Recent and Intense Dynamics in a Formerly Static Pyrenean Treeline

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Abstract

Alpine treelines are considered monitors of the effects of climate on forest growth and dynamics. Treelines are expected to react to current climate warming by showing upslope migrations. However, treeline dynamics are often characterized by lagged responses to rising temperatures, that is, treeline inertia. In addition, encroachment within the treeline ecotone seems to be a more widespread response to climate warming than treeline ascent. We investigate how the treeline responds to climate in a Pyrenean site with an intense Mountain pine (*Pinus uncinata*) regeneration but also abundant dead trees. We use dendrochronology to reconstruct treeline dynamics (growth, tree recruitment, and death) and to build an age structure of Pyrenean Mountain pine forests, and relate them to temperature reconstructions of the study area. We also describe the spatial structure and estimate the size reproductive threshold of pine recruits. The study treeline showed profuse pine recruitment in the 1980s. These recruits were spatially aggregated and reached the 50% probability of reproduction at 24 years old. Most Pyrenean Mountain pines were recruited in the first half of the 18th century, a warm period when growth was stable, while old treeline trees recruited not only in those decades but also in previous warm periods. Pine deaths concentrated in the cool transition between the mid 17th and the early 18th centuries and mainly from 1820 to 1860, when growth declined as a consequence of temperatures rapidly dropping at the end of the Little Ice Age. Only the amount of dead pines at the treeline was negatively related to temperatures, indicating that cool periods cause high adult mortality rates and trigger long-term treeline decline. But this decline was interrupted by intense regeneration and treeline encroachment, two features that characterize recent treeline dynamics in some mountains. This concurs with the view of a rapid response of alpine treelines to climate during the late 20th century.

Introduction

Alpine treelines represent conspicuous transitions from the subalpine forest limit to the alpine zone, and they are one of the ecotones that have attracted most interest from ecologists and biogeographers (von Humboldt and Bonpland, 1807; Troll, 1973; Tuhkanen, 1980; Arno, 1984; Holtmeier, 2009). Alpine treeline ecotones include the uppermost located trees, usually defined as 2-meter-tall arborescent individuals (cf. Kullman, 1979), whose growth and regeneration are mainly constrained by low soil temperatures and a short growing season (Wieser and Tausz, 2007; Körner, 2012). Because of low temperatures, treeline dynamics (i.e., the changes in growth, regeneration, and mortality of trees forming the treeline ecotone) are assumed to be highly sensitive to climate warming, particularly in extra-tropical areas (Smith et al., 2009). Nevertheless, the relationship between treeline elevation and interpolated isotherms is weak and corresponds to a coarse approximation given that the temperature of growing plant meristems is not the same as air temperature (Tranquillini, 1979; Grace et al., 2002).

A widespread upward shift of alpine treelines under currently warming conditions is expected. However, almost half the sites reviewed by Harsch et al. (2009) in their global meta-analysis of treelines did not respond to worldwide warming by migrating upward. Contrastingly, tree encroachment or densification within the treeline ecotone has been more widely observed than upslope

shifts of treelines (e.g., Camarero and Gutiérrez, 2004; Kullman, 2007; Batllori and Gutiérrez, 2008; Liang et al., 2011; Carrer et al., 2013; Mathisen et al., 2014). This lack of responsiveness, in terms of reduced treeline ascent, led to define the term *treeline inertia*, a phenomenon which can be caused by decoupled, lagged, or reduced responses of treelines to long-term climate change (Scuderi, 1994; Szeicz and MacDonald, 1995; Payette et al., 1985; Kullman, 2010).

Encroachment is a likely scenario of future treeline change in response to the ongoing rise in temperatures, but variable rates of upward treeline advance are also widely reported and linked to how tree growth and establishment occur near the treeline. To discern if broad-scale climate influences on tree regeneration and ecotone infilling are contingent on the local tree-to-tree interactions, which may correspond to facilitation, spatial analyses of tree establishment can be used (Batllori et al., 2010; Elliott, 2011). Furthermore, it must be considered that the disparate components of treeline dynamics (regeneration, radial growth, mortality) respond to different climate conditions at different rates (Lloyd and Graumlich, 1997; Daniels and Veblen, 2004; Holtmeier and Broll, 2005; Fajardo and McIntire, 2012).

Well-documented cases illustrate how linked or decoupled climate and treeline dynamics have been. For instance, impacts at treeline are often unnoticed until a bioclimatic threshold is crossed, as has been shown in climate-induced switches in tree establishment (Elliott, 2012). Several study cases document these abrupt changes

in regeneration across North American (Kupfer and Cairns, 1996; Lloyd and Graumlich, 1997; Danby and Hik, 2007) and South American mountains (Daniels and Veblen, 2004). In a long-term Holocene perspective, some 20th century treeline rapid upslope treeline shifts, as those detected in the Swedish Scandes, represent unprecedented ruptures or reversals of the long-term cooling trend and associated downslope treeline shifts reconstructed for the past five millennia (Kullman and Öberg, 2009; Kullman, 2010). In the Russian Urals, the forest limit has expanded upward rapidly during the past half century and vertical growth rate has also greatly increased, but the treeline elevation has remained stable (Shiyatov and Mazepa, 2011; Hagedorn et al., 2014). In Alaska, the lag between the first recruited seedlings and pronounced treeline densification was estimated to be approximately 150–200 years (Lloyd, 2005), that is, a similar timespan as the period elapsed since the end of the Little Ice Age (hereafter abbreviated as LIA), a cool period extending from about A.D. 1350 to 1850 (cf. Kullman, 1987). These cases exemplify nonlinear responses to climate and suggest that slow treeline dynamics during long-term cool periods (e.g., LIA) are interrupted by rapid responses to periods experiencing fast warming such as the 20th century (IPCC, 2013).

In this study, the long-term treeline dynamics (growth, regeneration, mortality) in relation to climate are described in a Pyrenean site (Fig. 1) where abundant regeneration has reversed a long-term decline characterized by adult mortality. We describe the recent regeneration pulse and we use dendrochronology to reconstruct growth and to date germination and death events so as to infer treeline dynamics and related climate variability during the past five centuries.

