Altitudinal shifts in tree species distribution and growth of Iberian mountains: a detectable fingerprint of climate change?

Advisor: Miguel Ángel Zavala

Reviewers: Laurent Augusto and Mark Bakker

Location: Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA), Centro de Investigación Forestal (CIFOR), Crta. de la Coruña, km. 7,5 28040 Madrid, Spain
ACKNOWLEDGMENTS

After having spent 5 months beginning a sentence in Spanish, following it in English and ending it in French, I hope to manage to write these acknowledgments in the each one’s language. With a few help, I admit.

Miguel, muchas gracias por haberte atrevido a aceptar mis prácticas pese a no hablar ni una palabra de español y no haber conseguido pronunciar una palabra en inglés la primera vez que nos vimos. A pesar de algunas pequeñas confusiones y malentendidos, al final hemos logrado entendernos y vuelvo a Francia enriquecida con una buena dosis de “ecological detective”, una cucharada de autonomía y un pellizco de seguridad suplementaria. Gracias por todo y sobre todo por haber confiado en mí.

Annabel et Sylvain merci d’avoir toujours été présents plus ou moins à distance et d’avoir nourri Lumino en tapas et en chocolat!

Raúl, te agradezco que me hayas enseñado: Access, el funcionamiento de la base de datos, el padel, ArcMap… ¡y el inglés! ¡Jejeje! ¡Y por encima de todo, gracias por tu paciencia cuando no lograba encontrar las palabras para que me entendieras!

Jesús y David, gracias por toda la información esencial que me habéis proporcionado sobre las especies y la geografía de España.

Gracias, Danke, Spas respectively to David, Marina, « the other » Raúl, Cristina, Katarina and Yusuf for your kindness , your good mood and your patience during our talks. In particular, I would like to thank Katarina for the proof reading, Marina for having been my personal translator and Cristina for her relevant advices.

Un clin d’œil à la Urli’s family qui n’est jamais très loin. Magie d’internet!

And to conclude: Let’s start a new chapter!
ABSTRACT

Species distribution ranges are extremely affected by climate warming. A critical issue is to determine the rate and the direction of tree distribution shift. Numerous studies based on modeling processes concluded on a northward and/or an upward shift in species distribution range. However, few observational studies assessed this hypothesis especially over a large scale. The aim of the study is to examine a potential altitudinal shift in occurrence, growth and relative abundance in Iberian mountain areas (Pyrenees and Sistema iberico) for two temperate species (*Quercus petraea* and *Fagus sylvatica*) and three Mediterranean ones (*Quercus faginea*, *Quercus suber* and *Quercus ilex*) over a ten year period. We analyzed huge datasets coming from the Second and the Third Spanish Forest Inventories (SFI) made in 1990 and 2000 respectively.

In general, our results showed an upward shift in occurrence for Mediterranean species whereas temperate ones presented a downward shift or no shift. Over the studied period, all the species presented a positive growth especially at low altitude for the temperate species and at high altitude for the Mediterranean ones. The relative abundance of the studied species decreased during the period which suggests that other species, not included in our analysis, increased in abundance between 1990 and 2000. However, differences in the pattern occurred between the mountains areas as Sistema iberico presented a more continental climate than the Pyrenees.

The unexpected downward shift observed for beech suggest that climate change is not the main factor influencing the species distribution in this area. Management and land-use changes played an important role in the Mediterranean region, especially at low altitude where land abandonment enhanced the dynamics of forest recovery.
TABLE OF CONTENTS

ACKNOWLEDGMENTS

ABSTRACT

TABLE OF CONTENTS

INTRODUCTION 1

MATERIALS AND METHODS 3

Study area 3
Data collection 4
Data processing 4
Species and specific study area choices 5
Statistical analysis 6

RESULTS 7

Climate of the studied mountain areas 7
Altitudinal shifts in tree species occurrence 8
Altitudinal shift in tree growth increment 10
Altitudinal shift in relative abundance 13

DISCUSSION 16

Altitudinal shift of species presence 16
Growth increase: fingerprint of climate change? 18
Change in species abundance 19
Conclusions 20

REFERENCES 21

APPENDIXES 25
**INTRODUCTION**

Rapid anthropogenic global changes such as climate warming, change in land use, nitrogen deposition and invasive species introduction interfere with many natural ecosystems. A critical issue is to understand how these changes will impact biodiversity (Bakkenes *et al.* 2002; Thomas *et al.* 2004; Thuiller *et al.* 2005; Walther, Berger & Sykes M.T. 2005), productivity (Hughes 2000), ecosystem services (Diaz, Tilman & Fargione 2003) and species distribution ranges (Bakkenes *et al.* 2002; Parmesan & Yohe 2003; Walther, Berger & Sykes 2005).

Phylogeographic and genetic studies allow to quantify the migration of tree species due to past climate changes. Paleoarchives (pollen, fossils) and genetic markers provide essential information to determine migration rates and directions of species and consequently to forecast future shifts of woody species distributions (Petit, Sheng Hu & Dick 2008; Bush, Silman & Urrego 2004). For example, pollen data revealed that spruce (*Picea* spp.) shifted northwards in the eastern United States as the climate warmed up at the end of the last glacial period (Davis & Shaw 2001). Moreover, a study based on haplotypes showed that holm oak (*Quercus ilex*) spread along several migration lines (westward and northward shifts) in the Mediterranean Basin during the Holocene (Petit, Hampe & Cheddadi 2005). However, the current increase of temperature occurs faster than this past global warming (IPCC 2001). Therefore, this study aims to investigate the response of tree species (adaption, migration or extirpation) under these important temperature variations (Davis & Shaw 2001; Aitken *et al.* 2008).

Are species distribution ranges altered by global changes?

The limit of species distribution ranges are characterized by complex processes and mechanisms which influence survival and migration. The northern limit called “leading edge” is controlled by rare long distance dispersal events whereas the southern limit (“rear edge”) consists in an eroding range margin where extirpation events occur (Hampe & Petit 2005).

