

A millennium-long perspective on high-elevation pine recruitment in the Spanish central Pyrenees

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Abstract: Long-term fluctuations in forest recruitment, at time scales well beyond the life-span of individual trees, can be related to climate changes. The underlying climatic drivers are, however, often understudied. Here, we present the recruitment history of a high-elevation mountain pine (*Pinus uncinata* Ram.) forest in the Spanish central Pyrenees throughout the last millennium. A total of 1108 ring-width series translated into a continuous chronology from 924 to 2014 CE, which allowed estimated germination dates of 470 trees to be compared against decadal-scale temperature variability. High recruitment intensity mainly coincided with relatively warm periods in the early 14th, 15th, 19th, and 20th centuries, whereas cold phases during the mid-17th, early 18th, and mid-19th centuries overlapped with generally low recruitment rates. In revealing the importance of prolonged warm conditions for high-elevation pine recruitment in the Pyrenees, this study suggests increased densification and even possible upward migration of tree-line ecotones under predicted global warming.

Key words: dendroecology, *Pinus uncinata*, subalpine forests, recruitment, tree rings.

Résumé : Les fluctuations à long terme du recrutement de semis en forêt, à des échelles de temps bien au-delà de la durée de vie des arbres individuels, peuvent être reliées aux changements climatiques. Toutefois, les facteurs climatiques sous-jacents sont souvent peu étudiés. Dans cette étude, nous présentons l'historique de recrutement d'une forêt de pin à crochets (*Pinus uncinata* Ram.) située en haute altitude dans les Pyrénées centrales espagnoles au cours du dernier millénaire. Au total, 1108 séries de cernes annuels ont été transformées en une chronologie continue couvrant la période de 924 à 2014 EC, ce qui nous a permis de relier les années de germination estimées pour 470 arbres à la variation décennale de température. De fortes intensités de recrutement ont surtout coïncidé avec des périodes relativement chaudes observées au début des 14^e, 15^e, 19^e et 20^e siècles, alors que les périodes froides observées au milieu du 17^e, au début du 18^e et au milieu du 19^e siècle correspondaient généralement à de faibles taux de recrutement. En révélant l'importance des périodes prolongées de réchauffement pour le recrutement de pin en haute altitude dans les Pyrénées, cette étude indique que le réchauffement climatique anticipé pourrait provoquer une augmentation de la densité des forêts et même une migration altitudinale des écotones de la limite des arbres. [Traduit par la Rédaction]

Mots-clés : dendroécologie, *Pinus uncinata*, forêts subalpines, recrutement, cernes annuels de croissance.

Introduction

Climate variability can alter ecological processes such as population dynamics (i.e., births or deaths), particularly in cold-limited environments (Kullman 1986). Long-term tree recruitment dynamics are not well understood because paleoecological reconstructions are rarely linked to the relevant temporal scale (10^2 – 10^3 years) dictated by tree life-spans, and annually resolved tree-ring studies are scarce in some regions because of the limited availability of well-conserved old trees (e.g., Zackrisson et al. 1995; Lloyd and Graumlich 1997; Kullman 2017). Therefore, we need a better understanding of past tree recruitment dynamics, which is relevant for developing ecological theory related to disturbance regimes (Frelich 2016), improving conservation and management, and refining forests models (Pilon et al. 2018). This gap of information should be filled to know how 21st century forests will respond to land-use abandonment and rising temperatures, especially in

high-elevation ecotones (Intergovernmental Panel on Climate Change (IPCC) 2014).

Dendrochronology represents a trade-off between mid- to long-term paleoecological reconstructions and short-term approaches (e.g., plot censuses). Thus, it is a valuable tool to infer tree population dynamics because it allows establishing annually resolved reconstructions of growth and recruitment (Fritts 1976). However, dendrochronology's utility in reconstructing these dynamics is limited by tree longevity and wood decomposition (Swetnam et al. 1999). Firstly, tree-ring chronologies represent imperfect records of forest dynamics as they do not usually provide ideal estimates of growth rates across age or size classes (Bowman et al. 2013) and thus cannot be used to assess demographic trends, including recruitment and mortality rates (Condit et al. 2017). Secondly, decomposed dead trees limit the capacity of tree-ring records to be used in reconstructions such as recruitment or mor-