Material and Methods

STUDY SITE AND SPECIES

The study site is a treeline ecotone located in Foratarruego (42°37′21″N, 0°06′46″E, 2200 m a.s.l.), in the buffer zone of the "Ordesa y Monte Perdido" National Park, Central Spanish Pyrenees. This treeline is located in a steep slope (36°), aspect W-SW (255°), and on calcareous and rocky soils. The ecotone is formed by open forest patches dominated by young saplings (usually 2–5 m tall) and standing dead Mountain pine (*Pinus uncinata* Ram.) trees (Fig. 1 and Fig. 2, part a). The understory is sparse and it is

FIGURE 1.   Views of the Pyrenean study treeline in 1999 and 2009 showing standing dead trees and abundant tree regeneration.
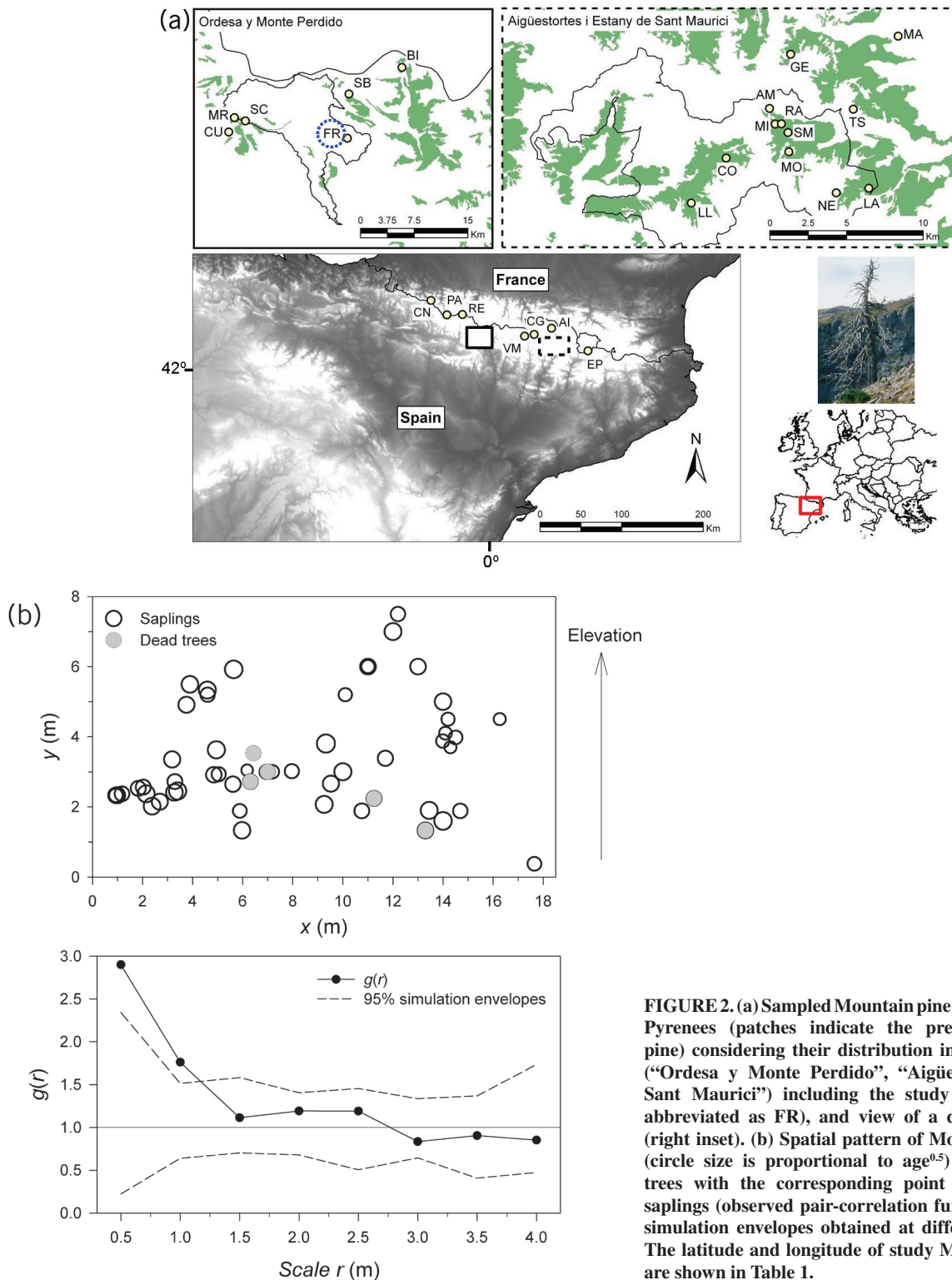
FIGURE 2. (a) Sampled Mountain pine stands in the Spanish Pyrenees (patches indicate the presence of Mountain pine) considering their distribution in two national parks ("Ordesa y Monte Perdido", "Aigüestortes i Estany de Sant Maurici") including the study site (Foratarruego, abbreviated as FR), and view of a dead Mountain pine (right inset). (b) Spatial pattern of Mountain pine recruits (circle size is proportional to age$^{0.5}$) and standing dead trees with the corresponding point pattern analysis of saplings (observed pair-correlation function $g(r)$ and 95% simulation envelopes obtained at different spatial scales). The latitude and longitude of study Mountain pine stands are shown in Table 1.

formed by shrubby *Juniperus communis* L. and *Thymelaea tinctoria* subsp. *nivalis* (Ram.) Nyman individuals. In the study site, we did not observe any signal of recent human use or disturbances (e.g., snow avalanches) such as charcoal, stumps, or grazing signals. The steepness and rockiness of the site make it relatively inaccessible to the main domestic grazers in the study area, namely sheep and cows. Climate is continental with cold winters and some

Mediterranean influence such as summer drought and autumn storms (Del Barrio et al., 1990). In the "Refugio de Góriz" meteorological station (42°40′N, 0°01′E, 2215 m a.s.l.), located 10.5 km away from the study site, mean annual temperature was 4.9 °C and total annual precipitation was 1694 mm for the period 1982–1999 (Camarero, 1999). According to homogenized and averaged data in a 0.5°-resolution grid corresponding to the Climate Research Unit

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(CRU) TS 3.1 data set (Harris et al., 2014), the annual temperature in the Spanish Pyrenees and in the 0.5-grid covering the study site increased by 0.015 °C year^{-1} and 0.019 °C year^{-1} during the 20th century, respectively (Galván et al., 2014).