Modeling processes is an option in order to put forward an hypothesis concerning possible shifts of the species distribution ranges. Two main kinds of distribution models exist: niche-based or bioclimatic model and process-based model. The first is based on the principle of the climatic envelope: it relates the current presence/absence of the species to environmental variables (Chuine, Thuiller & Morin 2004). It is applied to the continental scale and consequently to the whole distribution range of species because it is generally considered that the presence of the species is only determined by climate effects at this scale (Sykes, Prentice & Cramer 1996). Thuiller *et al.* (2005) projected distribution of 1350 European plant species with a climatic model named BIOMOD. They showed that more than half of the species could be vulnerable or threatened by 2080 according to the Application of the International Union for Conservation of Nature and Natural Resources Red List criteria. The results of simulations of BIOMOD are in agreement with the work of Iverson and Prasad (1998) (Chuine,
Thuiller & Morin 2004). They modeled the abundance of 80 tree species following climate change in the eastern United States: 36 species present the potential to shift at least 100 km to the north. However, these models present several disadvantages: it does not take the biological features of the species like its migration speed, plasticity, local adaptation, biotic interactions or land use into account (Thuiller et al. 2005). Contrary to this, process-based models deal with the physiological features of the species. PHENOFIT, a typical example of this kind of model, takes the role of the synchronization of the species timing of development to seasonal climatic variation into account. Using this model, Morin et al. (2008) simulated the distribution of 16 North American tree species at continental scale for the 21st century and showed a loss of habitat southward and a northward colonization for many species. However, process-based models need an important step of development and a great knowledge of the species physiology but little has been published so far (Aitken et al. 2008). Overall, the two kinds of models suggested a northward and/or an upward shift of tree species distribution, even if niche-based models tend to predict a stronger level of extirpation and a higher proportion of migration than the process-based models. Indeed, process-based models, focusing on the modeling of fundamental niches (based on ecophysiological responses to abiotic variables), are less pessimistic than niche-based models, which focus on the realized niche of the species (based on distributional data in nature).

Although field monitoring and observations are hardly executable on the whole range of species distribution, no other way exists to check the model predictions. Only the use of surveys could give a good approximation of the shift for the entire distribution range: Woodall et al. (in press) studied latitudinal shifts of tree seedling distribution of northern, southern and general species in the eastern United States: the northern species migrated northwards whereas southern species did not present any shift despite a greater regeneration at higher altitudes and general species showed an expansion southwards. Similar studies were realized along altitudinal gradients by Lenoir et al. (2008) and Kelly and Goulden (2008). They revealed an upward shift in species optimum elevation averaging 29 m (171 forest plant species) and 22.7 m (10 dominant species of 141 ones) per decade, respectively. Generally, most of the studies have focused on a single boundary of the species distribution. In many cases the treeline was observed and generally colonization events at high altitudes were detected for different species: Larix sibirica (Devi et al. 2008; Shi hayatov, Terent’ev & Fomin 2005; Shi hayatov et al. 2007; Shi hayatov & Mazepa 2007), Picea glauca (Danby & Hik 2007), Abies procera (Magee & Antos 1992), Pinus peuce (Meshinev, Apostolova & Koleva 2000). These colonization events equally appeared at the northern limits of species distribution and led to an northward shift of this edge (Jonstone & Chapin 2003; Lescop-Sinclair & Payette 1995; Sturm, Racine & Tape 2001). By contrast, very few studies take the rear edge into account. However, Peñuelas and Boada (2003) showed an upward shift of forest beech (Fagus sylvatica) at its southern limit with a degradation and extirpation of beech populations at medium and low elevations respectively. In conclusion, observation studies seem to confirm the
direction of model predictions but not the migration speed. However, it is necessary to verify further model predictions using large scale datasets or data from populations inhabiting vulnerable regions (e.g. populations at the rear edge of the species distribution range and mountain areas).

During the next century, the increase of temperature in mountain areas is expected to be two or three times higher than during the 20th century (Nogués-Bravo et al. 2007). Furthermore, Mediterranean ecosystems are vulnerable to global change and lot of changes in biodiversity are expected: Sobrino et al. (2001) showed an increase of range expansion of thermophilic and invasive plants through the Iberian Peninsula probably due to global change. So the Mediterranean mountains present a double disadvantage: being mountains and being located in Mediterranean climate (Nogués-Bravo et al. 2008) (south limit of distribution for temperate tree species). Moreover, Sala et al (2000) showed that land use could have stronger effects on terrestrial ecosystems in the future than climate change. This is particularly the case for Mediterranean mountain ecosystems which have been especially altered by humans through agriculture, stockbreeding and forestry (Nogués-Bravo et al. 2008).

The aim of this study is to examine a potential altitudinal shift in tree species in mountain areas in the Iberian Peninsula using comparable data of 10 year-separated national forest inventories. The Spanish forest inventory aims to obtain an extensive database concerning the forest resources (species, dendrometry data, health status, etc.) in order to develop suitable management strategies for the different ecosystems (Alia et al. 2009). These data are useful to investigate how Mediterranean mountains will cope to climate change. Five species, beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*), cork oak (*Quercus suber*), Portugese oak (*Quercus faginea*) and holm oak (*Quercus ilex*) and two mountain areas (Pyrenees and Sistema iberico) were selected. The specific questions of this study are: (i) Is an upward shift of species distribution observed? (ii) Can we detect an altitudinal shift in growth for these species? (iii) If these hypotheses are true, do climate or land use play a major role in these shifts?

**MATERIALS AND METHODS**

**Study area**

The Continental Spain (492173 km²) is included between 36°N and 43.5°N, and 9°W and 3°E which represents a striking altitudinal gradient (sea level – 3500 meters) (Montoya et al. in press). Mountains cover 51% of the national surface area and more than 20% of these mountain areas, 10 millions of hectares, are forest-covered (3rd SFI, Inventario Forestal Nacional 2007). The study area contains a large range of climates (from semiarid to Mediterranean and humid Atlantic climates) and a great variety of natural and managed landscapes: forests, savannas, shrublands, grasslands, agriculture fields and urban areas (Montoya et al. in press).
**Data collection**

The study area constitutes about 50 provinces and was surveyed by two forest inventories: the Second Spanish Forest Inventory (2\textsuperscript{nd} SFI, Inventario Forestal Nacional 1995) established between 1986 and 1996, and Third Spanish Forest Inventory (3\textsuperscript{rd} SFI, Inventario Forestal Nacional 2007) between 1997 and 2007. The SFI consists in a systematic sampling of permanent plots with a measurement interval of 10 years. These surveys contain circular plots distributed on a square grid of 1km over the total forested area. Each plot is located with Universal Transverse Mercator (UTM) coordinates. 205 416 plots were surveyed, a code was attributed for each of them during the third inventory to specify if the plot was new or in case it was created during the SFI2, if its coordinates were correct. For this study only the A1 plots (151 368) were selected because they are common in the two inventories and they are secure in terms of relocalization.