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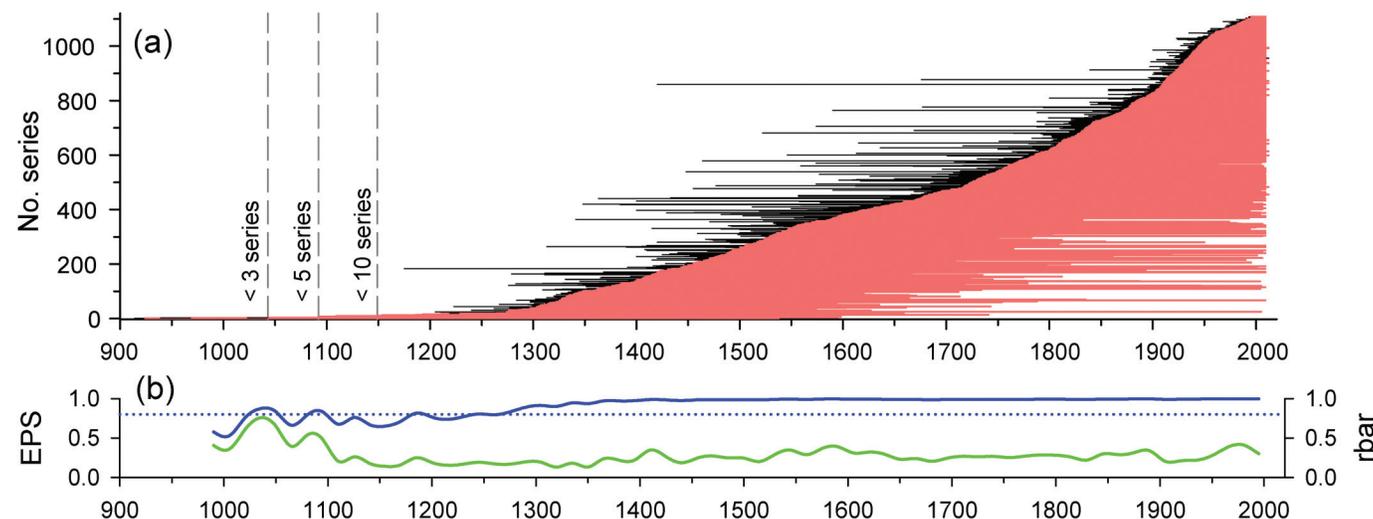
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Table 1. Dendrochronological statistics for the different tree-ring datasets used to build the final chronology shown in the last row of the table.

Dataset (reference)	Time span	Time span (>5 series)	No. of trees/ No. of radii	Tree-ring width \pm SD (mm)	MSL (years)	AC	ms _x	EPS
Büntgen 08 (Büntgen et al. 2008)	924–2005	1265–2005	106/201	0.63 \pm 0.27	209	0.76	0.21	0.89
Büntgen 17 update (Büntgen et al. 2017)	1093–2012	1109–2012	138/290	0.63 \pm 0.30	206	0.76	0.22	0.92
Cabanes Lake	1186–2007	1279–2006	117/132	0.64 \pm 0.29	252	0.79	0.22	0.87
Camarero (Galván et al. 2014)	1325–2009	1443–2009	29/67	0.53 \pm 0.23	300	0.79	0.21	0.88
Esper (Esper et al. 2015)	1529–2009	1560–2009	191/418	1.01 \pm 0.47	124	0.88	0.20	0.92
Final chronology	924–2012	1093–2012	581/1108	0.71 \pm 0.32	186	0.76	0.22	0.91

Note: SD, standard deviation; MSL, mean segment length; AC, first-order autocorrelation; ms_x, mean sensitivity; EPS, expressed population signal. Tree-ring width, AC, ms_x, and EPS variables were calculated for the common period 1560–2007. EPS values above 0.85 are considered well-replicated periods.

Fig. 1. (a) Temporal distribution of the 1108 tree-ring series (581 trees) ordered by the earliest measured tree ring. The horizontal black lines show the distance estimation from the last measured ring to the pith. Note the reduction in sample size (less than five series) prior to 1092 CE. (b) Expressed population signal (EPS; upper line, blue in online version) and mean correlation among series (\bar{r} ; lower line, green in online version) calculated over 30-year periods and lagged by 15 years. The dashed line represents the 0.85 EPS threshold. [Colour online.]



tality rates and thereby bias estimates of actual population dynamics (Johnson et al. 1994). For instance, few trees dating to a certain period may be the result of reduced recruitment, high mortality rates, or a combination of both factors.