Pyrenean treelines are mainly formed by Mountain pine, which is a long-lived (usually up to 825 years old) and shade-intolerant conifer with a wide ecological tolerance regarding topography (slope, exposure, altitude) and soil type (Cantegrel, 1983; Bosch et al., 1992; Camarero, 1999). It is found in subalpine forests from the Alps, the Pyrenees (elevation range 1800–2300 m), and the Iberian System. Most radial growth of *P. uncinata* occurs from May to June, and wood formation is enhanced by warm late autumn and spring temperatures before and during tree-ring formation, respectively (Camarero et al., 1998; Tardif et al., 2003). Near the treeline, Mountain pine usually forms low-density stands and grows as isolated individuals. In the Central Pyrenees, Scots pine (*Pinus sylvestris* L.) also appears at subalpine forests subjected to continental conditions, but it is dominant at lower elevations (mainly 1400–1900 m) than Mountain pine.

FIELD SAMPLING

Sampling was carried out in late July 2009. We measured the size (diameters at base and at breast height, or 1.3 m dbh, and total height) of all living pines located within a rectangular plot with sides of lengths 10 m and 20 m. The plot was located within the treeline ecotone so as to include the uppermost trees of at least 2 m tall and most dead trees. The longest side of the plot was located perpendicular to the maximum slope. We also mapped the relative Cartesian coordinates of all pine recruits (i.e., 3 < basal diameter < 25 cm, dbh < 20 cm, 0.5 < height < 5.0 m) located within the plot using tapes and a compass, and correcting for the change in slope. The age of pine recruits was estimated by counting the number of annual internodes along the main stem. Basal sections were taken in a subsample of pine recruits (n = 12) to correct for underestimations of age, which were on average 5 years. This allowed obtaining germination dates of pine recruits since the early 1960s. The presence of cones in living pines was also recorded. We defined the reproductive age threshold (see Wright et al., 2005) of young Mountain pines when the 50% probability of reproduction is reached by fitting a binary logistic regression to the data of cone presence as a function of tree age using SPSS version 19.0 (IBM SPSS Statistics for Windows, Armonk, New York).

UNIVARIATE POINT PATTERN ANALYSIS OF TREE LOCATIONS

To characterize the spatial patterns of the treeline saplings, we used point pattern analysis that allows us to describe spatial tree patterns and to infer the underlying processes (Camarero et al., 2000). We used the pair-correlation function $g(r)$, which depends on the probability of finding a point (e.g., tree stem) at a given distance from another point and it is suitable for small spatial scales (Wiegand and Moloney, 2004). Because we assumed that environmental heterogeneity (e.g., topography, soil features) influences the spatial tree patterns, we used the inhomogeneous version of the $g(r)$. The univariate $g_{11}(r)$ statistic was used to describe the spatial patterns of *P. uncinata* saplings. A heterogeneous Poisson process was employed as a null model corresponding to Complete Spatial Randomness in order determine if the observed pattern was random, clumped, or regularly spaced. The intensity function was based on a kernel smoothing algorithm applied to tree density data, which involves the selection of an appropriate radius of the mov-

ing window (Wiegand and Moloney, 2004). In our case, 3 m was selected as the radius of the moving window, which was similar to the maximum scale of analysis (4 m). Then, the upper or lower 99% simulation envelopes based on 999 Monte Carlo simulations were compared with the observed data. If the calculated $g_{11}(r)$ was above or below the upper or lower simulation envelopes, the pattern was considered to be significantly aggregated or hyperdispersed (regular) at the analyzed spatial scale. Since spatial relationships for Mountain pine treelines were previously detected at small scales of 0.5–2.0 m (Camarero et al., 2000), the statistic $g_{11}(r)$ was calculated using a resolution of 0.5 m. The Programita software was used to carry out the point pattern analyses (Wiegand and Moloney, 2004, 2014).

DENDROCHRONOLOGY

We used dendrochronology to estimate the exact dates of tree birth or germination and the approximate dates of tree death, and to reconstruct growth (Fritts, 2001). All standing or lying dead trees located within the plot (Fig. 1) and showing branch and stem or bark remains that corresponded to old Mountain pine morphologies (e.g., twisted trunk, large lateral branches, sparse and lopsided crowns with flattened tops; see similar criteria for identifying old ponderosa pine trees in Huckaby et al., 2003) were considered for dendrochronological estimations of their germination and death dates (n = 12). We assumed that all dead trees were Mountain pines given that this is the only pine species present at the study treeline site. Well-preserved sections with partially decomposing sapwood and heartwood always present were cut from each dead tree at 1–1.3 m height from the tree base. The exact date of germination was established for dead trees based on dendrochronological dating. However, it is not possible to determine the date of death due to wood decay and weathering composition. Therefore, first the missing sapwood rings were estimated based on the associations between dbh and the area and number of rings in the heartwood and sapwood observed in sections taken for living mature Mountain pines growing in high-elevation sites. For instance, the relationship between tree age and heartwood area was positive and highly significant (R^2 = 0.57, P < 0.001, n = 21 trees). Second, we added 45 years to the last dated ring according to relationships between age since death and decay (Bosch and Gutiérrez, 1999).

In addition, 21 living and mature (age > 150 yr) Mountain pines located near the sampling plot in an open stand were sampled using a Pressler increment borer. Two 5-mm-diameter cores were collected per living tree. To compare Mountain pine growth variability and responses to climate with that of Scots pine, 15 mature Scots pine trees situated at ~3 km from the sampling site, and forming also an open stand located at lower elevations (1800–1900 m) and in a slope with similar aspect, were sampled.

