the probability of occurrence indicated colonization events at the higher altitudes (Fig. 3c, Table 2).

Regarding the Mediterranean species, *Q. ilex* and *Q. suber*, their overall distributions remained almost identical over the investigated time period in the Pyrenees, with no changes in the probability of occurrence function ($pdiff.ext + pdiff.col$ equal to +3 and -5, respectively). In the Iberian system, *Q. suber* optimum altitude presented a moderate downward shift (-30 m) and no change in overall probabilities of occurrence ($pdiff.ext + pdiff.col = +2$; Table 2). For *Q. ilex*, some colonization events were observed, as indicated by $pdiff.col = +38$ throughout the altitudinal gradient (Fig. 3d,e, Table 2).

Climatic trends over 20 yr

Both in the Pyrenees and the Iberian system, a significant increase in mean annual temperature was observed, with a 0.38 °C and 0.24 °C increase per decade, respectively (Fig. 4). In the Pyrenees, this phenomenon corresponded to an increase of minimum winter temperature (+0.67 °C·decade⁻¹) and a decrease of maximum summer temperature (-0.42 °C·decade⁻¹). In the Iberian system, minimum temperature increased by 0.45 °C·decade⁻¹, whereas maximum summer temperature remained even over the considered period (+0.01 °C·decade⁻¹, not significant).

Discussion

Bioclimatic envelope models have predicted that the suitable climatic areas of Mediterranean species such as *Pinus halepensis*, *Quercus coccifera*, *Quercus ilex* and *Juniperus oxycedrus* would expand whereas those of temperate species such as *Abies alba*, *Picea abies*, *Larix deciduas* and *Fagus*

Table 1. Optimum altitude (Alt_{opt}) and shift in optimum (Shift) per species and mountain range.

Species	Mountain Area	Period	Model	Alt_{opt} (m)	CI Inf. (m)	CI Sup. (m)	Shift (m)
<i>Fagus sylvatica</i>	Pyrenees	1990s	Logistic	1330	1304	1357	-34
		2000s	Logistic	1296	1272	1320	
	Ib. system	1990s	HOF V	1528	1492	1564	-1
		2000s	HOF V	1527	1490	1564	
<i>Quercus petraea</i>	Pyrenees	1990s	HOF V	1195	1130	1260	+36
		2000s	HOF V	1231	1131	1332	
	Ib. system	1990s	HOF V	1393	1203	1583	+181
		2000s	HOF V	1574	1395	1753	
<i>Quercus faginea</i>	Pyrenees	1990s	HOF V	670	646	694	+93
		2000s	HOF V	763	734	793	
	Ib. system	1990s	Logistic	1068	1053	1082	+25
		2000s	Logistic	1094	1080	1108	
<i>Quercus suber</i>	Pyrenees	1990s	HOF IV	170	155	186	-3
		2000s	HOF IV	167	151	184	
	Ib. system	1990s	HOF IV	527	471	584	-30
		2000s	HOF IV	496	443	548	
<i>Quercus ilex</i>	Pyrenees	1990s	Logistic	370	326	414	+22
		2000s	Logistic	392	348	436	
	Ib. system	1990s	HOF V	927	913	940	+24
		2000s	HOF V	951	937	966	

Altitudes of the optimum of the probability of occurrence for the five studied species (Alt_{opt} , m) and 95% confidence intervals (CI, m), for both years of the forest survey (1990s and 2000s) within each mountain area (Pyrenees and Iberian system). The model type is indicated as logistic = symmetric logistic model, HOF IV = HOF symmetric model or HOFV = HOF skewed model (Huisman et al. 1993). Shifts (m) were calculated as differences in Alt_{opt} for each species and mountain range. Bold characters indicate non-overlapping 95% CI.

sylvatica would be at risk of higher extinction rates (Ohlemüller et al. 2006) in response to current global change. However, field evidence of species distribution shifts in Southern Europe is scarce. We show here that the altitudinal distributions of some sub-Mediterranean and temperate species were substantially altered during the last decade (1990s–2000s), whereas we could not detect any shift for the two Mediterranean species. This comparison suggests that for tree species located at the limit of their distribution area, rapid shifts in altitudinal distribution have occurred, which could be interpreted as signs of extirpation or migration in response to current global change.

