

Tree growth patterns associated with extreme longevity: implications for the ecology and conservation of primeval trees in Mediterranean mountains

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Authors' contributions

GP, GDV, AS, ADF, conceived the research idea and designed the methods; ADF, AD, MB, GP, EPS, AS, VM collected the data; MB, AD, GP, ADF, FB developed tree-ring series and performed dendrochronological analyses; GP and FB were primarily responsible for the manuscript text; all authors contributed critically to the drafts and gave final approval for publication.

Abstract

We dendrochronologically analyzed 177 Heldreich’s pines growing on the Pollino Massif, in southern Italy, for understanding climatic and human impacts on old trees. Most of the large-diameter trees currently living became established in the late Medieval to Renaissance periods under a snowy wet climate and low anthropic influence. Millennium-old (i.e., > 900 years of age) trees in remote sites escaped Medieval human impacts, then a wave of pine stands established in the late 14th and 16th centuries following recurrent human plague epidemics. Stem growth histories showed that both millennium-old and the majority of century-old trees grew along similar trajectories. These old trees have survived long-lasting climatic reversals, clearly a sign of their resilience to extreme events. Cliff habitats played a strategic environmental role for tree conservation during periods of land exploitation; such biodiversity refugia may serve as stepping stones for rewilding mountain landscapes. In recent decades, land abandonment following the collapse of sheep-herding, together with climate warming, have led to a new pulse of tree recruitment. Since 1850, low-frequency variability (50-70-year periods) in tree growth has been in synchrony with the Atlantic Multidecadal Oscillation. Recently observed growth increases counter widespread reports of tree and forest decline in Mediterranean environments, and suggest that extreme longevity does not necessarily reduce stem increment. Discovering, studying, and preserving primeval trees in forest landscapes remains a priority for biodiversity conservation in the Anthropocene. Heldreich’s pine resilience to current global changes bodes well for sustainable development in the Mediterranean mountains they inhabit, and similar studies are needed for threatened habitats and iconic trees of other ecoregions in order to assess their probable survival into the future.

25 **Key words:** old trees; cliff habitat; tree growth pattern; North Atlantic Oscillation; Atlantic

26 Multidecadal Oscillation; rewilding

27

28 **Highlights:**

29 - Old *Pinus heldreichii* trees of southern Italy have survived at high elevations in cliff habitats.

30 - Most large trees established during human demographic crises of the late Medieval period.

31 - Lifetime diameter growth curves revealed that old trees have followed similar growth trajectories
32 over time.

33 - Enhanced growth in modern times indicates that trees are coping well despite recent warming.

34 - Ecological dynamics of this iconic pine species reflect changes in both climate and human
35 society, making it a witness of the Anthropocene.

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38 INTRODUCTION

39

40 Placing accurate boundaries on maximum and average tree age, and on how these boundaries vary
41 with environmental conditions, helps understand demographic and growth processes that lead to
42 diverse forest structures (Stephenson et al., 2014; Di Filippo et al., 2017). Within human-modified
43 forest ecosystems, knowledge of tree longevity and growth processes is an essential premise for
44 locating the least impacted areas, which in turn yield the oldest trees, and therefore ultimately
45 become top candidates for conservation (Keddy and Drummond, 1996). Large old trees are a
46 keystone ecological component (Lindenmayer et al., 2014), and are also habitat to a number of
47 species, thereby contributing to forest biodiversity (Lindenmayer, 2016). Tree-dwelling lichens,
48 for instance, occur in close connection with stem age, which in turn is an indicator of habitat
49 persistence within a landscape, a necessary condition for the survival of niche-specific and/or
50 dispersal-limited species (Ranius et al., 2008; Fritz et al., 2009; Zemanová et al., 2017). Overall,
51 understanding the time span required for recruiting and retaining the oldest trees allows the
52 development of sound management practices for old-growth stands (Lindenmayer and Laurance,
53 2017).

54 The study of tree longevity and growth rates, especially when dendrochronologically
55 evaluated, is a well-established discipline (Molisch, 1938; Schulman, 1954). Locating, sampling,
56 and dating the oldest individuals of tree species that form annual xylem increments has allowed
57 dendrochronologists to date archaeological structures (Douglass, 1929), reconstruct changes in
58 climate (Fritts, 1976) and forest dynamics (Veblen et al., 2003), and provide reliable standards for
59 the calibration of the radiocarbon time scale (Bowman, 1990). In recent years, information on tree
60 longevity has been further acquired through dendroecological investigations of old-growth forests

(Di Filippo et al., 2012), strip-bark formation (Bunn et al., 2003), and extremely large individuals (Drobyshev and Niklasson, 2010; Patrut et al., 2007).

Lively debate has focused on the current and future health of large old trees, given the risk factors that may threaten their survival (Lindenmayer and Laurance, 2017). Because of current and expected widespread mortality episodes caused by climatic stress (Allen et al., 2015; Meddens et al., 2015), together with observed differences in growth patterns of individual life histories (Stephenson et al., 2014), it is crucial to improve our knowledge of functional ecology processes in different forest settings and with contrasting growth features (e.g. large old trees growing in open forest vs. those in closed forest; growth decline vs. increase; browning vs greening). Understanding how growth rates vary with tree age and dimension is also necessary for modelling forest functioning under a changing environment (Michaletz et al., 2014). Stem age and size are weakly correlated in natural old-growth late-successional forests (Piovesan et al., 2005), and the two components should be considered separately when assessing long-term tree and stand development. Old trees are also likely to yield new insights in the connections between ecophysiology and genomics (e.g. genetic and epigenetic regulation), particularly those related to senescence and ageing (Lanner and Connor, 2001; Flanary and Kletetschka, 2005; Thomas, 2013).

Slow, continuous stem growth is usually a premise for tree longevity (Bigler and Veblen, 2009; Johnson and Abrams, 2009; Piovesan et al., in review). Smaller tree-ring size and higher wood density may improve vascular plasticity to withstand climate stress and enhance resilience to recurrent canopy disturbance events throughout exceptionally long lifetimes (Di Filippo et al., 2012). Some species, such as European beech (*Fagus sylvatica* L.), seem negligibly affected by the progressive deterioration of physiological functions associated with age (Mencuccini et al., 2005; Peñuelas and Munné- Bosch, 2010; Mencuccini, 2014), confirming the existence of “negative senescence” phenomena (Munné-Bosch, 2015). Slow growth in old trees may thus

85 largely be dependent on long-term environmental constraints and physical damage rather than
86 ageing (Mencuccini et al., 2005; Mencuccini, 2014). In closed-canopy forests, shade-tolerant trees
87 may spend centuries in the understory, where competition for light reduces stem growth, while
88 gap dynamics introduce alternating periods of growth suppression and release (Piovesan and
89 Lüttge, 2018). In open-canopy forests, shade-intolerant trees are often more limited in their growth
90 by environmental factors than by competition, and the oldest individuals are found in areas of low
91 fertility and/or reduced growing seasons (Larson et al., 2000a).

92 In Europe and the Mediterranean Basin, one of the tree species with the longest-living
93 individuals is Heldreich's pine (*Pinus heldreichii* H. Christ, also called *Pinus leucodermis*
94 Antoine), whose populations in the highlands of Greece and south Italy have recently been found
95 to include two dendrochronologically dated trees older than a thousand years (Köster et al, 2017;
96 Piovesan et al., 2018a). Since numerous old trees were previously found in the Pollino massif of
97 southern Italy (Serre-Bachet, 1985; Biondi, 1992), it was necessary to determine if this
98 Mediterranean mountain was being affected by increased mortality among the oldest trees,
99 possibly as a sign and a consequence of forest decline (e.g. Dorado-Liñán et al., 2017) during the
100 Anthropocene. It should be noted that our definition of the Anthropocene is not linked to an
101 absolute date, rather it is based on identifying the human capacity for ecosystem engineering
102 (Niche Construction Theory) to search for the past large-scale impacts of human societies on
103 natural species and ecosystems in connection with changing environmental and cultural contexts
104 (Smith and Zeder, 2013; Ruddiman, 2018).

105 In this study, we used data from a comprehensive new field collection to uncover the
106 establishment date and growth dynamics of primeval Heldreich's pines. Our main objective was
107 to determine growth trajectories in Heldreich's pine of various ages and dimensions, with the
108 overarching motivation of evaluating the health of extremely old trees in the age of global

environmental change. After locating some Heldreich's pines of great longevity, we investigated how old trees in this high-elevation Mediterranean environment survived land use changes and long-lasting climatic episodes such as the Medieval warm period, the Little Ice Age, and lately global change. Considering the temporal, environmental and cultural contexts that influenced the stem growth histories of this old pine population expands our knowledge on ecological history and lays a foundation for nature conservation policy in mountain landscapes (Gillson and Marchant 2015).

MATERIALS AND METHODS

Study area

Heldreich's pine forests are protected habitat in southern Europe under the Natura 2000 Directive (95A0 High Oro-Mediterranean pine forests). This open forest habitat is restricted to mountains of the southern Balkans, northern Greece, and southern Italy, where it characterizes the timberline environment with limited undergrowth formed by sparse grasslands on often stony or rocky soils (Fig. 1). Sampled trees were selected during a three-year research campaign aimed at clarifying the biology and ecology of Heldreich's pine stands distributed throughout the Pollino massif (Fig. 2). Several rugged peaks (Pollino, Pollinello, Serra Dolcedorme, Serra delle Ciavole and Serra di Crispo) occur at elevations between 1675 and 2267 m a.s.l., aligned in an amphitheater formation covering about 12 km² of high mountain landscapes (Todaro et al., 2007). Our field collections uncovered the oldest tree in Europe (Piovesan et al., 2018a), which we named *Italus* and was shown to be 1230-years old by a combination of tree-ring and radiocarbon dating applied to stem and root cores (Piovesan et. al., 2018b).

133 *Tree-ring analysis*

134 Large individuals were preferred, so that wood increment cores were collected from stems with
135 diameter at breast height (DBH) greater than 50 cm (average of 92 cm and maximum of 180 cm).
136 A total of 240 cores (177 trees) were collected (120 cores included the stem pith), mostly at breast
137 height, during 2013-2016 at elevations ranging from 1837 to 2143 m a.s.l. All increment cores
138 were mounted, sanded, and surfaced with metal scalpels, then ring widths were measured to the
139 nearest 0.01 mm using a CCTRMD (Computer Controlled Tree Ring Measure Device, Aniol,
140 1987) interfaced with the software CATRAS (Aniol, 1983). After visual (Stokes and Smiley,
141 1996) and statistical (Wigley et al., 1987) crossdating, tree-ring series revealed that mean stem age
142 was 492 ± 171 years, with a few individuals exceeding 900 years. To reconstruct growth patterns
143 while minimizing age- and size-related trends, ring-width series were standardized by fitting a
144 cubic smoothing spline with a 50% frequency response for 100-yr periods (Cook and Peters,
145 1981). New *Pinus heldreichii* chronologies were compared to existing ones using Student's *t*-
146 values and Gleichläufigkeit (GLK), a measure of the percentage of common signs of year-to-year
147 growth change between two series (Buras and Wilmking, 2015).

148 Tree establishment date was calculated considering only the cores with the pith and adding
149 to the stem age 18 years to account for the average estimated time needed to reach ~1.3 m in
150 height (mean height growth rate is 7.1 cm yr^{-1} according to Vitali et al. 2019). We grouped tree
151 recruitment data into 30-year bins following the approach of Sangüesa-Barreda et al. 2018 to
152 account for uncertainty in age estimations.

153 Growth trajectories were computed either for individual trees or by age classes (<400
154 years, 400-600 years, 600-900 years, and > 900 years) to focus on old trees while allowing enough
155 samples ($n \geq 5$) in each interval. We used ring areas to quantify basal area increment, a proxy for
156 annual biomass production (BAI; Di Filippo et al., 2012). BAI chronologies obtained by averaging

individual series, and the Atlantic Multidecadal Oscillation (AMO) time series at annual resolution (Enfield et al., 2001; <https://www.esrl.noaa.gov/psd/data/timeseries/AMO/>), were smoothed using the Gaussian function of the Past software (Hammer et al., 2001). Wavelet transform was used for inspection of BAI chronologies at different scales using the Morlet function, and the significance level (p-value <0.05) was plotted as a contour (chi-squared test according to Torrence and Compo, 1998) using a red-noise model with the estimated first order moving average autocorrelation coefficient.

Growth-climate relationships were quantified using bootstrapped correlation functions (Zang and Biondi, 2015) and the prewhitened BAI chronology obtained using all cores, including those without the pith. Monthly time series of mean air temperature and total precipitation were obtained, respectively, from Brunetti et al. (2009a) and Brunetti et al. (2009b).

Spatial analysis

The location of every tree was recorded with a hand-held GPS unit during field work. Stem coordinates were then mapped using QGIS (2015) on a grid of 20-m² cells derived from the Italian national 20-m resolution DEM. The oldest tree in each cell was plotted at the cell centroid coordinates, and the Clark-Evans aggregation index (Clark and Evans, 1954) was then calculated using the R package “spatstat” (Baddeley and Turner, 2005) to evaluate spatial distribution patterns (e.g. clustered or random tree distribution). The aggregation index was calculated 1) for all trees; 2) for trees older than 600 years; 3) for trees younger than 600 years. The geographical area in each analysis was the same rectangular box to avoid any spurious results caused by changes in the area under study.

RESULTS

Tree establishment, climate, and anthropogenic impacts

The age distribution of sampled trees was bell-shaped (Shapiro-Wilk test = 0.93, p-value < .0001), even though the oldest trees (dbh $\geq$ 90 cm) introduced an asymmetry (Fig. 3a). The majority of surviving trees with dbh > 50 cm became established between 1400 and 1650 CE, with a peak around 1500 CE, during a persistently negative phase of the North Atlantic Oscillation (Fig. 4a Baker et al., 2015). In the same historical period, human populations were decimated by repeated plague epidemics (Porter, 2009) over most of Europe, potentially allowing a rewilding of mountain landscapes that favored the establishment of Heldreich's pine (Fig. 4b).

In open stands located above 1850 m a.s.l., trunk diameter was directly correlated with age (Fig. 3b), but this relation lost significance when considering trees with dbh > 90 cm. Subdividing the samples based on a 90-cm stem DBH threshold highlighted the more complex age distribution of the largest trees (Fig. 3a), which included the oldest individuals.

Sampled trees were spatially clustered (Clark-Evans test: $R = 0.27$, p-value < 0.001). These forest stands are located near treeline up to 2200 m elevation, above which the dominant plant species are shrubs or grasses (Fig. 5). Trees whose age was less than 600 years were less spatially clustered (Clark-Evans test: $R = 0.32$, p-value < 0.001) than older trees (Clark-Evans test: $R = 0.19$, p-value < 0.001), which were typically found in few cliff sites. Millennium-old trees, i.e. individuals older than 900 years, were not randomly distributed over the landscape, as they concentrated in the most remote and topographically complex areas. Most of the oldest trees were located on west-facing summit cliffs between 2000 and 2100 m elevation. The oldest pine, named *Italus* (Piovesan et al., 2018a), however, was located at lower elevation (1850 m) and on a very

steep south-west facing, ragged and sparsely vegetated slope. Elevation and slope were not correlated with tree age (Fig. S1).