Temperature-limited ecosystems such as high-elevation or sub-alpine forests are suitable settings to reconstruct tree recruitment dynamics in response to temperature changes because both growth and recruitment are particularly sensitive to temperature changes (e.g., Esper and Schweingruber 2004; Tardif et al. 2003; Shiyatov 2003; Büntgen et al. 2017). The effects of temperature oscillation have also been reported in other cold ecosystems such as the tundra, where shrub recruitment was linked to temperature at time lags of 2–6 years (Büntgen et al. 2015). However, understanding climate-driven tree population dynamics remains challenging because of the lack of well-replicated and adequately resolved records over long time periods.

Here, we present a millennium-long dendrochronological reconstruction of mountain pine (*Pinus uncinata* Ram.) recruitment at a high-elevation Pyrenean forest in northeastern Spain. This study represents the first long-term recruitment reconstruction in this region and one of the best replicated in high-elevation forests worldwide. We correlated the best-replicated (13th–20th century) recruitment estimates with regional temperature reconstructions to test whether long-term recruitment changes cohere with temperature changes. We also explored the relationships between tree growth and recruitment. We hypothesize that recruitment pulses are linked to warmer conditions at decadal time scales.

Material and methods

Study area and tree species

The study area is the basin (ca. 70 ha) surrounding Gerber Lake (42°37'N, 0°59'E, 2200–2350 m above sea level (a.s.l.)) and Cabanes Lake (42°37'N, 1°01'E, 2100–2300 m a.s.l.; situated 2.5 km from Gerber lake). Both sites are located at the northern fringe of the “Aigüestortes i Estany de Sant Maurici” National Park in the central Spanish Pyrenees (Camarero and Gutiérrez 2004; González de Andrés et al. 2015). Radial growth of the species is enhanced by warm previous-November and current-May conditions (Camarero et al. 1998; Büntgen et al. 2010; Tardif et al. 2003); however, it has been demonstrated to be drought-sensitive under global warming (Galván et al. 2015).

Mountain pine is a long-lived (up to 1000 years; Galván et al. 2014), shade-intolerant conifer with a large ecological amplitude regarding topography and soil type and dominates subalpine forests in the Spanish Pyrenees (Camarero and Gutiérrez 2004; González de Andrés et al. 2015). Radial growth of the species is enhanced by warm previous-November and current-May conditions (Camarero et al. 1998; Büntgen et al. 2010; Tardif et al. 2003); however, it has been demonstrated to be drought-sensitive under global warming (Galván et al. 2015).

Field sampling and dendrochronological methods

Wood disks ($n = 361$; 62% of the total dataset) and cores ($n = 220$; 38% of the total dataset) were randomly collected from standing and lying dead trees, well-preserved logs found inside the lakes, and living trees (cores; Supplementary Fig. S1¹). All samples corre-

¹Supplementary figures are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2018-0025>.

sponded to mature trees and therefore had a stem diameter at breast height (DBH) greater than 15 cm. The wood samples were air-dried and polished using a series of successively finer sandpaper grits until rings were clearly visible. The disks were taken as close as possible to the root collar and the wood cores were taken at a 1.3 m height following standard dendrocronological methods (Fritts 1976). Tree-ring widths were then measured at a precision of 0.01 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany) and cross-dated using the program COFECHA (Grissino-Mayer 2001). We estimated the germination year (birth) of each tree by considering the pith on disc and core samples. In those cases where samples missed the pith, we estimated the pith offset by fitting a geometric pith locator to the innermost rings and converting this distance into the number of missing rings (Galván et al. 2014). In wood cores, we dealt with the bias of age estimation due to the core height by grouping the recruitment years into age classes (see next section for further details).

A regional chronology was built encompassing different previously developed datasets of tree ring widths from the study area, including Cabanes Lake (see previous section; Table 1; Supplementary Fig. S2¹). We checked the homogeneity of the growth signal and used the regional curve standardization (RCS) method (Esper et al. 2003) to remove nonclimatic age trends (Fritts 1976), while preserving low-frequency variability (Cook et al. 1995). We used the software ARSTAN for these analyses (Cook 1985).

