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Climate–human interactions contributed to historical forest recruitment dynamics in Mediterranean subalpine ecosystems

Gabriel Sangüesa-Barreda[1] | Jan Esper[2] | Ulf Büntgen[3,4,5,6] | J. Julio Camarero[7] | Alfredo Di Filippo[8] | Michele Baliva[8] | Gianluca Piovesan[8]

[1]EiFAB-iuFOR, University of Valladolid, Soria, Spain
[2]Department of Geography, Johannes Gutenberg University, Mainz, Germany
[3]Department of Geography, University of Cambridge, Cambridge, UK
[4]Swiss Federal Research Institute (WSL), Birmensdorf, Switzerland
[5]Global Change Research Institute of the Czech Academy of Sciences (CzechGlobe), Brno, Czech Republic
[6]Department of Geography, Faculty of Science, Masaryk University, Brno, Czech Republic
[7]Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza, Spain
[8]DendrologyLab, Department of Agriculture and Forest Sciences (DAFNE), University of Tuscia, Viterbo, Italy

Correspondence
Gabriel Sangüesa-Barreda, Universidad de Valladolid, EiFAR-iuFOR, Campus Duques de Soria s/n, 42004 Soria, Spain.
Email: gbsanguesa@gmail.com

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Abstract

Long-term tree recruitment dynamics of subalpine forests mainly depend on temperature changes, but little is known about the feedbacks between historical land use and climate. Here, we analyze a southern European, millennium-long dataset of tree recruitment from three high-elevation pine forests located in Mediterranean mountains (Pyrenees, northeastern Spain; Pollino, southern Italy; and Mt. Smolikas, northern Greece). We identify synchronized recruitment peaks in the late 15th and early 16th centuries, following prolonged periods of societal and climate instability. Major European population crises in the 14th and 15th centuries associated with recurrent famines, the Black Death pandemic, and political turmoil are likely to have reduced the deforestation of subalpine environments and caused widespread rewilding. We suggest that a distinct cold phase in the Little Ice Age around 1450 CE could also have accelerated the cessation of grazing pressure, particularly in the Pyrenees, where the demographic crisis was less severe. Most pronounced in the Pyrenees, the enhanced pine recruitment from around 1500–1550 CE coincides with temporarily warmer temperatures associated with a positive phase of the North Atlantic Oscillation. We diagnose that a mixture of human and climate factors has influenced past forest recruitment dynamics in Mediterranean subalpine ecosystems. Our results highlight how complex human–climate interactions shaped forest dynamics during pre-industrial times and provide historical analogies to recent rewilding.

KEYWORDS
dendroecology, ecological history, *Pinus heldreichii*, *Pinus uncinata*, recruitment, rewilding, subalpine forests, tree-rings

1 | INTRODUCTION

Alpine and subalpine ecosystems are particularly sensitive to temperature changes (Holtmeier & Broll, 2005). As a result, recent climate warming has led to tree encroachment and upward treeline shifts (Camarero & Gutiérrez, 2004; Camarero et al., 2017; Du et al., 2018; Esper & Schweingruber, 2004; Harsch, Hulme, McGlone, & Duncan, 2009; Kirdyanov et al., 2012). In many cases, along with rising air temperatures, a reduction in human pressure has also contributed to recent forest recolonization (Ameztegui, Coll, Brotons, & Ninot, 2015; Camarero & Gutiérrez, 2007; Gehrig-Fasel, Guisan, & Zimmermann, 2007; Harsch et al., 2009; Körner, 2012; Vitali, Camarero, Garbarino, Piermattei, & Urbinati, 2017; Vitali et al., 2019). Unravelling current forest dynamics is challenging since the impacts of climatic and anthropogenic drivers are hard to distinguish due to both the absence of precise records (Piovesan, 2019; Piovesan et al., 2019) and the presence of cascading effects resulting from climate–human feedbacks (Buma, 2015). However, disentangling the strength of each driver is key to forecasting future changes in forest structure, composition, and treeline shifts (Camarero et al., 2017; Carlson et al., 2014). In addition, historical legacy effects and tree longevity must be considered when estimating changes in the global carbon budget because old-growth forests (Wirth, Messier, Bergeron, Frank, & Fankhänel, 2009) represent long-term carbon pools (Büntgen et al., 2019; Körner, 2017).

Since the mid-Holocene, human pressure in mountain systems has resulted in extensive deforestation through forest clearing, fire, and livestock grazing (Kaplan, Krumhardt, & Zimmermann, 2009), particularly important in historically human-modified areas such as the Mediterranean Basin (Blondel, 2006). In the Middle Ages alone, an estimated 50%–70% of European forests were deforested (Navarro & Pereira, 2012). The Medieval Warm Period (hereafter MWP) provided the opportunity to establish an extensive farming system that exploited subalpine forests and alpine grasslands for grazing, inducing rapid deforestation and forest ecosystem degradation (Schoolman, Mensing, & Piovesan, 2018; Walsh et al., 2014). In the Pyrenees, human activity and landscape transformation increased significantly during the Middle Ages (Galop, Rius, Cugny, & Mazier, 2013), and grazing became the main economic resource (Fillat, García-González, Gómez, & Reiné, 2008; Pascua Echegaray, 2012). This is confirmed by high-elevation paleoecological records (above 2,000 m a.s.l.) that, through drops in arboreal pollen levels and evidence of severe paleofires, reveal intense deforestations at local to regional scales (Ejarque et al., 2009; Leigh, Gragson, & Coughlan, 2016; Leunda et al., 2017; Miras, Ejarque, Riera Mora, Orengo, & Palet Martinez, 2015). In the Apennines (central Italy), extensive grazing promoted a landscape transformation from primary forests and secondary woodland to grassland as many settlements ascended into high-elevation environments (Mensing et al., 2013; Piovesan, Mercuri, & Mensing, 2018; Schoolman et al., 2018), which is also supported by palynological studies from southern Italy (Florenzano, 2019). In northern Greece, archaeological evidence points to pastoral exploitation of upland areas in the Pindus Mountains (Chang & Tourtelotte, 1993).