Growth variability in time

Radial increment of individual trees usually declined during the first decades of their life, followed by fluctuations around a generally decreasing overall trend, as it is typical of shade-intolerant conifer species (Fig. 6a; Fritts, 2012; Biondi and Qeadan, 2008). The analysis of life-history radial increment by age class showed overlapping growth performance, with millennium-old trees replicating patterns identified in trees about half that age. The lowest increments during the tree lifetime were observed in the 600-899 year age class. The growth trajectories of *Italus* and the other 4 nearly millenium-old pines enveloped most growth trajectories of multi-century old trees of smaller dimension (DBH < 90 cm; see Fig. 6b). The ecological habitats of millenium-old trees lie between lower elevation, fertile sites (e.g. near the upper margin of the beech forest or secondary grasslands, at 1850-1900 m a.s.l), and high elevation, unproductive cliff sites where we found the slowest growing millennium-old tree (lowest green line in Fig. 6b). In general, trees with DBH > 90 cm but lower age were normally found in areas characterized by faster growth rates, i.e. greater fertility (Fig. 7). When all sampled trees were considered, an inverse correlation existed between stem age and average annual growth (Fig. 8a-b).

The *Italus* tree-ring chronology is well synchronized with other long term *Pinus heldreichii* chronologies (Table S1a). The highest correlations (Table S1) were found with the chronology developed by Biondi (1992) from a few Pollino sites, closely followed by correlations with the chronology developed for Serra delle Ciavole by Serre-Bachet (1985) as well as by correlations with the new millennium-long chronology developed from the samples recently collected throughout the Pollino massif (Fig. S2, Table S1; see Fig. S3 for sample replication). Relatively

high correlations were also found with the *Pinus heldreichii* chronology from Albania (Seim et al., 2012), clearly suggesting that the Pollino and Albania mountains experience similar climatic variability. Lower, but still 99.9% significant, correlations were observed between *Italus* and the oldest trees (age > 900 years), of which three were discovered during the recent sampling campaign (Fig. S2b, Table S1b).

The standardized ring-index series of millennium-old pines and the master tree-ring chronology for the Pollino massif show an increasing growth trend in recent years (Fig. S2). Basal area increment chronologies (see Table S2), a proxy for tree biomass increment, confirmed the growth increase in recent decades for all age classes (Fig. 9). Multidecadal growth variations were coherent between different age classes (Fig. 9) with the 600-899 age class showing the lowest growth rates. In the last two centuries, trees in the youngest age class have been more productive and responsive to environmental variations, while the oldest trees have shown the steepest declining trend, which has then reversed in the last decades. This recent, common growth spur is unusual compared to previous centuries, especially for the youngest trees (Fig. 9).

Using a moving-window multiple regression model based on single-tree data, we found that BAI was directly related to stem size (DBH) and inversely related to stem age (Fig. 10). The model-explained variance changed in time, with a decreasing trend in modern times that has reversed in the last few years.

Variability of BAI since the late 1800s was dominated by multidecadal variability with extreme oscillations corresponding to the highest and lowest increments (Fig. 9). Wavelet analysis revealed increasing power in the 50-70 year periods during recent decades (Fig. 11a). The growth behavior of all age classes during the last 150 years was in phase with the Atlantic Multidecadal Oscillation (AMO; Fig. 11c and Fig. S4). The autocorrelation function of both AMO and BAI time series followed similar patterns too (Fig. 11b). Finally, the AMO was correlated with time-

related changes in variance explained by the multiple regression model for BAI mentioned above (Fig. 11d). Potential climatic linkages with the AMO are related to its effect on subalpine Mediterranean environments (O'Reilly et al., 2017), since bootstrapped correlation functions highlighted a positive relationship between air temperature and stem growth during the current year and a negative relationship with previous July precipitation (Fig. S5).

DISCUSSION

Old tree ecology

Millennium-old Heldreich's pines, located on rocky slopes in remote mountains, have been able to survive because of a combination of factors. In particular, they have been traditionally protected from logging and they have avoided wildfires because of the relative lack of fuels on the ground. The species is able to survive the lightning strikes and glaze storms that occur at these high elevations, while growing very slowly for most of its lifetime. The extreme longevity of Heldreich's pines in the Pollino area has a counterpart in the similarly maximum ages of European beech (*Fagus sylvatica* L.) in the same area. Our samples indicate the presence of beech trees with ages of about five-six centuries, hence approaching and likely exceeding the maximum life span for deciduous hardwoods (Di Filippo et al., 2015; Piovesan et al. in review). On these Mediterranean mountains, maximum age of pines is about twice that of beech, in general agreement with the global pattern of finding conifers older than hardwoods within the same environment (Oldlist, <http://www.rmtrr.org/oldlist.htm>). These extreme-longevity trees, located in old-growth stands that survived loggings in the late 1800s and early 1900s (Piovesan et al. in review), are bioindicators of wild landscapes that deserve to be preserved for future generations (Lindenmayer 2016; Lindenmayer and Laurance 2017; Lutz et al. 2018).

Overall, tree-ring series of old Heldreich's pines are characterized by relatively large tree-ring widths in the first cambial years, followed by a drop towards a very long sequence of extremely small rings, a typical growth pattern of isolated trees (Fritts, 1976; Biondi and Qeadan, 2008). Given the stringent limits to wood growth imposed by site conditions, sensitivity to climate is high (see also bootstrapped correlation functions in Fig. S5), thereby facilitating tree-ring dating even for the oldest samples. The growth trajectory of most Heldreich's pines younger than 600 years resembles that of millennium-old individuals, but trees of intermediate ages (600-900 years) experienced on average lower annual increments. Since the *Italus* growth trajectory is replicated by those of other millennium-old trees in the same area, we expect a relevant pool of actually smaller (DBH < 90 cm) - and younger - Heldreich's pines in the Pollino massif to continue growing, provided they can survive potential future threats caused by Anthropocene changes.

Tree longevity is commonly assumed to be inversely proportional with growth vigor (Fig. 1 in Black et al., 2008; Fig. 5.5 of Briffa and Melvin, 2011; Fig. 3 in Seim et al., 2012; Di Filippo et al., 2017; Piovesan et al. in press). When examining the growth trajectories of Heldreich's pine in the Pollino area, most of the millennium-old individuals occupy the middle-lower portion of the graph, suggesting both that extreme tree longevity requires slow growth and that extremely harsh conditions are detrimental to long life. Our dataset also showed that millennium-old Heldreich's pines in the Pollino area have maintained similar growth patterns regardless of appreciable differences in tree age. In temperate closed old-growth forests, tree diameter has generally no connection with age because of the very complex growth histories of older trees, characterized by slow growth and by suppression and release periods (Di Filippo et al., 2017). Instead, in the open pine stands we sampled, located above the high-mountain beech belt, larger individuals were likely to be very old especially when located on rocky slopes. It remains to be determined if this

299 finding is linked to peculiar ecological conditions and/or human management, which may possibly
300 have altered demographic processes.

301

302 *Historical ecology*

303 Anthropogenic influence on these mountain environments cannot be discounted, although it is
304 difficult to quantify the impact of past logging, fire use, and domestic grazing at the highest
305 elevations (above 1850 m). In the lower stem of most large trees it was possible to notice scars not
306 reaching the ground that were most likely caused by shepherds many years ago to collect wood
307 (“alberi castorati”) for various uses, ranging from illumination to incense replacement (Biondi and
308 Visani, 1993). However, as in the case of natural disturbance, the sampled trees were able to cope
309 with this anthropogenic impact, probably because of the abundant resin that sealed the wound
310 protecting the exposed xylem from pests and infections.

311 One can hypothesize multiple land use changes in the study area, starting for instance with
312 the transition from hunter-gatherers to farmers and shepherds that took place in this region around
313 the 11th Century BCE, when the local Enotri people were ruled by King *Italus*. Medieval
314 settlements expanded in central Italy in association with fortified castles starting in the middle of
315 the IX century, leading to both human population growth and to local deforestation pressure
316 (Schoolman et al., 2018). Deforestation should have then continued for about four centuries, as
317 suggested by the onset of erosive processes and by the decline of tree pollen in terrestrial and
318 marine sediment records from south-central Italy (Piovesan et al., 2018c). Anthropic utilization to
319 support the flourishing medieval societies could explain why only a few millennium-old
320 individuals could still be found in today’s landscapes.

321 Then between 1300 and 1600 CE the European population was decimated by recurrent
322 plagues, whose death toll was particularly high in Italy in the mid-1300s (Porter, 2009; Fig. 4b).

323 Medieval agrarian transformation of forested landscapes came to an end, and was slowly replaced
324 by regeneration through a rewilding of the forest landscape (“natural silviculture reaction”,
325 Piovesan et al., 2018c). Establishment of old-growth survivors in the Pollino area centers in the
326 1500s (Fig. 4), which is the time of a forest pollen peak in central Italy (Mensing et al., 2016).
327 This period was also characterized by negative anomalies of the North Atlantic oscillation (Baker
328 et al., 2015). The NAO is considered to favor greater winter precipitation in this region (López-
329 Moreno et al., 2011), thereby leading to greater and more persistent snowpacks (Diodato et al.
330 2018). In this mountain area, the accumulation and persistence of snow, possibly until June, would
331 have prevented livestock grazing in high mountain environments for most of the year. Land
332 abandonment following a crash in human population could have favored tree densification,
333 thereby providing an example of the complex interactions between human land use changes,
334 climate, and vegetation dynamics.

335 The human demographic crisis that started in the 14th century (Fig. 4b) should have
336 contributed to the 15th-century decision by the King of Naples to assign the Pollino Massif and
337 adjacent lands extending towards the sea to the Albanian refugees that were fleeing from Turkish
338 invaders. Several villages were then either established (see dots in Fig. 2) or repopulated (Fig. 1 in
339 Bracco et al., 2015) starting at the end of the 15th century. This recolonization of the hillsides and
340 mountain slopes took place in ways that led the Albanian settlers to maintain their cultural and
341 religious identities until modern times. Demographic expansion and increased presence of grazing
342 domestic animals, with their associated annual migrations to fresh pastures (“transumanza”), led to
343 greater human impacts on mountain landscapes during the second half of the 16th century (Russo
344 and Salvemini 2007, Russo, 2016). The number of families in the area was recorded at that time
345 using the number of fireplaces (Fusco, 2009; Anselmi, 2011), and those records are inversely
346 correlated with the establishment dates of Heldreich’s pines. During this period, North Atlantic

347 Oscillation (NAO) and Snow severity Index (SSI) are not concordant with tree establishment,
348 suggesting the return to a leading role of the human factor in landscape dynamics (Fig. 4).

349 Other declines in human population, such as during the 1656-1658 plague, did not
350 correspond to a rewilding comparable to what took place during the late Medieval-Renaissance
351 establishment of the current Heldreich's pine metapopulation. Because the high recruitment phase
352 (from about 1300 up to about 1550 CE) coincides with similar pulses in pine demography at high
353 elevation in the Spanish central Pyrenees (Sangüesa-Barreda et al., 2018), it is possible that cold
354 spells during the Little Ice Age interacted with human factors in determining the past dynamics of
355 tree establishment in Mediterranean mountains. Lagged effects of extreme climatic events on tree
356 growth, reproduction, and recruitment can complicate the recovery from either cold or dry periods
357 (e.g. Li et al. 2019).

358 Recently, natural regeneration and reforestation have increased again (Vitali et al. 2019;
359 Piovesan in press), most likely in connection with reduced anthropic pressure during the last
360 decades because of migration from the mountains to the cities (Todaro et al., 2007) as well as the
361 protection of rewilding afforded by the Natural Park. In this case forest expansion is not linked to
362 a decrease in human population, but to a migration from rural to urban areas, which is typical of
363 societies as they transition from primarily agrarian to primarily industrial economies (Keddy and
364 Drummond, 1996). Moreover, this new pulse of tree recruitment is occurring in a generally
365 warmer climate than the one experienced by the 1300-1700 CE wave of regeneration. Current
366 warming is enhancing pine growth (see discussion below) and recruitment in Mediterranean high
367 mountains, contributing to tree densification and upward movement of the tree line ecotone
368 (Sangüesa-Barreda et al. 2018; Vitali et al. 2019). This means that temperature is still the leading
369 climatic factor, controlling the pace of growth and recruitment as in most of the alpine zone
370 worldwide (Körner 2012; Silva et al., 2016). The positive association between warming, tree

growth, and establishment may not be stable in time (Fajardo and McIntire, 2012; Sangüesa-Barreda et al. 2018), hence the complex response of seedlings, saplings, and trees to climatic variability and human impacts (Andrus et al., 2018; Sidgel et al. 2018) deserves additional consideration.

Growth variability, temperature, and AMO trends

Italus and the majority of Heldreich's pines on the Pollino Massif have shown a growth increase in recent decades (Figs. 9 and 11). Such pattern – also found in bristlecone pine (Salzer et al. 2009) – contradicts the growth decline of tree-ring width that typically occurs as cambial age increases (Fritts 1976; Biondi and Qeadan, 2008), and it does not match the widespread growth decline and tree dieback that various Mediterranean ecosystems have recently experienced (Dorado-Liñán et al., 2017). Our research is only a first step towards uncovering how growth history of these old pines is influenced by complex non-linear processes linked to human impacts in a changing environment, such as local land use (see Todaro et al., 2007; Vitali et al. 2019), global increases in greenhouse gases, and regional changes in atmospheric pollution. Further studies on the driving factors behind the resumed growth since the 1980s should therefore consider as possibilities higher air temperature under non-limiting water stress (Granda et al., 2017), carbon dioxide fertilization, trends in ultraviolet radiation, and the deposition of air pollutants.

The high-elevation bioclimatic belt, where the oldest trees were found, is mainly limited by low temperature, as expected in subalpine forests worldwide (e.g. Salzer et al. 2009, Silva et al. 2016, but see Sigdel et al. 2018 for the relevant role of precipitation in arid climates). Both the significant variables in bootstrapped correlation functions and the growth variability agreement with the AMO suggest a direct connection with temperature. A leading positive correlation with

395 AMO has also been recently reported for tree growth in mountain pine forests of central-southern
396 Spain (see Fig. 2 in Madrigal-Gonzales et al., 2017). The AMO has been linked to surface air
397 temperature variation over Europe (O'Reilly et al., 2017), and generally with northern hemisphere
398 temperature on timescales longer than 30 years (McCarthy et al. 2015; Wang et al., 2017). Tree
399 growth responses to AMO phases can be linked to the positive effect of a warmer growing season
400 (Todaro et al., 2007). A longer duration of the growing season, mainly due to an earlier onset of
401 cambial activity in spring, had already been identified in Heldreich's pine as a driving factor for
402 increased wood growth under warmer air temperature conditions (Deslauriers et al., 2008). While
403 temperature oscillation is the candidate factor to explain the high correlation between Heldreich's
404 pine BAI and AMO timeseries, the relation may not be stable in time.

