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RESEARCH PAPER

Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees

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ABSTRACT

Aim To assess the effects of climate change, past land uses and physiography on the current position of the tree line in the Catalan Pyrenees and its dynamics between 1956 and 2006.

Location More than 1000 linear kilometres of sub-alpine tree line in the Catalan Pyrenees (north-east Spain)

Methods Using aerial photographs and supervised classification, we reclassified the images into a binary raster with 'tree' and 'non-tree' values, and determined canopy cover in 1956 and 2006. We then determined the change in position of the tree line between 1956 and 2006 based on changes in forest cover. We used the distance from the position of the tree line in 1956 to the theoretical potential tree line – determined from interpretation of aerial photographs, identifying the highest old remnants of forest for homogeneous areas of the landscape in terms of bioclimatic conditions, bedrock, landform and exposure – as a surrogate of intensity of past land uses.

Results Our analyses showed that the Pyrenean tree line has moved upwards on average almost 40 m (mean advance ± SE: 35.3 ± 0.5 m, $P < 0.001$), although in most cases it has remained unchanged (61.8%) or advanced moderately, i.e. between 25 and 100 m (23.7%); only 9.2% of the locations have advanced more than 100 m. Upward shifts of the tree line were significantly larger in locations heavily modified in the past by anthropogenic disturbance (mean advance 50.8 ± 1.1 m) compared with near natural tree line locations (19.7 ± 0.8 m, $P < 0.001$), where the mean displacement was much lower than expected and was not related to changes in temperature along the study period.

Main conclusions Our results stress the impact of the cessation of human activity in driving forest dynamics at the tree line in the Catalan Pyrenees, and reveal a very low or even negligible signal of climate change in the study area.

Keywords
Anthropogenic disturbances, climate change, high mountain, land-use changes, Pyrenees, tree line.

INTRODUCTION

During the last decades, temperatures have increased worldwide, particularly at high elevations and latitudes (IPCC, 2007). Temperature during the vegetative period is broadly considered as the main factor driving the global position of the tree line (Körner, 1998; Jobbágy & Jackson, 2000; Körner & Paulsen, 2004) and hence it might be logical to expect a general advance of the tree line tracking the reported increase in temperatures. However, despite the ubiquity of warming trends, an advancing tree line is not a world-wide phenomenon: in a meta-analysis of the dynamics of 166 tree lines during the last decades, Harsch

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et al. (2009) reported that in about a half of the cases studied the tree line had remained stable despite a reported increase in temperature.

Several causes have been suggested to explain the variability in the observed responses (Holtmeier & Broll, 2005; Case & Duncan, 2014). For instance, temperature can be modified by, or interact with, other factors such as wind exposure, radiation, soil properties, snow cover or disturbance (Harsch *et al*., 2009; Löffler *et al*., 2011; Case & Duncan, 2014), and non-uniform local patterns of temperature change can emerge due to the complex topography that characterizes mountain areas (Beniston, 2003). Furthermore, positive feedback mechanisms (i.e. the facilitative effect provided by existing trees or boulders that ameliorate environmental conditions) have also been described (Bekker, 2005; Elliott, 2011). Lastly, the importance of land-use changes for tree line dynamics, although initially underestimated, is increasingly acknowledged, particularly in areas with a long history of intense anthropogenic influence such as the European mountains (Gehrig-Fasel *et al*., 2007; Batllori *et al*., 2010; Palombo *et al*., 2013).

In most of these mountains, the main changes in land use during recent decades include drastic changes in the type, abundance and behaviour of their main herbivore populations (Garcia-Ruiz & Lasanta, 1990). Herbivores can interact with climate change, strengthening or relaxing its impacts depending on the stocking density or the identity of the tree species that constitutes the tree line (Cairns & Moen, 2004; Cairns *et al*., 2007). In many managed ecosystems, the removal of animals or the reduction in animal activity has led to increases in seedling establishment above the current tree line, which have not always been translated into upslope advances of the tree line (Camarero & Gutiérrez, 2007; Gehrig-Fasel *et al*., 2007; Palombo *et al*., 2013).

In the Pyrenees, the tree line has been recurrently lowered, in most cases to increase the availability of grazing areas, and its current position mostly occurs well below its potential location due to the long history of anthropogenic disturbances (Carreras *et al*., 1996; Ninot *et al*., 2008). In the last 50 years, the intensity and spatial organization of the Pyrenean economy have drastically changed – including rural exodus and the decline of traditional practices – with major consequences for the configuration of the landscape (Lasanta, 1990; Garcia-Ruiz *et al*., 1996). In parallel, temperatures have also increased by at least 1 °C in the same period (Bucher & Dessens, 1991). Both factors (changes in climate and land use) have contributed to a general expansion of forest areas (Ameztegui *et al*., 2010) but their combined effect on the position of the tree line remains unclear. Previous studies in the area report a variety of responses, with general increases in recruitment and stand density across the ecotone from pasture to forest that are not necessarily translated into shifts in the position of the tree line (Camarero & Gutiérrez, 2004, 2007; Batllori & Gutiérrez, 2008). Most of these studies have been conducted at local scales or are based on a limited number of plots, and no regional assessment of the dynamics of the Pyrenean tree line exists to date.