European societies were struck by severe famines, wars, and recurrent pandemics such as the Black Death which decimated populations from the 14th to the early 15th century (Gottfried, 1983). These demographic crises potentially reduced or even reversed deforestation and land exploitation in certain periods (Navarro & Pereira, 2012). This possible reduction in detrimental human pressure on subalpine forests may have translated into a landscape-scale rewilding (i.e., a return to natural pre-anthropogenic dynamics), although it would only have been effective in the context of long-lasting warm temperatures to promote and enhance tree establishment (Zasada, Sharik, & Nygren, 1992). Improved climatic conditions would unbalance forest dynamics toward higher tree recruitment rates and lower mortality rates in contrast to the previous situation of low recruitment rates and high mortality or a combination of both as a result of grazing practices.

Subsequent to the MWP, during the Little Ice Age (hereafter LIA) from the 15th to 19th centuries, climate shifted toward cooler and more unstable conditions (Esper et al., 2018). In the Mediterranean Basin, the LIA is associated with a weaker winter North Atlantic Oscillation (NAO) Index, beginning approximately at the middle of 15th century (Trouet et al., 2009). The societal implications of such noteworthy climate change toward increased variability are still uncertain, although climate will have inevitably affected a society that essentially relied on local farming and the exploitation of natural resources. During the coldest periods of the LIA, persistently low temperatures and late snow melting could have limited the grazing activities in the high-elevation belt, potentially a contributing factor in reducing deforestation (Galop et al., 2013; Piovesan et al., 2019). Overall, these findings diagnose an inter-related mixture of human and climatic disturbances occurring simultaneously during this transient period from the 14th to 15th centuries, affecting historical forest dynamics.

In this article, we analyze potential climate and human impacts on the long-term tree recruitment in Mediterranean subalpine pine forests. Local temperature records have been shown to correlate with long-term tree establishment in the Pyrenees (Sangüesa-Barreda, Camarero, Esper, Galván, & Büntgen, 2018), but the wider significance of these findings, as well as the effects of historical human practices and the role of potential synoptic climatic drivers, has not been explored (but see Piovesan et al., 2019). We take advantage of three unique tree-ring collections from ecotones in the Pyrenees (Gerber lake; north-eastern Spain; Büntgen, Frank, Grudd, & Esper, 2008; Büntgen et al., 2017, 2019; Esper et al., 2010, 2015; Sangüesa-Barreda et al., 2018), Pollino massif (southern Italy; Piovesan et al., 2019), and Mt. Smolikas (northern Greece; Esper et al., 2020; Klippel et al., 2017). These massively replicated high-elevation tree-ring datasets have been used to reconstruct tree establishment dynamics over the last millennium. We analyze tree establishment pulses in the 15th and 16th centuries as potential indicators of a previous human demographic crisis and consequent reduction in grazing in high-elevation forests. We also analyze how the beginning of the LIA and local temperature patterns may have influenced tree recruitment dynamics, and discuss potential associations with anthropogenic disturbance regimes. Even though the three Mediterranean high-elevation sites are fairly remote and the access requires long hikes, documental and proxy (paleoecology) records reconstruct periods of intense human pressure during the Middle Ages at local to regional scales.

2 | MATERIALS AND METHODS

2.1 | Sites of old-living trees and sampling strategy

Lake Gerber (42.63°N, 0.99°E) is located in the "Aigüestortes i Estany de Sant Maurici" National Park, central Spanish Pyrenees (Figure 1). The surrounding area of the lake includes open high-elevation Mountain pine (*Pinus uncinata* Ram.) forests up to the treeline ecotone at c. 2,400 m a.s.l. Mountain pine is a long-lived (up to c. 1,000 years old), slow-growing, and shade-intolerant conifer that prevails in subalpine environments in the Spanish Pyrenees (Camarero & Gutiérrez, 2004; Galván, Camarero, & Gutiérrez, 2014). Since 2005 and in diverse field campaigns, disc and core samples from 581 living