405 Reconstructed Atlantic multidecadal variability shows no evidence of a distinct decadal or
406 centennial spectral peak (Singh et al., 2018). This is also the case in the pre-instrumental period of
407 the BAI growth series, despite a reddening spectrum at the multidecadal timescale (>50 years). An
408 amplification of the AMO multidecadal power since the onset of the industrial era was previously
409 reported by Moore et al. (2017). Modeling studies have provided evidence that a sizeable part of
410 the observed AMO variability since 1854 may be externally forced (Bellomo et al., 2018), and for
411 the same period the wavelet coherence between Northern Hemisphere mean May to August
412 temperature anomaly and solar forcing showed a reactivation of the cycle (see Fig. 15 in
413 Anchukaitis et al. 2017).

414 Even in old age, trees can respond to favorable environmental conditions (Phillips et al.,
415 2008; Salzer et al., 2009; Sillett et al., 2015), thereby reversing the long-term trend of radial
416 increment and raising questions on their senescence process (Peñuelas and Munné-Bosch, 2010;
417 Thomas, 2013). For the oldest trees in our sample, BAI was directly linked to DBH but inversely
418 correlated with age, connections that are typically difficult to separate cleanly (see Foster et al.,

2016 for a discussion). In the last two centuries the predictive power of DBH and age on stem increment showed a decreasing trend. At the same time, older trees had lower BAI compared to younger ones of similar dimension. This growth pattern is unique during the last 700 years, suggesting that younger trees may have become more productive in a warming climate (e.g. Camarero et al., 2015). However, since mature trees are more resilient than saplings to global warming (e.g. Zhang et al., 2015), the acclimation capacity of the new cohort is uncertain.

Conservation management implications

Pollino National Park is the largest protected natural area in Italy, and our study has shown that the Park harbors a unique concentration of old-growth stands, with several trees either older than 900 years or likely to reach that advanced age. Current conservation policies in the Park ensure the preservation of this majestic and primeval tree population within strict reserves using an approach that is landscape-scale and longstanding. Additional social and cultural benefits (Blicharska and Mikusiński, 2014) derive from the fact that Heldreich's pine is an iconic species for biological conservation in mountains of the northern Mediterranean Basin. Reconstructing the growth history of the oldest trees therefore helps consolidating the territorial identity and collective well-being of the local people, which need to be directly involved in order to guarantee the wilderness status of the protected areas. Raising public awareness of the importance to preserve these old-growth stands while maintaining a sustainable development has in fact allowed the Park to become locally accepted and cherished, after being initially met with opposition at the time of its creation in the 1990s, which led to the torching of the "Zi Peppe" tree, a symbol for the newly designated Park.

Our dendrochronological study has confirmed the importance of cliff environments for yielding some of the oldest trees on the planet (Larson et al., 2000a; Sandel and Svenning, 2013; Piovesan et al., 2018a). The ecological factor that governs the appearance of extreme longevity in

trees may then simply be the presence of vertical rock that restricts fire and limits access by humans and their livestock (Larson et al., 2000a). In the Pollino area, these primeval trees are habitat for a number of species, such as obligate saproxylic invertebrates. For example we recently found under the canopy of *Italus* a *Buprestis splendens*, which is a saproxylic coleopter that has disappeared from most of Europe; this species is currently endangered, and on the verge of extinction (see <http://www.iucnredlist.org/details/3334/0>). Species like *Buprestis splendens* have been faced with heavy habitat losses because of the disappearance of large/old conifer trees (Carpaneto et al., 2015; Eckelt et al., 2017). Discovering, studying, preserving and restoring large old trees in the forest landscape remains a priority task for biodiversity conservation (Lindenmayer and Laurance, 2017).

Conclusion

Millennium-old trees and their growth trends are emblematic and unique environmental indicators in this age of global changes. Old Heldreich's pines escaped medieval human impacts in remote cliff sites of the Pollino massif, then a wave of pine stands established after a human demographic crisis during the late 14th and 16th centuries, further intertwined with the late 15th century establishment of small rural communities by people coming from Albania (Arbësh). Remote mountains and cliff habitat confirmed to be long-term stable refugia for wildlife conservation (Larson et al. 2000b; Pimm 2008; Tang et al. 2018), especially Heldreich's pine, as in the case of other relict plants from the Tertiary era in different ecoregions (e.g., Tang et al., 2015; Qian et al., 2016; White et al., 2016). These unique environments are understudied (Covy et al., 2019), but cliffs can protect a wide range of organisms during periods of land exploitation, hence they become stepping stones during rewilding phases of the landscape. Modern land abandonment from the collapse of sheep-herding and climate warming have generated a new pulse of tree

recruitment, leading to a high-altitude tree densification, in accordance with other mountains of Southern Europe (Sangüesa-Barreda et al. 2018; Vitali et al. 2019). While threatened habitat and species may be in danger of extinction from climate change impacts (e.g., Pimm 2008), the Pollino high mountain pine population showed resilience to current climate change, and is even spreading in an unusual environment, the high mountain old-growth beech forest (Piovesan. in press).

When considering *Italus*, its establishment occurred within the cold period of the Dark Age (400 – 865 CE; Helama et al., 2017). The oldest trees have then survived through the Medieval Warm period, the Little Ice Age, and the recent warming, which corresponds to a renewed increase in stem growth. Trees capable of long life and of tolerating climatic changes are particularly relevant to management strategies aimed at increasing carbon storage in forested landscapes over long time periods (Körner, 2017; Musavi et al. 2017). Further studies should be aimed at determining if just the oldest trees or rather the entire Heldreich's pine population has peculiar genetic features or simply a plastic response to climatic shifts.

Since 1850, low-frequency variability (50-70-year periods) in tree growth has been in synchrony with changes in the Atlantic Multidecadal Oscillation (AMO). The historical ecology of Heldreich's pine therefore reflects changes in climate and in societal processes, making this iconic tree a special witness of the Anthropocene.

Tree longevity and growth patterns of the oldest trees were appropriate indicators for the assessment of naturalness in forest ecosystems (Di Filippo et al., 2017). Natural regeneration of Heldreich's pine in its bioclimatic belt has recently been favored by the disappearance of traditional pastoral practices (Fig. 12; Todaro et al., 2007; Piovesan, in press). The Pollino Massif has therefore experienced a rewilding process, possibly extending back to the post-Renaissance period. While carbon fixation in long-lived trees contributes to removing carbon dioxide from the atmosphere, some attention should also be given to the somewhat counter-intuitive possibility that

higher growth rates may expose these remarkable old trees to a higher risk of death because of the tradeoff between growth and longevity (Bigler and Veblen, 2009; Di Filippo et al., 2015; Piovesan et al. in review). For this reason, continuous monitoring of tree health and growth status will be an important step to understand the impact of climatic change on Heldreich's pine lifespan. The protection of biodiversity, ecosystems and wildlife in mountains is a strategic development goal of the UN 2030 Agenda for sustainable development (<https://sustainabledevelopment.un.org/topics/mountains>). The protection afforded to these old-growth stands by the Pollino National Park is only one of many conservation efforts that are required to maintain these invaluable populations for future generations. Similar studies would be needed for threatened habitats and iconic trees of other ecoregions worldwide, in order to assess their probable survival into the future.

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Abstract

We dendrochronologically analyzed 177 Heldreich's pines growing on the Pollino Massif, in southern Italy, for understanding climatic and human impacts on old trees. Most of the large-diameter trees currently living became established in the late Medieval to Renaissance periods under a snowy wet climate and low anthropic influence. Millennium-old (i.e., > 900 years of age) trees in remote sites escaped Medieval human impacts, then a wave of pine stands established in the late 14th and 16th centuries following recurrent human plague epidemics. Stem growth histories showed that both millennium-old and the majority of century-old trees grew along similar trajectories. These old trees have survived long-lasting climatic reversals, clearly a sign of their resilience to extreme events. Cliff habitats played a strategic environmental role for tree conservation during periods of land exploitation; such biodiversity refugia may serve as stepping stones for rewilding mountain landscapes. In recent decades, land abandonment following the collapse of sheep-herding, together with climate warming, have led to a new pulse of tree recruitment. Since 1850, low-frequency variability (50-70-year periods) in tree growth has been in synchrony with the Atlantic Multidecadal Oscillation. Recently observed growth increases counter widespread reports of tree and forest decline in Mediterranean environments, and suggest that extreme longevity does not necessarily reduce stem increment. Discovering, studying, and preserving primeval trees in forest landscapes remains a priority for biodiversity conservation in the Anthropocene. Heldreich's pine resilience to current global changes bodes well for sustainable development in the Mediterranean mountains they inhabit, and similar studies are needed for threatened habitats and iconic trees of other ecoregions in order to assess their probable survival into the future.

Key words: old trees; cliff habitat; tree growth pattern; North Atlantic Oscillation; Atlantic Multidecadal Oscillation; rewilding

Highlights:

- Old *Pinus heldreichii* trees of southern Italy have survived at high elevations in cliff habitats.
- Most large trees established during human demographic crises of the late Medieval period.
- Lifetime diameter growth curves revealed that old trees have followed similar growth trajectories over time.
- Enhanced growth in modern times indicates that trees are coping well despite recent warming.
- Ecological dynamics of this iconic pine species reflect changes in both climate and human society, making it a witness of the Anthropocene.

INTRODUCTION

Placing accurate boundaries on maximum and average tree age, and on how these boundaries vary with environmental conditions, helps understand demographic and growth processes that lead to diverse forest structures (Stephenson et al., 2014; Di Filippo et al., 2017). Within human-modified forest ecosystems, knowledge of tree longevity and growth processes is an essential premise for locating the least impacted areas, which in turn yield the oldest trees, and therefore ultimately become top candidates for conservation (Keddy and Drummond, 1996). Large old trees are a keystone ecological component (Lindenmayer et al., 2014), and are also habitat to a number of species, thereby contributing to forest biodiversity (Lindenmayer, 2016). Tree-dwelling lichens, for instance, occur in close connection with stem age, which in turn is an indicator of habitat persistence within a landscape, a necessary condition for the survival of niche-specific and/or dispersal-limited species (Ranius et al., 2008; Fritz et al., 2009; Zemanová et al., 2017). Overall, understanding the time span required for recruiting and retaining the oldest trees allows the development of sound management practices for old-growth stands (Lindenmayer and Laurance, 2017).

The study of tree longevity and growth rates, especially when dendrochronologically evaluated, is a well-established discipline (Molisch, 1938; Schulman, 1954). Locating, sampling, and dating the oldest individuals of tree species that form annual xylem increments has allowed dendrochronologists to date archaeological structures (Douglass, 1929), reconstruct changes in climate (Fritts, 1976) and forest dynamics (Veblen et al., 2003), and provide reliable standards for the calibration of the radiocarbon time scale (Bowman, 1990). In recent years, information on tree longevity has been further acquired through dendroecological investigations of old-growth forests

(Di Filippo et al., 2012), strip-bark formation (Bunn et al., 2003), and extremely large individuals (Drobyshev and Niklasson, 2010; Patrut et al., 2007).

Lively debate has focused on the current and future health of large old trees, given the risk factors that may threaten their survival (Lindenmayer and Laurance, 2017). Because of current and expected widespread mortality episodes caused by climatic stress (Allen et al., 2015; Meddens et al., 2015), together with observed differences in growth patterns of individual life histories (Stephenson et al., 2014), it is crucial to improve our knowledge of functional ecology processes in different forest settings and with contrasting growth features (e.g. large old trees growing in open forest vs. those in closed forest; growth decline vs. increase; browning vs greening). Understanding how growth rates vary with tree age and dimension is also necessary for modelling forest functioning under a changing environment (Michaletz et al., 2014). Stem age and size are weakly correlated in natural old-growth late-successional forests (Piovesan et al., 2005), and the two components should be considered separately when assessing long-term tree and stand development. Old trees are also likely to yield new insights in the connections between ecophysiology and genomics (e.g. genetic and epigenetic regulation), particularly those related to senescence and ageing (Lanner and Connor, 2001; Flanary and Kletetschka, 2005; Thomas, 2013).

Slow, continuous stem growth is usually a premise for tree longevity (Bigler and Veblen, 2009; Johnson and Abrams, 2009; Piovesan et al., in review). Smaller tree-ring size and higher wood density may improve vascular plasticity to withstand climate stress and enhance resilience to recurrent canopy disturbance events throughout exceptionally long lifetimes (Di Filippo et al., 2012). Some species, such as European beech (*Fagus sylvatica* L.), seem negligibly affected by the progressive deterioration of physiological functions associated with age (Mencuccini et al., 2005; Peñuelas and Munné- Bosch, 2010; Mencuccini, 2014), confirming the existence of “negative senescence” phenomena (Munné-Bosch, 2015). Slow growth in old trees may thus

largely be dependent on long-term environmental constraints and physical damage rather than ageing (Mencuccini et al., 2005; Mencuccini, 2014). In closed-canopy forests, shade-tolerant trees may spend centuries in the understory, where competition for light reduces stem growth, while gap dynamics introduce alternating periods of growth suppression and release (Piovesan and Lüttge, 2018). In open-canopy forests, shade-intolerant trees are often more limited in their growth by environmental factors than by competition, and the oldest individuals are found in areas of low fertility and/or reduced growing seasons (Larson et al., 2000a).

In Europe and the Mediterranean Basin, one of the tree species with the longest-living individuals is Heldreich's pine (*Pinus heldreichii* H. Christ, also called *Pinus leucodermis* Antoine), whose populations in the highlands of Greece and south Italy have recently been found to include two dendrochronologically dated trees older than a thousand years (Könter et al, 2017; Piovesan et al., 2018a). Since numerous old trees were previously found in the Pollino massif of southern Italy (Serre-Bachet, 1985; Biondi, 1992), it was necessary to determine if this Mediterranean mountain was being affected by increased mortality among the oldest trees, possibly as a sign and a consequence of forest decline (e.g. Dorado-Liñán et al., 2017) during the Anthropocene. It should be noted that our definition of the Anthropocene is not linked to an absolute date, rather it is based on identifying the human capacity for ecosystem engineering (Niche Construction Theory) to search for the past large-scale impacts of human societies on natural species and ecosystems in connection with changing environmental and cultural contexts (Smith and Zeder, 2013; Ruddiman, 2018).

In this study, we used data from a comprehensive new field collection to uncover the establishment date and growth dynamics of primeval Heldreich's pines. Our main objective was to determine growth trajectories in Heldreich's pine of various ages and dimensions, with the overarching motivation of evaluating the health of extremely old trees in the age of global

environmental change. After locating some Heldreich's pines of great longevity, we investigated how old trees in this high-elevation Mediterranean environment survived land use changes and long-lasting climatic episodes such as the Medieval warm period, the Little Ice Age, and lately global change. Considering the temporal, environmental and cultural contexts that influenced the stem growth histories of this old pine population expands our knowledge on ecological history and lays a foundation for nature conservation policy in mountain landscapes (Gillson and Marchant 2015).

MATERIALS AND METHODS

Study area

Heldreich's pine forests are protected habitat in southern Europe under the Natura 2000 Directive (95A0 High Oro-Mediterranean pine forests). This open forest habitat is restricted to mountains of the southern Balkans, northern Greece, and southern Italy, where it characterizes the timberline environment with limited undergrowth formed by sparse grasslands on often stony or rocky soils (Fig. 1). Sampled trees were selected during a three-year research campaign aimed at clarifying the biology and ecology of Heldreich's pine stands distributed throughout the Pollino massif (Fig. 2). Several rugged peaks (Pollino, Pollinello, Serra Dolcedorme, Serra delle Ciavole and Serra di Crispo) occur at elevations between 1675 and 2267 m a.s.l., aligned in an amphitheater formation covering about 12 km² of high mountain landscapes (Todaro et al., 2007). Our field collections uncovered the oldest tree in Europe (Piovesan et al., 2018a), which we named *Italus* and was shown to be 1230-years old by a combination of tree-ring and radiocarbon dating applied to stem and root cores (Piovesan et. al., 2018b).