Cores and sections were air-dried, sanded, and visually cross-dated, and tree-ring widths were measured using a Lintab-TSAP semi-automatic measuring table (F. Rinn, Heidelberg, Germany). The resulting time series were detrended using Hugershoff growth curves to remove age- and size-related trends at long to mid time frequencies from the data (Fritts, 2001). The autocorrelation of these series was modeled and partially removed to obtain residual ring-width indices. The indexed series were finally averaged using the arithmetic mean to form well-replicated residual chronologies of Mountain and Scots pines reaching back to 1700. Chronology building was done using the program Turbo Arstan (Cook and Krusic, 2005). The change in quality of the site chronologies through time was assessed by calculating (1) correlations between the chro-

TABLE 1

Geographical, topographical, and ecological characteristics of the Mountain pine stands sampled across the Spanish Pyrenees (see sites in Fig. 2, part a). The study site (FR) is emphasized in bold characters. Values are means ± SD.

Site (code)	Latitude (N)	Longitude (E / W)	Altitude (m a.s.l.)	Aspect	Slope (°)	Dbh (cm)	Age at 1.3 m (years)
Estanys de la Pera (EP)	42°27′	1°35′E	2360	SW	30	65.2 ± 11.0	339 ± 117
Mata de València (MA)	42°38′	1°04′E	2019	N-NW	19	43.2 ± 3.6	237 ± 72
Estany de Lladres (LA)	42°33′	1°03′E	2120	NW	35	52.1 ± 9.8	313 ± 123
Airoto (AI)	42°42′	1°02′E	2300	W	37	58.5 ± 13.5	288 ± 100
Tessó de Son (TS)	42°35′	1°02′E	2239	N-NE	42	74.5 ± 18.8	346 ± 202
Estany Negre (NE)	42°33′	1°02′E	2451	SE	35	71.0 ± 26.0	411 ± 182
Estany Gerber (GE)	42°37′	0°59′E	2268	W	15	53.5 ± 14.6	426 ± 147
Estany d'Amitges (AM)	42°35′	0°59′E	2390	S-E	40	69.0 ± 26.0	355 ± 106
Mirador (MI)	42°35′	0°59′E	2180	SE	33	55.1 ± 25.8	401 ± 132
Ratera (RA)	42°35′	0°59′E	2170	N	40	28.3 ± 8.1	380 ± 146
Sant Maurici (SM)	42°35′	0°59′E	1933	S-SE	16	38.2 ± 5.7	204 ± 23
Monestero (MO)	42°34′	0°59′E	2280	SE	28	64.4 ± 16.1	346 ± 110
Corticelles (CO)	42°34′	0°56′E	2269	W-NW	24	83.1 ± 28.8	509 ± 177
Barranc de Llacs (LL)	42°32′	0°55′E	2250	N-NW	44	71.7 ± 20.0	616 ± 175
Conangles (CG)	42°37′	0°44′E	2106	S-SW	43	56.0 ± 14.5	318 ± 117
Vall de Mulleres (VM)	42°37′	0°43′E	1800	N-NE	34	69.0 ± 26.0	437 ± 184
Bielsa (BI)	42°42′	0°11′E	2100	E	60	45.1 ± 9.4	270 ± 67
Sobrestivo (SB)	42°40′	0°06′E	2296	S	38	61.7 ± 17.5	341 ± 97
Foratarruego (FR)	42°37′	0°06′E	2031	W	37	49.5 ± 18.3	433 ± 50
Senda de Cazadores (SC)	42°38′	0°03′W	2247	N	39	60.9 ± 16.5	357 ± 145
Mirador del Rey (MR)	42°38′	0°04′W	1980	SW	25	53.3 ± 15.3	117 ± 18
Las Cutas (CU)	42°37′	0°05′W	2150	S-SW	20	33.3 ± 8.3	129 ± 16
Respomuso (RE)	42°49′	0°17′W	2350	S	30	49.5 ± 15.1	280 ± 83
Pic d'Arnousse (PA)	42°48′	0°31′W	1940	NW	32	65.4 ± 5.1	248 ± 83
Larra-La Contienda (CN)	42°57′	0°46′W	1750	SW	38	46.4 ± 14.0	350 ± 108

nologies and (2) the Expressed Population Signal (EPS; Wigley et al., 1984). A value of EPS ≥ 0.85 is considered as acceptable for a well-replicated chronology. Correlations between the two species chronologies were calculated for 20-year intervals shifted along the time series from 1800 until 2009.

Several dendrochronological statistics were calculated for the common period 1900–2008 to characterize the chronologies (Briffa and Jones, 1990): mean, standard deviation and first-order autocorrelation of raw tree-ring widths; and mean sensitivity (a measure of the year-to-year variability in width of consecutive tree rings), mean between-trees correlation, and the percentage of variance explained by the first principal component of residual ring-width indices.

GROWTH RESPONSES TO CLIMATE

To quantify growth responses to climate of both pine species, their residual chronologies were correlated with monthly mean maximum (TMax) and minimum (Tmin) temperatures

obtained from the corresponding CRU TS 3.1 grid and for the period 1901–2008. We obtained Pearson correlation coefficients between growth indices and temperature from the prior October up to September of the year of tree-ring formation. Precipitation data were not considered because (1) reliable data were lacking in the first half of the 20th century in the study area, and (2) tree growth at high elevation mainly responds to temperature in the Pyrenees (Tardif et al., 2003). We considered three probability levels ($0.05 \leq P$; $0.05 < P \leq 0.01$; $0.01 < P \leq 0.001$) in these analyses.

