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

Article Type: Research Paper

Keywords: old trees; cliff habitats; tree growth pattern; North Atlantic Oscillation; Atlantic Multidecadal Oscillation; landscape rewilding

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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.



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Viterbo, Italy, 5th March 2019

Dear Editor and Associate Editor,

Please find attached a fully revised version of the manuscript.

We would like to thank you and the reviewers for the valuable suggestions that have allowed us to improve the manuscript. Changes were made with particular reference to the suggestions noted on the pdf file downloaded from the Anthropocene website.

We carefully considered all comments made by the reviewers, and our detailed answers are included below using italic font.

Reviewer #1:

This is much improved over the first version of the paper I reviewed, and the author(s) has done an admirable job with their arguments that the oldest age trees are temporally and spatially unique. I especially enjoyed reading about the human history they've been able to gather in regard to the trees' history; of course one great advantage to having these trees growing in Italy is that there is a long and well-known human history to draw upon! Overall this will be a valuable addition to the ecological history of this region, and to better understanding and management of these unique forests and trees.

Minor comments:

Abstract (and elsewhere in the discussion): "late XIV and XVI centuries), further intertwined with the late XV century"; not sure why the use of Roman numerals, please change to Hindu-Arabic.

Response: Changed as suggested.

The last paragraph of the first section of the results ("Establishment of the sampled trees took place mainly between 1300 and 1600 CE...") I think really should be moved to the discussion; seems more like interpretation of the actual results. These observations could easily be incorporated to other parts of the discussion.

Response: Changed We partially rewrote this paragraph and we kept the text to present Fig. 5 .

Figures: several of the axes labels are either very small (e.g., violin plots in Fig 3a) or otherwise indistinct (t- and R2-values in Fig 10); not sure how large these figures may end up in the published paper but I suggest enlarging and/or otherwise changing the axes to make them easier to read.

Response: Changed We reworked the requested figures.

Finally, the photographs in Fig 12 and included in the graphical abstract make me curious if the authors have also sampled the dead trees. It appears to be quite a lot of snags and logs, but I take it from this paper and other research I have seen from the Mount Pollino area that only living trees have been cored? I would expect that the dead trees have quite a story to tell as well, and trust that those are being sampled, which would add to the early history for the area.

Response: Changed Dead trees were not considered in this study. That's why we changed the photo in the graphical abstract. In the course of the sampling campaigns we have sampled some dead trees but since the ages do not differ from the average of the pine population we have not gone beyond at least for now.

Reviewer #2:

Using a large sample of old trees on the Pollino massif, the manuscript, 'Tree growth patterns associated with extreme longevity: implications for the ecology and conservation of primeval trees in a changing world', provides a rich overview on the growth of old trees in one region over the course of centuries in the context of changes in human demography, politics, and variations in climate. The images are gorgeous and add much to the study, as do many of the figures. The manuscript is well written and there is much learned from their results and discussion.

However, the title intimates a general pattern of tree growth patterns and implications for the future of old trees. The introduction makes a strong case as to why old/big trees are important to ecology and conservation, but the authors do not fully come back to those main points. There is much to learn from a study of >170 old trees in a population, but it is limited to one species (Limitation #1). Similarly, some of the citations are limited to a region or species and does not reflect much of what is known about other species. There is much literature from the western U.S. and others related to this topic that are not cited. The second limitation of the manuscript is the use of indices of climatic oscillations. What is

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the mechanism of this implied result? Related, the NAO is used to identify the establishment of these trees. However, most of these trees were cored at DBH. This is the last limitation. It is a significant limitation.

Limitation #1: Can the Heldreich's pine tree represent all species?

How do these results compare to other tree species? Can the Heldreich's pine tree be representative of the growth of old trees as the title implies? It is not evident. One solution is to restrict the title to the region or species. Another solution is to use data from the International Tree Ring Databank of trees from around the world to identify growth patterns associated with extreme longevity.

Response: Changed Heldreich's pine is a relict species of the Tertiary which occupies a subalpine belt in the mountains of southern Italy and the Balkans. As suggested by the reviewer, we have restricted the title to the Mediterranean mountain region.

The new title is therefore: "Tree growth patterns associated with extreme longevity: Implications for the ecology and conservation of primeval trees in Mediterranean mountains".

Limitation #2: Climate Response

The authors tie growth to the AMO. The figure plotting growth vs AMO is compelling, but how does the AMO influence growth? What is the mechanism? What are the climatic variables that drive the growth of these trees? The answers to these questions are not fully discussed. The authors presumably have the data to answer these questions. It is not clear why a climatic response is not calculated from the growth data. Presenting the climatic response would be easy to do and better help the reader understand why the AMO appears important to Heldreich's pine tree growth.