Tree-ring analysis

Large individuals were preferred, so that wood increment cores were collected from stems with diameter at breast height (DBH) greater than 50 cm (average of 92 cm and maximum of 180 cm). A total of 240 cores (177 trees) were collected (120 cores included the stem pith), mostly at breast height, during 2013-2016 at elevations ranging from 1837 to 2143 m a.s.l. All increment cores were mounted, sanded, and surfaced with metal scalpels, then ring widths were measured to the nearest 0.01 mm using a CCTRMD (Computer Controlled Tree Ring Measure Device, Aniol, 1987) interfaced with the software CATRAS (Aniol, 1983). After visual (Stokes and Smiley, 1996) and statistical (Wigley et al., 1987) crossdating, tree-ring series revealed that mean stem age was 492 ± 171 years, with a few individuals exceeding 900 years. To reconstruct growth patterns while minimizing age- and size-related trends, ring-width series were standardized by fitting a cubic smoothing spline with a 50% frequency response for 100-yr periods (Cook and Peters, 1981). New *Pinus heldreichii* chronologies were compared to existing ones using Student's *t*-values and Gleichläufigkeit (GLK), a measure of the percentage of common signs of year-to-year growth change between two series (Buras and Wilmking, 2015).

Tree establishment date was calculated considering only the cores with the pith and adding to the stem age 18 years to account for the average estimated time needed to reach ~1.3 m in height (mean height growth rate is 7.1 cm yr^{-1} according to Vitali et al. 2019). We grouped tree recruitment data into 30-year bins following the approach of Sangüesa-Barreda et al. 2018 to account for uncertainty in age estimations.

Growth trajectories were computed either for individual trees or by age classes (<400 years, 400-600 years, 600-900 years, and > 900 years) to focus on old trees while allowing enough samples ($n \geq 5$) in each interval. We used ring areas to quantify basal area increment, a proxy for annual biomass production (BAI; Di Filippo et al., 2012). BAI chronologies obtained by averaging

individual series, and the Atlantic Multidecadal Oscillation (AMO) time series at annual resolution (Enfield et al., 2001; <https://www.esrl.noaa.gov/psd/data/timeseries/AMO/>), were smoothed using the Gaussian function of the Past software (Hammer et al., 2001). Wavelet transform was used for inspection of BAI chronologies at different scales using the Morlet function, and the significance level (p-value <0.05) was plotted as a contour (chi-squared test according to Torrence and Compo, 1998) using a red-noise model with the estimated first order moving average autocorrelation coefficient.

Growth-climate relationships were quantified using bootstrapped correlation functions (Zang and Biondi, 2015) and the prewhitened BAI chronology obtained using all cores, including those without the pith. Monthly time series of mean air temperature and total precipitation were obtained, respectively, from Brunetti et al. (2009a) and Brunetti et al. (2009b).

Spatial analysis

The location of every tree was recorded with a hand-held GPS unit during field work. Stem coordinates were then mapped using QGIS (2015) on a grid of 20-m² cells derived from the Italian national 20-m resolution DEM. The oldest tree in each cell was plotted at the cell centroid coordinates, and the Clark-Evans aggregation index (Clark and Evans, 1954) was then calculated using the R package “spatstat” (Baddeley and Turner, 2005) to evaluate spatial distribution patterns (e.g. clustered or random tree distribution). The aggregation index was calculated 1) for all trees; 2) for trees older than 600 years; 3) for trees younger than 600 years. The geographical area in each analysis was the same rectangular box to avoid any spurious results caused by changes in the area under study.

RESULTS

Tree establishment, climate, and anthropogenic impacts

The age distribution of sampled trees was bell-shaped (Shapiro-Wilk test = 0.93, p-value < .0001), even though the oldest trees (dbh $\geq$ 90 cm) introduced an asymmetry (Fig. 3a). The majority of surviving trees with dbh > 50 cm became established between 1400 and 1650 CE, with a peak around 1500 CE, during a persistently negative phase of the North Atlantic Oscillation (Fig. 4a Baker et al., 2015). In the same historical period, human populations were decimated by repeated plague epidemics (Porter, 2009) over most of Europe, potentially allowing a rewilding of mountain landscapes that favored the establishment of Heldreich's pine (Fig. 4b).

In open stands located above 1850 m a.s.l., trunk diameter was directly correlated with age (Fig. 3b), but this relation lost significance when considering trees with dbh > 90 cm. Subdividing the samples based on a 90-cm stem DBH threshold highlighted the more complex age distribution of the largest trees (Fig. 3a), which included the oldest individuals.

Sampled trees were spatially clustered (Clark-Evans test: $R = 0.27$, p-value < 0.001). These forest stands are located near treeline up to 2200 m elevation, above which the dominant plant species are shrubs or grasses (Fig. 5). Trees whose age was less than 600 years were less spatially clustered (Clark-Evans test: $R = 0.32$, p-value < 0.001) than older trees (Clark-Evans test: $R = 0.19$, p-value < 0.001), which were typically found in few cliff sites. Millennium-old trees, i.e. individuals older than 900 years, were not randomly distributed over the landscape, as they concentrated in the most remote and topographically complex areas. Most of the oldest trees were located on west-facing summit cliffs between 2000 and 2100 m elevation. The oldest pine, named *Italus* (Piovesan et al., 2018a), however, was located at lower elevation (1850 m) and on a very

steep south-west facing, ragged and sparsely vegetated slope. Elevation and slope were not correlated with tree age (Fig. S1).

Growth variability in time

Radial increment of individual trees usually declined during the first decades of their life, followed by fluctuations around a generally decreasing overall trend, as it is typical of shade-intolerant conifer species (Fig. 6a; Fritts, 2012; Biondi and Qeadan, 2008). The analysis of life-history radial increment by age class showed overlapping growth performance, with millennium-old trees replicating patterns identified in trees about half that age. The lowest increments during the tree lifetime were observed in the 600-899 year age class. The growth trajectories of *Italus* and the other 4 nearly millenium-old pines enveloped most growth trajectories of multi-century old trees of smaller dimension (DBH < 90 cm; see Fig. 6b). The ecological habitats of millenium-old trees lie between lower elevation, fertile sites (e.g. near the upper margin of the beech forest or secondary grasslands, at 1850-1900 m a.s.l), and high elevation, unproductive cliff sites where we found the slowest growing millennium-old tree (lowest green line in Fig. 6b). In general, trees with DBH > 90 cm but lower age were normally found in areas characterized by faster growth rates, i.e. greater fertility (Fig. 7). When all sampled trees were considered, an inverse correlation existed between stem age and average annual growth (Fig. 8a-b).

The *Italus* tree-ring chronology is well synchronized with other long term *Pinus heldreichii* chronologies (Table S1a). The highest correlations (Table S1) were found with the chronology developed by Biondi (1992) from a few Pollino sites, closely followed by correlations with the chronology developed for Serra delle Ciavole by Serre-Bachet (1985) as well as by correlations with the new millennium-long chronology developed from the samples recently collected throughout the Pollino massif (Fig. S2, Table S1; see Fig. S3 for sample replication). Relatively

high correlations were also found with the *Pinus heldreichii* chronology from Albania (Seim et al., 2012), clearly suggesting that the Pollino and Albania mountains experience similar climatic variability. Lower, but still 99.9% significant, correlations were observed between *Italus* and the oldest trees (age > 900 years), of which three were discovered during the recent sampling campaign (Fig. S2b, Table S1b).

The standardized ring-index series of millennium-old pines and the master tree-ring chronology for the Pollino massif show an increasing growth trend in recent years (Fig. S2). Basal area increment chronologies (see Table S2), a proxy for tree biomass increment, confirmed the growth increase in recent decades for all age classes (Fig. 9). Multidecadal growth variations were coherent between different age classes (Fig. 9) with the 600-899 age class showing the lowest growth rates. In the last two centuries, trees in the youngest age class have been more productive and responsive to environmental variations, while the oldest trees have shown the steepest declining trend, which has then reversed in the last decades. This recent, common growth spur is unusual compared to previous centuries, especially for the youngest trees (Fig. 9).

Using a moving-window multiple regression model based on single-tree data, we found that BAI was directly related to stem size (DBH) and inversely related to stem age (Fig. 10). The model-explained variance changed in time, with a decreasing trend in modern times that has reversed in the last few years.

Variability of BAI since the late 1800s was dominated by multidecadal variability with extreme oscillations corresponding to the highest and lowest increments (Fig. 9). Wavelet analysis revealed increasing power in the 50-70 year periods during recent decades (Fig. 11a). The growth behavior of all age classes during the last 150 years was in phase with the Atlantic Multidecadal Oscillation (AMO; Fig. 11c and Fig. S4). The autocorrelation function of both AMO and BAI time series followed similar patterns too (Fig. 11b). Finally, the AMO was correlated with time-

related changes in variance explained by the multiple regression model for BAI mentioned above (Fig. 11d). Potential climatic linkages with the AMO are related to its effect on subalpine Mediterranean environments (O'Reilly et al., 2017), since bootstrapped correlation functions highlighted a positive relationship between air temperature and stem growth during the current year and a negative relationship with previous July precipitation (Fig. S5).

DISCUSSION

Old tree ecology

Millennium-old Heldreich's pines, located on rocky slopes in remote mountains, have been able to survive because of a combination of factors. In particular, they have been traditionally protected from logging and they have avoided wildfires because of the relative lack of fuels on the ground. The species is able to survive the lightning strikes and glaze storms that occur at these high elevations, while growing very slowly for most of its lifetime. The extreme longevity of Heldreich's pines in the Pollino area has a counterpart in the similarly maximum ages of European beech (*Fagus sylvatica* L.) in the same area. Our samples indicate the presence of beech trees with ages of about five-six centuries, hence approaching and likely exceeding the maximum life span for deciduous hardwoods (Di Filippo et al., 2015; Piovesan et al. in review). On these Mediterranean mountains, maximum age of pines is about twice that of beech, in general agreement with the global pattern of finding conifers older than hardwoods within the same environment (Oldlist, <http://www.rmtrr.org/oldlist.htm>). These extreme-longevity trees, located in old-growth stands that survived loggings in the late 1800s and early 1900s (Piovesan et al. in review), are bioindicators of wild landscapes that deserve to be preserved for future generations (Lindenmayer 2016; Lindenmayer and Laurance 2017; Lutz et al. 2018).

Overall, tree-ring series of old Heldreich's pines are characterized by relatively large tree-ring widths in the first cambial years, followed by a drop towards a very long sequence of extremely small rings, a typical growth pattern of isolated trees (Fritts, 1976; Biondi and Qeadan, 2008). Given the stringent limits to wood growth imposed by site conditions, sensitivity to climate is high (see also bootstrapped correlation functions in Fig. S5), thereby facilitating tree-ring dating even for the oldest samples. The growth trajectory of most Heldreich's pines younger than 600 years resembles that of millennium-old individuals, but trees of intermediate ages (600-900 years) experienced on average lower annual increments. Since the *Italus* growth trajectory is replicated by those of other millennium-old trees in the same area, we expect a relevant pool of actually smaller (DBH < 90 cm) - and younger - Heldreich's pines in the Pollino massif to continue growing, provided they can survive potential future threats caused by Anthropocene changes.

Tree longevity is commonly assumed to be inversely proportional with growth vigor (Fig. 1 in Black et al., 2008; Fig. 5.5 of Briffa and Melvin, 2011; Fig. 3 in Seim et al., 2012; Di Filippo et al., 2017; Piovesan et al. in press). When examining the growth trajectories of Heldreich's pine in the Pollino area, most of the millennium-old individuals occupy the middle-lower portion of the graph, suggesting both that extreme tree longevity requires slow growth and that extremely harsh conditions are detrimental to long life. Our dataset also showed that millennium-old Heldreich's pines in the Pollino area have maintained similar growth patterns regardless of appreciable differences in tree age. In temperate closed old-growth forests, tree diameter has generally no connection with age because of the very complex growth histories of older trees, characterized by slow growth and by suppression and release periods (Di Filippo et al., 2017). Instead, in the open pine stands we sampled, located above the high-mountain beech belt, larger individuals were likely to be very old especially when located on rocky slopes. It remains to be determined if this

finding is linked to peculiar ecological conditions and/or human management, which may possibly have altered demographic processes.

Historical ecology

Anthropogenic influence on these mountain environments cannot be discounted, although it is difficult to quantify the impact of past logging, fire use, and domestic grazing at the highest elevations (above 1850 m). In the lower stem of most large trees it was possible to notice scars not reaching the ground that were most likely caused by shepherds many years ago to collect wood (“alberi castorati”) for various uses, ranging from illumination to incense replacement (Biondi and Visani, 1993). However, as in the case of natural disturbance, the sampled trees were able to cope with this anthropogenic impact, probably because of the abundant resin that sealed the wound protecting the exposed xylem from pests and infections.

One can hypothesize multiple land use changes in the study area, starting for instance with the transition from hunter-gatherers to farmers and shepherds that took place in this region around the 11th Century BCE, when the local Enotri people were ruled by King *Italus*. Medieval settlements expanded in central Italy in association with fortified castles starting in the middle of the IX century, leading to both human population growth and to local deforestation pressure (Schoolman et al., 2018). Deforestation should have then continued for about four centuries, as suggested by the onset of erosive processes and by the decline of tree pollen in terrestrial and marine sediment records from south-central Italy (Piovesan et al., 2018c). Anthropic utilization to support the flourishing medieval societies could explain why only a few millennium-old individuals could still be found in today’s landscapes.

Then between 1300 and 1600 CE the European population was decimated by recurrent plagues, whose death toll was particularly high in Italy in the mid-1300s (Porter, 2009; Fig. 4b).

Medieval agrarian transformation of forested landscapes came to an end, and was slowly replaced by regeneration through a rewilding of the forest landscape (“natural silviculture reaction”, Piovesan et al., 2018c). Establishment of old-growth survivors in the Pollino area centers in the 1500s (Fig. 4), which is the time of a forest pollen peak in central Italy (Mensing et al., 2016). This period was also characterized by negative anomalies of the North Atlantic oscillation (Baker et al., 2015). The NAO is considered to favor greater winter precipitation in this region (López-Moreno et al., 2011), thereby leading to greater and more persistent snowpacks (Diodato et al. 2018). In this mountain area, the accumulation and persistence of snow, possibly until June, would have prevented livestock grazing in high mountain environments for most of the year. Land abandonment following a crash in human population could have favored tree densification, thereby providing an example of the complex interactions between human land use changes, climate, and vegetation dynamics.