Here we present a comprehensive assessment of the dynamics of the tree line in the Catalan Pyrenees based on the comparison of multiple pairs of aerial photographs. This method allows us to perform a regional assessment of recent tree line dynamics while incorporating information at different spatial scales. In particular, we aim to quantify changes in the position of the tree line in recent decades and unravel the role of land-use history and climate change in the observed dynamics. Due to the lack of data on past land uses at the required level of spatial resolution, we used the distance from the tree line in 1956 to the potential position of the tree line as an indicator of the intensity of past disturbance regimes of anthropogenic origin, assuming that sites located far from the potential tree line were subject to more diverse and intensive practices than those located closer to their potential limit. We hypothesize that the areas that were located in 1956 far from their potential position will correspond to those where tree line displacements should be mostly observed as a result of a relaxation in the perturbation pressure. At the same time, considering the recent trends of increasing temperature, we expect to find at the regional level a general upward shift of the tree line according to the hypothesis of equilibrium between climate and vegetation dynamics.

MATERIALS AND METHODS

Study area

The study area covers the Catalan Pyrenees, which extend over more than 6000 km^2 and are located south-east of the Pyrenean range (Fig. 1). The large study area spans a broad range of environmental conditions, with a patent elevational gradient of temperature and precipitation due to the abrupt terrain. The proximity of the Mediterranean Sea also entails a marked gradient, with lower precipitation and a smaller temperature range as we approach the coastline. The study area can be divided into three main bioclimatic regions: western, south-eastern and central. The south-eastern region is characterized by a greater influence of the Mediterranean Sea, so some summer drought and maritime influence seem to be related to a moderate potential tree line elevation. The central region is characterized by a continental-alpine climate, and is where the highest elevations can be found. The western region has a stronger oceanic influence (a great part of it is actually on the northern slopes of the Pyrenees) and consequently has a milder climate and higher precipitation, and shows a moderate potential tree line elevation.

The tree line runs, by definition, in the transition between sub-alpine and alpine elevational belts, which in the study area corresponds on average to an elevation of 2000–2300 m a.s.l. (Table 1). The climate at these elevations is typically alpine, characterized by a short growing period (4–5 months), cold winters and a significant portion of the total precipitation falling as snow. The vegetation in the alpine belt is strongly restricted by a short growing season and low temperatures, and is limited to herbaceous or shrubby plants, whereas the sub-alpine belt (from 1600 m a.s.l to the tree line) is dominated by mountain pine

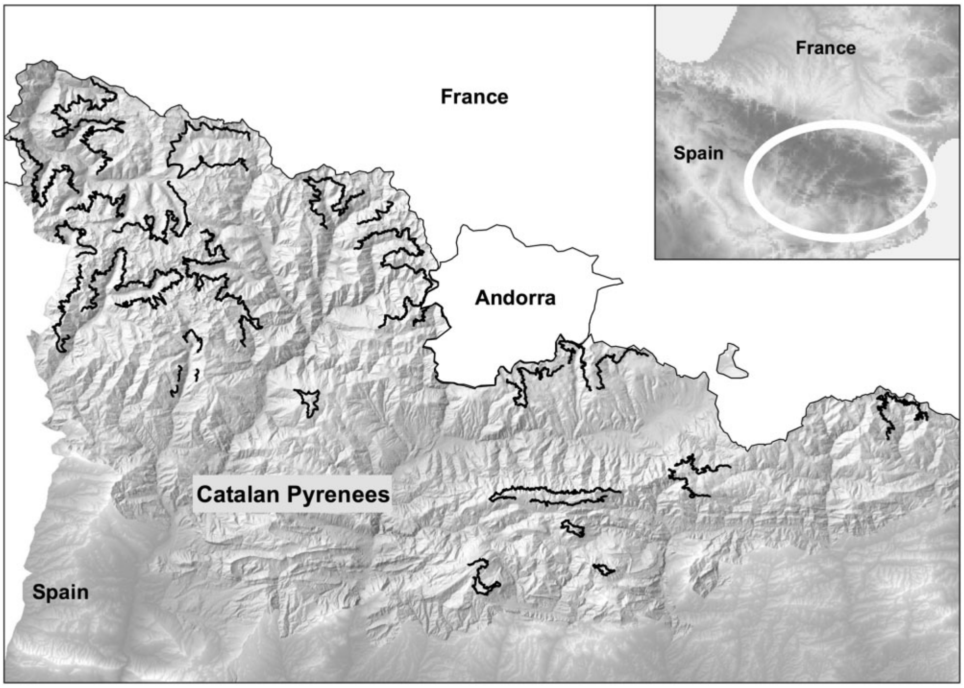

Figure 1 Location of the study area – the Catalan Pyrenees – in the Pyrenean range, and position of the current tree line as determined for this study.

Table 1 Descriptive statistics of the main physiographic, climatic and land-use variables that characterize past and current tree line locations in the Catalan Pyrenees. *P*-values and effect sizes (Cohen's *d*) refer to differences between values for past and current tree lines. Medium and large effect sizes ($d > 0.5$) are indicated in bold.