LONG-TERM RECRUITMENT, DEATH, AND TEMPERATURE PATTERNS

Finally, we evaluated if long-term temperature variability was coupled with treeline dynamics at the study site and changes in the Mountain pine age structure for a Pyrenean data set of high-elevation Mountain pine forests. The age data set of high-elevation Mountain pine forests was based on 28 forests located in
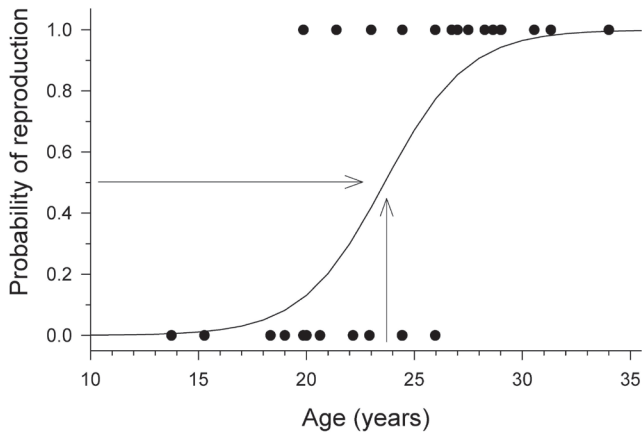
FIGURE 3. Probability of reproduction (cone presence) in treeline Mountain pine recruits as a function of their ages. According to the fitted binomial model (line, equation: $y = e^{(0.52x-12.32)}/(1 + e^{(0.52x-12.32)})$), the probability of reproduction equal to 0.5 is reached at an age of 24 years as illustrated by the two arrows.

the Spanish Pyrenees and including four treeline sites. Sampled sites are described in Table 1 (see more details in Gutiérrez et al., 1998; Camarero et al., 2015). We emphasize that the trees sampled in the study site represent a small proportion ($n = 33$ trees) as compared with the whole Pyrenean data set of adult Mountain pine trees ($n = 544$ trees), which also includes tree sampled at treeline sites ($n = 79$ trees). We compared several temperature reconstructions with the estimated dates of germination and death of Mountain pines at treeline and with the frequency of Mountain pines germinated in Pyrenean forests. Both data sets were expressed in 20-year classes. Here it must be noted that: (1) the reconstruction of tree age structures involving the dating of living and dead trees is the result of changes in recruitment and/or mortality rates (Johnson et al., 1994), and (2) the historical death estimates do not fully account for the individual and temporal variability of actual tree death rates (Zens and Peart, 2003). Mountain pine data were compared with several long-term climate reconstructions, namely (1) annual temperatures for northern Spain based on speleothems (Martín-Chivelet et al., 2011),

(2) seasonal temperatures for the Pyrenees based on dendrochronological proxies such as summer (June to August) temperature based on maximum wood density (Büntgen et al., 2008; hereafter abbreviated as B-2008), and (3) growing-season (May to September) temperature based on tree-ring widths and maximum wood density (Dorado Liñán et al., 2012; hereafter abbreviated as DL-2012). We selected non-dendrochronological proxies such as spelothems and dendrochronological proxies of temperature to provide complementary climate reconstructions, and to avoid circular arguments based on age and temperature reconstructions derived of tree-ring sources. The comparisons between temperature reconstructions, the age structure of Pyrenean Mountain pine forests and the frequency of germinated and dead trees in the study treeline was quantified using the Spearman correlation coefficient (rs). To compare these variables, Mountain pine age data were calculated for 20-year classes, whereas temperatures were standardized by subtracting the mean and dividing them by the standard deviation, and then averaged for the same classes considering the period 1500–1860 ($n = 18$ classes). We restricted the analyses to this period to avoid two biases of tree data due to (1) the sampling of mature trees usually older than 150 years in dendrochronological samplings of Pyrenean forests, and (2) the decay and decomposition of young trees recruited but later dead in the treeline site and elsewhere.

Results

RECENT AND AGGREGATED RECRUITMENT OF YOUNG MOUNTAIN PINES WITHIN THE TREELINE ECOTONE

Mountain pine recruits ($n = 43$) showed similar sizes (means ± SE of the mean, basal diameter = 14.1 ± 1.9 cm; dbh = 11.1 ± 2.0 cm; height = 2.4 ± 0.2 m) and ages (24 1 ± 1 years, range 14–34 years). This means that all sampled Mountain pines were recruited in a short timespan. Specifically, 67% of all recruits germinated in the 1980s with a mean germination year of 1986. The remaining 33% of young Mountain pines were born in the early 1990s. Based on the aforementioned size and age estimates, most pines can be considered as saplings recruited from 1980s until 1990, but showing high vertical growth rates nowadays, since 59% of saplings reached heights between 2 and 3 m. Mountain pine saplings also presented significant spatial aggregation up to 1 m apart, initiating clustered foci of infilling within the ecotone (Fig. 1 and Fig. 2, part b). Saplings were also reproductively precocious, reaching the 50% probability of reproduction at 24 years (Fig. 3).

TREE-RING WIDTH CHRONOLOGIES AND CLIMATE-GROWTH ASSOCIATIONS

The chronologies of Mountain and Scots pines were well replicated since 1505 and 1790, respectively, when they reached EPS-values above the 0.85 threshold. Both species presented similar first-order autocorrelation values but Mountain pine showed on average narrower rings than Scots pine and a higher mean sensitivity, i.e. more year-to-year variability in width of consecutive rings (Table 2). The higher correlation values between trees and percent variance accounted for the first principal component in Mountain pine indicate that growth series of trees were more coherent and responded more strongly to climate variables than in the case of Scots pine.

Several periods of low and high growth rates were observed in the ring-width chronologies (Fig. 4, part a). During the 18th

TABLE 2

Dendrochronological statistics obtained for the Mountain and Scots pine ring-width chronologies considering the common period 1900–2008.