The human demographic crisis that started in the 14th century (Fig. 4b) should have contributed to the 15th-century decision by the King of Naples to assign the Pollino Massif and adjacent lands extending towards the sea to the Albanian refugees that were fleeing from Turkish invaders. Several villages were then either established (see dots in Fig. 2) or repopulated (Fig. 1 in Bracco et al., 2015) starting at the end of the 15th century. This recolonization of the hillsides and mountain slopes took place in ways that led the Albanian settlers to maintain their cultural and religious identities until modern times. Demographic expansion and increased presence of grazing domestic animals, with their associated annual migrations to fresh pastures (“transumanza”), led to greater human impacts on mountain landscapes during the second half of the 16th century (Russo and Salvemini 2007, Russo, 2016). The number of families in the area was recorded at that time using the number of fireplaces (Fusco, 2009; Anselmi, 2011), and those records are inversely correlated with the establishment dates of Heldreich’s pines. During this period, North Atlantic

Oscillation (NAO) and Snow severity Index (SSI) are not concordant with tree establishment, suggesting the return to a leading role of the human factor in landscape dynamics (Fig. 4).

Other declines in human population, such as during the 1656-1658 plague, did not correspond to a rewilding comparable to what took place during the late Medieval-Renaissance establishment of the current Heldreich's pine metapopulation. Because the high recruitment phase (from about 1300 up to about 1550 CE) coincides with similar pulses in pine demography at high elevation in the Spanish central Pyrenees (Sangüesa-Barreda et al., 2018), it is possible that cold spells during the Little Ice Age interacted with human factors in determining the past dynamics of tree establishment in Mediterranean mountains. Lagged effects of extreme climatic events on tree growth, reproduction, and recruitment can complicate the recovery from either cold or dry periods (e.g. Li et al. 2019).

Recently, natural regeneration and reforestation have increased again (Vitali et al. 2019; Piovesan in press), most likely in connection with reduced anthropic pressure during the last decades because of migration from the mountains to the cities (Todaro et al., 2007) as well as the protection of rewilding afforded by the Natural Park. In this case forest expansion is not linked to a decrease in human population, but to a migration from rural to urban areas, which is typical of societies as they transition from primarily agrarian to primarily industrial economies (Keddy and Drummond, 1996). Moreover, this new pulse of tree recruitment is occurring in a generally warmer climate than the one experienced by the 1300-1700 CE wave of regeneration. Current warming is enhancing pine growth (see discussion below) and recruitment in Mediterranean high mountains, contributing to tree densification and upward movement of the tree line ecotone (Sangüesa-Barreda et al. 2018; Vitali et al. 2019). This means that temperature is still the leading climatic factor, controlling the pace of growth and recruitment as in most of the alpine zone worldwide (Körner 2012; Silva et al., 2016). The positive association between warming, tree

growth, and establishment may not be stable in time (Fajardo and McIntire, 2012; Sangüesa-Barreda et al. 2018), hence the complex response of seedlings, saplings, and trees to climatic variability and human impacts (Andrus et al., 2018; Sidel et al. 2018) deserves additional consideration.

Growth variability, temperature, and AMO trends

Italus and the majority of Heldreich's pines on the Pollino Massif have shown a growth increase in recent decades (Figs. 9 and 11). Such pattern – also found in bristlecone pine (Salzer et al. 2009) – contradicts the growth decline of tree-ring width that typically occurs as cambial age increases (Fritts 1976; Biondi and Qeadan, 2008), and it does not match the widespread growth decline and tree dieback that various Mediterranean ecosystems have recently experienced (Dorado-Liñán et al., 2017). Our research is only a first step towards uncovering how growth history of these old pines is influenced by complex non-linear processes linked to human impacts in a changing environment, such as local land use (see Todaro et al., 2007; Vitali et al. 2019), global increases in greenhouse gases, and regional changes in atmospheric pollution. Further studies on the driving factors behind the resumed growth since the 1980s should therefore consider as possibilities higher air temperature under non-limiting water stress (Granda et al., 2017), carbon dioxide fertilization, trends in ultraviolet radiation, and the deposition of air pollutants.

The high-elevation bioclimatic belt, where the oldest trees were found, is mainly limited by low temperature, as expected in subalpine forests worldwide (e.g. Salzer et al. 2009, Silva et al. 2016, but see Sidel et al. 2018 for the relevant role of precipitation in arid climates). Both the significant variables in bootstrapped correlation functions and the growth variability agreement with the AMO suggest a direct connection with temperature. A leading positive correlation with

AMO has also been recently reported for tree growth in mountain pine forests of central-southern Spain (see Fig. 2 in Madrigal-Gonzales et al., 2017). The AMO has been linked to surface air temperature variation over Europe (O'Reilly et al., 2017), and generally with northern hemisphere temperature on timescales longer than 30 years (McCarthy et al. 2015; Wang et al., 2017). Tree growth responses to AMO phases can be linked to the positive effect of a warmer growing season (Todaro et al., 2007). A longer duration of the growing season, mainly due to an earlier onset of cambial activity in spring, had already been identified in Heldreich's pine as a driving factor for increased wood growth under warmer air temperature conditions (Deslauriers et al., 2008). While temperature oscillation is the candidate factor to explain the high correlation between Heldreich's pine BAI and AMO timeseries, the relation may not be stable in time.

Reconstructed Atlantic multidecadal variability shows no evidence of a distinct decadal or centennial spectral peak (Singh et al., 2018). This is also the case in the pre-instrumental period of the BAI growth series, despite a reddening spectrum at the multidecadal timescale (>50 years). An amplification of the AMO multidecadal power since the onset of the industrial era was previously reported by Moore et al. (2017). Modeling studies have provided evidence that a sizeable part of the observed AMO variability since 1854 may be externally forced (Bellomo et al., 2018), and for the same period the wavelet coherence between Northern Hemisphere mean May to August temperature anomaly and solar forcing showed a reactivation of the cycle (see Fig. 15 in Anchukaitis et al. 2017).

Even in old age, trees can respond to favorable environmental conditions (Phillips et al., 2008; Salzer et al., 2009; Sillett et al., 2015), thereby reversing the long-term trend of radial increment and raising questions on their senescence process (Peñuelas and Munné-Bosch, 2010; Thomas, 2013). For the oldest trees in our sample, BAI was directly linked to DBH but inversely correlated with age, connections that are typically difficult to separate cleanly (see Foster et al.,

2016 for a discussion). In the last two centuries the predictive power of DBH and age on stem increment showed a decreasing trend. At the same time, older trees had lower BAI compared to younger ones of similar dimension. This growth pattern is unique during the last 700 years, suggesting that younger trees may have become more productive in a warming climate (e.g. Camarero et al., 2015). However, since mature trees are more resilient than saplings to global warming (e.g. Zhang et al., 2015), the acclimation capacity of the new cohort is uncertain.

Conservation management implications

Pollino National Park is the largest protected natural area in Italy, and our study has shown that the Park harbors a unique concentration of old-growth stands, with several trees either older than 900 years or likely to reach that advanced age. Current conservation policies in the Park ensure the preservation of this majestic and primeval tree population within strict reserves using an approach that is landscape-scale and longstanding. Additional social and cultural benefits (Blicharska and Mikusiński, 2014) derive from the fact that Heldreich's pine is an iconic species for biological conservation in mountains of the northern Mediterranean Basin. Reconstructing the growth history of the oldest trees therefore helps consolidating the territorial identity and collective well-being of the local people, which need to be directly involved in order to guarantee the wilderness status of the protected areas. Raising public awareness of the importance to preserve these old-growth stands while maintaining a sustainable development has in fact allowed the Park to become locally accepted and cherished, after being initially met with opposition at the time of its creation in the 1990s, which led to the torching of the "Zi Peppe" tree, a symbol for the newly designated Park.

Our dendrochronological study has confirmed the importance of cliff environments for yielding some of the oldest trees on the planet (Larson et al., 2000a; Sandel and Svenning, 2013; Piovesan et al., 2018a). The ecological factor that governs the appearance of extreme longevity in

trees may then simply be the presence of vertical rock that restricts fire and limits access by humans and their livestock (Larson et al., 2000a). In the Pollino area, these primeval trees are habitat for a number of species, such as obligate saproxylic invertebrates. For example we recently found under the canopy of *Italus* a *Buprestis splendens*, which is a saproxylic coleopter that has disappeared from most of Europe; this species is currently endangered, and on the verge of extinction (see <http://www.iucnredlist.org/details/3334/0>). Species like *Buprestis splendens* have been faced with heavy habitat losses because of the disappearance of large/old conifer trees (Carpaneto et al., 2015; Eckelt et al., 2017). Discovering, studying, preserving and restoring large old trees in the forest landscape remains a priority task for biodiversity conservation (Lindenmayer and Laurance, 2017).

Conclusion

Millennium-old trees and their growth trends are emblematic and unique environmental indicators in this age of global changes. Old Heldreich's pines escaped medieval human impacts in remote cliff sites, then a wave of pine stands established after a human demographic crisis during the late 14th and 16th centuries, further intertwined with the late 15th century establishment of small rural communities by people coming from Albania (Arbësh). Remote mountains and cliff habitat confirmed to be long-term stable refugia for wildlife conservation (Larson et al. 2000b; Pimm2008; Tang et al. 2018), especially Heldreich's pine, as in the case of other relict plants from the Tertiary era in different ecoregions (e.g., Tang et al., 2015; Qian et al., 2016; White et al., 2016). These unique environments are understudied (Covy et al., 2019), but cliffs can protect a wide range of organisms during periods of land exploitation, hence they become stepping stones during rewilding phases of the landscape. Modern land abandonment from the collapse of sheep-herding and climate warming have generated a new pulse of tree recruitment, leading to a high-

altitude tree densification, in accordance with other mountains of Southern Europe (Sangüesa-Barreda et al. 2018; Vitali et al. 2019). While threatened habitat and species may be in danger of extinction from climate change impacts (e.g., Pimm 2008), the Pollino high mountain pine population showed resilience to current climate change, and is even spreading in an unusual environment, the high mountain old-growth beech forest (Piovesan. in press).

When considering *Italus*, its establishment occurred within the cold period of the Dark Age (400 – 865 CE; Helama et al., 2017). The oldest trees have then survived through the Medieval Warm period, the Little Ice Age, and the recent warming, which corresponds to a renewed increase in stem growth. Trees capable of long life and of tolerating climatic changes are particularly relevant to management strategies aimed at increasing carbon storage in forested landscapes over long time periods (Körner, 2017; Musavi et al. 2017). Further studies should be aimed at determining if just the oldest trees or rather the entire Heldreich's pine population has peculiar genetic features or simply a plastic response to climatic shifts.

Since 1850, low-frequency variability (50-70-year periods) in tree growth has been in synchrony with changes in the Atlantic Multidecadal Oscillation (AMO). The historical ecology of Heldreich's pine therefore reflects changes in climate and in societal processes, making this iconic tree a special witness of the Anthropocene.

Tree longevity and growth patterns of the oldest trees were appropriate indicators for the assessment of naturalness in forest ecosystems (Di Filippo et al., 2017). Natural regeneration of Heldreich's pine in its bioclimatic belt has recently been favored by the disappearance of traditional pastoral practices (Fig. 12; Todaro et al., 2007; Piovesan, in press). The Pollino Massif has therefore experienced a rewilding process, possibly extending back to the post-Renaissance period. While carbon fixation in long-lived trees contributes to removing carbon dioxide from the atmosphere, some attention should also be given to the somewhat counter-intuitive possibility that

higher growth rates may expose these remarkable old trees to a higher risk of death because of the tradeoff between growth and longevity (Bigler and Veblen, 2009; Di Filippo et al., 2015; Piovesan et al. in review). For this reason, continuous monitoring of tree health and growth status will be an important step to understand the impact of climatic change on Heldreich's pine lifespan. The protection of biodiversity, ecosystems and wildlife in mountains is a strategic development goal of the UN 2030 Agenda for sustainable development (<https://sustainabledevelopment.un.org/topics/mountains>). The protection afforded to these old-growth stands by the Pollino National Park is only one of many conservation efforts that are required to maintain these invaluable populations for future generations. Similar studies would be needed for threatened habitats and iconic trees of other ecoregions worldwide, in order to assess their probable survival into the future.

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Figure legends

Figure 1. Winter landscape view of the Pollino mountain. Old-growth beech forests occupy the area below cliff habitats that harbor the open high-mountain Heldreich's pine belt.

Figure 2. Location of sampled *Pinus heldreichii* stands in the Pollino massif. Arbëreshe villages are marked by dots, Italian villages are marked by squares (from Fiorini et al., 2007).

Figure 3. (a) Violin plots and histograms of tree establishment date, given by stem age plus 18 years to account for the average estimated time to reach ~1.3 m height (*: significant difference in mean establishment date according to Welch's *t*-test with $p < 0.05$). (b) Relationship between stem diameter and age, which was modeled by a simple linear regression.

Figure 4. (a) Smoothed trends (100yr) in tree establishment dates, North Atlantic Oscillation (NAO) proxies (Baker et al., 2015) and Snow Severity Index (SSI, Diodato et al., 2019). The NAO proxy (stalagmite record) is inversely correlated with the NAO index. Only cores that included the tree pith were considered, and stem age was increased by 18 years to account for the estimated time to reach 1.3 m of height. A Gaussian smoothing filter with standard deviation set to 1/5 of the window size was applied to the data. (b) Smoothed trends in tree establishment dates (inverted Y axis), South Italian population since 1300 AD (Malanima, 2005), and population of North Calabria and Basilicata based on the number of "fireplaces" (Fusco, 2009; 4.5 persons for each fireplace according to Anselmi, 2011).

Figure 5. Spatial distribution of sampled *Pinus heldreichii* stands plotted on a Google Earth image using colors to represent tree maximum age within a 20x20-m grid cell.

Figure 6. (a) Gaussian smoothed (50-yr) average tree-ring growth rates by age class. Cambial age refers to breast height (~1.3 m); different colors were used to identify age classes (years). The number of trees (n) included in each age class is shown in the legend, and only the portion of each age class curve based on at least five trees was plotted.

(b) Lifetime growth trajectories (DIB = diameter inside bark at breast height) for the Heldreich's pine population. Color lines represent millennium-old pines (in red *Italus* and in green the other three millennium-old pines discovered in this study; the dashed line refers to a millennium-old pine sampled by Biondi 1992); black lines represent pines that were 600-899 years old.

Figure 7. Tree age plotted against average tree-ring width in large trees (dbh > 90 cm). Symbol color was used to represent elevation, and a horizontal dotted line shows the 600-year threshold. A power law function (blue line) with confidence intervals (grey shading) was overlaid to indicate a potentially non-linear relationship. Lower tree ages were normally found in areas characterized by greater fertility, hence faster growth rates.

Figure 8. Tree age plotted against average tree-ring width (dbh > 50 cm). Symbol color was used to represent (a) elevation and (b) sampled site (see legend). A horizontal dotted line shows the 600-year threshold. A power law function (blue line) with confidence intervals (grey shading) was overlaid to indicate a potentially non-linear relationship.

Figure 9. Average basal area increment (BAI) chronologies by age class, smoothed using a 50-yr Gaussian filter with standard deviation set to 1/5 of the window size. Different colors were used to identify age classes (years). The number of trees (n) included in each age class is shown in the legend. Only tree-ring series with pith were used to build age-class curves, and only BAI curves with $n \geq 5$ are shown. Tree-ring statistics are reported in Table S2.