	Tree line in 1956				Tree line in 2006					
Variable	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	*P*-value	Cohen's *d*
Physiography										
Elevation (m a.s.l.)	2111.8	220.1	1318.9	2582.5	2142.7	214.9	1320.0	2554.5	< 0.001	0.064
Slope (degrees)	52.9	22.8	0.0	211.8	51.7	23.5	0.0	211.8	< 0.001	0.052
Aspect (degrees)	88.6	52.0	0.0	180.0	87.8	51.9	0.0	180.0	0.082	0.020
Curvature	0.03	1.22	–20.1	15.8	0.03	1.29	–15.6	18.6	0.525	0.007
Roughness	13.5	5.9	0.0	60.4	13.2	6.1	0.0	58.1	< 0.001	0.053
Climate										
MAT (°C)	3.7	1.3	0.6	8.9	5.0	1.1	2.3	8.8	< 0.001	**1.085**
MAP (mm)	1089.4	110.4	781.7	1378.4	884.6	98.1	640.5	1157.1	< 0.001	**1.959**
Summer temp. (°C)	11.0	1.2	8.2	15.9	13.5	1.1	10.7	17.0	< 0.001	**2.214**
Winter temp. (°C)	–2.9	1.3	–5.9	2.3	–1.9	1.1	–4.5	1.8	< 0.001	**0.833**
Radiation ($\mathrm{kJ \cdot m^{-2} \cdot day^{-1}}$)	2311.6	386.0	1268.1	2839.9	2314.6	381.2	1267.7	2839.9	0.827	0.001
Land uses										
Population change (1950s–2000s)	100.0	56.2	16.0	214.0	100.5	56.3	16.0	214.0	0.391	0.010
Current population density	6.8	7.6	0.77	49.0	6.8	7.8	0.77	49.0	0.387	0.010
Percentage of labour force in the primary sector	11.8	8.3	0.0	42.0	11.8	8.5	0.0	42.0	0.699	0.004
Percentage of pastures	22.0	9.4	1.7	39.1	22.2	9.2	1.7	39.1	0.128	0.018
Land-use legacies (distance to potential tree line, m)	508.4	502.5	–90.6	1990.6	490.0	498.2	–90.6	1930.2	< 0.001	0.039

MAT, mean annual temperature; MAP, mean annual precipitation.

(*Pinus uncinata* Ram. ex DC.), a shade-intolerant species that can grow in all kinds of soils and forms all the tree lines in the study area, finding its potential tree line elevation between 2200 and 2450 m a.s.l. depending on continentality, exposure and landform (Ninot *et al.*, 2007).

Climatic and land-use changes in the study area

In the last decades, the Pyrenees have gone through major changes in land organization (Garcia-Ruiz & Lasanta, 1990). Strong depopulation trends in rural areas have led to massive abandonment of farmland and major changes in the type, abundance and behaviour of the main herbivore populations. Over the last 50 years, the southern Pyrenees moved from a transhumance system – in which sheep for wool production were favoured, and there was an extensive utilization of most available food sources – to a system in which the overall livestock pressure is notably lower, and beef cattle and breeding mares have partially substituted sheep herds (Garcia-Ruiz & Lasanta, 1990; Lasanta, 1990). Therefore, human-driven pressure concentrated on the most productive areas, whereas many pastures that were suitable for sheep are now unused (Balcells, 1983). Along with these land-use changes, climate in the Pyrenees has also changed during the last century, with annual mean temperature and annual mean minimum temperature increasing by 0.83 °C and 2.11 °C, respectively (Bucher & Dessens, 1991).

Identification of the position of the tree line in 1956 and 2006

To determine the position of past and current tree lines, we used more than 200 pairs of aerial photographs taken in 1956 and 2006. Following the method described in Ameztegui *et al.* (2010), we reclassified the images into a binary raster with 'tree' and 'non-tree' values, and determined canopy cover in 1956 and 2006 on a 50 m × 50 m sampling grid that covered the whole surface of the study area. We focused the study in the tree line ecotone (referred as the tree line hereafter) which comprises the transition from timber line (i.e. the forest limit, defined by the presence of continuous forest cover) to the tree line (i.e. the last upright trees reaching 2 or 3 m in height) (Harsch *et al.*, 2009; Case & Duncan, 2014). However, since aerial photographs do not allow us to determine tree height, we identified the position of the tree line using a criterion based on canopy cover thresholds, as follows. First, we established that a cell in the 50 m × 50 m grid was 'forested' if its canopy cover was equal to or greater than 10%. This threshold has also been used in the Spanish National Forest Inventory (Direccion General para la Biodiversidad, 2007) and in previous studies to differentiate forest from grasslands (Coop & Givnish, 2007; Ameztegui *et al.*, 2010). Second, the centre of a cell was identified as constituting part of the tree line when it met two criteria: (1) there was at least another forested cell in its neighbourhood (defined with the Moore neighbourhood criterion, i.e. the eight cells surrounding the central cell); and (2) it was the highest forested cell in the surrounding area.