Reconstruction of tree recruitment and temperature proxies

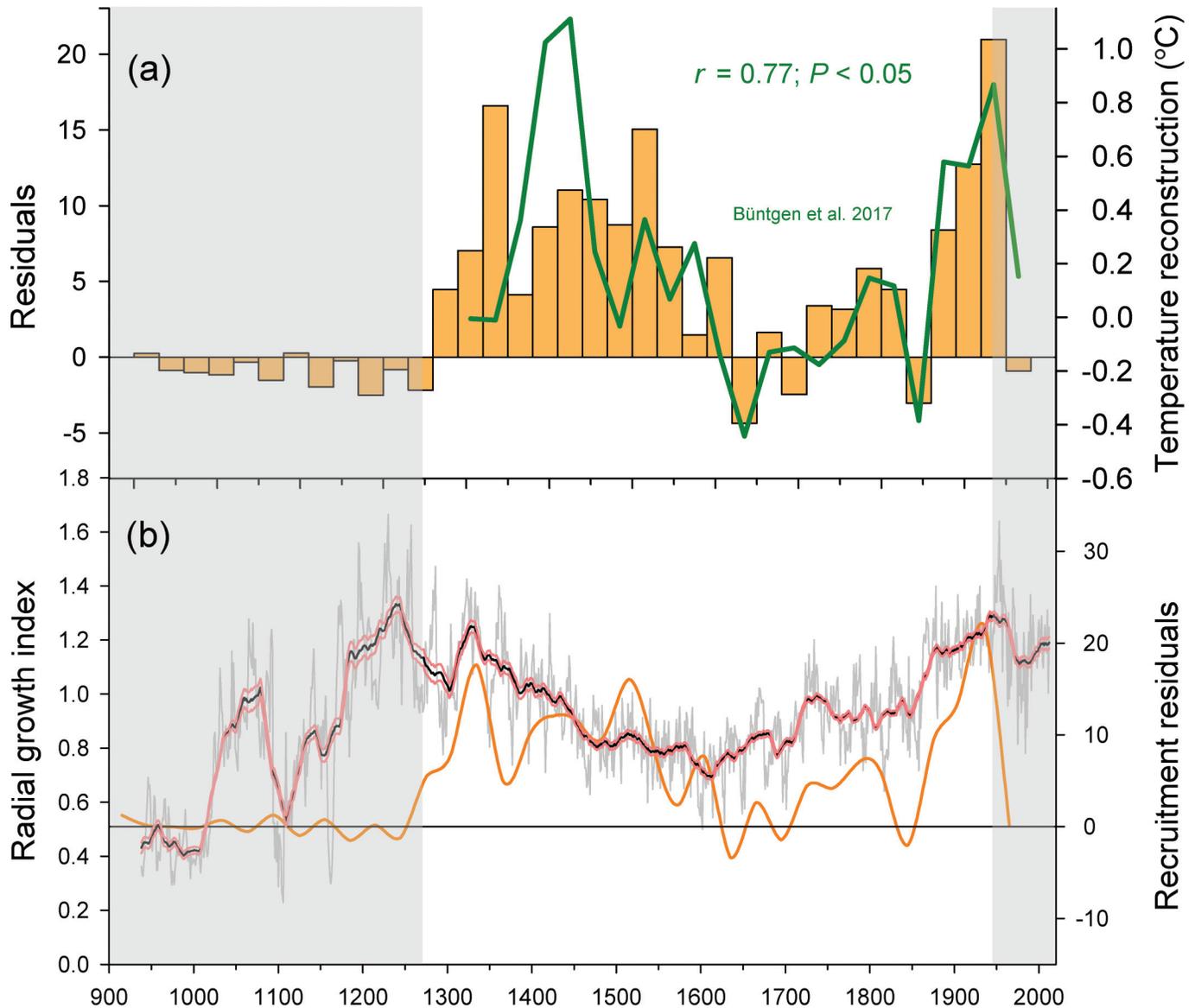
Long-term recruitment dynamics were assessed by reconstructing individual-tree germination dates over the best-replicated period 1275–1935. This period was defined based on a minimum replication of 25 series and coherence exceeding an expressed population signal (EPS) >0.80 among ring-width indices (see Fig. 1; Table 1; Supplementary Fig. S2¹). We truncated the recruitment analyses in 1935 because we did not consider recent tree recruitment, as very young trees were not sampled. We grouped tree recruitment data into classes of 10, 20, or 30 years to assess the uncertainty in age estimations. In this analysis, we used trees with dated piths ($n = 134$ trees; 43% cores and 57% disks), samples with pith-offset estimations equal to or lower than 25 rings ($n = 241$ trees; 47% cores and 53% disks), and samples with pith-offset estimations higher than 25 rings ($n = 95$ trees; 33% cores and 67% disks). Finally, we selected class size of 30 years because it was wider than the main uncertainty interval (25 years; 80% of the samples) and had an adequate temporal resolution for assessing long-term recruitment trends. We fitted exponential and power functions to the frequency of recruitments grouped into the 30-year class assuming either constant recruitment and mortality rates or constant recruitment but variable (age-dependent) mortality rates, respectively (Hett and Loucks 1976; Szeicz and Macdonald 1995). The selection of either negative exponential or power functions was based on the lowest Akaike information criterion (AIC) and the highest explained variance (R^2). The residuals of the best-fitting functions were related to temperature reconstructions derived from diverse proxies (see Table 2): a reconstruction derived from long-term changes in chrysophyte cysts from a nearby lake (Pla and Catalán 2005), a European summer temperature reconstruction (Luterbacher et al. 2016), and a reconstruction for northern Spain based on stalagmite $\delta^{13}\text{C}$ (Martín-Chivelet et al. 2011). We also used a recent spring–summer temperature reconstruction based on tree-ring wood density from the study site (Büntgen et al. 2008, 2017). We checked the relationships between recruitment and temperature reconstructions using Pearson correlations. Finally, we performed cross-correlations between growth and recruitment data considering up to three recruitment classes (90-year-long lags).