<table>
<thead>
<tr>
<th>DBH classes (cm)</th>
<th>SAR\textsubscript{j} (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7.5&lt;DBH&lt;12.49</td>
<td>5</td>
</tr>
<tr>
<td>12.5&lt;DBH&lt;22.49</td>
<td>10</td>
</tr>
<tr>
<td>22.5&lt;DBH&lt;42.49</td>
<td>15</td>
</tr>
<tr>
<td>DBH&gt;42.5</td>
<td>25</td>
</tr>
</tbody>
</table>

Table 1. Sampling area radius (SAR\textsubscript{j}) measured as the distance from the center of the plot on the circular sampled plot as a function of the tree DBH class \( j \).

The SFIs are composed of two dendrometric classes of trees: large trees (Lt) and small trees (St). Lt is constituted all trees with a diameter at breast height over 7.5 cm (DBH, m, measured at 1.3 m of height). Their sampling area is a circle whose radius from the centre of the plot is increasing as a function of their DBH (Table 1). The Lt database contains individual level data: tree species and two perpendicular tree diameters. St represents the regeneration and takes into account all trees with a DBH lower than 7.5 cm. These trees were sampled in a 5m-radius area. Contrary to the Lt, the St database contains plot level data only: presence / absence per tree species (Inventario Forestal Nacional 2007).

**Data processing**

Data were extracted and compiled with Access (Microsoft Office 2003 and 2007, Redmond, WA, USA). Firstly, the different tables of province level data were joined into one single table, for the Lt and St respectively and for each inventory.

For each Lt Database’s tree, an individual diameter \((DNi, \text{mm})\) was calculated by averaging the two measured perpendicular diameters. Depending on this \(DNi\) the sampling area radius \((SARj, m)\) was deduced following the previously mentioned rules (Table 1). Then these tree level data were aggregated...
by plot and species to obtain information about presence and absolute values of basal area (AbsBA, m².ha⁻¹) for each species per plot (Plot level per species):

\[
AbsBA_{p,s} = \sum_{i=1}^{n} \pi \left( \frac{DN_i}{2000} \right)^2 \times \frac{10000}{\pi (SAR_j)^2}
\]

where \(n\) is the total number of trees of the species \(s\) in the plot \(p\). Then the relative value of BA (RelBA) was calculated as follows:

\[
RelBA_{p,s} = \frac{AbsBA_{p,s}}{\sum_{s=1}^{m} AbsBA_{p,s}}
\]

where \(m\) is the total number of species in the plot \(p\).

The establishment of a species code correspondence between the two inventories allowed us to reunite the data about Lt and St (e.g. presence/absence for each class (Lt, St), AbsBA \(_{p,s}\), RelBA \(_{s,p}\)) for the Second and the Third inventory per plot and per species: The relative increment in absolute basal area (ΔBAr) corresponding to tree growth increment and the absolute increment in relative basal area (Δp) corresponding to species relative abundance change were calculated according to:

\[
\Delta BA_{r,p,s} = \frac{AbsBA_{3,p,s} - AbsBA_{2,p,s}}{AbsBA_{2,p,s}}
\]

\[
\Delta p_{p,s} = RelBA_{3,p,s} - RelBA_{2,p,s}
\]

where 2 and 3 represent the number of the inventory.

**Species and specific study area choices**

5 hardwood tree species were selected and were arranged in two groups: the temperate species (*Fagus sylvatica* and *Quercus petraea*) and the Mediterranean species (*Quercus suber*, *Quercus faginea* and *Quercus ilex*). *F. sylvatica* and *Q. petraea* are typical species for central and occidental Europe. They are located in the northern mountains of Spain. The distribution of *Q. suber* and *Q. faginea* is restricted to the west of the Mediterranean area. In Spain *Q. suber* is dominant in the western sector of the country whereas *Q.faginea* is present everywhere except in the North-East. *Q. ilex* is a typical Mediterranean species whose distribution area expands to all countries bordering the Mediterranean Sea (Alia et al. 2009). In Spain, the temperate studied species are situated at their rear edge whereas the Mediterranean ones are in the core of their distribution range.

For each species, different specific study areas were selected including all Spain and one or two mountain areas according to the distribution of the species and the number of existing plots (Table 2, Appendix 1). Each area was defined with ArcMap (ESRI ArcMap 9.2, Redlands, CA, USA) and by using provenance maps (Alia et al. 2009).
Table 2. Specific study area and associated number of plots for each species

<table>
<thead>
<tr>
<th>Species</th>
<th>Specific study areas</th>
<th>Number of plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fagus sylvatica</td>
<td>Spain</td>
<td>2123</td>
</tr>
<tr>
<td></td>
<td>Pyrenees</td>
<td>640</td>
</tr>
<tr>
<td></td>
<td>Sistema iberico</td>
<td>430</td>
</tr>
<tr>
<td>Quercus petraea</td>
<td>Spain</td>
<td>948</td>
</tr>
<tr>
<td></td>
<td>Pyrenees</td>
<td>555</td>
</tr>
<tr>
<td>Quercus suber</td>
<td>Spain</td>
<td>3159</td>
</tr>
<tr>
<td>Quercus faginea</td>
<td>Spain</td>
<td>6852</td>
</tr>
<tr>
<td></td>
<td>Pyrenees</td>
<td>1518</td>
</tr>
<tr>
<td></td>
<td>Sistema iberico</td>
<td>2497</td>
</tr>
<tr>
<td>Quercus ilex</td>
<td>Spain</td>
<td>23075</td>
</tr>
<tr>
<td></td>
<td>Pyrenees</td>
<td>4611</td>
</tr>
<tr>
<td></td>
<td>Sistema iberico</td>
<td>5197</td>
</tr>
</tbody>
</table>

Climatic data including mean annual temperature ($T$, °C), mean minimum temperature ($T_{min}$, °C), mean maximum Temperature ($T_{max}$, °C), annual Precipitation ($P$, mm) and the minimum of summer precipitation ($MSP$, mm) were associated to each plot. The data was provided from a model of Julián Gonzalo Jiménez (Gonzalo 2007).