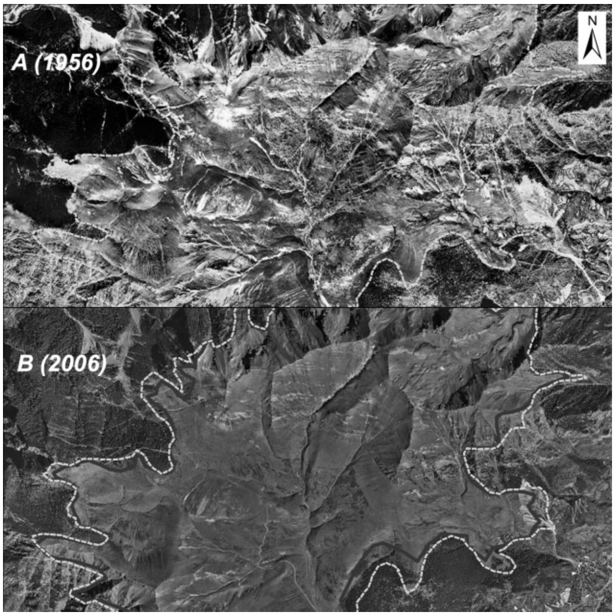

Figure 2 Example of an area showing tree line shift in the Catalan Pyrenees. The position of the tree line in 1956 is indicated by a dashed line, whereas the current tree line is showed in a dark solid line. In the current image (bottom), both lines are shown for comparative purposes. Both photos represent a land area that measures 7000 m × 3500 m, located in the western part of the Aigüestortes i Estany de Sant Maurici National Park.

For each of the 17,806 locations that were identified as constituting the tree line in 1956, we determined the closest point in Euclidean distance that constituted the tree line in 2006. Then, we computed the elevational shift in the tree line as the difference in elevation between each pair of points (Fig. 2). We also classified tree line elevational shift in four categories, based on the amount of elevational displacement: (1) retreat, when the new position of the tree line was at least 25 m below its position in 1956; (2) no shift, when the elevational shift was less than 25 m (either positive or negative); (3) moderate advance, when the shift was between 25 and 100 m; and (4) large advance, when the tree line in 2006 was located more than 100 m above the tree line in 1956.

Explanatory variables

For each of the study locations we determined physiographic, climatic and land-use variables that had a potential influence on tree line dynamics. Physiographic variables were obtained from a digital elevation model with a resolution of 10 m, and included elevation, slope, aspect, curvature and roughness (Table 1). Curvature was defined as the first derivative of the slope, whereas roughness was calculated as the greatest difference in elevation between a given cell and the surrounding ones. Monthly mean climatic variables between 1951 and 2010 were gathered from continuous maps developed using the method of the Climatic Atlas of the Iberian Peninsula (Ninyerola *et al.*, 2000) from information provided by the Spanish National Meteorological Agency (AEMET). Selected climatic variables included mean annual temperature (MAT) and precipitation (MAP), mean summer and winter temperature and solar radiation (Table 1). For each cell in the climatic maps we fitted linear regression models relating each climatic variable and year, and changes in climate were determined for each location in the tree line as the difference between the value predicted by the regression for 2006 and for 1956.

Given the difficulty of obtaining good-quality data on past land use at a detailed resolution, we used the distance from tree line in 1956 to the potential tree line as a proxy for past land use. We used the potential tree line delimited by Carreras *et al.* (1996), defined as the theoretical natural border of the supra-forest zone in the absence of anthropogenic disturbances. The potential tree line was determined from the interpretation of aerial photographs at detailed spatial scales, identifying the highest old remnants of forest for homogeneous areas of the landscape in terms of bioclimatic conditions, bedrock, landform and exposure. First, the study area was divided into the three main bioclimatic regions, south eastern, central and western, and each of these three regions was then subdivided into several sub-regions based on their geobotanical features. Each sub-region was further divided into granite, slate and lime based on the nature of the bedrock. Moreover, north-facing and south-facing slopes were considered separately, to take into account the effect of exposure. Finally, concave and convex areas were also treated separately to account for landform effects (see Carreras *et al.*, 1996, for a more detailed description of the procedure). The potential tree line was assumed to be relatively constant for each of the zones defined based on bioclimate, bedrock, landform and exposure, and its exact position within each zone was then deduced from the highest locations of forest remains, i.e. small forest spots or tree groups saved from anthropogenic deforestation, and thus indicating environmental suitability for sub-alpine forest (Carreras *et al.*, 1996; Ninot *et al.*, 2008). Therefore, we interpreted the discrepancy between the position of the observed tree line and the potential tree line as a surrogate of human disturbance, chiefly the occurrence of sub-alpine grasslands or other open areas. In this way, we assume that sites located further from the potential tree line hosted more diverse and intensive practices (range pasture, shepherd intensification, agriculture) than those located closer to their potential limit (Garcia-Ruiz & Lasanta, 1990; Lasanta, 2002). We established three disturbance categories according to the distance between the position of the tree line and the potential tree line, based on Ninot *et al.* (2008): (1) little modified, when the observed tree line was located within 100 m elevation from potential tree line; (2) moderately modified, when the observed tree line was between 100 and 400 m lower than the potential tree line; and (3) heavily modified, when the observed tree line was more than 400 m below its potential location. We determined these categories for the 1956 and 2006 datasets.