Altitudinal shifts of species distribution

We used two successive National Forest Inventories to investigate the existence or absence of a shift over a 10-yr period in tree species, repeating the analysis over two mountain ranges in Spain. Overall, we found an average shift of +31 m·decade⁻¹ in optimum altitude, ranging between -34 m and +181 m·decade⁻¹. Similar to our observations, empirical data-based studies have found that tree species or genus distribution could present shifts of the same magnitude along altitudinal gradients during the last decades or century (Beckage et al. 2008; Kelly & Goulden 2008; Lenoir et al. 2008; Parolo & Rossi 2008; Bertrand et al. 2011; Feeley et al. 2011) in response to global

change. Using presence–absence data gathered from six different French mountain ranges, altitudinal shifts varied between -157 m and +120 m·decade⁻¹, depending on the woody species studied ($n = 56$; Lenoir et al. 2008). In the Santa Rosa Mountains of California, tree and shrub species shifted upward from 28 m to 142 m·decade⁻¹ (Kelly & Goulden 2008). The upward or downward movements observed in these studies were not always straightforward to interpret. Upward shifts are generally interpreted as a response to climate change, species moving towards milder temperature in response to climate warming (Breshears et al. 2008; Kelly & Goulden 2008). Downward shifts would result either from changes in biotic interactions as a result of land-use or climate change (Hampe & Jump 2011). Crimmins et al. (2011) underlined the downward shifts of plant species as inconsistent with current increasing temperatures, and rather a response to increased water balance at lower elevations. Lenoir et al. (2010) proposed a conceptual model where climate change would induce release in species competition that could explain climate-inconsistent downward shifts. We observed a general warming of the studied areas between 1980 and 2000 (0.24 °C and 0.38 °C·decade⁻¹), and models predict a warming of Mediterranean mountains by 0.35 °C to 0.50 °C·decade⁻¹ between 1990 and 2055 (Nogués Bravo et al. 2008). Considering these diverse elements, we thus expected differences in the pattern of