Figure 10. Multiple linear regression model linking mean annual basal area increment (BAI) with stem diameter (DBH) and age at breast height. Regression results were calculated in 10-year moving windows from 1700 to 2016 CE using only those tree-ring series ($n=100$) completely covering the entire period. Lines (left y axis): t -values of the two predictors (black: diameter; grey: age). Grey bars (right y axis): variance explained by the regression. Values were assigned to the last year of each time window.

Figure 11. Comparison of the long-term tree growth variability of *Pinus heldreichii* with the Atlantic Multidecadal Oscillation (AMO; Enfield et al., 2001). (a) Wavelet transform of unsmoothed BAI chronology of the Pollino Massif performed with the Morlet basic function. The “cone of influence” is plotted in black to show the region where boundary effects are present. The significance level corresponding to $p=0.05$ is plotted as a black contour for a red-noise (lag-1 autoregressive) background spectrum with the given MA(1) autocorrelation coefficient estimated using an ARMA model. (b) Autocorrelation function of the *Pinus* BAI and AMO unsmoothed time series. (c) Mean basal area increment (BAI) chronology of the Pollino Massif compared with the yearly AMO ($R^2=0.59$). (d) Time variation of adjusted R^2 from the multiple regression model of single tree BAI (see Fig. 10) compared with the yearly AMO. A Gaussian smoothing filter with

standard deviation set to 1/5 of the window size (50 years) was applied to the data presented in Figs c and d.

Figure 12. Natural regeneration of *Pinus heldreichii* above the beech forest (> 1900-2000 m a.s.l.) as a consequence of land use change (abandonment of pastoral activities and subsequent vegetation rewilding).