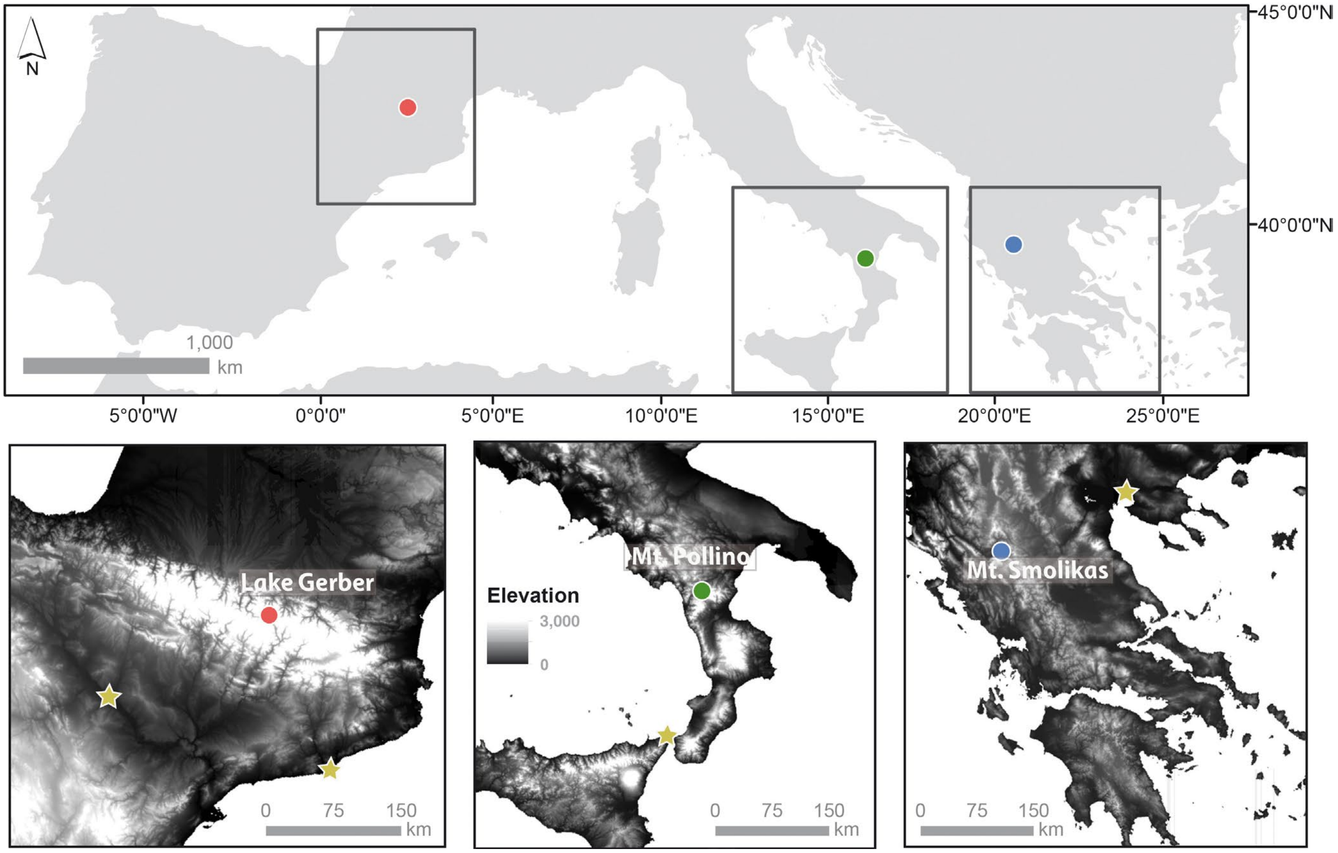

FIGURE 1 Location of the study populations within the Mediterranean basin. The yellow stars indicate the nearby cities utilized to assess human population trends in southern Europe: Gerber (Zaragoza and Barcelona, north-eastern Spain), Pollino (Messina, southern Italy), and Mt. Smolikas (Thessaloniki, northern Greece). The gray scales represent elevation, increasing from black to white [Colour figure can be viewed at wileyonlinelibrary.com]

and dead Mountain pine trees were collected (Büntgen et al., 2008, 2017, 2019; Esper et al., 2010, 2015; Sangüesa-Barreda et al., 2018). From this collection, 361 trees were sampled through wood discs, and 220 with increment cores. 37.9% of the sampled trees were living and 62.1% dead. Discs from well-preserved standing and fallen dead trees were sampled close to the tree base, whereas the wood cores were collected at 1.3 m height (Fritts, 1976). More details of the site and sampling strategy are given in Sangüesa-Barreda et al. (2018).

The Pollino massif is situated in southern Italy (39.94°N, 16.13°E) and it harbors open Bosnian pine (*Pinus heldreichii* H. Christ) forests between c. 1,675 and 2,267 m a.s.l. Bosnian pine is a subalpine shade-intolerant conifer with a scattered distribution in the Pollino massif and Balkans. In Pollino, Bosnian pines include the so-called *Italus*; with a life span of about 1,230 years currently the oldest known tree in Europe (Piovesan, Biondi, et al., 2018). The high-elevation individuals in the treeline ecotone are restricted to extensive rocky and remote areas (Piovesan, 2019). Between 2013 and 2016, wood cores from 177 large (with diameter at breast height, DBH > 50 cm) living trees were collected, 120 of them including the stem pith. Further details on this site can be found in Piovesan et al. (2019).

Mt. Smolikas (40.10°N, 20.93°E) is the highest peak in the Pindus range in northern Greece. The treeline ecotone is formed by old-living Bosnian pines (Esper et al., 2020), with ages up to 1,075 years such as the notable tree named *Adonis* (Konter, Krusic, Trouet, & Esper, 2017). Bosnian pines are located between 2,000 and 2,200 m a.s.l. in an open forest with shallow soils. Over four field campaigns since 2013, 388 trees were sampled (208 living and 180 dead trees). Disc samples from dead standing and fallen trees were taken as close as possible to the root collar. Further information on this site can be found in Esper et al. (2020).