We also selected several indirect measures tied to the socio-economic characteristics of the municipalities, including: (1) *population change*, defined as the ratio between the current population and that of 1951, aimed at capturing the large differences in depopulation patterns across municipalities (Molina, 2002); whereas (2) *current population density*, (3) *importance of primary sector* – defined as the proportion of employees dedicated to the primary-sector – and (4) *proportion of sub-alpine pastures* were used to assess differences in economic structure across municipalities (Table 1). The economic and demographic variables (1, 2 and 3) were obtained from the Spanish National Statistics Institute (INE) or the Catalan Statistics Institute (IDESCAT), whereas the proportion of sub-alpine pastures (4) was calculated from the Land Cover Maps of Catalonia (Ibanez *et al.*, 2002).

Data analyses

We tested for differences in the elevation of the tree line in 1956 and 2006 with the Wilcoxon signed-rank test, and determined the differences in the mean value of each explanatory variable between 1956 and 2006 via multiple *t*-tests. The statistical significance of the mean elevational shift in the tree line was tested with a one-sample *t*-test. We also quantified the proportion of study locations that fell into each of the pre-defined categories of shift (retreat, no shift, moderate advance and large advance), and performed an ANOVA to test for differences in the mean values of the explanatory variables across these categories. We excluded from this analysis those locations at which the tree line had retreated – they represented 5% of the total sample – on the assumption that the retreat was due to recent disturbance events. To assess the role of land-use legacies on tree line dynamics, we determined the elevational shift in the tree line for each category of past land use – as calculated from the distance to the potential tree line in 1956 – and compared values across categories via ANOVA. Finally, we tested for potential interactions between climate change and land-use legacies by fitting different linear models on the response of the tree line to climate variables for each category of past land use, taking into account spatial autocorrelation.

Given the large sample size, the results of the statistical tests were assessed through Cohen's d as a measure of effect size. Cohen's d indicates the standardized difference between two means, and is independent of sample size. Therefore it is preferred to traditional statistical significance tests, which for very large samples can lead to small or trivial effects producing statistically significant results. Following Cohen (1988), we considered an effect size as small when $d < 0.2$, moderate when $d \approx 0.5$, and large when $d > 0.8$. All the analyses were performed using R v.3.0.3 (R Development Core Team, 2014).

RESULTS

Past and current tree line

The current tree line in the Catalan Pyrenees was located on average at an elevation of 2142.7 m, whereas the average elevation in 1956 was only slightly lower (2111.8 m, Cohen's $d = 0.06$). Cohen's effect size value suggested low practical sig-

Table 2 Proportion of tree line in 1956 and 2006 (in per cent) according to categories of distance to the potential tree line as defined in Ninot *et al.* (2008), and split into north-facing and south-facing slopes.

	Tree line in 1956		Tree line in 2006	
Distance to potential tree line	North-facing	South-facing	North-facing	South-facing
Little modified (< 100 m)	23.0	20.1	25.3	22.4
Moderately modified (100–500 m)	40.5	41.2	40.4	39.6
Heavily modified (> 500 m)	36.5	38.7	34.3	37.9

nificance of the differences in physiographic variables (elevation, slope, aspect, curvature and roughness) between the tree line locations in both years (Table 1). During the study period, the climate in the area became warmer (ΔMAT = +1.3 °C, Cohen's $d = 1.08$) and drier (ΔMAP = −17%, Cohen's $d = 1.95$), and the difference in temperatures was greater for summer (+2.5 °C, Cohen's $d = 2.21$) than for winter (+1 °C, Cohen's $d = 0.83$; see Appendix S1 in the Supporting Information for the evolution of climatic variables throughout the study period). More than 70% of the study locations were moderately or heavily modified in 1956, i.e. the tree line was located at least 100 m below its potential location, with no differences across aspect (Table 2).

Elevational shifts of the tree line (1956–2006) and potential causes

The mean elevational shift of the tree line between 1956 and 2006 was 35.3 m, with a moderate effect size (Cohen's $d = 0.53$). Nevertheless, the span of observed shifts was very large, and ranged from retreats of more than 100 m to upward displacements of greater than 300 m (Fig. 3). Most of the tree line (62% of the locations) remained unchanged between the two periods (i.e. shifts in position were less than 25 m) and only 5% of the locations were at lower positions in 2006 than in 1956 (Fig. 3).

Effects of physiography, climate and climate change

Those locations in which the tree line had largely moved upwards (elevational shift > 100 m) were situated at lower elevations in 1956 than those for which the displacement had been small or null (1971.6 vs. 2127.2 m; Cohen's $d = 0.87$), and also at slightly steeper and more south-facing slopes, but the effect of these two variables was moderate to low (Cohen's $d = 0.47$ and 0.42, respectively; Table 3). No practical significant differences between groups were observed for roughness and curvature. Locations where the tree line had experienced a large upslope shift also had a milder climate in 1956 (annual, winter and summer mean temperatures were on average 1 °C higher), but no effect of precipitation or radiation was observed. The change in climate (temperature, precipitation, radiation) between 1956 and 2006 was similar across categories of tree line elevational shift, as indicated by the low effect size of the differences (Table 3).