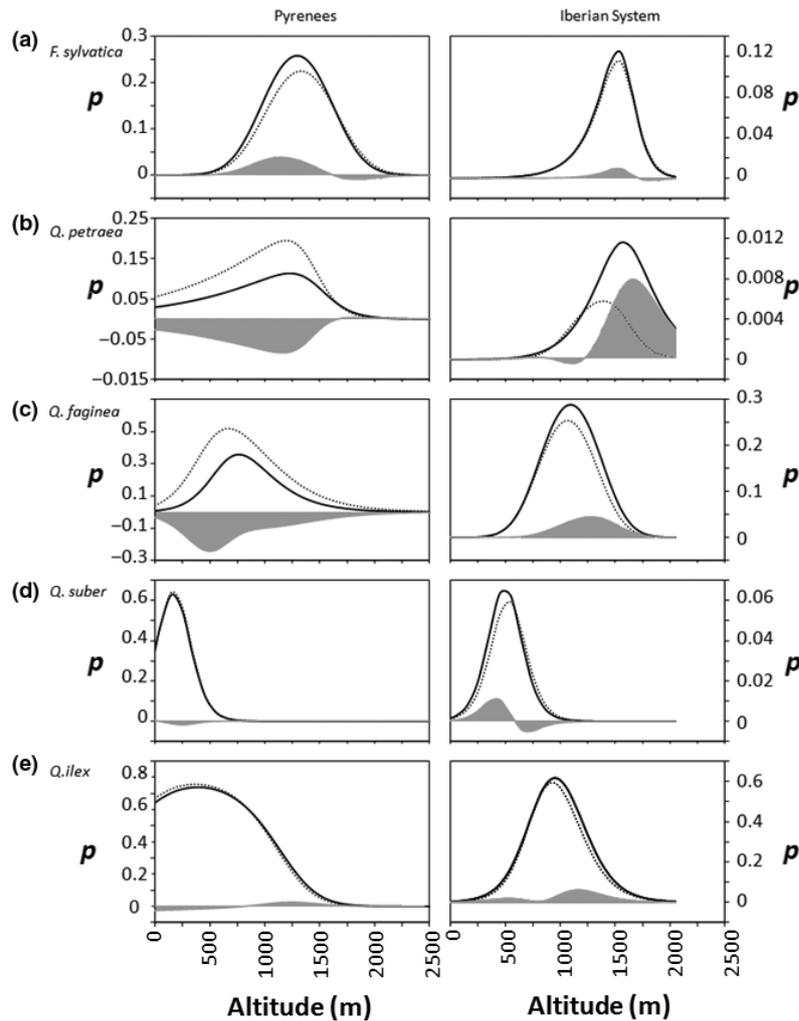


Fig. 3. Altitudinal species distributions and difference in species occurrence over a 10-yr period. The lines correspond to the fitted distributions of the probability of occurrence (p) along the altitudinal gradient for the 1990 forest inventory (dotted line) and the 2000 forest inventory (full line) in the Pyrenees Mountains (left panel) and in the Iberian System (right panel) for the five species: (a) *F. sylvatica*, (b) *Q. petraea*, (c) *Q. faginea*, (d) *Q. suber* and (e) *Q. ilex*. Grey areas represent the altitudinal distributions of difference in probability of occurrence between the 2000 and 1990 surveys. Positive values indicate tree colonisation event whereas negative values correspond to tree extirpation.

altitudinal distribution and change depending on the species type (Mediterranean/sub-Mediterranean, temperate), the mountain area (Pyrenees/Iberian system) and their sensitivity to the mediterranean climate.

Sub-Mediterranean and temperate species

Quercus petraea and *Q. faginea* were the two species whose distributions presented the most important shifts in the Spanish mountains over the 10-yr period studied. In the Iberian system, *Q. faginea* range did not change, either in optimum altitude or in probabilities of occurrence, but the species was already absent at lower altitudes (600–1700 m) compared to this species in the Pyrenees (100–1800 m). The magnitude of the shift in optimum alti-

tude in the Pyrenees ($93 \text{ m}\cdot\text{decade}^{-1}$) corresponded to extreme values encountered in the literature (Kelly & Goulden 2008; Lenoir et al. 2008), and a 10-yr period is sufficient to detect such fast-migrating species. This upward shift in optimum altitude resulted primarily from extirpation at the lowest altitudes, as indicated by the large values of $pdiff.ext$. This phenomenon is clearly a signature of a retraction in the species distribution area and could be considered one of the first stages in the response of species distribution to climate change (Maggini et al. 2011). A modelling study investigating the distributions of *Q. faginea* and *Q. ilex* demonstrated a drastic drop in *Q. faginea* presence in response to increases in drought duration, leading to its quasi-disappearance after a 30-d increment of the drought period (Purves et al. 2007). However, as under-

Table 2. Colonization (*pdiff.col*) and extirpation (*pdiff.ext*) events per species and mountain range.

Species	Mountain area	p_{1990s}	p_{2000s}	<i>pdiff.col</i>	<i>pdiff.ext</i>
<i>Fagus sylvatica</i>	Pyrenees	177	197	24	-3
	Ib. system	55	58	3	0
<i>Quercus petraea</i>	Pyrenees	209	126	1	-85
	Ib. system	4	8	5	0
<i>Quercus faginea</i>	Pyrenees	474	270	0	-204
	Ib. system	164	191	27	0
<i>Quercus suber</i>	Pyrenees	221	216	0	-5
	Ib. system	25	27	3	-1
<i>Quercus ilex</i>	Pyrenees	812	815	15	-12
	Ib. system	379	417	38	0

p_{1990s} and p_{2000s} (m per prob. units) correspond to the areas under the altitudinal distributions of probability of occurrence (*p*) for the 1990s and 2000s surveys, respectively. *pdiff.col* and *pdiff.ext* (m per prob. units) describe the area under the *pdiff* curve when *pdiff* > 0 and *pdiff* < 0, respectively. Bold characters indicate significant events.

