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

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ABSTRACT

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

Location More than 1,000 linear kilometers of subalpine treeline in the Catalan Pyrenees (NE 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 treeline position between 1956 and 2006 based on changes in forest cover. We used the distance from the treeline position in 1956 to the theoretical potential treeline – 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 treeline has moved upwards on average almost 40 m (mean advance ± SE: 35.3 ± 0.5 m; $P < 0.001$), although in most cases has remained unchanged (61.8 %) or advanced moderately, i.e. between 25 and 100 m (23.7%), and only 9.2% of the locations have advanced largely (more than 100 m). Treeline upward shifts were significantly larger in locations heavily modified in the past by anthropogenic disturbance (mean advance: 50.8 ± 1.1 m) compared to near natural treeline locations (19.7 ± 0.8 m; $P < 0.001$), where the mean displacement was much

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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 treeline in the Catalan Pyrenees, and reveal a very low or even negligible signal of climate change in the study area.

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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 treeline (Körner, 1998; Jobbágy & Jackson, 2000; Körner & Paulsen, 2004) and hence it might be logic to expect a general treeline advance tracking the reported increase in temperatures. However, despite the ubiquity of warming trends, treeline advance is not a worldwide phenomenon: in a meta-analysis of the dynamics of 166 treelines during the last decades, Harsch *et al.* (2009) reported that in about a half of the cases studied treeline had remained stable despite a reported increase in temperatures.

Several causes have been suggested to explain the variability in the observed responses. (Case & Duncan, 2014; Holtmeier & Broll, 2005). 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; Case & Duncan, 2014; Löffler *et al.*, 2011); 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 on treeline dynamics, although initially underestimated, is increasingly acknowledged, particularly in areas

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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 treeline (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 treeline, which have yet not always been translated into upslope advances of the treeline (Camarero & Gutiérrez, 2007; Gehrig-Fasel *et al.*, 2007; Palombo *et al.*, 2013).

In the Pyrenees, treeline 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 (Ninot *et al.*, 2008; Carreras *et al.*, 1996). 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 sharp consequences in the landscape configuration (Garcia-Ruiz *et al.*, 1996; Lasanta, 1990). In parallel, temperatures have also increased by at least 1 degree in the same period (Bucher & Dessens, 1991). Both factors (changes in climate and land-uses) have contributed to a general expansion of forest areas (Ameztegui *et al.*, 2010) but their combined effect on treeline position 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 on the treeline position (Camarero & Gutiérrez, 2004; Batllori & Gutiérrez, 2008; Camarero & Gutiérrez, 2007). 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 treeline exists to date.

Here we present a comprehensive assessment of the dynamics of the treeline in the Catalan Pyrenees based on the comparison of multiple pairs of aerial photographs. This methodology allows performing a regional assessment of recent treeline dynamics while incorporating information at different spatial scales. In particular, we aim to quantify changes in the position of the treeline in recent decades and unravel the role of land-use history and climate change on 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 treeline in 1956 to the potential treeline position as an indicator of the intensity of past disturbance regimes of anthropogenic origin, assuming that sites located far from the potential treeline 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 treeline displacements should be mostly observed as a result of a relax in the perturbation pressure. At the same time, considering the recent trends in temperature increase, we expect to find at the regional level a general upward shift of the treeline according to the hypothesis of equilibrium between climate and vegetation dynamics.

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MATERIALS AND METHODS

Study area

The study area covers the Catalan Pyrenees, which extend over more than 6,000 km^2 and are located south-east of the Pyrenean range (Figure 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 precipitations and less thermal amplitude as we approach the coastline. The study area can be divided into three main bioclimatic regions: western, southeastern and central. Southeastern region is characterized by a greater influence of the Mediterranean Sea, so some summer drought and maritime influence seem to be related to moderate potential treeline elevations. Central region is characterized by a continental-alpine climate, and is where the highest elevations can be found. Western region has a stronger oceanic influence (a great part of it is actually on the northern slopes of the Pyrenees) and consequently has milder climate and higher precipitations, and show moderate elevations for potential treeline.