Figures

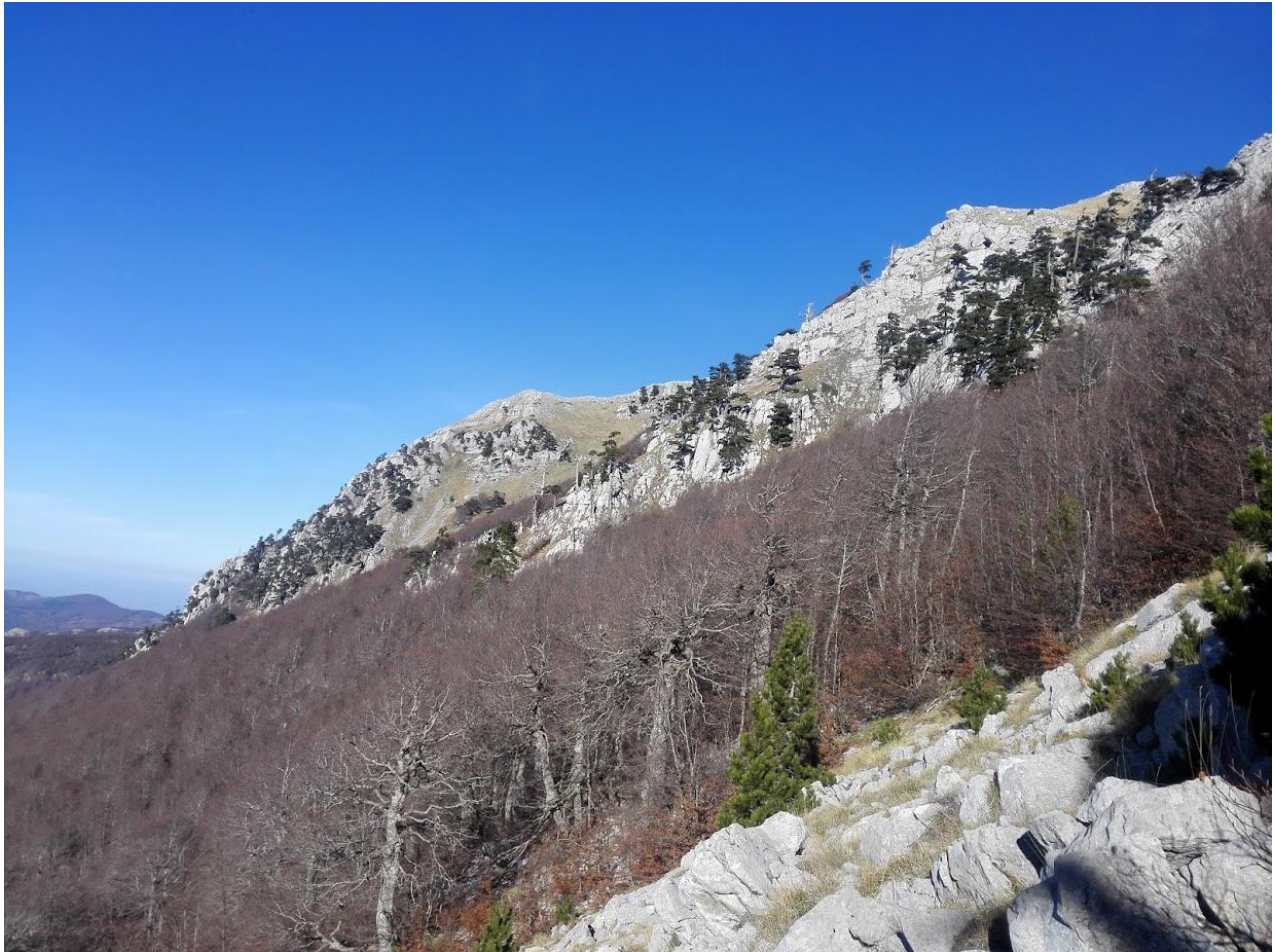


Fig. 1

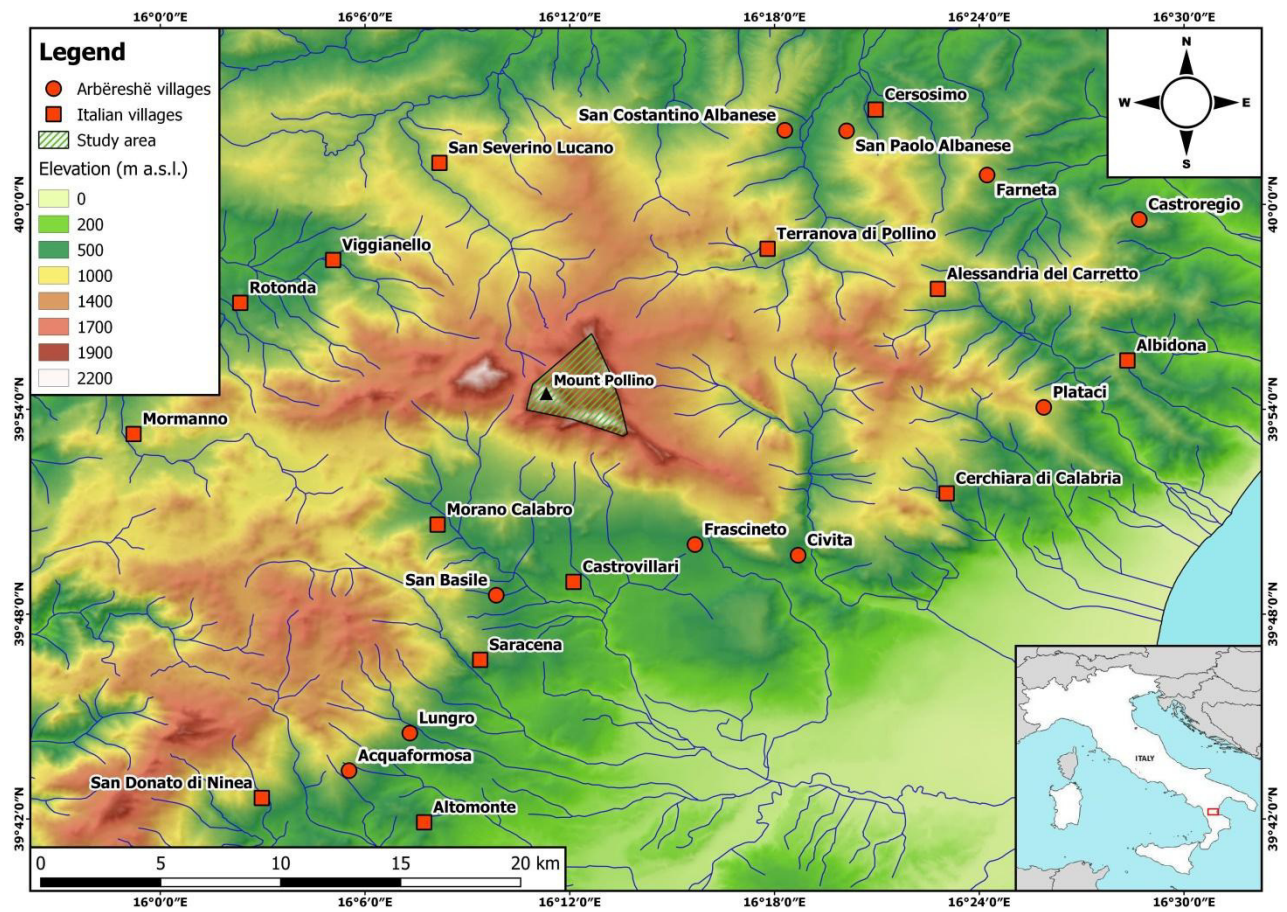


Fig. 2

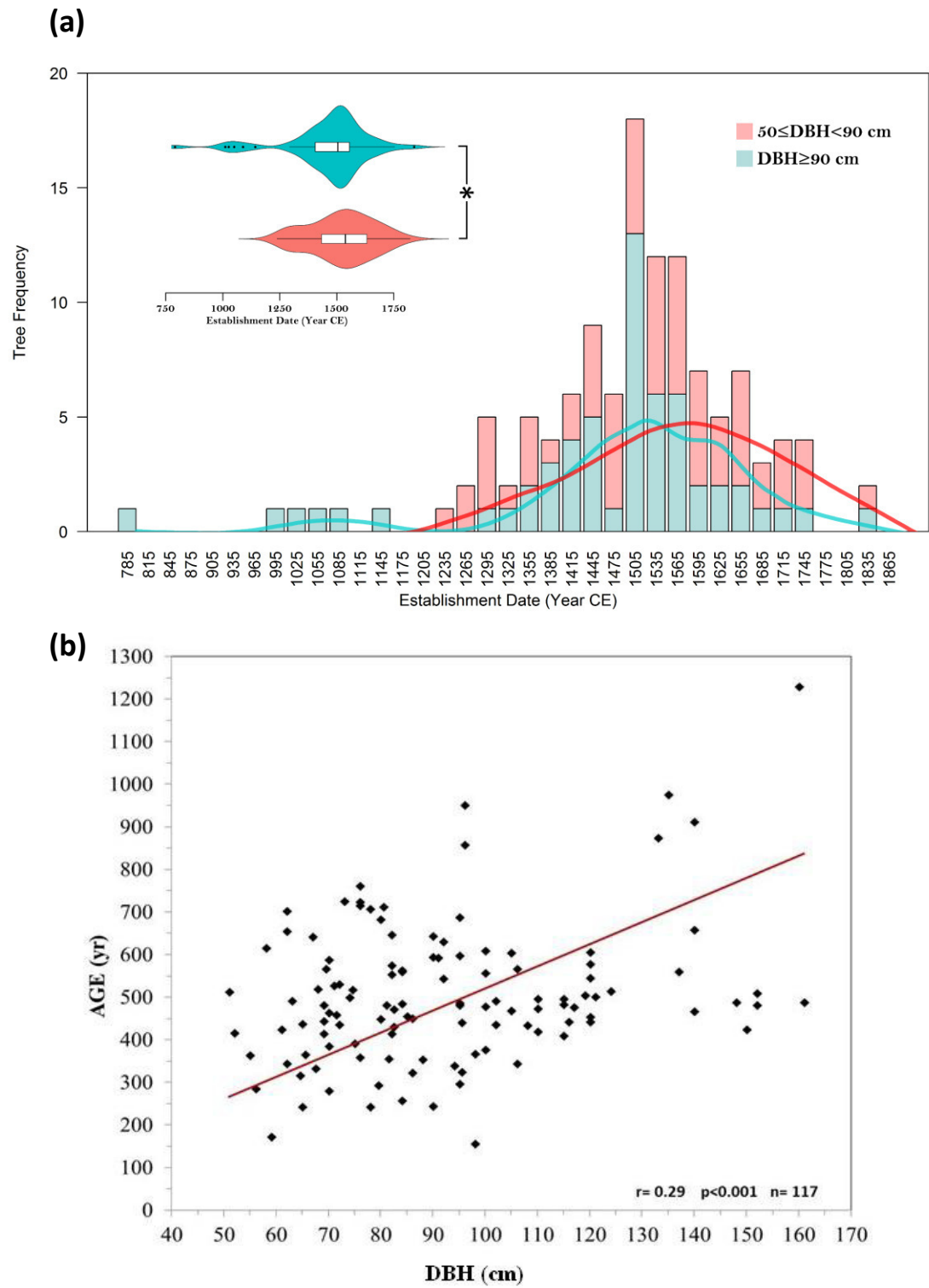


Fig.3

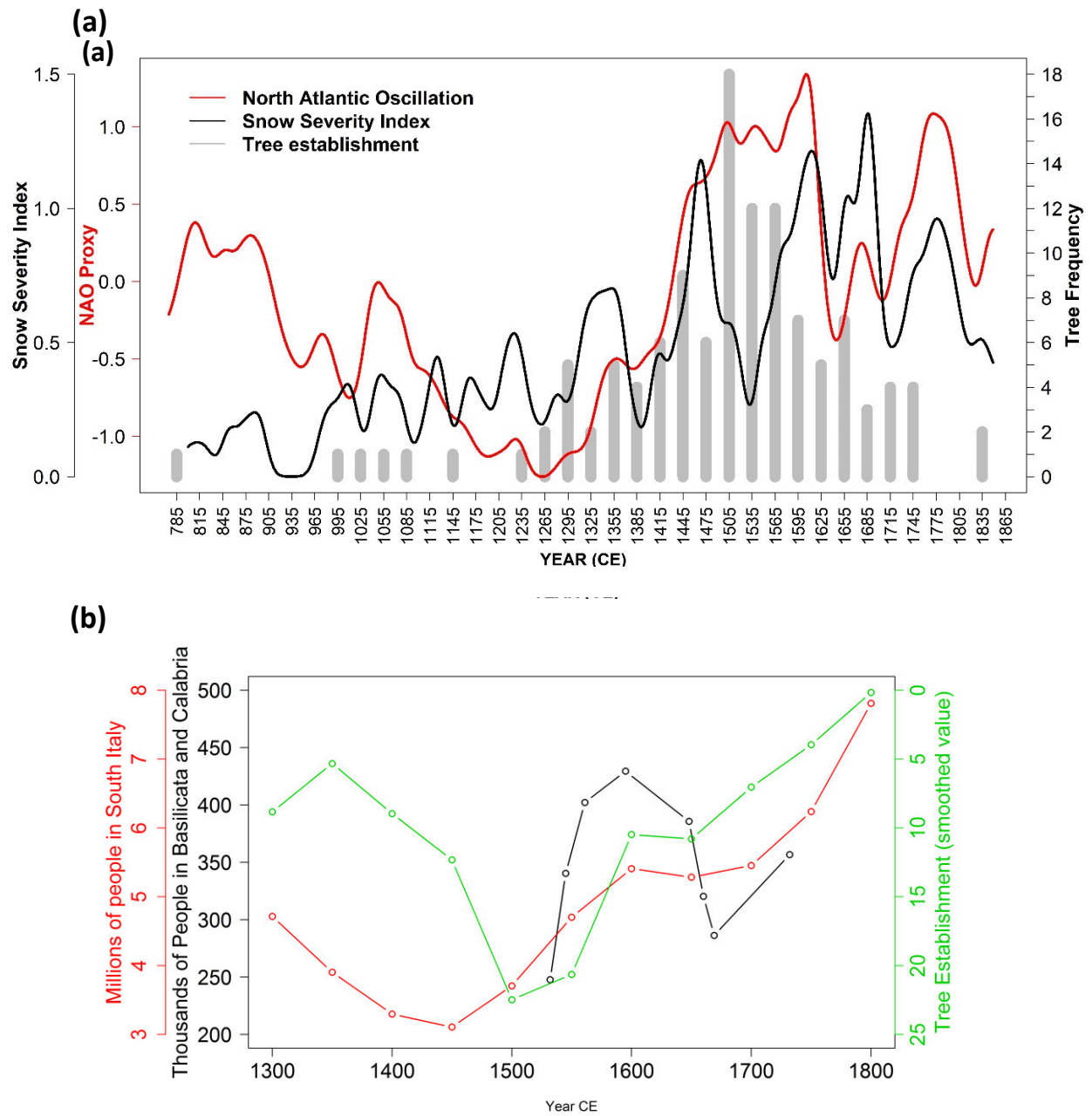


Fig. 4

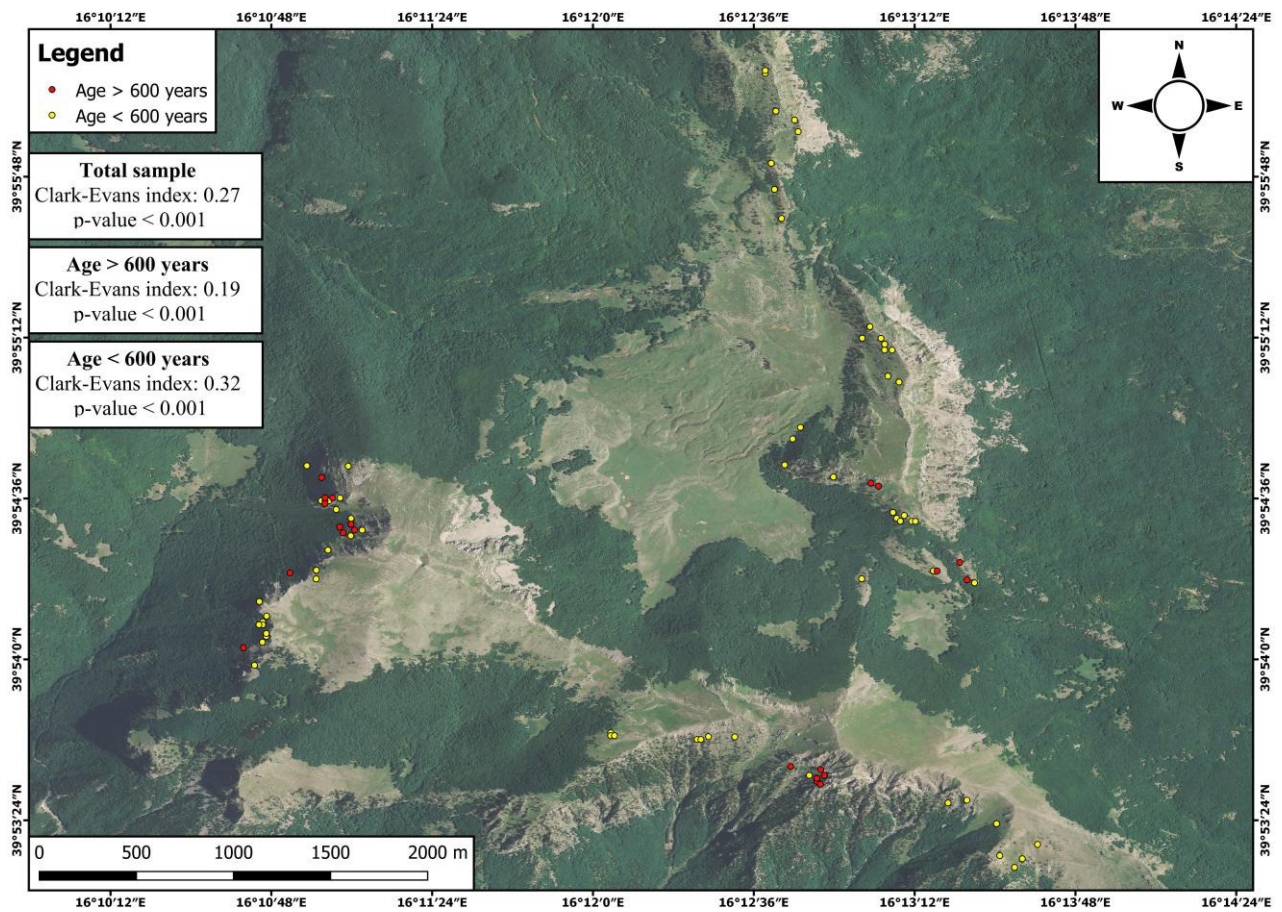


Fig. 5

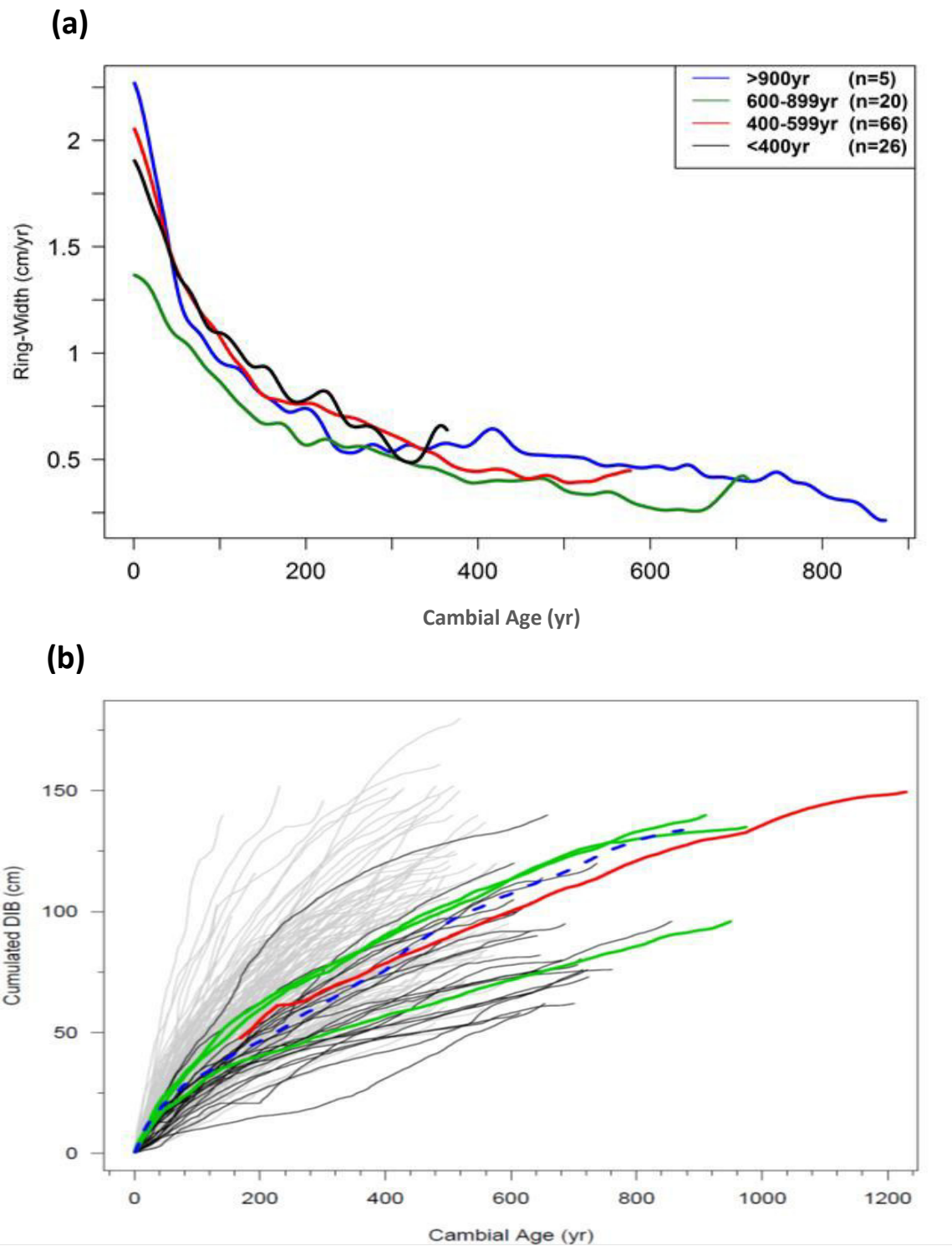


Fig. 6

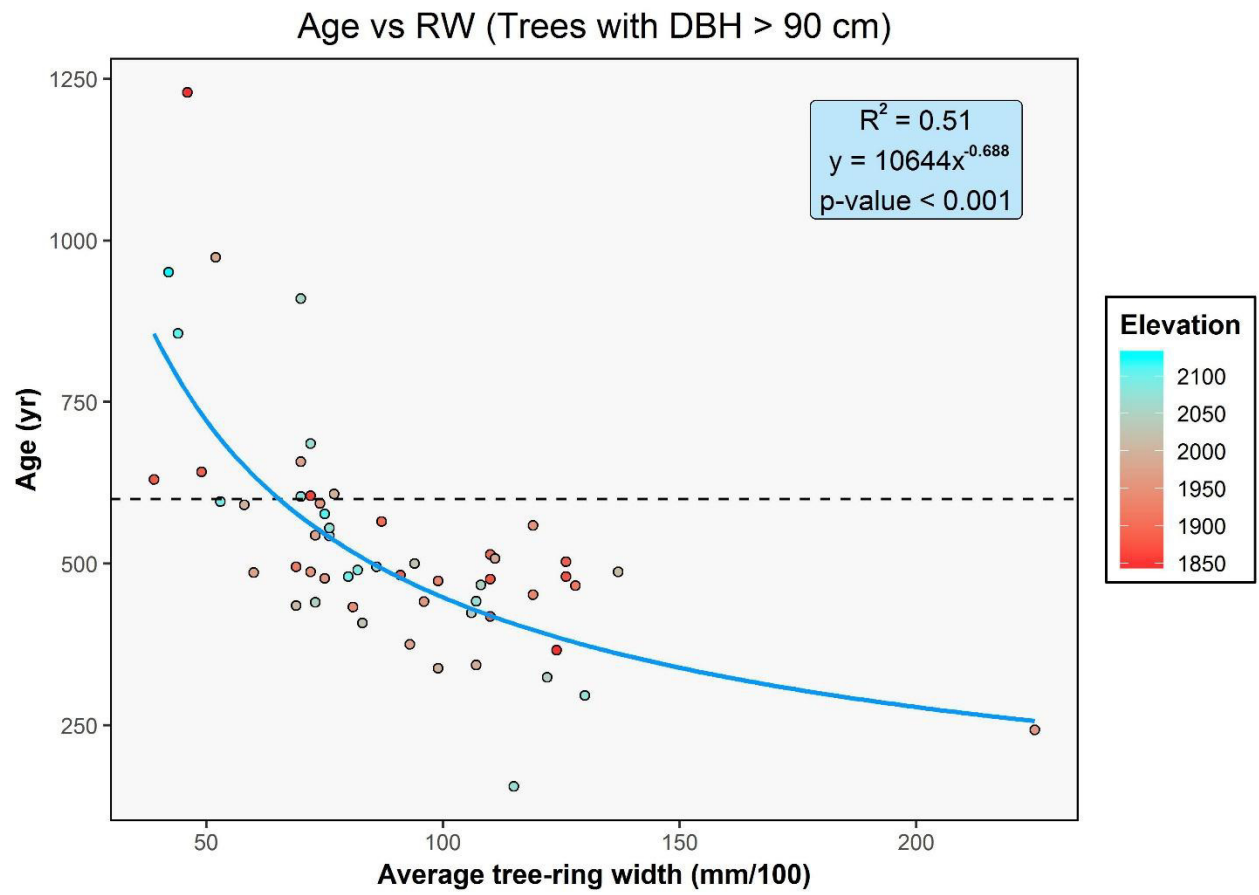


Fig. 7

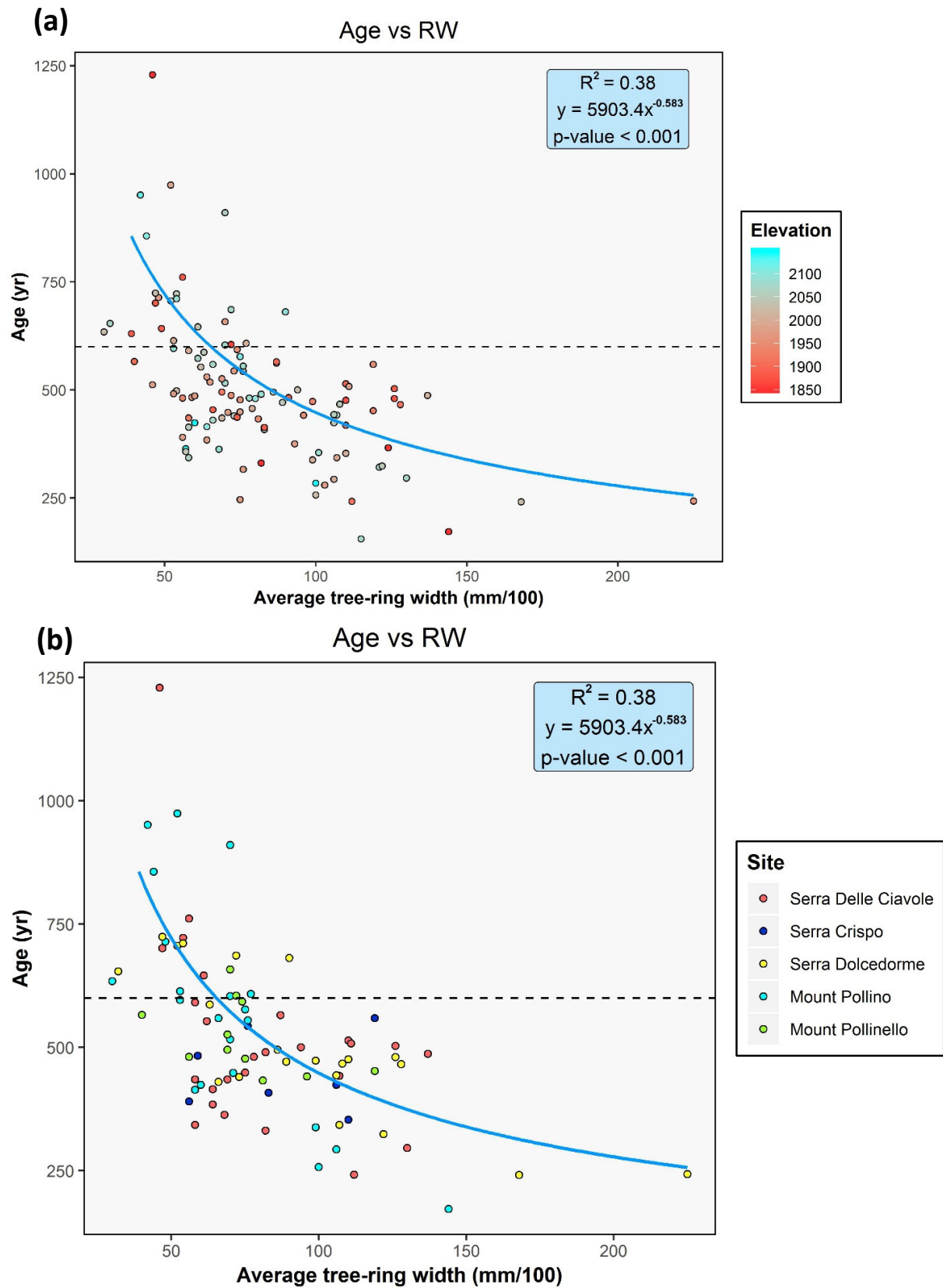


Fig. 8

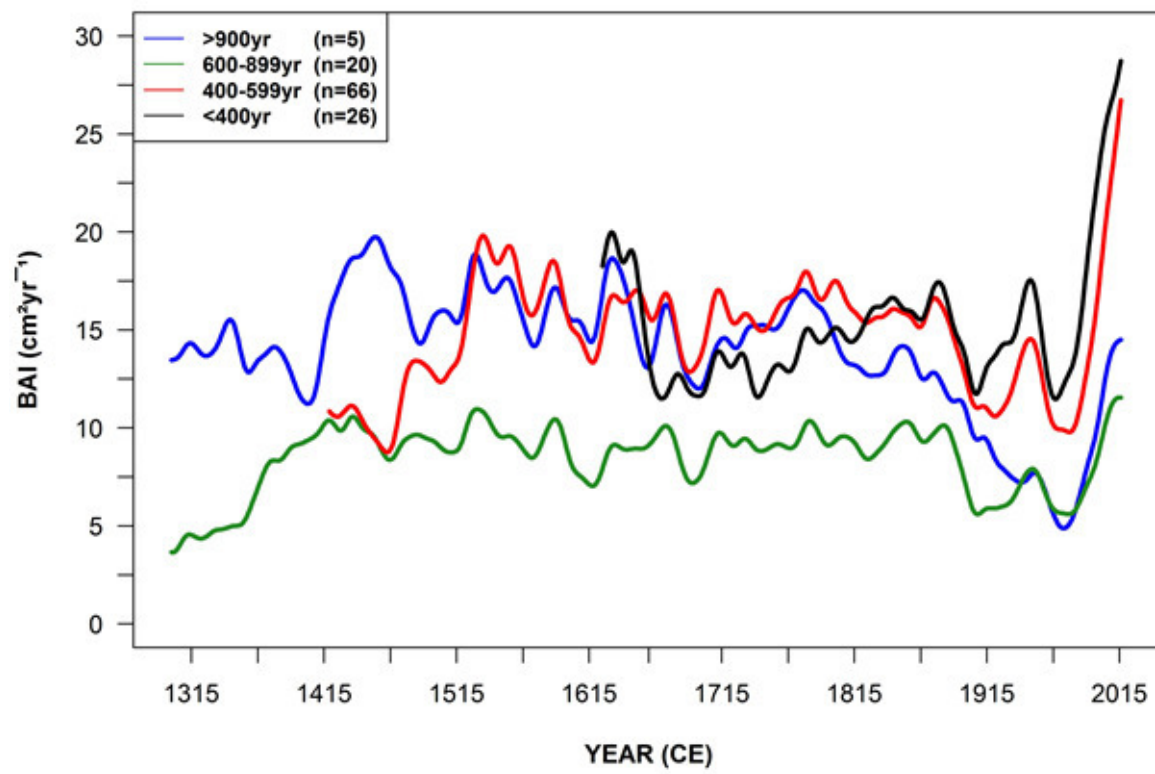


Fig. 9