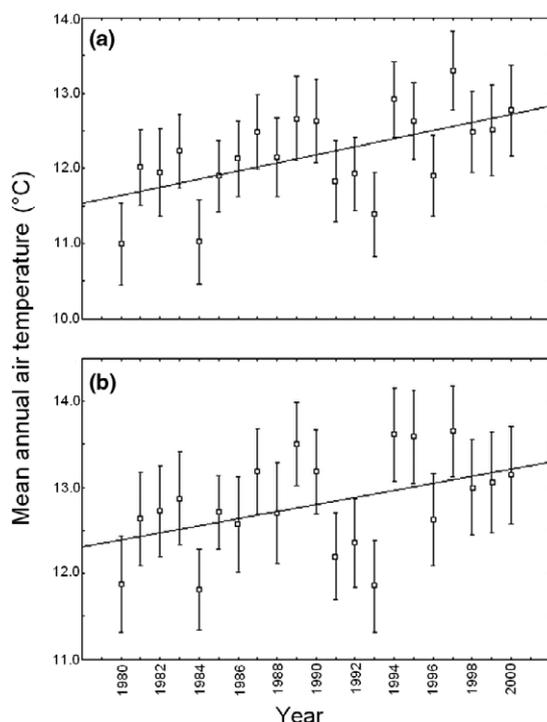


Fig. 4. Trends in mean annual temperature between 1980 and 2000 (a) in the Pyrenees mountains (b) in the Iberian System. (a) In the Pyrenees mountains, each square corresponds to the mean of 89 weather stations ($\pm 95\%$ confidence interval). The line indicates the significant tendency: $T = 11.6412 + 0.054 \cdot \text{year}$ ($P = 0.0069$). (b) In the Iberian System, each square corresponds to the mean of 98 weather stations ($\pm 95\%$ confidence interval). The line indicates the significant tendency: $T = 12.39 + 0.0412 \cdot \text{year}$ ($P = 0.0414$).

lined in a recent study on the local dynamics of *Q. faginea* – *Q. ilex* – *J. thurifera* mixed ecosystems, changes in climatic conditions and in land use (e.g. a decrease in cattle pres-

sure) may operate simultaneously, making it difficult to disentangle the role of the two processes (Olano et al. 2012). The sub-Mediterranean climate area is expected to dramatically decrease by 2080 (Sanchez de Dios et al. 2009; Ruiz-Labourdette et al. 2012), and the current distribution pattern and dynamics we observed in both Spanish mountain areas demonstrated extirpation at the lowest altitudes. Thus, we can hypothesize that *Q. faginea* is already experiencing the consequences of living at its rear edge limit under suboptimal climatic conditions, and that its extirpation is likely to accelerate in the years ahead.

For *Q. petraea*, the upward shifts in optimum altitude experienced in both the Pyrenees ($+36 \text{ m-decade}^{-1}$) and the Iberian system ($+181 \text{ m-decade}^{-1}$) were not significant. A limited non-significant downward shift in optimum altitude was found ($-28 \text{ m-decade}^{-1}$) in the French mountains (Lenoir et al. 2008); the same authors (Lenoir et al. 2009) suggested, however, a recent upward shift of the species, as indicated by the seedling optimum of occurrence, which was 346 m higher than that for adult trees. Our results could confirm this element, although the future 4th inventory would be necessary to be fully conclusive. In the Iberian system, the occurrence of colonization events at the highest altitudes demonstrated the early stage of upward shifts in patterns (Maggini et al. 2011). Although resulting from different demographic mechanisms, early signs of upward shifts have also been observed for this species in the Pyrenees, with important low-altitude extirpation events – equivalent to a trailing edge retraction (Maggini et al. 2011). In Spain, *Q. petraea* is already located at the rear edge of its latitudinal distribution (Ducousso & Bordacs 2004); its location in the Iberian system already corresponds to the most southern location of this species and we demonstrated that the current shift in the Iberian system is also placing it at the tree line (maximum altitude 1800 m) of the mountain range itself (1850–2050 m), making it almost impossible to escape upward in the future (highest altitudinal point 2313 m). In addition, a recent modelling study predicted that *Q. petraea* would suffer the largest reduction in its bioclimatic envelope by 2080 relative to other Spanish temperate broad-leaved trees (Benito Garzon et al. 2008). As temperatures are increasing in both mountain areas and as the phenomenon is expected to continue during the next century (Nogués Bravo et al. 2008), we can infer that *Q. petraea* will be at risk of extirpation in the southern range of its distribution in Europe.