2.2 | Tree-ring analysis and tree recruitment dynamics

All samples were air-dried and polished until tree-rings were unmistakably distinguishable. Tree-ring width (TRW) was measured at a resolution of 0.01 mm using LINTAB measuring systems and a Computer Controlled Tree Ring Measure Device (Aniol, 1987) controlled by the software CATRAS (Aniol, 1983). TRW data were visually (Stokes & Smiley, 1996) and statistically (Holmes, 1983) cross-dated. We established the germination year of each tree by resolving the calendar date of its pith. In those cases where the pith was missing on a sample, a pith offset was estimated by considering the width and curvature of the innermost rings. For the trees sampled using increment cores at 1.3 m height, we added 20 years to the stem age to estimate the tree age at the root collar according to Piovesan et al. (2019).

We assessed the long-term recruitment dynamics by reconstructing individual tree germination dates. The tree recruitment data were grouped into 30 year classes to mitigate potential uncertainties in the process of age estimation (Piovesan et al., 2019; Sangüesa-Barreda et al., 2018), but with enough temporal resolution for assessing multi-centurial recruitment trends. Finally, we rearranged the recruitment data considering diameter thresholds (small vs. large trees in each site) and the tree status (living vs. dead trees).

To enhance the comparability between the recruitment trends of each pine population, we standardized the frequency of recruitments grouped into 30 year classes using the mean and the standard deviation of the well-replicated AD 1000–1900 period. Values higher and lower than zero represent high and low recruitment rates, respectively.

2.3 | Human population trends

We gathered information on demographic trends in each of the regions of the three sites by considering the new high-resolution dataset of urban population (Reba, Reitsma, & Seto, 2016). We selected the closest cities that contained information of the period 1200–1800 CE. For Gerber, these are Zaragoza and Barcelona, located at distances of 190 and 168 km, respectively, from the sampling site. For Pollino, we used Messina (195 km), and for Mt. Smolikas, Thessaloniki (155 km). Although the distance between the cities and the studied sites is quite substantial, the longer term demographic trends detailed for these cities are likely to be representative at regional to inter-regional scales (Reba et al., 2016). In the case of Pollino, we additionally used an Italian database of historical population since 1300 CE (Malanima, 2005). This repository contains information of demographic trends in relation to city size. We obtained the rural population by subtracting the urban population from the total population in southern Italy.

2.4 | Land use and grazing trends at site scale

We used the KK09 Anthropogenic land use change index proposed by Kaplan et al. (2009). This dataset contains annually resolved high-resolution time series of anthropogenic deforestation for all Europe and the period from 1000 BC to AD 1850. The model integrates diverse information, such as climate and soils data and population density estimations. The land use index is standardized from 0 to 1 and includes both cultivation and grazing. We considered the low and high uncertainty scenarios in past population estimations. The data were downloaded from Kaplan and Krunhardt (2018) PANGAEA repository considering a 5′ × 5′ grid (c. 85 km^2). The study forests were located in the following grids: Gerber, 42.58–42.67°N, 0.92–1°E; Pollino, 39.92–40°N, 16.08–16.17°E; and Mt. Smolikas, 40.08–40.17°N, 20.92–21°E). The land use index was extracted every 50 years during the AD 1100–1700 period. Since the model considers all major European ranges (Alps, Pyrenees, and Carpathians) to be unusable due to climate limitations (Kaplan et al., 2009), the land use index in Gerber (Pyrenees) was substantially underestimated. For this reason, we excluded this site from this analysis.

Additionally, we obtained the historical pasture area from the HYDE 3.1 dataset (Goldewijk, Beusen, Van Drecht, & De Vos, 2011). This is a spatially explicit global reconstruction (12,000 years) of grazing intensity based on the combination of satellite information and specific allocation algorithms. The model considers, among other factors: population density trends, distance to water, natural herbaceous area, soil suitability, topography, and temperature. The database distinguishes between cropland and pasture activities, but we focused on the latter. The data were downloaded from the History Database of the Global Environment (https://themasites.pbl.nl/tridion/en/themasites/hyde/index.html) for the same 5′ × 5′ grids and period used before. Due to the methodological differences in both datasets and the uncertainties associated with past estimations, we focused on long-term trends rather than absolute values (Gaillard et al., 2010; Goldewijk & Verburg, 2013).

2.5 | Climate forcings: North Atlantic Oscillation (NAO), local temperature reconstructions, and climate–recruitment links

The tree recruitment trends were compared to several yearly NAO index and temperature reconstructions: (a) a winter NAO reconstruction based on tree-rings and speleothems (Trouet et al., 2009), (b) a NAO proxy based on stalagmite records (Baker, Hellstrom, Kelly, Mariethoz, & Trouet, 2015), (c) an ensemble of 48 annually resolved NAO proxy records combined through multivariate regressions (Ortega et al., 2015), (d) an evolving functional network analysis of different paleoclimate proxy records (Franke, Werner, & Donner, 2017), (e) a spring–summer temperature reconstruction based on tree-ring maximum latewood density data (MXD) from the Gerber site (Büntgen et al., 2017), and (f) a long-term summer temperature reconstruction derived from MXD data from the Mt. Smolikas site (Esper et al., 2020). The different NAO reconstructions were low-pass filtered using a 30 year moving average to allow their comparability.