The treeline runs, by definition, in the transition between subalpine and alpine elevational belts, which in the study area corresponds on average to an elevation of 2,000 – 2,300 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 short growing season and low temperatures, and is limited to herbaceous or shrubby plants, whereas the subalpine belt (from 1600 m a.s.l to treeline) is dominated by mountain pine (*Pinus uncinata* Ram. ex DC.), a shade-intolerant species that can grow in all kinds of soils and forms all the treelines in the study area, finding its potential treeline elevation between 2,200 and 2,450 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 led to massive farmland abandonment and major changes in the type, abundance and behaviour of their main herbivore populations. Over the last 50 years, the southern Pyrenees moved from a transhumant 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 treeline position in 1956 and 2006

To determine the position of past and current treeline, we used more than 200 pairs of aerial photographs taken in 1956 and 2006. Following the methodology 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 x 50 m sampling grid that covered the whole surface of the study area. We focused the study in the treeline ecotone (referred as treeline onwards) which comprises the transition from timberline (i.e., the forest limit, defined by the presence of continuous forest cover) to treeline (i.e. the last upright trees reaching two or three meters in height) (Case & Duncan, 2014; Harsch *et al.*, 2009). However, since aerial photographs do not allow determining tree height, we identified treeline position using a criteria based on canopy cover thresholds, as follows. First, we established that a cell in the 50 x 50 m grid was 'forested' if its canopy cover was equal 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 center of a cell was identified as constituting part of the treeline when it met two criteria: (i) 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 (ii) it was the highest forested cell in the surrounding area.

For each of the 17,806 locations that were identified as constituting the treeline in 1956, we determined the closest point in Euclidean distance that constituted the treeline in 2006. Then, we computed treeline elevational shift as the difference in elevation between each pair of points (Figure 2). We also classified treeline elevational shift in four categories, based on the amount of elevational displacement: (i) retreat, when the new

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position of the treeline was at least 25 m below its position in 1956; (ii) no shift, when the elevational shift was lower than 25 m (either positive or negative); (iii) moderate advance, when the shift was between 25 and 100 m; and (iv) large advance, when the treeline in 2006 was located more than 100 m above the treeline in 1956.

Explanatory variables

We determined for each of the study locations physiographic, climatic, and land-use variables with a potential influence on treeline dynamics. Physiographic variables were obtained from a Digital Elevation Model with a resolution of 10 meters, 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 highest 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 methodology 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 and precipitation, 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 treeline as the difference between the value predicted by the regression for 2006 and for 1956.

Given the difficulty to obtain quality data on past land-uses at a detailed resolution, we used the distance from treeline in 1956 to potential treeline as a proxy for past land-uses.

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We used the potential treeline 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 treeline was determined from 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: Southeastern, 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 bedrock. Moreover, north-facing and south-facing slopes were considered separately, to take into account for 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 treeline 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 subalpine forest (Carreras *et al.*, 1996; Ninot *et al.*, 2008). Therefore, we interpreted the discrepancy between the position of the observed treeline and the potential treeline as a surrogate of human disturbance, chiefly the occurrence of subalpine grasslands or other open areas. In this way, we assume that sites located further from the potential treeline hosted more diverse and intensive practices (range pasture, shepherd intensification, agriculture) than those located closer to their

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potential limit (Garcia-Ruiz & Lasanta, 1990; Lasanta, 2002). We established three disturbance categories according to the distance between the position of treeline and potential treeline, based on Ninot *et al.* (2008): (i) little modified, when the observed treeline was located within 100 elevation meters from potential treeline; (ii) moderately modified, when the observed treeline was between 100 and 400 m lower than the potential treeline; and (iii) heavily modified, when the observed treeline 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 lied to the socioeconomic 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 subalpine pastures* were used to assess differences in economic structure across municipalities (Table 1). 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 subalpine pastures was calculated from the Land Cover Maps of Catalonia (Ibanez *et al.*, 2002).

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Data analyses

We tested for differences in the elevation of treeline in 1956 and 2006 with 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 treeline elevational shift 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 treeline had retreated – they represented 5% of the total sample – in the assumption that the retreat was due to recent disturbance events. To assess the role of land-use legacies on treeline dynamics, we determined the treeline elevational shift for each category of past land-use – as calculated from the distance to potential treeline in 1956 – and compared values across categories via ANOVA. Last, we tested for potential interactions between climate change and land-use legacies by fitting different linear models on the response of treeline 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 standardised 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

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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).

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RESULTS

Past and current treeline

The current treeline in the Catalan Pyrenees was located in average at an elevation of 2,142.7 m, whereas the average elevation in 1956 was only slightly lower (2,111.8 m, Cohen's d = 0.06). Cohen's effect size value suggested low practical significance of the differences in physiographic variables (elevation, slope, aspect, curvature and roughness) between the treeline locations at both years (Table 1). During the study period, the climate in the area became warmer (ΔMAT = +1.3 ºC, 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 ºC, Cohen's d = 2.21) than for winter (+1 ºC, Cohen's d = 0.83; see Appendix S1 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 treeline was located at least 100 m below its potential location, with no differences across aspect (Table 2).