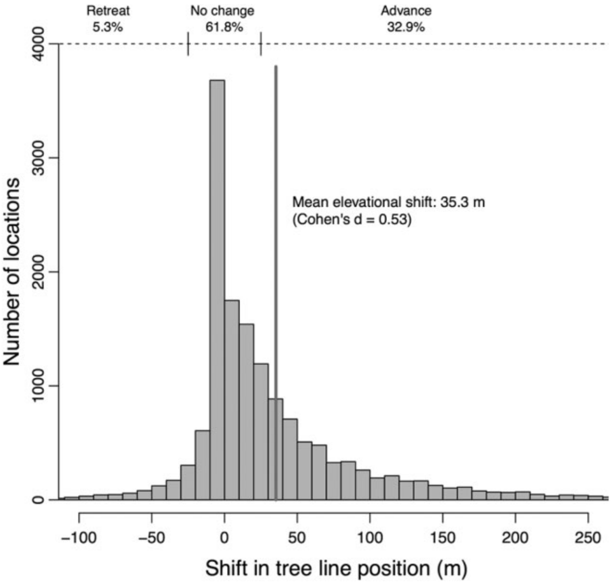

Figure 3 Histogram of the elevational shift of the tree line in the Catalan Pyrenees between 1956 and 2006, showing mean tree line advance (grey vertical line) and percentage of the tree line that has experienced retreat, advance or no change (see text for details on these categories).

Effects of land-use and land-use legacies and their interaction with climate change

None of the socio-economic variables tested at the municipality level (population change, current population density, importance of the primary sector, and percentage of sub-alpine pastures) were different across categories of tree line advance, as indicated by their low effect size (Cohen's $d < 0.2$; Table 3). Nevertheless, those locations where the tree line had shifted more between 1956 and 2006 corresponded to those that were more heavily modified by land uses in 1956, as indicated by their greater distance to potential tree line (716.7 vs. 479.4 m; Cohen's $d = 0.75$). Moreover, for heavily modified tree lines (those located in 1956 at least 500 m lower than the potential tree line), the mean tree line displacement was 50.8 m, almost twice the displacement observed for moderately modified tree lines (29.3 m) and 2.5 times larger than those little modified (19.7 m, Fig. 4).

The results of linear modelling revealed an interaction between the intensity of land-use legacies and changes in climate. Changes in mean annual and winter temperature exerted no effect on tree line displacement for moderately or

Table 3 Mean values of physiography, land-use and climatic variables (including difference in climate between the decades of 1950 and 2000), as a function of observed elevational shift of the tree line between 1956 and 2006 in the Catalan Pyrenees. Values in parentheses indicate the effect size (Cohen's *d*) between that category of change and the reference category (no change). Medium and large effect sizes ($d > 0.5$) are indicated in bold. See main text for details on the definition of categories of tree line advance.

	Categories of tree line elevational shift		
Variables	No change	Moderate advance	Large advance
Physiography			
Elevation (m a.s.l.)	2127.2 (–)	2053.3 (0.34)	**1971.6 (0.87)**
Slope (degrees)	51.2 (–)	58.5 (0.32)	60.9 (0.42)
Aspect (degrees)	91.5 (–)	77.4 (0.27)	67.0 (0.47)
Curvature	0.05 (–)	–0.06 (0.09)	–0.13 (0.15)
Roughness	13.1 (–)	14.9 (0.31)	15.6 (0.43)
Climate in 1950s			
MAT (°C)	3.5 (–)	4.1 (0.40)	**4.5 (0.81)**
MAP (mm)	1093.2 (–)	1072.9 (0.18)	1076.2 (0.15)
Summer temperature (°C)	10.9 (–)	11.4 (0.44)	**11.8 (0.86)**
Winter temperature (°C)	–3.0 (–)	–2.5 (0.39)	**–2.0 (0.81)**
Radiation ($kJ \cdot m^{-2} \cdot day^{-1}$)	2300.0 (–)	2355.1 (0.14)	2366.3 (0.17)
Climate change (differences between 1950s and 2000s)			
ΔMAT (°C)	1.4 (–)	1.4 (0.01)	1.3 (0.25)
ΔMAP (mm)	–205.2 (–)	–203.9 (0.02)	–211.5 (0.07)
Δ summer temperature (°C)	2.6 (–)	2.5 (0.09)	2.4 (0.40)
Δ winter temperature (°C)	1.1 (–)	1.0 (0.02)	0.9 (0.39)
Δ radiation ($kJ \cdot m^{-2} \cdot day^{-1}$)	1.4(–)	1.8 (0.05)	1.0 (0.05)
Land uses			
Population change (1950s–2000s)	99.4 (–)	104.8 (0.10)	88.8 (0.19)
Current population density	6.6 (–)	8.1 (0.20)	5.6 (0.13)
Percentage of labour force in the primary sector	11.8 (–)	11.7 (0.01)	12.2 (0.05)
Percentage of pastures	22.2 (-)	20.7 (0.16)	21.4 (0.10)
Land-use legacies (distance to potential treeline in 1956, m)	479.4 (–)	625.6 (0.34)	**716.7 (0.75)**

MAT, mean annual temperature; MAP, mean annual precipitation.

heavily modified tree line locations, whereas for slightly modified ones there was a small positive effect of changes in temperature on tree line displacement (Table 4). Conversely, upward displacement of the tree line was negatively affected by increases in summer temperatures, but only in locations with moderately or heavily modified tree lines. However, all these trends disappeared when the spatial autocorrelation was taken into account.