**Statistical analysis**

All statistical analyses were performed with the STATISTICA software (v 7.0, StatSoft Inc., Tulsa, OK, USA).

A discriminant analysis using the topographic (altitude) and climatic ($T$, $T_{min}$, $T_{max}$, $P$ and $MSP$) variables was carried out for the plots figuring each area (Pyrenees, Sistema iberico, the rest of Spain) to check the topographic and climatic homogeneity between areas.

The normality of the data was checked with Kolmogorov-Smirnov test (data not shown). If the data was normal distributed, Student test and ANOVA were used, if not Mann-Withney test U and Kruskall-Wallis ANOVA were performed.

Two way analysis of variance (ANOVA) allowed to determine the respective effects of species and mountains on mean altitude of the species occurrence. Student tests with dependent samples were used for each species and each area to test the difference of mean altitude of the species presence between the two inventories. The difference between the mean altitude of the species presence in SFI2 and the colonized plots in SFI3 (e.g. plots for which the species was not present as St or Lt in SFI2 and
it is present as St orLt in SFI3) was tested with Student tests with independent samples for each species and each area.

For each analysis with $\Delta BAr$ data, the monospecific and plurispecific plots were considered whereas for the analyses with $\Delta p$ data only the plurispecific plots were taken into account because of the definition of this variable.

$\Delta BAr$ and $\Delta p$ were analysed separating the plots in three categories: plots that demonstrated a positive value of the variable, plots with negative values and plots that presented values equal to 0. One way ANOVA allowed to evaluate the difference of mean altitude between these categories for $\Delta BAr$ and $\Delta p$ for each species and each area. The effects of species and mountains on the mean altitude of the plots for each categories of the grouping variable were tested with two ways ANOVA.

Equivalent to non parametric Student test, Mann-Withney U-test allowed to test the difference of $\Delta BAr$ and $\Delta p$ respectively between categorical variables of altitude defined as:

$$\begin{cases}
\text{LOW if Altitude < MA} \\
\text{HIGH if Altitude > MA}
\end{cases}$$

where MA is the mean altitude of the SFI2 and the SFI3. The MA is different for each species and each area. The effects of mountains on $\Delta BAr$ and $\Delta p$ were tested with Kruskall-Wallis ANOVAs.

**RESULTS**

*Climate of the studied mountain areas*

A discriminant analysis ordered the plots across two components. The first axis explained 74% of the variance and is defined by minimum summer precipitations (MSP) and $T_{\text{min}}$ at the positive extreme and $T$ and $T_{\text{max}}$ at the negative one. The second axis represented 26% of the total variance and is correlated with Altitude, $T_{\text{max}}$ and $T_{\text{min}}$ at the positive values, and $T$ and $P$ at the negatives ones (Table 3, Figure 1).

| Table 3. Results of the discriminant analysis: Variance explained by each axis and variables defining the axes with standardized weights. |
|----------------------------------|----------|----------|
| **Variance extracted (%)**      | Axis 1   | Axis 2   |
| Altitude                         | 0.23     | 0.50     |
| MSP                              | 1.31     | 0.20     |
| P                                | 0.00     | -0.92    |
| T                                | -1.54    | -2.59    |
| $T_{\text{max}}$                 | -0.54    | 0.82     |
| $T_{\text{min}}$                 | 1.68     | 1.49     |

This analysis and more precisely the axis 1 ordinated the two mountain areas from the rest of the plots by their climatic features. The annual, minimum and maximum temperatures were lower in
the Pyrenees than in the Sistema iberico whereas the mean summer precipitations were more important in the Pyrenees than in the Sistema iberico which is subject to a more continental climate.

![Figure 1](image.jpg)

**Figure 1.** Ordination by discriminant analysis of the plots situated in Pyrenees (green circles) and Sistela iberico (red squares) compared to the rest of the plots (blue circles).

**Altitudinal shifts in tree species occurrence**

The mean altitude of species presence in 2000 (i.e. during the SFI3) was different between each species: 940 m for *Q. petraea*, 895 m for *Q. faginea*, 760 m for *Q. ilex*, 390 m for *Q. suber* and 1065 m for *F. sylvatica* (One-way ANOVA, F-test=2038.68, p<0.0001, Newmann-Keuls test). For all species together, mountains presented a significant effect on mean altitude which were different between each mountain areas (i.e Pyrenees, Sistema iberico and the rest of the plots in Spain) (One-way ANOVA, F-test=4852.2, p<0.0001).

For *F. sylvatica*, we observed a significant downward shift between the two inventories in all areas (but not significant in Sistema iberico): 15 m, 7 m and 5 m in the whole Spain, in the Pyrenees and in the Sistema iberico respectively). In opposition, all *Quercus* species exhibited upward shifts except *Q. petraea* in the whole Spain but this trend was only significant for *Q. faginea* in the Pyrenees (Figure 2, left).
Figure 2. Mean altitude and standard error of species presence of SFI2 (white bars) and SFI3 (gray bars) (left) and of SFI2 (white bars) and the colonized plots in SFI3 (black bars) (right) for each species and each location: (a) Spain, (b) Pyrenees, (c) Sistema Iberico. Qp: Q. petraea, Qf: Q. faginea, Qi: Q. ilex, Qs: Q. suber and Fs: Fagus sylvatica. Results of Student test with dependent samples between SFI2 and SFI3 and with independent samples between SFI2 and colonized plots in SFI3 (***, **, * are respectively p<0.001, p<0.01 and p<0.05, ns: not significant).

Mean altitude differences were more important when comparing second inventory plots and colonized plots in SFI3 (Figure 2, right). A downward shift is once observed in all areas for F. sylvatica (140 m, 65 m and 48 m in the whole Spain, in the Pyrenees and in the Sistema Iberico respectively) but only the shift in the whole Spain was significant. To the contrary, all Quercus
species except Q. petraea and Q. faginea in the whole Spain showed upward shifts. In the case of Q. ilex in the whole Spain this shift was particularly great: 350 m.

**Altitudinal shift in tree growth increment**

Tree growth increment corresponds to the percentage of change in basal area ($\Delta BAr$) of each species between the two inventories. For each species, the mean of this variable is positive which indicates that each species demonstrated a positive growth in basal area between 1990 and 2000. Kruskall-Wallis ANOVAs by area showed a significant effect of species on the mean of $\Delta BAr$ (Figure 3). In Spain, Q. faginea had the higher growth rate whereas Q. suber presented the lowest basal area increment. In the Pyrenees and Sistema iberico mountains, Q. ilex is the species with the higher radial growth. For each species except for Q. suber (which was only studied on the whole Spain), the effect of mountain areas on $\Delta BAr$ was significant (Kruskall-Wallis ANOVAs). Tree growth increment was higher for the plots situated in the Pyrenees and in the Sistema iberico compared to the rest of the plots located in Spain (open circles of the maps in Appendix 1).