Treeline elevational shifts (1956-2006) and potential causes

The mean elevational shift of the treeline 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 greater than 300 m (Figure 3). Most of the treeline (62% of the locations) remained unchanged between periods (i.e. shifts in position were lower than 25 m), and only 5% of the locations were at lower positions in 2006 than in 1956 (Figure 3).

Effects of physiography, climate and climate change

Those locations in which the treeline 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 treeline had experienced large upslope shift also had a milder climate in 1956 (annual, winter and summer mean temperatures were on average 1ºC 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 treeline elevational shift, as indicated by the low effect size of the differences (Table 3).

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

None of the socioeconomic variables tested at the municipality level (*population change*, *current population density*, *importance of the primary sector*, and *percentage of subalpine pastures*) were different across categories of treeline advance, as indicated by their low effect size (Cohen's $d < 0.2$; Table 3). Nevertheless, those locations where treeline had shifted more between 1956 and 2006 corresponded to those more heavily modified by land-uses in 1956, as indicated by their greater distance to potential treeline (716.7 *vs*. 479.4 m; Cohen's $d = 0.75$). Moreover, for heavily modified treelines (those located in 1956 at least 500 m lower than the potential treeline), the mean treeline

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displacement was 50.8 m, almost twice the displacement observed for moderately modified treelines (29.3 m), and 2.5 times larger than those little modified (19.7 m, Figure 4).

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

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DISCUSSION

Recent treeline dynamics: effect of land-use legacies and climate

We observed a slight to moderate mean upward displacement of Eastern Pyrenean treeline between 1956 and 2006, although in 60% of the analyzed treeline 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 treeline position corresponded to those located further from the potential treeline. In this study, we used the distance from observed to potential treeline as an indicator of the intensity of past disturbance regimes of anthropogenic origin, assuming that sites located in 1956 far from their potential treeline 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 treeline 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), or the Scandes (Bryn, 2008; Lundberg, 2011; Penniston & Lundberg, 2014).

Arguably, several environmental factors are likely to change along the gradient from nearly natural treeline to those heavily modified (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

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temperatures and greater duration of growing season) in heavily modified treeline areas than in undisturbed ones (Resler, 2006). Although soil characteristics were not included in our study due to the lack of information at an adequate scale, soils are likely to have 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 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 milder climate and better soil quality could undoubtedly have contributed to foster encroachment at heavily modified treeline, but are not enough in themselves 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 (Albert *et al.*, 2008; Gehrig-Fasel *et al.*, 2007; 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 directly testing their effect in the eastern Pyrenees. To try to fill this gap, we used various indirect variables reflecting the main socioeconomic 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 treeline dynamics. Socioeconomic changes at the municipality level have been found to explain forest

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encroachment and densification patterns in the Pyrenees, but it is worthy to note that these processes mostly occurred at low- and mid- range lands (Ameztegui *et al.*, 2010). In contrast, the Pyrenean treeline is often located close to subalpine pastures that in many valleys are still in use (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 socioeconomic changes at the municipal level (Domínguez, 2002; Molina, 2002).

The role of climate change on treeline dynamics

Contrary to our expectations, the climate-change signal (i.e. the shift in the position of the treeline 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 ºC increase in mean annual temperature between 1956 and 2006, and considering a vertical temperature change of 0.65ºC per 100 m, this would result in a rise in treeline position of c. 160 m). The poor role of the differences in climate between 1956 and 2006 as predictors of treeline dynamics further confirms the scarce influence of climate change on treeline position. Modest responses or lags of treeline tracking increases in temperatures have been previously observed in various mountain systems worldwide (Szeicz & Macdonald, 1995; Juntunen *et al.*, 2002; Gehrig-Fasel *et al.*, 2007; Paulsen *et al.*, 2000). Also in the Pyrenees, where infilling processes – increases in recruitment and density in the transition zone between forest and the treeline – are more common that true upward shifts of the forest limit (Batllori *et al.*, 2009, 2010; Camarero