In order to relate tree recruitment and local climate, we used the methodology proposed by Szeicz and MacDonald (1995). Because of the absence of climate reconstructions in Pollino, we restricted the analysis to Gerber and Mt. Smolikas. We fitted power functions to the frequency of recruitments grouped into 30 year classes as the best predictors of long-term recruitment trends (Sangüesa-Barreda et al., 2018). We focused on the AD 1300–1800 period when the peak of tree recruitment occurred. We selected the power function which provided the highest amount of explained variance. In Mt. Smolikas, we did not consider recent tree recruitment, as very young trees were not sampled, and so we used the same power function in both sites. Finally, the residuals of the fitted functions were related to reconstructed local temperature.

3 | RESULTS

We identified a period of high intensity tree recruitment in the late 15th and early 16th centuries, although this was most notable in Pollino and Mt. Smolikas (Figure 2). This period of high recruitment rates was detected from tree samples regardless of species (*P. uncinata* or *P. heldreichii*), diameter (small or large trees), and current life status (living or dead trees).

Regarding the regional human population fluctuations in the three regions (northeastern Spain, southern Italy, and northern Greece), we detected a drop in the population size in the 14th and 15th centuries, especially in southern Italy and northern Greece which reached a historical low around 1400–1450 CE (Figure 3). In southern Italy, the trend was similar whether considering the urban population (Messina city) or the rural population, although the drop

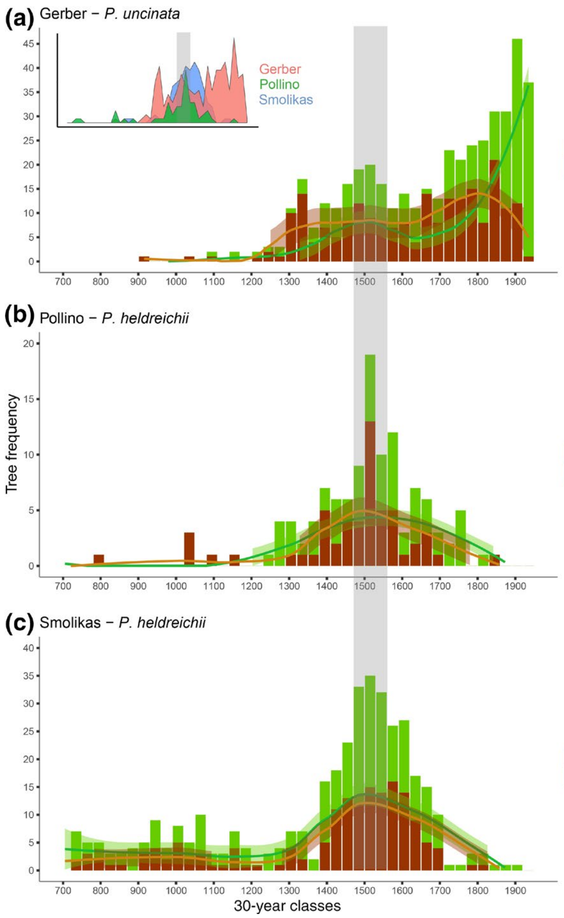

FIGURE 2 Tree recruitment dynamics in the three mountain populations: (a) Gerber (*Pinus uncinata*; north-eastern Spain), (b) Pollino (*Pinus heldreichii*; southern Italy), and (c) Mt. Smolikas (*P. heldreichii*; northern Greece) considering tree diameter at breast height (DBH; small vs. large trees). Note that different diameter thresholds were used depending on site characteristics, including 30, 90, and 60 cm in Gerber, Pollino, and Smolikas, respectively. The long-term trends of tree recruitment dynamics as a function of tree diameter are shown as splines. The top-left inset shows tree recruitment considering only large and living trees. The vertical gray bar highlights peak tree recruitment in the late 15th and early 16th centuries [Colour figure can be viewed at wileyonlinelibrary.com]

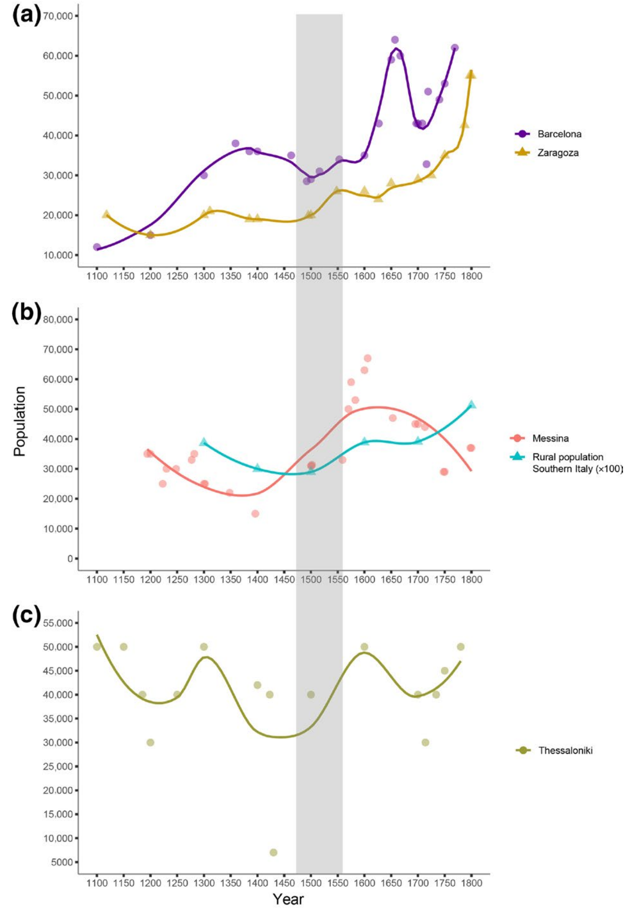

FIGURE 3 Human population trends in the cities closest to the tree sites in (a) Gerber (*Pinus uncinata*; north-eastern Spain), (b) Pollino (*Pinus heldreichii*; southern Italy), and (c) Mt. Smolikas (*P. heldreichii*; northern Greece). Human population data were derived from Reba et al. (2016) and Malanima (2005). The long-term trends are emphasized using splines. The vertical gray bar shows the peak in tree recruitment in the late 15th and early 16th centuries [Colour figure can be viewed at wileyonlinelibrary.com]