Table 2. Relationships between different temperature reconstructions and 30-year classes of tree-recruitment residuals (see Fig. 2b).

Source of temperature reconstructions	Proxy	Reconstruction	Localization	Distance to the sampling zone (km)	Time span (CE)	r	P
Luterbacher et al. (2016)	Tree-ring records, historical documents	Summer temperature	Europe	—	755–2011	0.66	0.036
Martín-Chivelet et al. (2011)	Stalagmite $\delta^{13}\text{C}$	Temperature	North Spain	400	–1949–2000	0.49	0.268
Pla and Catalán (2005)	Chrysophyte cysts	Winter–spring temperature	Lake Radon, Spanish Pyrenees	18	578–1994	0.70	0.026
Büntgen et al. (2008, 2017)	Tree-ring maximum latewood density	Spring–summer temperature	Lake Gerber, Spanish Pyrenees	0.1	924–2014	0.77	0.003

Note: Correlations were calculated for the common period 1275–1935 considering 30-year intervals. Significant correlations ($P < 0.05$) are highlighted in boldface type.

Fig. 2. (a) Recruitment residuals ($n = 470$ trees) after fitting a power function compared with a spring–summer reconstruction based on tree-ring maximum density (line refers to Büntgen et al. 2017). Regression statistics correspond to the relationship observed between recruitment residuals and the temperature reconstructions for the 1275–1935 period (see also Table 2). (b) Standard chronology after 20-year low-pass filtering (black line) and its uncertainty range and yearly variability (red and grey lines, respectively). The orange line indicates the 30-year residuals of recruitment shown as a spline. The shaded areas indicate periods with poor replication. [Colour online.]



Results

The replication of the whole TRW dataset was adequate between 1275 and 2012 (Fig. 1; Table 1; Supplementary Fig. S2¹), whereas it was lower before and decreased to one series in the early 10th century (year 924). Almost half (47%) of all dated trees ($n = 581$) were at least 75 to 200 years old and the oldest dated tree reached 675 years (Supplementary Fig. S3¹).

The power function was selected because it explained 77% of the variability in tree recruitment and showed the lowest AIC, whereas the exponential function explained 73% (Supplementary Fig. S4¹). We detected low recruitment periods from 1550 to 1750 CE, with evident drops in the mid-17th century and the early 18th century and also in the 1850s coinciding with the end of the Little Ice Age (LIA) (Fig. 2a). Those periods of low recruitment coincided with cold conditions according to non-tree-ring and tree-ring proxies (Fig. 2a and Table 2). High recruitment occurred during relatively warm phases from ca. 1400 to 1500, as well as in

the early 14th and 19th centuries. Whereas the recruitment residuals were significantly ($P < 0.05$) related to temperature reconstructions (Fig. 2a; Table 2), the 30-year averages of growth indices were not correlated with tree recruitment ($r = 0.34$, $P = 0.13$; Fig. 2b). Cross-correlations between growth and recruitment data considering (up to) three recruitment class lags were all insignificant (results not presented). Ring-width indices reached a minimum in the early 17th century, whereas recruitment residuals declined from the mid-17th to the early 18th centuries (Fig. 2b). On the other hand, ring-width indices peaked in the early 13th, early 14th, and mid-20th centuries, whereas recruitment residuals culminated in the mid-14th, early 16th, and mid-20th centuries.