![Figure 3](image)

**Figure 3.** Mean value of $\Delta BAr$ and standard error for each species and each location. For the species legend, see Fig. 2. Different letters above columns indicates the significant differences (p<0.05) between species by location (Results of Kruskall-Wallis ANOVA).

Figure 4 presents the mean altitudes for three different categories of change in tree growth increment per species and mountain areas (plots presenting a positive, negative and null change). For Q. petraea, mean altitude was not significantly different among the categories of $\Delta BAr$ for Spain and the Pyrenees. For Q. faginea, the mean altitude of plots with null change was lower than one of plots with positive and negative changes whatever the study area, but this difference was not significant in the Sistema iberico. The effect of Mountains was significant on mean altitude of Q. faginea but the interaction “Mountains*$\Delta BAr$ category” had no effect (Appendix 2). For Q. ilex the mean altitude of plots with negative change was lower than the altitude of plots with positive and null changes in the whole Spain whereas in the two mountain areas (i. e. Pyrenees and Sistema iberico) the mean altitude of plots with null change was lower than one of plots with positive and negative changes. The
mountain areas and the interaction “Mountains*ΔBAr Category” had a significant effect on holm oak’s altitude (Appendix 2).

For *Q. suber*, the mean altitude of the plots with a null change in basal area was higher than the altitude of the plots with positive and negative values of basal area increments. On the contrary, beech plots with a null change in basal area presented a lower altitude than plots with positive and negative ones in the whole Spain (but no difference in the Pyrenees and the Sistema iberico). Mountains has an effect on mean altitude of each category for this species but not the interaction “Mountains*ΔBAr category” (Appendix 3).

Figure 5 shows the mean of tree growth increment for the plots situated below the mean altitude of the two inventories for the considered species per area (low altitude) and above this limit (high altitude). Over whole Spain, the mean ΔBAr was higher at high altitude for *Q. faginea*, *Q. ilex* and *Q. suber*. In opposition, for *Q. petraea* we found a higher value of mean basal area increment at low altitude. Only *F. sylvatica* had equal mean of ΔBAr between low and high altitudes, over

![Figure 4](image-url)
whole Spain. On the opposite in the Pyrenees, growth increment of *F. sylvatica* at high altitude was close to zero whereas it was equal to 0.7 at low altitude. There was no significant difference in mean $\Delta BAr$ between the categories of altitude for the others species in the Pyrenees, even if the basal area increment was more important at low altitude for *Q. petraea* and at high altitude for *Q. faginea*. No species presented significant differences in the Sistema iberico.

**Figure 5.** $\Delta BAr$ (Mean and SE) for each species and each location, for plots observed at low (white bars) and high (gray bars) altitudes. See Fig. 2 for the legend of species and location. Results of Mann-Withney-U test (***, **, * are respectively p<0.001, p<0.01 and p<0.05, ns: not significant).
**Altitudinal shift in relative abundance**

The relative abundance change ($\Delta p$) was close to zero or negative except for beech in the Pyrenees (Figure 6). It means that the proportion of the species tended not to change or slightly decrease in average over the 10 years studied period. Over whole Spain $Q. faginea$ and $Q. suber$ presented the higher decrease in relative abundance whereas beech showed a lesser decrease. In the Pyrenees, the proportion of this last species increased whereas it decreases in the Sistema iberico. In the Pyrenees, the relative abundance of the others species decreases. In the Sistema Iberico, the proportion of $Q. faginea$ dramatically decreased over the 10 years period. Kruskall-Wallis ANOVAs showed that for all the species except cork oak the effect of mountains on $\Delta p$ was significant.

![Figure 6. Mean value of $\Delta p$ and standard error for each species and each location. For the species legend, see Fig. 2. Different letters above columns indicates the significant differences ($p<0.05$) between species by location (Results of Kruskall-Wallis ANOVA).](image)

The comparison of mean altitude of each category (plots with a positive, negative and null change in relative abundance) is shown on Figure 7. For all *Quercus* species, plots with null change in $\Delta p$ were located at higher altitude than those with positive and negative changes in the whole Spain whereas $F. sylvatica$ presented no difference between the categories of $\Delta p$. $Q. petraea$ and $Q. ilex$ exhibited the same pattern in the Pyrenees. For $Q. faginea$, in this mountain area, it was no difference between altitudes for each category of relative abundance changes whereas in the Sistema iberico, mean altitude of the plots with positive values of $\Delta p$ were located at higher altitude than those with negative and null changes. For this species, Mountains and the interaction “Mountains*$\Delta p$ category” had significant effects on mean altitude (Appendix 3). At last, for *Fagus sylvatica*, plots with positive values of relative abundance change were located at lower altitude than those with negative values in Pyrenees whereas no difference was detected in Sistema iberico. Indeed, we observed a significant effects of Mountains and interaction “Mountains*$\Delta p$ category” (Appendix 3).
Figure 7. Mean altitude and standard error of $\Delta p$ for each species and each location, for plots presenting a positive (white bars), negative (dark gray bars) or null change (light gray bars). See Fig.2 for legend of species and location. Different letters above columns indicates significant differences ($p<0.05$) between each category by species and location according to one-way ANOVA.

Over whole Spain, the decrease in $Q. petraea$, $Q. faginea$, $Q. ilex$ and $F. sylvatica$ relative abundance was more important at high altitude but only the difference of $F. sylvatica$ was significant. The opposite pattern (i.e., the decrease in the species proportion was higher at low altitude) occurred for $Q. suber$. In the Pyrenees, the decrease in $\Delta p$ between altitudes was not significantly different for $Q. petraea$ and $Q. ilex$. In the same mountain area, $Q. faginea$ and $F. sylvatica$ presented both an increment in species proportion at low altitudes and a decrease at high one. In the Sistema iberico,
only *Q. faginea* showed a significant difference between the two categories of altitude: the decrement was higher in low altitude plots compared to high altitude plots (Figure 8).