Response: Changed We calculated and discussed the climate variables that drive tree growth (Fig. S5). Moreover we introduced another climate index for snowfall that is correlated with the Atlantic Multidecadal Oscillation/AMO, and we partially rewrote and further explained the link between tree growth and AMO.

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The authors cored most of these trees at DBH, presumably 1.4 m above the ground, prompting the question: how long does it take these trees to reach this height? What is the variance around the estimation of how long it takes these trees to reach this height? It does not seem likely that the authors have these data. If so, this analysis should likely be removed from the study. Or, if the authors have the data, a more direct analysis should be done like the work of (Villalba and Veblen 1997).

Response: Changed As indicated in the manuscript for calculating the ages of tree establishment we added 15 years to the age measured at 1.30 m height using cores with the pith. Thanks to the recent work of Vitali et al. 2019 we used average height growth data for this pine species to calculate the average age (18 years) needed to reach 1.30 m height. The data were then merged into 30-year-old windows following the Sangüesa-Barreda et al. 2018 approach. It should be considered that Pinus heldreichii trees grow in low-density, open stands where saplings do not compete with each other. This results in low variability of height growth, and in relatively large average growth increments in early life stages (Fig. 6a).

Besides the specific changes mentioned above, we fully revised the text in accordance to the reviewer's suggestions.

Yours sincerely,

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Professor e-mail: piovesan@unitus.it

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1 **Tree growth patterns associated with extreme longevity:**
2 **implications for the ecology and conservation of primeval**
3 **trees in Mediterranean mountains**
4

5 **Gianluca Piovesan^{1,*} Franco Biondi², Michele Baliva¹, Anna Dinella^{1,3}, Luca Di Fiore²,**
6 **Vittoria Marchiano⁴. Emanuele Presutti Saba¹, Giuseppe De Vivo⁴, Aldo Schettino⁴, Alfredo**
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17 University of Tuscia, Via SC de Lellis, Viterbo, Italy; E-mail: piovesan@unitus.it
18

19
20 Short Running title: **Establishment and Growth patterns of old trees**
21

22 **Authors' contributions**

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

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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.

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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37

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

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

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

77 Slow, continuous stem growth is usually a premise for tree longevity (Bigler and Veblen,
78 2009; Johnson and Abrams, 2009; Piovesan et al., in review). Smaller tree-ring size and higher
79 wood density may improve vascular plasticity to withstand climate stress and enhance resilience to
80 recurrent canopy disturbance events throughout exceptionally long lifetimes (Di Filippo et al.,
81 2012). Some species, such as European beech (*Fagus sylvatica* L.), seem negligibly affected by
82 the progressive deterioration of physiological functions associated with age (Mencuccini et al.,
83 2005; Peñuelas and Munné-Bosch, 2010; Mencuccini, 2014), confirming the existence of
84 “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 (Könter 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

109 environmental change. After locating some Heldreich's pines of great longevity, we investigated
110 how old trees in this high-elevation Mediterranean environment survived land use changes and
111 long-lasting climatic episodes such as the Medieval warm period, the Little Ice Age, and lately
112 global change. Considering the temporal, environmental and cultural contexts that influenced the
113 stem growth histories of this old pine population expands our knowledge on ecological history and
114 lays a foundation for nature conservation policy in mountain landscapes (Gillson and Marchant
115 2015).

116

117 MATERIALS AND METHODS

118

119 *Study area*

120 Heldreich's pine forests are protected habitat in southern Europe under the Natura 2000 Directive
121 (95A0 High Oro-Mediterranean pine forests). This open forest habitat is restricted to mountains of
122 the southern Balkans, northern Greece, and southern Italy, where it characterizes the timberline
123 environment with limited undergrowth formed by sparse grasslands on often stony or rocky soils
124 (Fig. 1). Sampled trees were selected during a three-year research campaign aimed at clarifying
125 the biology and ecology of Heldreich's pine stands distributed throughout the Pollino massif (Fig.
126 2). Several rugged peaks (Pollino, Pollinello, Serra Dolcedorme, Serra delle Ciavole and Serra di
127 Crispo) occur at elevations between 1675 and 2267 m a.s.l., aligned in an amphitheater formation
128 covering about 12 km² of high mountain landscapes (Todaro et al., 2007). Our field collections
129 uncovered the oldest tree in Europe (Piovesan et al., 2018a), which we named *Italus* and was
130 shown to be 1230-years old by a combination of tree-ring and radiocarbon dating applied to stem
131 and root cores (Piovesan et. al., 2018b).

132

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

157 individual series, and the Atlantic Multidecadal Oscillation (AMO) time series at annual resolution
158 (Enfield et al., 2001; <https://www.esrl.noaa.gov/psd/data/timeseries/AMO/>), were smoothed using
159 the Gaussian function of the Past software (Hammer et al., 2001). Wavelet transform was used for
160 inspection of BAI chronologies at different scales using the Morlet function, and the significance
161 level (p-value <0.05) was plotted as a contour (chi-squared test according to Torrence and Compo,
162 1998) using a red-noise model with the estimated first order moving average autocorrelation
163 coefficient.