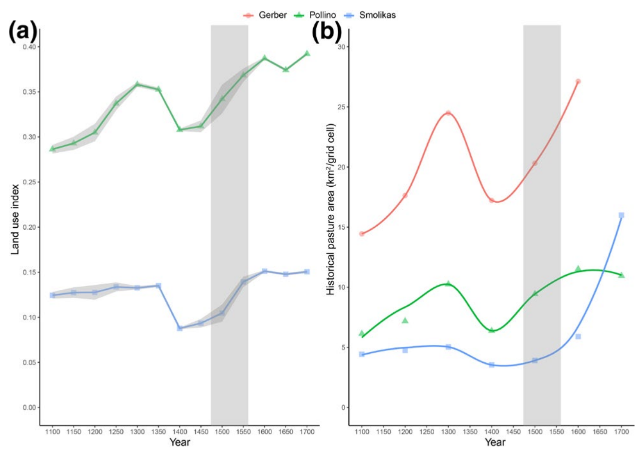

FIGURE 4 (a) Values of the land use index for the study pine populations according to Kaplan et al. (2009). The gray areas above and below the lines show the range of uncertainty in past population estimations. (b) Historical pasture area based on the HYDE 3.1 database (Goldewijk et al., 2011). The vertical gray boxes show the peak in tree recruitment in the late 15th and early 16th centuries [Colour figure can be viewed at wileyonlinelibrary.com]

in human population was more prolonged in rural areas. By contrast, human population in the Spanish cities closest to the Pyrenees did not experience such a decline. At site scale, we observed a common drop in the land use index and the grazing area in 1400 CE (Figure 4). The land use change hiatus occurred after 150–200 years (c. 1150–1350 CE) of increasing anthropogenic activity and lasted for 100–150 years (c. 1350–1500 CE). After the 1500s, the local land use began to increase while tree recruitment rates decreased.

A colder phase of the LIA, recorded in Gerber and Mt. Smolikas as severe drops in temperature, was also linked to drops in NAO in 1450 CE (Figure 5a). However, the peak in tree recruitment (late 15th and early 16th centuries) overlapped with relatively warm phases between cold intervals associated with the LIA in Gerber (Figure 5b,c). These warm conditions concurrent with positive NAO phases were more relevant after the 1500s. By contrast, in Mt. Smolikas, low temperatures prevailed during the peak in tree recruitment. Finally, the climate–recruitment relationships in the AD 1300–1800 period were positive but not significant in Gerber (Spearman correlation coefficient, r_s = .40; p = .10), and negative and significant in Mt. Smolikas (r_s = −.55; p < .05; Figure 5d).