For *F. sylvatica*, a temperate species also located at the southern limit of its distribution, we could not detect any shifts in the Spanish mountains. The species distribution did not change in the Iberian system and moved slightly downwards during the investigated period in the Pyrenees

($-34 \text{ m-decade}^{-1}$ in the optimum plus colonization events at the lower altitudes). It could be that our time period was too short to detect any shift for this species; 55 m and 12.5 m upward shifts per decade were found in the French mountains (Lenoir et al. 2008) and the Spanish Montseny mountains (Penuelas & Boada 2003), respectively. Comparing seedling and adult tree distributions, a downward shift of the species could be suggested (optimum altitude difference of -16 m ; Lenoir et al. 2009). According to Penuelas & Boada (2003), the persistence of this temperate species at the southern latitudes of Spain is already the result of ancient upward movements that allowed the land to reach altitudes with favourable climatic conditions. The distribution patterns that we observed (maximum altitude of 2100 m) confirm that *F. sylvatica* has already reached the tree line in the Pyrenees (Penuelas & Boada 2003; Battlori & Gutierrez 2008) and almost the rock limit (2500 m), such that upward colonization events will be unlikely in the future.

Mediterranean species

In this study, we demonstrated the current resilience of the Mediterranean species *Q. ilex* and *Q. suber*, since hardly any movement was observed during the investigated period, as underlined by small shifts in the optimum or absolute values of probabilities of presence along both altitudinal gradients. In the literature, we found no similar studies on these species; however, local stand demographic assessments clearly demonstrated that the total area of *Q. ilex* was expanding in the Montseny mountains (Penuelas & Boada 2003) and that colonization events could be observed in *J. thurifera* stands in central Spain (Olano et al. 2012). Similarly, modelling studies based on climatic envelopes (Benito Garzon et al. 2008; Ruiz-Labourdette et al. 2012) or on seed dispersal processes (Purves et al. 2007) predicted the maintenance or expansion of *Q. ilex* range in response to global change in the Iberian Peninsula until 2020, followed by strong extirpations by 2080. Our results rather suggest the current stability of the altitudinal distribution of these species. Olano et al. (2012) noted that *Q. ilex* colonization events observed in central Spain occurred in plots having the same climatic conditions in both 1992 and 2002. *Q. ilex* dynamics seemed to be largely influenced by abiotic factors such as drought stress at the regeneration stage (Resco de Dios et al. 2007) as well as temperature (Sanchez de Dios et al. 2009). The climatic envelope of *Q. suber* should already be reduced by 2020 according to the models (Benito Garzon et al. 2008), and this species is known to be less stress tolerant than *Q. ilex* (David et al. 2007). However, our results did not confirm these assumptions as no movement was detected. Our study thus suggested that both Spanish mountain areas

still represent suitable climatic environments for the two Mediterranean oaks.

Both of these Mediterranean oaks are at the core of their latitudinal distribution area in Spain (Pyrenees and Iberian system), which could explain why changes in environmental conditions did not result in detectable changes over a 10-yr period and would suggest a longer stability of their distribution area under current global changes.