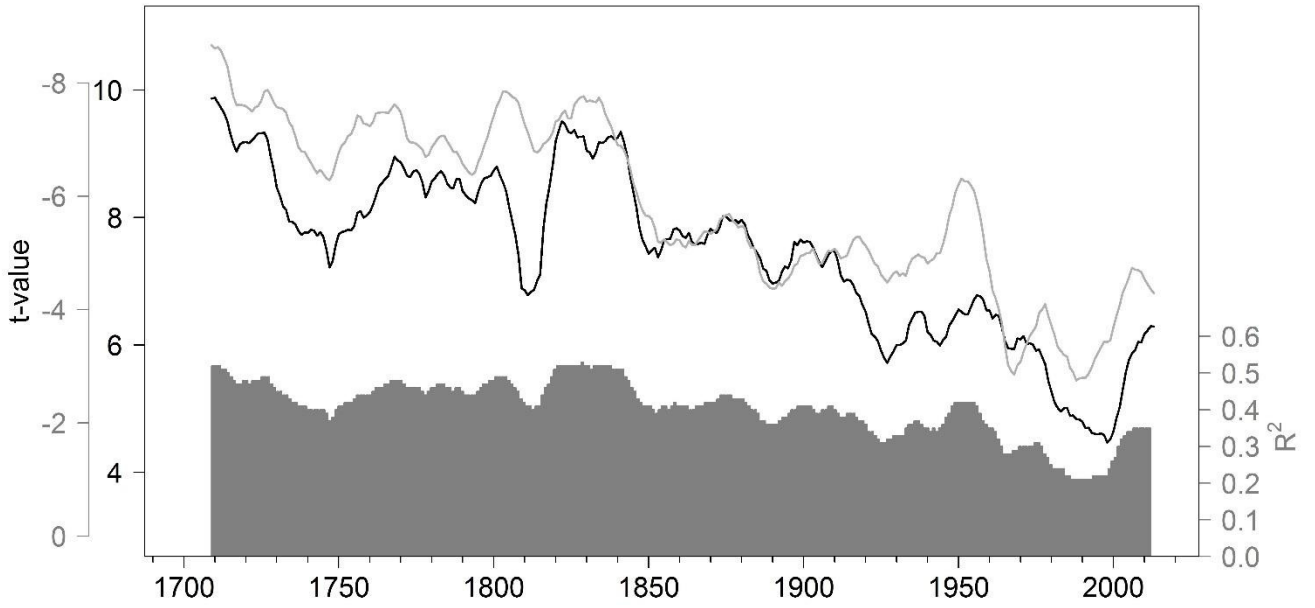


Fig. 10

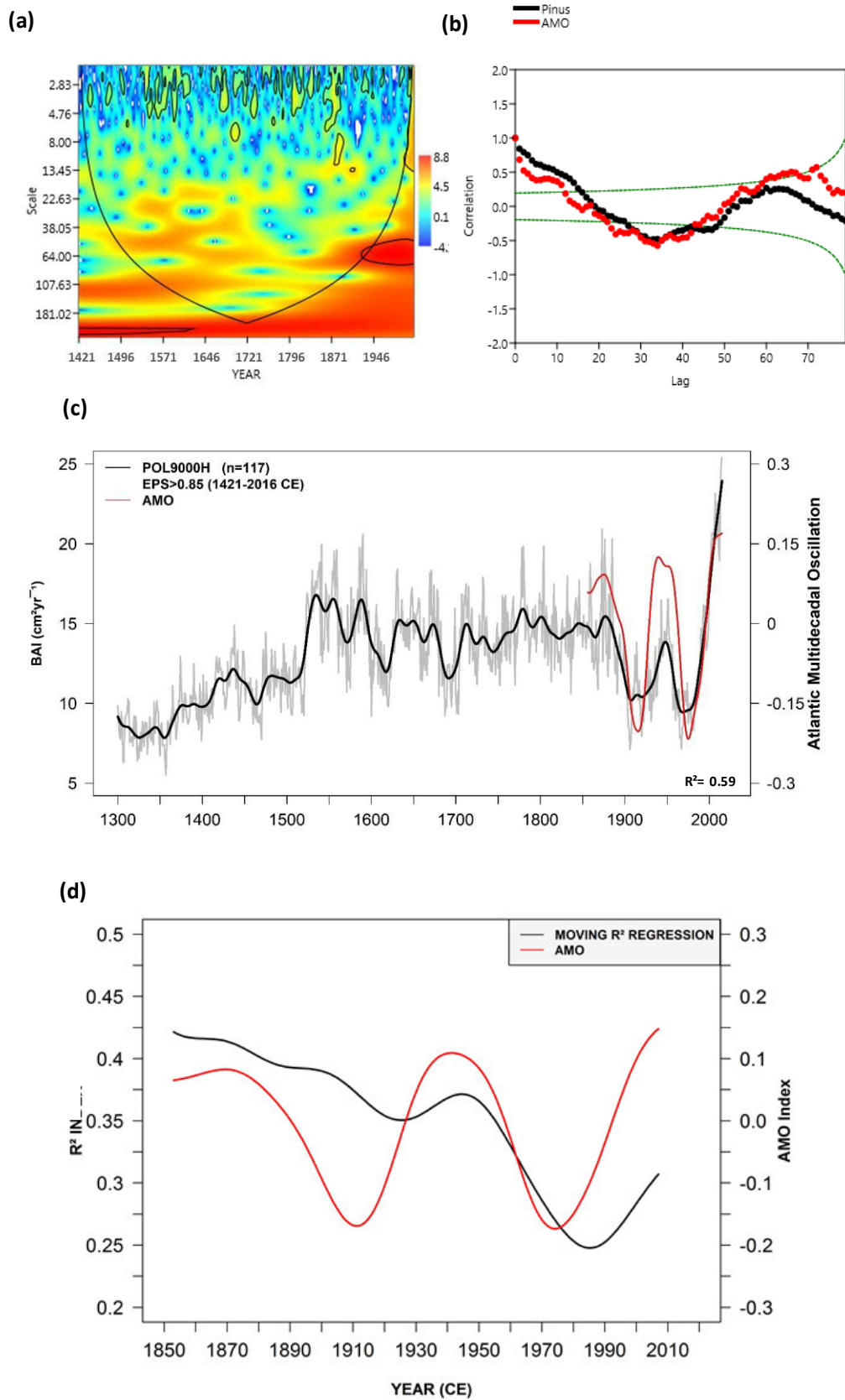


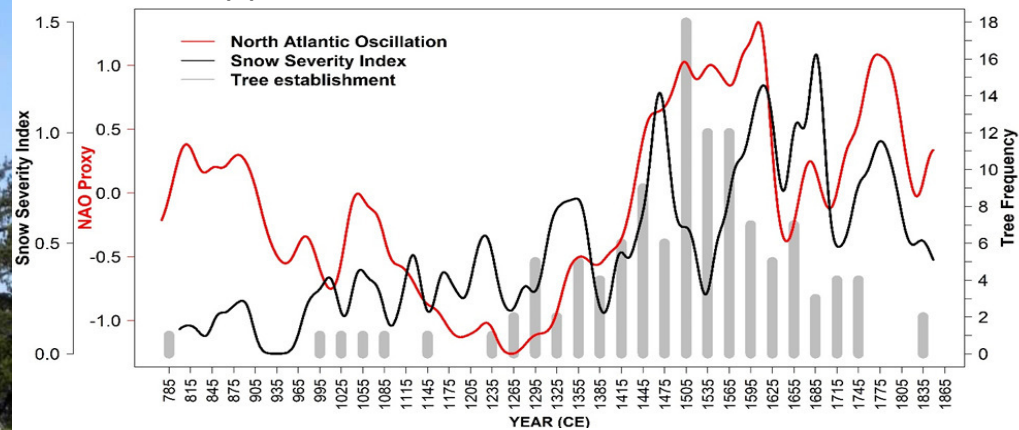
Fig. 11



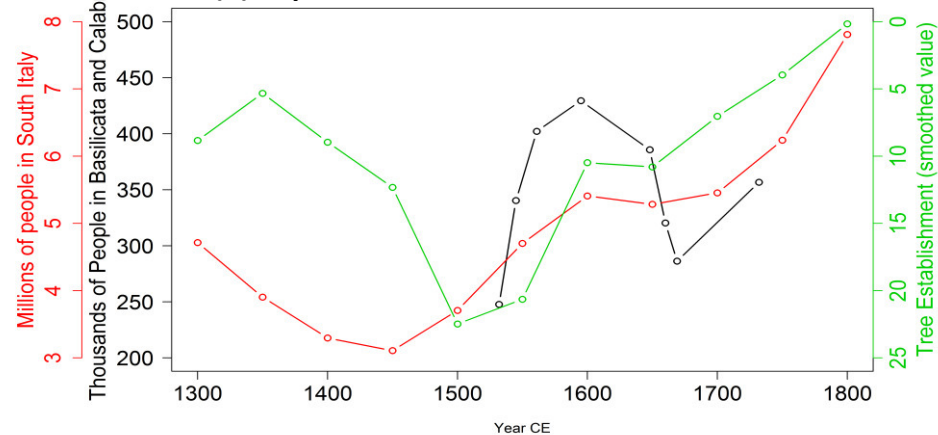
Fig. 12



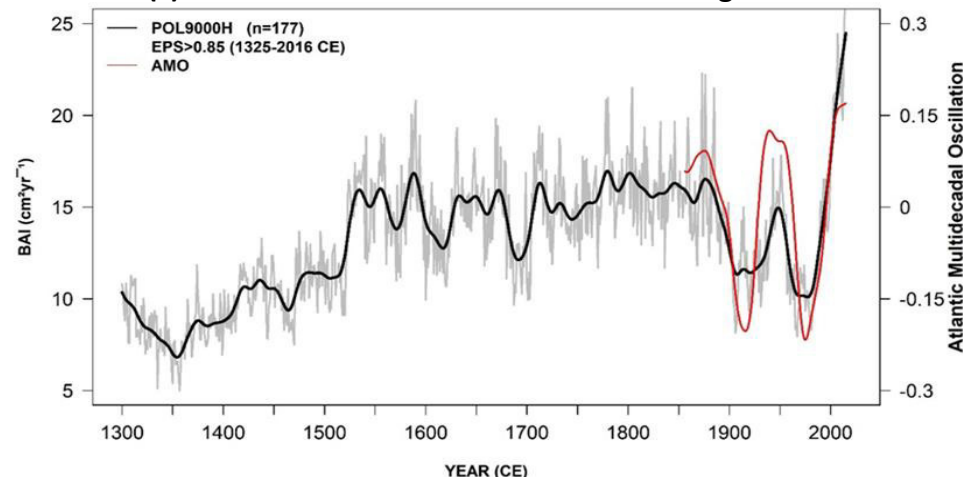
(a) Climate variations vs tree establishment



(b) Population trends vs tree establishment



(c) Atlantic multidecadal oscillation vs tree growth



Supplementary material

[Click here to download e-components: Anthropocene_Supporting Information.docx](#)