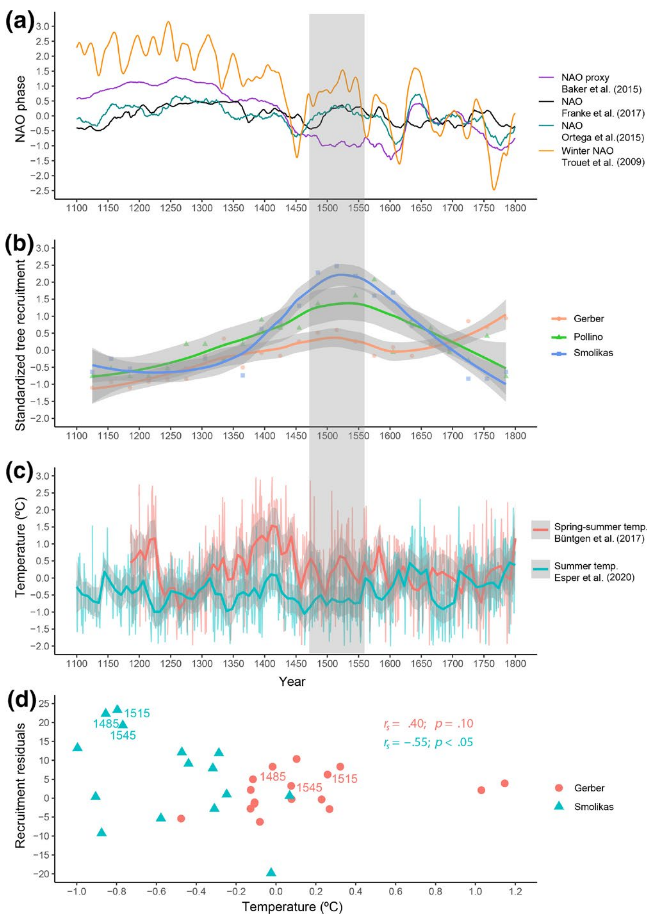

FIGURE 5 (a) Thirty year low-pass filtered North Atlantic Oscillation (NAO) reconstructions derived from different proxies (Baker et al., 2015; Franke et al., 2017; Ortega et al., 2015; Trouet et al., 2009). (b) Standardized tree recruitment patterns in each of the three study populations. (c) Tree-ring-based local temperature reconstructions in Gerber, Spain (red curves; Büntgen et al., 2017), and Mt. Smolikas, Greece (blue curves; Esper et al., 2020). The gray areas show the standard error. The vertical gray box in (a), (b), and (c) highlights peak tree recruitment in the late 15th and early 16th centuries. (d) Relationships (Spearman correlation coefficients, r_s) between the recruitment residuals after fitting a power function and local temperature reconstructions for the 1300–1800 period in Gerber and Smolikas. The 30 year classes in the peak of tree recruitment (1485, 1515, and 1545) are highlighted [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Through a long-term temporal perspective of tree recruitment at timescales beyond the Industrial Era and based on three well-preserved high-elevation forests in the Mediterranean Basin, we identified a widespread and persisting peak of tree establishment in the late 15th and early 16th centuries. This similitude in tree establishment in mountain forests located thousands of kilometers away points toward regional and coupled human–climate interactions as drivers of forest dynamics. However, region-specific differences are also evident and can be discussed in terms of different incidences of climate and human factors in Spain with respect to southern Italy and northern Greece. Consistent with our initial hypothesis, we found different pieces of evidence that illustrate interactions between historical human practices and climate changes that resulted in an apparent landscape rewilding in subalpine southern Europe c. 500 years ago.

The high tree recruitment intensity found in the 15th and 16th centuries, that followed a period of lower recruitment associated with widespread human activity, is evidenced by numerous paleoecological records in the Pyrenees. The alpine lake Marboré in the central Pyrenees (2,612 m a.s.l. and c. 70 km distant from Gerber) captured a reduction in the arboreal pollen during the Middle Ages and high amounts of pine pollen around 500 BP (Leunda et al., 2017). These results are in line with paleoecological studies in the eastern Pyrenees (Bassa Nera; 1,891 m a.s.l. and c. 40 km distant from the study site; Garcés-Pastor et al., 2017), and the nearest records just 24 km distant from Gerber that showed strong reductions in the arboreal pollen from approximately the 11th to 14th centuries alongside macrocharcoal remains indicating active fire regimes (Estanilles peat bog; 2,200 m a.s.l.; Pérez-Obiol, Bal, Pèlachs, Cunill, & Soriano, 2012). In a similar manner, the pine pollen concentration in the eastern pre-Pyrenees (Estanya lake; 670 m a.s.l. and c. 70 distant) reached minimum and maximum values in 1350 and 1430 CE, respectively (Morellón et al., 2011). In central Italy, our findings agree with paleoecological evidences in the Lungo lake (371 m a.s.l. and 400 km distant from the study site; Mensing et al., 2016; Piovesan, Mercuri, et al., 2018) which captured steep drops in the arboreal pollen in the Medieval times and high tree pollen amounts starting from the 15th century. Indeed, the forest taxa pollen showed a significant inverse relationship with the Italian population trends (Piovesan, Mercuri, et al., 2018). In southern Greece, high-resolution sedimentary records from Lake Stymphalia showed large-scale erosion into the lake during the Middle Ages, suggesting an intensive use of the landscape (Seguin et al., 2019).

Before 1400 CE, despite the favorable climate context during the MWP through positive and lasting NAO phases (Figure 5a), the three sites showed low establishment values corresponding to low recruitment rates, high mortality rates, or both (Figure 2). According to the significant correlations between tree recruitment and temperature shown in the Pyrenees (Sangüesa-Barreda et al., 2018) but also in other cold, high-elevation sites (e.g., Du et al., 2018; Kharuk, Im, Dvinskaya, & Ranson, 2010; Liang et al., 2016), warm and stable conditions should have resulted in high tree recruitment rates. In fact, in the Pyrenees, the association between tree establishment and temperature was more intense after the 1500s (Sangüesa-Barreda et al., 2018). During Medieval times, a high human pressure on subalpine ecosystems through grazing and surface fires could have reduced forest expansion. Wood decomposition rates and the species lifespan have limited available tree records from this time, but we identified a period of 150–200 years in the 13th and 14th centuries of increasing human land use intensity (Figure 4), and thus a decisive influence of human practices on mountain forest dynamics.

Regional human population fluctuations and land use changes at a local scale showed analogous trends (Figures 3 and 4), while those trends and the reported tree recruitment data were decoupled between the 14th and 16th centuries, suggesting a cause–effect relationship with a lag time coherent with reproductive biology of mountain pines (Figures 2 and 4). In agreement with these ideas, the greater decline in human population in northern Greece was translated into the highest tree establishment rates. In Greece, the 14th and early 15th centuries were characterized by large-scale depopulation in rural areas associated with major plague outbreaks, wars, and the invasion of the Ottoman Turks (Bintliff, 2012; Seguin et al., 2019). In Italy, population was especially affected by recurring devastating plagues, most notably the Black Death in the mid-1300s (Porter, 2009; Schoolman et al., 2018). The Pyrenean case could be different since the death toll from the Black Death pandemic in the 14th century was lower than in the rest of Europe (Álvarez-Nogal & Prados de la Escosura, 2013), as reflected in the lower loss of urban population and a more moderate increase of tree establishment at this time (Figures 2 and 3). Some palynological records from the northern slope of the Pyrenees suggest that the consequences of the late-medieval crisis were spatially heterogeneous (Galop et al., 2013). Despite the reported epidemics and social problems in some valleys, metallurgical activities could have maintained a strong pressure on local forests (Galop et al., 2013). However, our results indicate that this was not the case in remote, high-elevation forests, since we detected a major change in grazing intensity on Gerber (Figure 4). Nonetheless, the different methodologies and uncertainties in the estimations of past land use and grazing intensity suggest that the absolute values should be considered with caution, and that the long-term trends are a better indicator than inter-population comparisons (Gaillard et al., 2010; Goldewijk & Verburg, 2013).