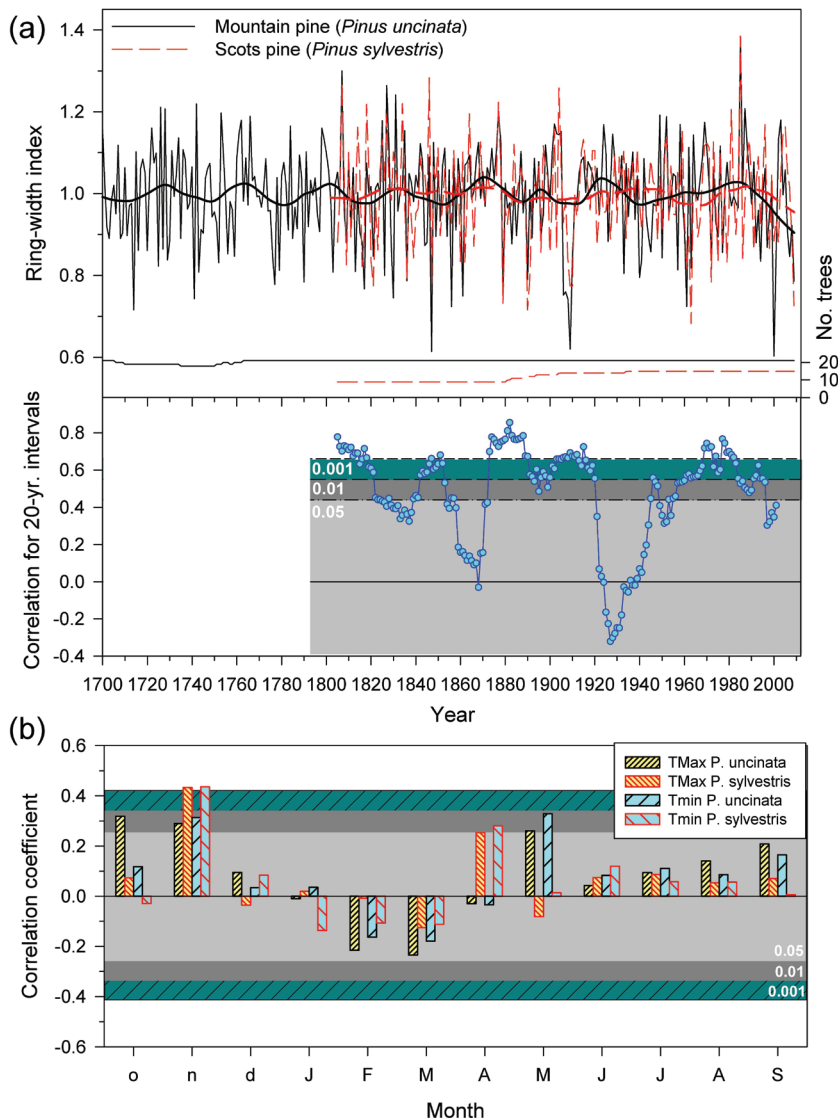| Variables	Mountain pine (*Pinus uncinata*)	Scots pine (*Pinus sylvestris*)
No. trees (No. radii)	33 (65)	15 (30)
Mean tree-ring width (mm)	0.429	0.765
Standard deviation (mm)	0.136	0.244
First-order autocorrelation	0.663	0.659
Mean sensitivity	0.313	0.263
Correlation between trees	0.385	0.249
Variance accounted for by the first principal component (%)	45.10	30.75

FIGURE 4. Tree-ring width chronologies of Mountain and Scots pines displayed for their corresponding (a) well-replicated timespans and (b) temperature-growth relationships for both species. In the upper plot the residual indexed chronologies and their smoothed functions are shown (smoothing was done with 0.1-long loess functions). The right *y*-axis shows the number of sampled trees. The 20-year moving correlations calculated between both species chronologies are displayed with three probability levels shown as areas with different colors. In the lower plot, the bars show Pearson correlation coefficients calculated between monthly mean maximum (TMax) and minimum (Tmin) temperatures and ring-width indices from previous October up to current September during the period 1901–2008. Months abbreviated by lowercase and uppercase letters correspond to the prior and current years, respectively. The areas with different colors indicate significance levels.

century, relatively stable growth conditions were observed, while low growth indices were found in both pine species in the 1840s, 1900s, early 1960s, and late 1990s. High growth indices were frequent in both Mountain and Scots pines in the 1800s, 1870s, 1890s, and particularly in the 1980s. The major drop in growth indices was observed in the beginning of the 20th century. The apparent growth decline of the Mountain pine chronology during the late 20th century is probably an artifact of slow growth rates of dead trees used in the chronology. Finally, both species show coupled growth indices throughout most of the analyzed period, except during the late 19th century (approximately 1860–1880) and between 1920 and 1940 when growth indices were moderate and showed little temporal variability.

The calculated temperature-growth associations confirmed the abovementioned assumption because Mountain pine ring-width indices were significantly and positively related to previous-November (both maximum and minimum) and current-May (mainly minimum) temperatures (Fig. 4, part b). In contrast, Scots pine indices were similarly related to November temperatures but showed smaller, albeit significant, correlations with April temperatures than Mountain pine showed in the case of May temperatures. These different growth responses to spring temperatures suggest phenological shifts of the two species, probably explained by the contrasting elevation of the sampled trees since the two stands shared similar slope aspect. Lastly, warmer conditions in the previous October were also linked to enhanced growth in Mountain pine, whereas warmer March conditions were nonsignificantly associated with growth reduction in both species.