**Figure 8.** Δp (Mean and SE) for each species and each location, for plots observed at low (white bars) and high (gray bars) altitudes. See Fig. 2 for the legend of species and location. Results of Mann-Whitney-U test (***, **, * are respectively p<0.001, p<0.01 and p<0.05, ns: not significant).
This retrospective analysis of SFI datasets allowed us to evidence that Mediterranean species (Q. faginea, Q. ilex and Q. suber) shifted upwards in occurrence whereas temperate ones (Q. petraea and F. sylvatica) shifted downwards or no shift. All the species presented an increase in growth over the studied period whatever the area. However, the Mediterranean species showed a higher increase in growth at high altitude whereas temperate ones exhibited the highest increase at low altitude. In addition, the relative abundance of all the species decreased during the studied period, except for F. sylvatica in the Pyrenees. Finally, we will discuss these results in a context of change in climate and land use to determine their relative role in the Mediterranean ecosystems.

Altitudinal shift of species presence

The comparison of the mean altitude of the species presence between the two inventories revealed that whatever the areas, oak species generally presented a 10 m upward shift in average between SFI2 and SFI3 and Q. faginea a significant 20 m upward shift in the Pyrenees. The two inventories that we studied are separated by ten years only, this period of time is relatively short to detect a significant change in the mean altitude over the whole altitudinal distribution for each species knowing that this phenomena is species dependent (Resco de Dios, Fischer & Colinas 2007). However, we found similar results compare with those found in the literature; Lenoir et al. (2008) compared the optimum altitude of 171 forest species over a larger period (between 1905 and 1985, and 1986 and 2005) and an altitudinal gradient in west Europe and showed an upward shift of 29 m per decade in average for the 56 woody species and a larger shift (more than 100 m) for the species restricted to the mountainous habitat. These trends were also observed for more specific areas. Indeed, in southern California’s Santa Rosa Mountains, Kelly and Goulden (2008) showed that the average elevation of the dominant plant species of two surveys made in 1977 and 2006-2007 rose by 65 m which corresponded to a 22 m upward shift per decade. The comparison of historical records (1954-1958) and recent surveys (2003-2005) allowed to detect a 23.9 m upward shift of vascular plants along a 730 m continuous altitudinal transect in the Rhaetian Alps (North Italy) (Parolo & Rossi 2008).

In addition in our study, the differences were more important when considering the SFI2 plots’s mean altitude and the altitude of the colonized plots in SFI3 which indicates a future shift of the whole distribution. In average, colonization of new plots by the Mediterranean species occurred at higher altitude than the mean altitude of the SFI2 species distribution especially, for holm oak which presented a 350 m and 90 m upward shift over the whole Spain and in the Pyrenees, respectively. A similar upward shift was observed in the North-East Pyrenees (Catalonia) in the Montseny mountains where Q. ilex replaced F. sylvatica forests at medium altitude (Penuelas & Boada 2003). Benito Garzon et al. (2008) modeled the current and future distribution under climate change of Mediterranean, submediterranean and temperate
species in the Iberian Peninsula and showed that the Mediterranean forest composed by *Q. faginea*, *Q. ilex* and *Q. suber* will rise in altitude and latitude. The same study showed that the temperate species such as *Q. petraea* and *F. sylvatica* will suffer from a reduced distribution range, being relegated in the northern mountains of Spain and at higher altitude than their current distribution. This hypothesis would be confirmed by the greater elevation of colonized plots of sessile oak that we observed in this study.

On the other hand, the results that we observed for beech are really unexpected: this species presents a downward shift in elevation in whole Spain and the Pyrenees mountains, between the two inventories as well as between the SFI2 and the colonized plots. In the Pyrenees, Peñuelas and Boada (2003) found the opposite result with a 70m upward shift over a 55 year period. Only one study revealed a downward shift in latitude for a tree species: Kullman (1996) observed a significant altitudinal retraction of the treeline of Norway spruce (*Picea abies*) in the Swedish Scandes between 1974 and 1994 due to successive cold and snowy winters in 1965 and 1966. However, this trend was transitory and a recent study showed a colonization of alpine region by *Picea abies*, *Pinus sylvestris*, *Sorbus aucuparia* and *Salix* spp. over 50 years (1950-2000) due to warmer winters and summers. The cold and precipitations cannot explain the downward shift of distribution of beech that we observed here as precipitation in the Pyrenees have begun to decrease before the 90’s (Lopez-Moreno 2005).

Human sylvopastoral practices have shaped the landscapes of Mediterranean countries since the last few millennia (Urbieta, Zavala & Marañon 2008). Land use changes that we can observe nowadays is a consequence of the transition from traditional intensive practices to modern industrialized extensive agriculture. Several species have been favored by cultivation in the past like holm and cork oaks whose distributions has expanded outside of their climatic limits (Urbieta, Zavala & Marañon 2008). But many studies revealed the current problem of regeneration of these species in the open woods also called *dehesas* which form important areas along the Mediterranean Basin (Cierjacks & Hensen 2004; Soto, Lorenzo & Gil 2007). *Dehesas* combines traditional extensive livestock grazing of sheep, hogs, goats, cattle with the cultivation of oats, barley and wheat and forestry uses such as acorns, cork, charcoal and firewood (Plieninger & Schaar 2008). The lack of regeneration of holm oak in these lowland areas probably results from the increase of acorn consumption by the cattle and unfavorable abiotic conditions for holm oak seedling establishment created by agricultural and pastoral uses (Plieninger 2006). It could explain the absence of upward shift of *Q. suber* and *Q. ilex* between the inventories and the presence of one between SFI2 plots and SFI3 colonized plots thanks to a better regeneration at high altitude. However, another effect of land-use occurred: the vegetation colonization is frequent on the slopes which have been abandoned in favor of more fertile areas (bottom of valleys) (Vicente-Serrano, Lasanta & Romo 2005). *F. sylvatica* has the capacity to form important and resistant seed banks and the seedlings are able to grow rapidly in diameter and height after a gap creation (Rozas 2003). These advantages would allow *F. sylvatica* to colonize lower altitude after land abandonment.
Moreover, in several local places, the downward shift of *F. sylvatica* could be explained by thermal inversion in the depression. Air stratification occurs in valleys surrounded by abrupt reliefs. The sun cannot reach the depth of the canyons and during more than half of the year, temperature is cooler at the bottom of the valley (Benito Alonso 2005). In the depression of Brasov in Romania the topoclimatic conditions led to vegetation inversions: spruce fir is located at lower altitude than beech and fir tree (Marcu & Huber 2003). Thermal inversions exist in some locations in Sistema iberico and Pyrenees. Beech could then colonized the bottom of the valley where this air stratification occurs and find their optimum conditions of temperature and precipitations at lower altitude. This downward shift could be accentuated by climate change. If its normal optimum condition area is reduced drastically by climate change and thanks to its ability to constitute seed bank, *F. sylvatica* could spread in new areas at low altitude where the conditions are better. In conclusion, such a phenomenon could influence the downward shift of beech although it could not explain the amplitude of the shift observed at the scale of the Pyrenees and whole Spain.