Discussion

The association between prolonged cold (e.g., 17th century, 1850s) and warm periods (e.g., 1350–1450, most 20th century) with low and high mountain pine recruitment values, respectively,

supports our main hypothesis (Fig. 2a; Table 2). The temperature oscillations were recorded in tree-ring proxies (Büntgen et al. 2008, 2010, 2017; Dorado-Liñán et al. 2012; Esper et al. 2015) but are also confirmed by other proxies (Pla and Catalán 2005; Morellón et al. 2012). Mountain pine growth was enhanced by warm spring conditions (Camarero et al. 1998), and thus it could be expected to co-vary with tree recruitment, but growth and recruitment were uncoupled, suggesting that they are driven by different thermal variables. Tree recruitment requires warm and stable climatic conditions lasting several decades to produce enough viable seeds to have germinated seeds ultimately recruit into trees (Zasada et al. 1992; Esper and Schweingruber 2004). However, established recruits can be killed by exceptional cold spells during winters without insulating snowpack (Camarero and Gutiérrez 2004). This agrees with the fitted power function (Supplementary Fig. S4¹), which is appropriate for age structures corresponding to high mortality rates in young trees (Hett and Loucks 1976). In fact, periods with low recruitment coincided with cold and unstable climatic conditions such as those observed towards the end of the LIA during the late 19th century (Büntgen et al. 2008, 2017; Morellón et al. 2012). Winter frost and drought due to freeze–thaw cycles, xylem embolism, and needle and shoot abrasion are climatic effects causing tree death and forest dieback in cold environments (Kullman 1996). These factors could explain the sharp drop in tree recruitment recorded during the cold 17th century, during which tree growth also decreased (Figs. 2b). Long-term cooling driven by orbital forcing or cold spells have caused the retreat or local extinction of tree-line populations (Kullman 1986, 1996; Helama et al. 2004). Therefore, recruitment and mortality are asymmetric processes in the dynamics of cold subarctic and subalpine forests.

Multiple studies from cold high-elevation and boreal environments worldwide have linked warm conditions to an increase in tree regeneration and extended cold periods to peaks of tree mortality, and thus they are in line with our main results. Positive relationships between spring–summer temperature and tree recruitment have also been observed in Pyrenean tree lines (Camarero and Gutiérrez 2004). Studies in other regions also confirm the links between warm periods and high tree recruitment. At Mongolian tree lines, tree recruitment was enhanced by warmer conditions in the late 19th century (Kharuk et al. 2010). In northeastern China, the ongoing rapid warming since 1985 is leading to an increase in tree recruitment across the tree line (Du et al. 2018). In northern Fennoscandia and Russia, tree recruitment at the tree line correlated with warm summer conditions (Kullman 1986; Esper and Schweingruber 2004; Kirilyanov et al. 2012; Kharuk et al. 2013). In the Tibetan Plateau, warmer and humid conditions also promoted tree recruitment (Liang et al. 2016). Finally, in boreal Scots pine forests, recruitment peaks followed warm periods (Zackrisson et al. 1995). In addition, these recruitment pulses have also been reconstructed in previous warm periods. For instance, in the Polar Urals tree line, enhanced tree recruitment occurred in response to the Medieval climate warming (11th–13th centuries), and such improved regeneration was also observed in response to the 20th-century warming (Shiyatov 2003; Mazepa 2005). However, mountain forests may also respond to other climate factors as reported from the Sierra Nevada (USA) tree line, where warm and dry conditions constrained recruitment due to a reduced snowpack (Lloyd 1997; Lloyd and Graumlich 1997).

The reconstruction of tree recruitment in similar climatic areas could be used as a proxy of centennial to millennial temperature fluctuations and ecosystem responses. If climate warming proceeds as it did during the 20th century in the Spanish Pyrenees (+0.01 °C·year⁻¹; Galván et al. 2014), enhanced pine growth and recruitment are expected, leading to tree invasion into alpine areas and confining these alpine communities to higher elevations or treeless microsites. Albeit we truncated the analyses in 1950s, our data indicate intense recruitment already during the

early 20th century, which coincides with observations across Pyrenean high-elevation forests and tree lines (Camarero et al. 2015). However, the positive association between temperature and tree establishment may not be consistent in the long term, because other factors (e.g., adequate moisture) may play a relevant role. In addition, our record is not robust enough in its earliest part so as to reflect improved recruitment in response to the High Medieval Warm Period (12th century) and earlier periods.

In summary, we found that tree recruitment in a tree-line ecotone in the Spanish central Pyrenees was enhanced during warm periods, whereas cold periods were associated with relatively low recruitment rates. Tree-ring records reveal that temperature is the major driver of long-term tree population dynamics in cold-limited environments.

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