LONG-TERM COUPLING BETWEEN MOUNTAIN PINE REGENERATION AND AIR TEMPERATURE

The most abundant age classes in Pyrenean high-elevation Mountain pine forests were formed by trees with ages from 240 up to 300 years, that is, trees recruited between 1700 and 1760, a period characterized by warmer conditions according to temperature reconstructions (Fig. 5, part a). In the study treeline, recruitment peaked in the late 20th century, and dead mature trees recruited between 1740 and 1760 and in the early 16th century. The periods with more abundant deaths were the first half of the 19th century, specifically from 1820 to 1860 when temperatures rapidly dropped, and the transition between the mid 17th and the early 18th centuries, which were also cool decades (Fig. 5, part b).
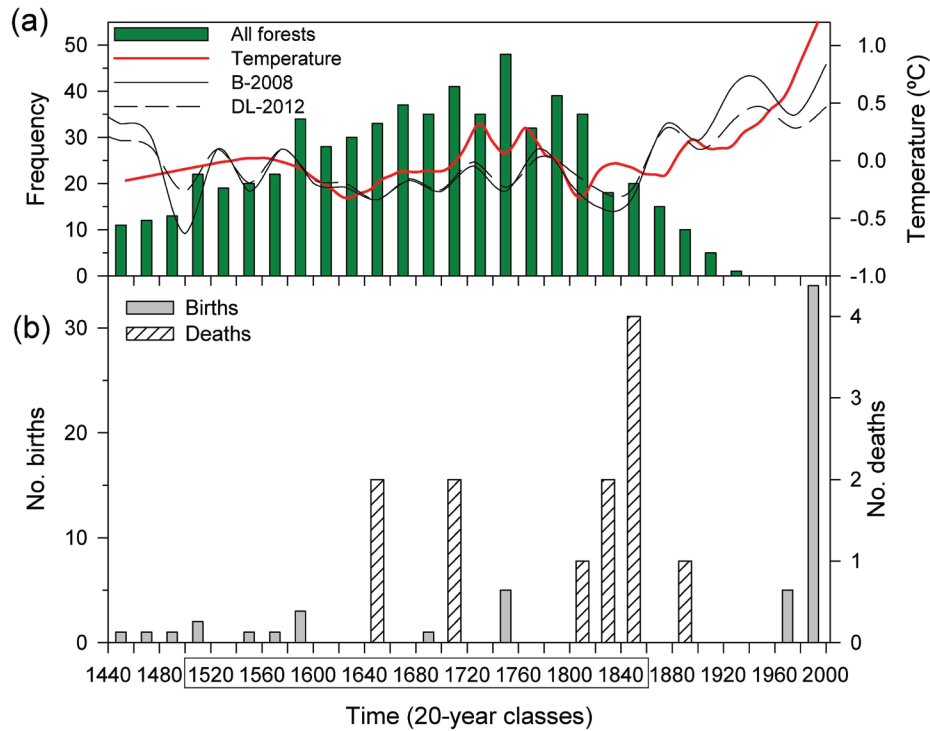
FIGURE 5. Trends of temperature anomalies in northern Spain and the Pyrenees derived from different proxies (red continuous line, speleothems; dendrochronologic reconstructions: black thin line, B-2008, Büntgen et al., 2008; dashed thin line, DL-2012, Dorado Liñán et al., 2012) as compared with (a) the age structure of Mountain pines sampled in the Spanish Pyrenees (modified from Camarero et al., 2015) and with (b) Mountain pine recruitment (births) and death events in the study treeline. In both panels age, recruitment, or death data are given in 20-year classes. The speleothem reconstruction was performed for northern Spain (Martín-Chivelet et al., 2011). Dendrochronological reconstructions of maximum summer (June–August) temperatures (B-2008) and May–September mean temperatures (DL-2012) are based on maximum wood density and tree-ring width, respectively. The box in the *x*-axis of the lowermost plot indicates the period considered to analyze relationships between temperature and pine data.

Mountain pine reconstructed age and germination data were not significantly related to temperature reconstructions (Table 3). Only the frequency of dead pines at treeline was negatively related to the temperature reconstructed using dendrochronological proxies. This is logical because both dendroclimatic reconstructions were significantly correlated ($rs = 0.96$, $P < 0.001$), but only the DL-2012 dendrochronological temperature reconstruction was related to the speleothem-based reconstruction ($rs = 0.47$, $P = 0.05$).

Discussion

Treeline conifer stands show intense and fast dynamics in response to recent climate warming that translate into new and abundant regeneration, stand encroachment, high growth rates particularly regarding vertical shoot growth, and less often upslope shifts. This process has been described in the presented Pyrenean study case but analogous cases exist elsewhere. For example, in the case of Scots pine treelines in the Swedish Scandes, successive warm summers and exceptionally mild winters in the 20th century enhanced growth and regeneration and in some cases facilitated upward treeline shifts (Kullman, 2000). The regeneration process at pine treelines requires several successive warm summers to ensure the formation of buds, flowering, and successful formation of viable seeds (Sarvas, 1962), while in the case of Mountain pine warmer spring conditions enhance recruitment and tree growth (Camarero and Gutiérrez, 2004).

TABLE 3

Associations (Spearman correlation coefficients) observed between reconstructed temperature series, either based on dendrochronological (B-2008, Büntgen et al., 2008; DL-2012, Dorado Liñán et al., 2012) or non-dendrochronological proxies (espeleothems, Martín-Chivelet et al., 2011), and the age structure of Pyrenean mountain pine forests or the frequency of trees germinated (births) or dead (deaths) in the study treeline. The *P* value of each correlation is indicated between parentheses.

Temperature reconstruction	Age structure of mountain pine forests	Mountain pine births at treeline	Mountain pine deaths at treeline
B-2008	–0.03 (0.92)	0.06 (0.82)	–0.65 (0.003)
DL-2012	–0.14 (0.58)	0.05 (0.83)	–0.58 (0.01)
Espeleothems	0.15 (0.56)	0.29 (0.24)	–0.40 (0.10)

According to the CRU data set, the 1980s and 1990s were among the warmest decades of the last half of the past century (mean = 5.4 °C), but they were also remarkable by experiencing rapid warming with an average rate of 0.091 °C yr^{-1}. Interestingly, the 1980s and 1990s were also decades with high year-to-year variability in annual temperatures (coefficient of variation, CV = 10.2%) if compared with colder decades such as the 1970s (mean = 4.7°, CV = 4.3%) or warmer periods such as the 2000s (mean = 6.1°, CV = 5.7%). Therefore, recent Mountain pine recruitment at the study treeline occurred during warm periods experiencing rapid warming but also high interannual variability in air temperature. This result partially agrees with what previously Camarero and Gutiérrez (2004) reported, since they also found intense pine recruitment during warm periods in Pyrenean treelines, but they argued that stable temperature conditions were necessary for continuous treeline encroachment and subsequent treeline ascent. Nevertheless, these findings are not conclusive given that the sample size of the study site (Fig. 5, part b) represents a small percentage (6%) of the whole Pyrenean data set of Mountain pine trees (Fig. 5, part a) (n = 544 trees), but this proportion increases if only treeline sites are considered (42%).