**Growth increase: fingerprint of climate change?**

Overall, we found an increase in tree growth over the studied period. Numerous studies showed that the temperature increase has promoted tree growth especially at medium and high latitudes in the Northern hemisphere (Vicente-Serrano, Lasanta & Romo 2005). Myneni et al. (1997) presented the evidence that growth and growing season length increased between 1981 and 1991 in the northern high latitudes by using satellite data. According to altitude, we found two opposite patterns between temperate and Mediterranean species: the first ones presented higher growth increment at low altitude whereas the second ones showed higher increment at high altitude.

In many studies the observations of growth increment are a fingerprint of climate change and coincide (Devi et al. 2008; Suarez, Binkley & Kaye 1999) or not (Villalba et al. 1997) with an altitudinal shift in species occurrence. But the trend we observed of higher growth at high altitude is only significant for the whole Spain but not in the mountain areas where the temperature increase is the most important. So climate change is not the main cause of this altitudinal growth shift. The previously cited studies are often located in areas where human activities are negligible (Vicente-Serrano, Lasanta & Romo 2005), but as we have seen previously, land use has important effects on our study area. The low growth of Mediterranean species at low altitude could be explained by the current land use which increased the pastoral pressure on seedlings.

Temperate species like *F. sylvatica* and *Q. petraea* are expected to present a greater radial growth with altitude because the studied area is located at the southern edge of their distribution range. Contrary to all expectation, over the ten studied years these species have been found to have a better growth at low altitude in Spain for *Q. petraea* and in the Pyrenees for *F. sylvatica* over the ten studied years. Our results are opposite to the ones by Jump et al. (2006) which observed a growth decline for beech at low altitude in
the southern edge of their distribution range (i.e. in the Pyrenees). At low altitude, *F. sylvatica* is limited by high temperature and low precipitation explaining the reduced growth. Therefore, our results suggest that climate change is not the most important factor influencing growth along the altitudinal gradient in the Iberian mountains. Land abandonment is the most likely hypothesis to explain the higher growth at low altitude for the temperate species. Vicente–Serrano *et al.* (2005) studied the vegetation cover and biomass in the Spanish central Pyrenees between 1982 and 2000 by using Normalized Difference Vegetation Index (NDVI) and they showed a significant increase of the plants activity explained by the temperature increase but also by the important land use changes that occurred in the Mediterranean mountains during 20th century. They revealed that the vegetation evolution is spatially heterogeneous and they find the highest growth in abandoned lands.

*Change in species abundance*

Climate change and land use lead to a shift in occurrence or in growth as we have seen previously. These changes in occurrence and growth cause modification in ecosystems composition and in between species interactions (Hughes 2000; Walther 2003). The study of relative abundance changes reflects the changes in the proportion of each species over the studied period and so gives us information on the evolution of forest composition in Spain, Pyrenees and Sistema iberico.

Over ten years, the change in species proportion is low but in majority the studied species seemed to decrease in proportion except for *F. sylvatica* in the Pyrenees. These results are unexpected because the Mediterranean species are more drought tolerant than temperate species and should show an increase in abundance relatively to *F. sylvatica* and *Q. petraea*. Ogaya and Peñuelas (2007) concluded that tree growth and mortality of holm oak forest increased among a drought gradient suggesting that drought-tolerant species could be favored in detriment of more mesic species. In the study of Ogaya and Peñuelas, *Q. ilex* is considered as a mesic species and *Arbutus unedo* as a drought tolerant one. The decrease in species proportion involves an increase in another species maybe more drought-tolerant than the Mediterranean studied ones.

The mean relative abundance of *Q. petraea* decreased in Spain and the Pyrenees between the two inventories. But no significant change was detected between its proportion at low and high altitude. *F. sylvatica* presented different proportion patterns among the areas. In Spain, its proportion demonstrated no change at low altitude but it decreased more at high altitude; moreover no difference in *Fagus* growth increment occurred between low and high altitude. In conclusion, others species are more abundant at high altitude than *F. sylvatica*. On the contrary, in the Pyrenees, *F. sylvatica* proportion increased at low altitude and decreased at high altitude which is coherent with the result of tree growth (better growth at low altitude in the Pyrenees). In the Pyrenees, land use played a determinant role in *F. sylvatica* abundance because *F. sylvatica* has the ability of a rapid colonization after land abandonment as showed in the study of Rozas (2003). The author advised to plant *Quercus robur* and to control *F. sylvatica* regeneration to
avoid the complete domination of *F. sylvatica* in the future beech-oak lowland forests in Cantabria, in the northern of Spain. These results are also coherent with the increase in *F. sylvatica* proportion in the Pyrenees. Its decrease in abundance in the Sistema iberico could be explained by the more extreme location within its distribution range.

Concerning the Mediterranean species, no proportion change was detected for *Q. ilex* whatever the area. *Q. faginea* presented two opposite patterns in proportion between the two mountains areas: a low decrease in abundance at high altitude in the Pyrenees and a large decrease in abundance at low altitude in Sistema iberico. *Q. faginea* is a submediterranean species. These results could support the hypothesis that submediterranean forest can replace temperate forest (Benito Garzon, Sanchez de Dios & Sainz Ollero 2008). These forests are situated in northern Spanish mountains areas. The continental climate of the Sistema iberico may be the origin of the decrease of the *Q. faginea* proportion. At last, *Q. suber* proportion decrease is important in Spain especially at low altitude which corresponds to the low increment of tree growth due to a reduction of wood demand and lack of regeneration. So others species could increase in detriment of this species like deciduous oak in the more humid areas (Urbieten, Zavala & Marañon 2008).