DISCUSSION

Recent tree line dynamics: effect of land-use legacies and climate

We observed a slight to moderate mean upward displacement of the eastern Pyrenean tree line between 1956 and 2006, although in 60% of the analysed tree line locations the changes in position during the study period were very small or null. As hypothesized, the locations where we observed greatest upward shifts in tree line position corresponded to those located further from the potential tree line. In this study, we used the distance from the observed to the potential tree line as an indicator of the intensity of past disturbance regimes of anthropogenic origin, assuming that sites located in 1956 far from their potential tree line were subject to more diverse and intensive practices than those located closer to their potential limit. Our results thus confirm the role of past anthropogenic disturbance regimes, or land-use legacies, as major drivers of recent tree line dynamics in the Pyrenees, as previously suggested (Ninot *et al*., 2008). Similar results have been previously reported in other European mountain systems with a long history of human use, including the Alps (Gehrig-Fasel *et al*., 2007; Albert *et al*., 2008), the Apennines (Palombo *et al*., 2013) and the Scandes (Bryn, 2008; Lundberg, 2011; Penniston & Lundberg, 2014).

Arguably, several environmental factors are likely to change along the gradient from a nearly natural tree line to a heavily modified one (Ninot *et al*., 2008). For instance, the latter were located at significantly lower elevations than undisturbed locations, so recruits that invade former pastures will face more favourable site conditions (warmer temperatures and a longer growing season) in areas with a heavily modified tree line than in undisturbed ones (Resler, 2006). Although soil characteristics were not included in our study due to a lack of information at an adequate scale, soils are likely to be of better quality at lower elevations, not only due to the milder climate but also to a potential fertilization effect after years of intense livestock breeding and agricultural activities. However, these areas already had suitable climatic and soil conditions for forest growth in 1956. Had it not been for the intense human activity that has

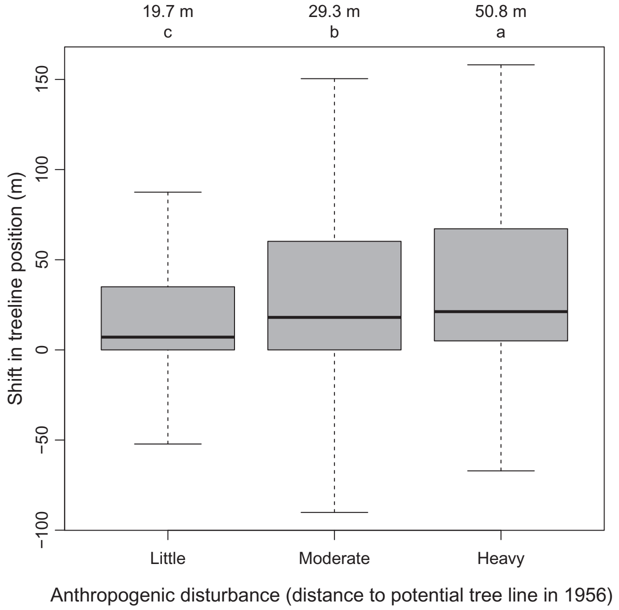

Figure 4 Distribution of tree line advance (elevation, m) per category of land use as defined by the distance from the tree line in 1956 to the potential tree line (see Table 2). The boxes denote the lower and upper quartiles, the horizontal bands are the medians, and whiskers extend to the lower 5% and upper 95% percentiles. Values above each box indicate mean tree line advance for that category, and different letters indicate a significant difference between values ($P < 0.05$).

occurred in the Pyrenean slopes for centuries (Garcia-Ruiz & Lasanta, 1990), these areas would probably have already been forested in 1956. Since tree invasion after the cessation of human activity is likely to be controlled by site conditions (Holtmeier & Broll, 2005; Bryn, 2008), the combination of a milder climate and better soil quality could undoubtedly have contributed to foster encroachment at heavily modified tree lines, but this is not enough in itself to explain the observed dynamics.

The importance of land-use changes in forest dynamics has been observed in most of the mountain ranges of southern Europe (Gehrig-Fasel *et al.*, 2007; Albert *et al.*, 2008; Palombo *et al.*, 2013) where there is a long history of landscape modification by human activities. However, the lack of adequate data at appropriate spatial and temporal scales prevented a direct test of their effect in the eastern Pyrenees. To try to fill this gap, we used various indirect variables reflecting the main socio-economic trends that this region has experienced in recent decades (Garcia-Ruiz & Lasanta, 1990; Lasanta *et al.*, 2005), but none of the variables at municipal level showed an effect on tree line dynamics. Socio-economic changes at the municipality level have been found to explain forest encroachment and densification patterns in the Pyrenees, but it is worth noting that these processes mostly occurred on low- and mid-range lands (Ameztegui *et al.*, 2010). In contrast, the Pyrenean tree line is often located close to sub-alpine pastures that are still in use in many valleys (Lasanta, 1990; Domínguez, 2002). These areas have traditionally been managed as pasture commons, often exploited by all livestock farmers in a valley, and the evolution of uses in them can be largely independent of socio-economic changes at the municipal level (Domínguez, 2002; Molina, 2002).