Strengths and limitations of the modelling approach

Considering that the time period considered in our study was short, it was all the more important to assess the parameters of the species distribution in the most unbiased way. Logistic regression is the most commonly used model in the analysis of species distributions along environmental gradients to fit binary data such as species presence-absence (see review of Austin 2007). However, Coudun & Gegout (2006) underlined that the main parameters of the distribution (among which the optimum of occurrence) could not be accurately estimated with this model when the theoretical optimum was located near an extreme of the gradient, i.e. when the distribution was skewed. When species distributions along ecological gradients do not exhibit a symmetric distribution, unimodal or skewed models should be tested instead (Austin 2002, 2007; Oksanen & Minchin 2002). The HOF models (Austin 2002) cover a set of symmetric and asymmetric models that were proposed as the best techniques to fit skewed distributions (Lawesson & Oksanen 2002; Oksanen & Minchin 2002). In our study, we found that species altitudinal distributions corresponded to skewed curves in 50% of the studied cases. The occurrence of skewed distributions was already present along various environmental gradients for 21–84% of the species studied (Minchin 1989; Lawesson & Oksanen 2002; Oksanen & Minchin 2002; Rydgren et al. 2003; Murphy et al. 2010). The use of symmetric models on a skewed distribution would clearly lead to significant biases in optimum altitude estimates, and thus we strongly encourage calculation of the optimum and confidence interval using the HOF V skewed model and the Delta method (Couallier et al. 2011). Moreover, as migration of tree species is slow, studies such as ours that consider rapid changes over one decade are probably incapable of providing evidence of changes over the whole altitudinal or latitudinal range, such as the contraction or expansion events demonstrated in Zhu et al. (2012). Migration can still be seen by studying signs such as leaning of the optimum towards higher or lower limits of the range or changes in abundance along the whole range (Breshears et al. 2008; Maggini et al. 2011). The models that we used (Huisman et al. 1993) and the developments we added to the estimations of optimum on skewed distributions (Couallier et al.

2011) offer an interesting method to quantify the magnitude of the changes along the whole altitudinal distribution of a species.

Conclusion

Our study demonstrated that over a short time period, using adequate models to quantitatively describe the altitudinal distribution of trees, we could determine that Mediterranean species distributions are still resilient to current global changes, whereas sub-Mediterranean and temperate species distributions were already changing, either in altitude of the optimum of occurrence or in probability of occurrence at high or low altitudes. These patterns resulted from changes in species colonization or extirpation events. For the Mediterranean species, located in the core of their distribution area, the absence of rapid shifts may be explained by the maintenance of local environmental conditions still corresponding to their ecological requirements. In contrast, for some sub-Mediterranean and temperate species, the magnitude of the changes suggests that local extirpations or upward colonizations are underway, probably as a sign of increasing lack of balance between prevailing conditions and the species fundamental niche. Considering the expected changes in climatic conditions, with warmer and drier conditions (Nogués Bravo et al. 2008; Kelley et al. 2012), the tree species shift rates that we observed are lower by a factor of 10–100 compared to the pace of land-use and climate change suggested in the models (Iverson et al. 2004; Morin et al. 2008; Bertrand et al. 2011). Thus the patterns observed in this study are likely to intensify in the future, with tree species distributions moving upwards as a consequence of enhanced high-altitude colonization events and low-altitude extirpations events.

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Supporting Information

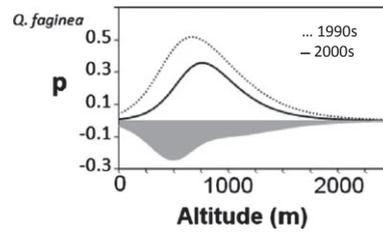
Additional supporting information may be found in the online version of this article:

Table S1. Total number of plots and number of A1 plots used in the analysis in each mountain range and for each national forest inventory survey.

Table S2. Values of the Akaike criterion (AIC).

Graphical Abstract

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Still little empirical evidence exists on tree species migrations in response to global change. Our work demonstrates that changes in altitudinal distribution could occur over a 10 year time period for tree species located at the southern limit of their distribution area whereas no movement was detected for Mediterranean oaks located in the core of their distribution area.