These results showed that climate change had impacts on species proportion between the two inventories but for some species, like beech and cork oak, land abandonment seems to have more effects on species abundance and it was not negligible over the studied period.

**Conclusions**

Shifts of species presence were detected over the studied period. But more upward shifts were showed comparing the mean altitude of the species distribution and that of the colonized plots 10 years after. Radial growth studies revealed changes which could not be detected with presence data on such a short period. Moreover the treeline position (expanded in this study to the high altitudes of the species distribution) may alternate periods of stasis with period of movement (Walther 2003) which makes difficult the understanding of the species shift over a 10 year period.

The Mediterranean oak species, *Q. suber* and *Q. ilex*, moved upward in colonization and growth but not with the same amplitude than the submediterranean oak species, *Q. faginea*. The temperate species, *Q. petraea* and *F. sylvatica*, presented sometimes unexpected patterns with a downward shift for beech. The Mediterranean Basin was subjected to important land use changes and this large management change can operate synergistically or in compensation with climate change. At last the slope, soil, etc. were not taken into account in this study.

This work was a starting point to study potential shifts in altitudinal distribution of five temperate and Mediterranean species at a large scale with all data from comparable plots. It would be interesting to pursue further with plots located at the treeline in order to determine if the shift found using the whole range of the species is similar at the treeline of the concerned species. This future work would be necessary to assess the species migration capacity above the treeline especially for temperate species.
REFERENCES


Plieninger T. (2006) Habitat loss, fragmentation, and alteration - Quantifying the impact of land-use changes on a Spanish dehesa landscape by use of aerial photography and GIS. *Landscape Ecology* 21, 91-105


APPENDIXES

### Appendix 2. Results of two-ways ANOVAs on mean altitude of category of $ΔBAr$ (DF: Degree of Freedom; MS: Mean Square; F: Fisher-test value; ***, **, * are respectively p<0.001, p<0.01 and p<0.05, ns: not significant).

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Q. petraea</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountains</td>
<td>1</td>
<td>12818</td>
<td>0.109</td>
<td>0.741 ns</td>
</tr>
<tr>
<td>$ΔBAr$ categories</td>
<td>2</td>
<td>17324</td>
<td>0.147</td>
<td>0.863 ns</td>
</tr>
<tr>
<td>$ΔBAr$ categories</td>
<td>2</td>
<td>35715</td>
<td>0.303</td>
<td>0.740 ns</td>
</tr>
<tr>
<td><strong>Q. faginea</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountains</td>
<td>2</td>
<td>875806</td>
<td>17.966</td>
<td>&lt;0.00001 ***</td>
</tr>
<tr>
<td>$ΔBAr$ categories</td>
<td>2</td>
<td>255649</td>
<td>5.244</td>
<td>0.005 **</td>
</tr>
<tr>
<td>$ΔBAr$ categories</td>
<td>4</td>
<td>87672</td>
<td>1.798</td>
<td>0.126 ns</td>
</tr>
<tr>
<td><strong>Q. ilex</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountains</td>
<td>2</td>
<td>8001696</td>
<td>89.714</td>
<td>&lt;0.00001 ***</td>
</tr>
<tr>
<td>$ΔBAr$ categories</td>
<td>2</td>
<td>891165</td>
<td>9.992</td>
<td>0.0005 ***</td>
</tr>
<tr>
<td>$ΔBAr$ categories</td>
<td>4</td>
<td>461189</td>
<td>5.171</td>
<td>0.0004 ***</td>
</tr>
<tr>
<td><strong>F. sylvatica</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountains</td>
<td>1</td>
<td>923940.7</td>
<td>11.170</td>
<td>0.0009 ***</td>
</tr>
<tr>
<td>$ΔBAr$ categories</td>
<td>1</td>
<td>1271</td>
<td>0.015</td>
<td>0.901</td>
</tr>
<tr>
<td>$ΔBAr$ categories</td>
<td>3</td>
<td>51923.6</td>
<td>0.628</td>
<td>0.597</td>
</tr>
</tbody>
</table>

### Appendix 3. Results of two-ways ANOVAs on mean altitude of category of $Δp$ (DF: Degree of Freedom; MS: Mean Square; F: Fisher-test value; ***, **, * are respectively p<0.001, p<0.01 and p<0.05, ns: not significant).

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Q. petraea</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountains</td>
<td>1</td>
<td>738022</td>
<td>6.364</td>
<td>0.012 *</td>
</tr>
<tr>
<td>$Δp$ categories</td>
<td>2</td>
<td>573346</td>
<td>4.944</td>
<td>0.007 **</td>
</tr>
<tr>
<td>$Δp$ categories</td>
<td>2</td>
<td>35615</td>
<td>0.307</td>
<td>0.736</td>
</tr>
<tr>
<td><strong>Q. faginea</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountains</td>
<td>2</td>
<td>1.553*10^7</td>
<td>318.830</td>
<td>&lt;0.00001 ***</td>
</tr>
<tr>
<td>$Δp$ categories</td>
<td>2</td>
<td>1.3*10^4</td>
<td>0.270</td>
<td>0.765</td>
</tr>
<tr>
<td>$Δp$ categories</td>
<td>4</td>
<td>1.39*10^5</td>
<td>2.860</td>
<td>0.022 *</td>
</tr>
<tr>
<td><strong>Q. ilex</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountains</td>
<td>2</td>
<td>5.177*10^7</td>
<td>556.280</td>
<td>&lt;0.00001 ***</td>
</tr>
<tr>
<td>$Δp$ categories</td>
<td>2</td>
<td>2.187*10^6</td>
<td>23.500</td>
<td>&lt;0.00001 ***</td>
</tr>
<tr>
<td>$Δp$ categories</td>
<td>4</td>
<td>9.53*10^5</td>
<td>10.240</td>
<td>&lt;0.00001 ***</td>
</tr>
<tr>
<td><strong>F. sylvatica</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountains</td>
<td>2</td>
<td>1.2518353</td>
<td>155.800</td>
<td>&lt;0.0001 ***</td>
</tr>
<tr>
<td>$Δp$ categories</td>
<td>2</td>
<td>645325</td>
<td>8.030</td>
<td>0.0003 ***</td>
</tr>
<tr>
<td>$Δp$ categories</td>
<td>4</td>
<td>369330</td>
<td>4.600</td>
<td>0.0011 **</td>
</tr>
</tbody>
</table>