The role of climate change in tree line dynamics

Contrary to our expectations, the climate change signal (i.e. the shift in the position of the tree line in those locations with little or null human influence) was very small, much lower than the rise in isotherms that would correspond to the reported increase in temperatures (for a 1.05 °C increase in MAT between 1956 and 2006, and considering a vertical temperature change of 0.65 °C per 100 m, this would result in a rise in the position of the tree line of *c.* 160 m). The poor role of the difference in climate between 1956 and 2006 as a predictor of tree line dynamics further confirms the small influence of climate change on tree line position. Modest responses or lags of the tree line tracking increases in temperatures have been previously observed in various mountain systems worldwide (Szeicz & Macdonald, 1995; Paulsen *et al.*, 2000; Juntunen *et al.*, 2002; Gehrig-Fasel *et al.*, 2007). This is also the case in the Pyrenees, where infilling processes – increases in recruitment and density in the transition zone between forest and the tree line – are more common than true upward shifts of the forest limit (Camarero & Gutiérrez, 2004; Batllori *et al.*, 2009, 2010). In a recent study conducted at a smaller scale, Batllori *et al.* (2010) reported similar recruitment patterns regardless of the past disturbance regime in 12 field plots across the Pyrenees, suggesting a greater influence of climate than reported here. However, all the plots analysed in that study were located above 2000 m and close to their natural potential limit, where similar microtopographic conditions and patterns of seedling recruitment commonly exist irrespective of disturbance history (Holtmeier & Broll, 2005; Resler, 2006). Under those conditions, trees invading former pastures above the tree line are at the limit of their physiological tolerance, are often impeded by the prevailing harsh site conditions and are more likely to be positively influenced by an increase in temperatures (Holtmeier & Broll, 2005). Our results show a more important role of climate change at tree line locations close to their potential limit, but the strength of this effect was still rather weak. In the Pyrenees, seedling recruitment at the sub-alpine–alpine ecotone usually occurs in aggregated spatial structures, suggesting the importance of favourable microhabitats for seedling recruitment (Batllori *et al.*, 2010). Facilitation by shrubs, tree islands or krummholz mats thus becomes crucial for successful seedling recruitment in the harsh environments of sub-alpine–alpine forests (Batllori *et al.*, 2009; Ameztegui & Coll, 2013; Grau *et al.*, 2013), and may have impeded the detection of a stronger climatic signal, as has already been reported in the Alps (Leonelli *et al.*, 2011), the Rocky Mountains (Elliott & Kipfmueller, 2010) and in tropical latitudes (Bader *et al.*, 2008).

Table 4 Parameter estimates for linear models testing the significance of the interaction between climate change and anthropogenic disturbance as predictors of elevational shift in the tree line for the Catalan Pyrenees, without considering spatial autocorrelation (a) and after accounting for spatial autocorrelation (b). Values in parentheses are *P*-values for the parameter estimate.

	Past anthropogenic disturbance (based on distance to potential tree line)		
	Little modified (< 100 m)	Moderately modified (100–500 m)	Heavily modified (> 500 m)
(a)Without spatial autocorrelation			
Change in mean annual temperature	3.426 (< 0.001)	n.s.	n.s.
Changes in mean summer temperature	n.s.	–4.658 (< 0.001)	–5.022 (< 0.001)
Changes in mean winter temperature	1.708 (0.017)	n.s.	n.s.
Change in mean annual precipitation	n.s.	n.s.	–0.026 (< 0.001)
(B) With spatial autocorrelation			
Change in mean annual temperature	n.s.	n.s.	n.s.
Changes in mean summer temperature	n.s.	n.s.	n.s
Changes in mean winter temperature	n.s.	n.s.	n.s.
Change in mean annual precipitation	n.s.	n.s.	n.s.

n.s, non-significant estimate at $P = 0.05$.

The Pyrenean tree line now and in the future

In line with available information (Ninot *et al*., 2008), most of the present tree line in the Catalan Pyrenees is still located well below its theoretical natural limit. This indicates that anthropogenic uses are still significantly conditioning the current position of the tree line and its dynamics. Future tree-line dynamics at the regional scale are thus likely to depend on future land uses, particularly on changes in extensive livestock practices in high mountain areas. Our results suggest that, regardless of the evolution of climatic conditions, the tree line would still have room for further upward displacement if a decrease in livestock pressure occurs in these areas. The ongoing increase in wild ungulate populations – mainly roe deer and chamois – could also affect their future dynamics, although recent studies suggest that the rate at which they consume seedlings is not sufficient to prevent recruitment in sub-alpine areas (Ameztegui & Coll, 2015).

Conclusion

We found recent tree line dynamics in our study area to be mostly driven by the past history of anthropogenic disturbance, with tree line locations that had been heavily modified in the past showing the greatest change in their position. We could not detect any significant influence of changes in climate – neither temperature nor precipitation – on tree line dynamics in our region, suggesting that the potential effect of climate change pales when compared with the shift from intense past anthropogenic disturbances to the recent lighter land uses. The variability of observed responses also suggests a high importance of local conditions – microtopograhic, microclimatic, edaphic – as ultimate drivers of tree line responses at the local scale. Nevertheless, the method used in this study – determination of the position of the tree line from forest cover at a spatial resolution of 50 m – allowed us to identify the main global trends, but cannot directly capture the effect of these factors acting at local spatial scales. A future challenge is thus to integrate information at the required scale to capture these processes in analyses at landscape or regional scales.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Evolution of climate in the study area between 1951 and 2010.

BIOSKETCH

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