We detected a lag of c. 50 years between the historical human population low and the peak of tree recruitment (Figures 2 and 3). After centuries of widespread impacts by grazing practices, high-elevation forests probably needed decades to restore stands with mature, reproductive trees in the landscape and the formation of disturbed soils capable of harboring pine seedlings. Furthermore, widespread tree recruitment requires warm and stable climatic conditions over many years to produce enough viable seeds to promote tree recruitment (Esper & Schweingruber, 2004; Zasada et al., 1992), and depending on the scale of the deforestation, the majority of seeds would need to move long distances from their source. This theory is confirmed by the gradual increase in tree recruitment until it reached maximum rates in the late 15th and early 16th centuries. In agreement with this idea, the current rewilding of the subalpine environments following the cessation of traditional land use in the second half of the 20th century is also showing a gradual conversion of subalpine grasslands to forests by increasing seedling recruitment (Vitali et al., 2017, 2019), analogous with the situation observed in the 15th century.

The LIA was associated with negative NAO phases and cold temperatures, with a significant cold phase c. in 1450 CE (Figure 3). The influence of the NAO in the Mediterranean Basin is not uniform, with a decreasing incidence eastward (Hurrell & Van Loon, 1997). Negative NAO phases are associated with abundant winter–spring precipitations (Hurrell, Kushnir, Ottersen, & Visbeck, 2003), which may have more relevance in the Pyrenees than in Greece. We speculate that the beginning of the LIA could have been a further contributing factor to the cessation of grazing activities in high-elevation forests, since the snowpack accumulation and the late snow melting associated with cold and lasting winters and springs could accelerate the abandonment of grazing. This may be particularly important in the Pyrenees, where winter snow precipitations should be higher during negative NAO phases and the drop in temperature stronger than in the East (Figure 5). While the demographic crisis was less severe in this region, the climatic component could have been decisive in reducing the grazing pressure of mountain pastures, which is in line with what Galop et al. (2013) suggested. The peak in tree recruitment was associated with relatively warm decades during positive NAO phases between cold intervals due to the LIA (Figure 5b,c). The warm temperature oscillation in the AD 1450–1550 period was especially marked in Gerber, suggesting a prominent role in this site. However, neither in Mt. Smolikas nor in Pollino, we found an increase in temperature important enough to uniquely explain the high recruitment intensity.

We detected not only similarities but also differences between other simultaneous processes of subalpine forest expansion and encroachment. In the Alps, pollen records reflected a reduction of the agro-pastoral activities during the 14th and 15th centuries as a result of military conflicts, recurrent famines and epidemics, and probably the first signs of the LIA (Walsh et al., 2014). However, at least in the Alps and in central France, the recuperation after the late-medieval crisis was faster, and in the 16th century, the transhumance economy was completely restored and grazing impact was as severe as in other periods in history (Servera Vives et al., 2014; Walsh et al., 2014). In contrast, in southern Europe, the impact of the late-medieval crisis was probably deeper and more lasting since we did not observe a total recovery of the previous land use rates until c. 1600 CE. Indeed, our data suggest that the late-medieval crisis was slightly longer than the period reconstructed by land use models, since the high rates of tree recruitment lasted up to c. 1530 CE, while models showed an increase of the land use after the second half of the 15th century. This idea is in line with the fact that the drop of human population in rural areas was more prolonged than the reported in urban population.

In conclusion, the historical peak in tree recruitment observed in the three mountain forests of southern Europe Peninsulas did not match a global temperature maximum. We provide evidence that suggests the major role of complex climate–human interactions on mountain forest dynamics before the 1500s CE, especially in the central-western Mediterranean Basin. We identify a late Medieval–Renaissance period of climatic and anthropogenic changes that could be decisive in driving past forest dynamics. This period should be more intensely studied in the future since it could be a historical analog to recent rewilding. The time interval since then and the longevity of the studied pine species may have allowed the current abundance of old individuals and remnants of old-growth forests in these remote, high-elevation sites (Wirth et al., 2009). In addition to other science disciplines such as paleoecology or archaeology, dendroecological reconstructions could improve our understanding of the historical landscape transformation of subalpine forest ecosystems at secular timescales.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

ORCID

Gabriel Sangüesa-Barreda https://orcid.org/0000-0002-7722-2424
Jan Esper https://orcid.org/0000-0003-3919-014X
Ulf Büntgen https://orcid.org/0000-0002-3821-0818
J. Julio Camarero https://orcid.org/0000-0003-2436-2922
Alfredo Di Filippo https://orcid.org/0000-0001-5863-8339
Michele Baliva https://orcid.org/0000-0001-9707-8688
Gianluca Piovesan https://orcid.org/0000-0002-3214-0839

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