& Gutiérrez, 2004). In a recent study conducted at a lower scale, Batllori *et al.* (2010) reported similar recruitment patterns regardless 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 2,000 m and close to their natural potential limit, where similar microtopographical conditions and patterns of seedling recruitment commonly exist irrespective of the disturbance history (Resler, 2006; Holtmeier & Broll, 2005). Under those conditions, trees invading former pastures above the treeline 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 treeline locations close to their potential limit, but the strength of this effect was still rather weak. In the Pyrenees, seedling recruitment at the subalpine-alpine ecotone usually occurs in aggregated spatial structures, suggesting the importance of favourable microhabitats to allow seedling recruitment (Batllori *et al.*, 2010). Facilitation by shrubs, tree islands or krummholz mats becomes thus crucial for successful seedling recruitment in the harsh environments of subalpine-alpine forests (Ameztegui & Coll, 2013; Batllori *et al.*, 2009; 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).

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Present and future of Pyrenean treeline

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

Conclusion

We found recent treeline dynamics in our study area to be mostly driven by the past history of anthropogenic disturbance, with treeline locations 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 treeline dynamics in our region, suggesting that the potential effect of climate change pales when compared to the shift from intense past anthropogenic disturbances to the recent lighter land-use. The variability of observed responses also suggests a high importance of local conditions – microtopograhic, microclimatic, edaphic – as ultimate drivers of treeline

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responses at the local scale. Nevertheless, the methodology used in this study – determination of treeline position from forest cover, 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. The future challenge is thus to integrate information at the required scale to capture these processes into analyses at landscape or regional scale.

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BIOSKETCH

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Table 1. Descriptive statistics of the main physiographic, climatic and land-use variables that characterize past and current treeline locations in the Catalan Pyrenees. *P* values and effect sizes (Cohen's d) refer to differences between values for past and current treeline. Medium and large effect sizes (d > 0.5) are indicated in bold. MAT: mean annual temperature; MAP: mean annual precipitation

	Treeline 1956				Treeline 2006				*P*	Cohen's
Variable	Mean	SD	Min	Max	Mean	SD	Min	Max	value	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 (ºC)	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 (ºC)	11.0	1.2	8.2	15.9	13.5	1.1	10.7	17.0	<0.001	**2.214**
Winter temp (ºC)	-2.9	1.3	-5.9	2.3	-1.9	1.1	-4.5	1.8	<0.001	**0.833**
Radiation ($KJ \cdot m^{-2} \cdot day^{-1}$)	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 treeline)	508.4	502.5	-90.6	1990.6	490.0	498.2	-90.6	1930.2	<0.001	0.039

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

Distance to potential treeline	Treeline1956		Treeline 2006	
	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

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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 treeline elevational shift 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 treeline advance

	Categories of treeline 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 (ºC)	3.5 (-)	4.1 (0.40)	**4.5 (0.81)**
MAP (mm)	1093.2 (-)	1072.9 (0.18)	1076.2 (0.15)
Summer temperature (ºC)	10.9 (-)	11.4 (0.44)	**11.8 (0.86)**
Winter temperature (ºC)	-3.0 (-)	-2.5 (0.39)	**-2.0 (0.81)**
Radiation (KJ·m^{-2}·day^{-1})	2300.0 (-)	2355.1 (0.14)	2366.3 (0.17)
Climate change (differences between 1950s and 2000s)			
Δ MAT (ºC)	1.4 (-)	1.4 (0.01)	1.3 (0.25)
Δ MAP (mm)	-205.2 (-)	-203.9 (0.02)	-211.5 (0.07)
Δ Summer temperature (ºC)	2.6 (-)	2.5 (0.09)	2.4 (0.40)
Δ Winter temperature (ºC)	1.1 (-)	1.0 (0.02)	0.9 (0.39)

Δ Radiation (KJ·m^{-2}·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)**

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Table 4 Parameter estimates for linear models testing the significance of the interaction between climate change and anthropogenic disturbance as predictors of treeline elevational shift for the Catalan Pyrenees, without consideration of spatial autocorrelation (a) and after accounting for spatial autocorrelation (b). Values in parentheses are *P*-values for the parameter estimate. n.s: non-significant estimate at *P* = 0.05.

	Past Anthropogenic Disturbance (based on distance to potential treeline)		
	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.

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FIGURE CAPTIONS

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

Figure 2. Example of an area showing treeline shift in the Catalan Pyrenees. Treeline position in 1956 is indicated by dashed line, whereas current treeline is showed in dark solid line. In the current image (below), both lines are shown for comparative purposes. Both photos represent a land area that measures 7,000 X 3,500 m, located in the western part of the Aigüestortes i Estany de Sant Maurici National Park.

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

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