Late autumn and spring temperatures were the major drivers of radial growth of treeline Mountain pine and downslope Scots pine trees. This agrees with previous research in nearby Pyrenean high-elevation forests and treeline sites (Gutiérrez et al., 1998; Tardif et al., 2003; Camarero and Gutiérrez, 2004; Galván et al., 2014). Therefore, periods of sustained and low ring-width indices corresponded to sudden drops in temperatures as occurred in the early 20th century. Warm periods as in the 1980s caused growth enhancement but also increased regeneration rates at the treeline. Old trees or shrubby krummholz individuals can persist, growing slowly and producing few viable seeds for centuries at treeline and then respond rapidly to climate warming by increasing their radial growth rates and initiating sexual reproduction (Shiyatov and Mazepa, 2011; Trant et al., 2011). The ability of individuals to persist with suppressed radial growth rates during adverse growing conditions may have significant implications for the rate at which these trees are able to respond when conditions become favorable. Further, warmer conditions and increased radial-growth rates could shift the reproductive size thresholds and make trees more precocious in reproductive terms, that is, by decreasing the minimum age of cone production.

Lastly, periods characterized by moderate and stable ring-width indices in both species coincided with the decoupling between the species chronologies. This suggests the prevalence of warm and stable climatic conditions in those periods (1860–1880, 1920–1940), which release trees from climatic constraints such as cold periods or climatic extremes and make them more dependent on local site factors (Tardif et al., 2003). It is interesting to emphasize that in those two periods, when climatic conditions were assumed to be stable and favorable to growth, no death event was detected in the treeline site. This suggests that the requirement of warm and stable climatic conditions for allowing treeline encroachment and ascent could mainly work on adult mortality rates (Camarero and Gutiérrez, 2004).

In addition, our research allows inferring that cold periods, such as the period 1840–1860 at the end of the LIA, lead to reduced growth rates and increased adult mortality rates. Long-term climatic controls over treeline may operate through stasis or lagged responses to climate (e.g., long-lived and slow-growing adult trees surviving under harsh environmental conditions) punctuated by intense recruitment or death events triggered by climatic extremes (Kullman, 1987, 1993). In long-lived treeline species such

as Mountain or Scots pines, abundant adult tree death caused by long-term cooling trends (e.g., LIA) or by extremely cold climatic events (e.g., the early 20th century in this study) is a more important process than recruitment failure in driving the decline of treeline populations (Kullman, 1987). However, the picture may be more complex since the W-SW aspect and the dominant rocky substrates of the study site could make it prone to drought stress. Drought is becoming a more important driver of growth trends in Pyrenean Mountain pine forests (Galván et al., 2014), particularly in sites with S-facing and steep slopes and rocky substrates (Galván et al., 2015). In addition, dry conditions prevailed in northern Spain during periods of high mortality levels in the study site such as the 1820s, 1830s, early 1850s, and 1860s (Esper et al., 2014). Therefore, dry summers and cold winter conditions, particularly with a shallow snow pack, could both contribute to drought- or cold-induced dieback, thus increasing tree mortality.

Cool periods, as the 1970s, also slow down treeline dynamics by reducing growth and regeneration rates as exemplified in the study Mountain pine treeline. Conversely, warm conditions enhance tree growth and increase recruitment rates as occurred during the 1980s and 1990s. These two decades were characterized by intense recruitment levels across Pyrenean treelines (Batllori and Gutiérrez, 2008; Batllori et al., 2012), which indicates that the study site is representative of Mountain pine regeneration trends at those marginal ecotones. Positive feedbacks caused by local processes could also lead to increased regeneration through facilitation or abundance of safe sites for seedling establishment (Batllori et al., 2009). Those feedbacks represent a major source of decoupling between climate and treeline dynamics because local factors (e.g., microtopography, snow depth, soils, aspect, shrub cover) override regional climate warming as drivers of regeneration (Elliott, 2011). The observed aggregation of tree recruits is coherent with the existence of positive feedbacks between neighboring trees (Batllori et al., 2009, 2010), probably modulated by snow deposition patterns and also related to the initial dispersal of seeds from adults (Camarero et al., 2005).

Overall, treeline dynamics during the late 20th century, specifically growth and regeneration rates, were rapid and intense in the studied Pyrenean treeline site. The presented research allows inferring that climate and treeline responses did not present remarkable time lags, that is, no treeline inertia was observed. Contrarily, current treeline dynamics are coupled with climate. The reconstruction of growth, regeneration, and death processes also indicate that recent treeline dynamics represent a new phase of recovery, which breaks the long-term decline observed at the study treeline characterized by high mortality rates during the LIA. These findings indicate that certain processes such as regeneration and mortality are appropriate and sensitive monitors of the effects of climate on alpine treelines. But, a long-term perspective (e.g., the past 1–5 millennia) is needed to properly appraise how vegetation will respond to future warming. The framework offered by the transition from the cold late 19th century to the very warm late 20th century seems to be unprecedented in a late-Holocene perspective (Kullman, 2001), and that could explain the rapid treeline dynamics observed nowadays. This opens the question on how warm or stable future climatic conditions must be to cause treeline densification and upslope migration. The comparisons between this study and regeneration dynamics in Pyrenean forest and treelines add generality to the presented findings, though we are fully aware that the lack of site replication limits our conclusions. Furthermore, geomorphic features of the study site such as its steepness and abundant rocky substrates could also limit the upslope advancement of the treeline ecotone by constraining

seedling establishment (Resler, 2006; Holtmeier and Broll, 2012; Macias-Fauria and Johnson, 2013). To lessen these shortcomings, treeline ecotones with diverse landforms and nearby forests could be compared by reconstructing their long-term post-LIA mortality and recruitment rates.

Acknowledgments

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