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

168

169 *Spatial analysis*

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

179

180

181 **RESULTS**

182

183 *Tree establishment, climate, and anthropogenic impacts*

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

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

195 Sampled trees were spatially clustered (Clark-Evans test: R = 0.27, p-value < 0.001). These
196 forest stands are located near treeline up to 2200 m elevation, above which the dominant plant
197 species are shrubs or grasses (Fig. 5). Trees whose age was less than 600 years were less spatially
198 clustered (Clark-Evans test: R = 0.32, p-value < 0.001) than older trees (Clark- Evans test: R =
199 0.19, p-value < 0.001), which were typically found in few cliff sites. Millennium-old trees, i.e.
200 individuals older than 900 years, were not randomly distributed over the landscape, as they
201 concentrated in the most remote and topographically complex areas. Most of the oldest trees were
202 located on west-facing summit cliffs between 2000 and 2100 m elevation. The oldest pine, named
203 *Italus* (Piovesan et al., 2018a), however, was located at lower elevation (1850 m) and on a very

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

206

207 *Growth variability in time*

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

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

228 high correlations were also found with the *Pinus heldreichii* chronology from Albania (Seim et al.,
229 2012), clearly suggesting that the Pollino and Albania mountains experience similar climatic
230 variability. Lower, but still 99.9% significant, correlations were observed between *Italus* and the
231 oldest trees (age > 900 years), of which three were discovered during the recent sampling
232 campaign (Fig. S2b, Table S1b).

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

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

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

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

257

258 **DISCUSSION**

259

260 *Old tree ecology*

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

276 Overall, tree-ring series of old Heldreich's pines are characterized by relatively large tree-
277 ring widths in the first cambial years, followed by a drop towards a very long sequence of
278 extremely small rings, a typical growth pattern of isolated trees (Fritts, 1976; Biondi and Qeadan,
279 2008). Given the stringent limits to wood growth imposed by site conditions, sensitivity to climate
280 is high (see also bootstrapped correlation functions in Fig. S5), thereby facilitating tree-ring dating
281 even for the oldest samples. The growth trajectory of most Heldreich's pines younger than 600
282 years resembles that of millennium-old individuals, but trees of intermediate ages (600-900 years)
283 experienced on average lower annual increments. Since the *Italus* growth trajectory is replicated
284 by those of other millennium-old trees in the same area, we expect a relevant pool of actually
285 smaller (DBH < 90 cm) - and younger - Heldreich's pines in the Pollino massif to continue
286 growing, provided they can survive potential future threats caused by Anthropocene changes.

287 Tree longevity is commonly assumed to be inversely proportional with growth vigor (Fig.
288 1 in Black et al., 2008; Fig. 5.5 of Briffa and Melvin, 2011; Fig. 3 in Seim et al., 2012; Di Filippo
289 et al., 2017; Piovesan et al. in press). When examining the growth trajectories of Heldreich's pine
290 in the Pollino area, most of the millennium-old individuals occupy the middle-lower portion of the
291 graph, suggesting both that extreme tree longevity requires slow growth and that extremely harsh
292 conditions are detrimental to long life. Our dataset also showed that millennium-old Heldreich's
293 pines in the Pollino area have maintained similar growth patterns regardless of appreciable
294 differences in tree age. In temperate closed old-growth forests, tree diameter has generally no
295 connection with age because of the very complex growth histories of older trees, characterized by
296 slow growth and by suppression and release periods (Di Filippo et al., 2017). Instead, in the open
297 pine stands we sampled, located above the high-mountain beech belt, larger individuals were
298 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). Anthropoc 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

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

375

376 *Growth variability, temperature, and AMO trends*

377 *Italus* and the majority of Heldreich's pines on the Pollino Massif have shown a growth increase
378 in recent decades (Figs. 9 and 11). Such pattern – also found in bristlecone pine (Salzer et al.
379 2009) – contradicts the growth decline of tree-ring width that typically occurs as cambial age
380 increases (Fritts 1976; Biondi and Qeadan, 2008), and it does not match the widespread growth
381 decline and tree dieback that various Mediterranean ecosystems have recently experienced
382 (Dorado-Liñán et al., 2017). Our research is only a first step towards uncovering how growth
383 history of these old pines is influenced by complex non-linear processes linked to human impacts
384 in a changing environment, such as local land use (see Todaro et al., 2007; Vitali et al. 2019),
385 global increases in greenhouse gases, and regional changes in atmospheric pollution. Further
386 studies on the driving factors behind the resumed growth since the 1980s should therefore
387 consider as possibilities higher air temperature under non-limiting water stress (Granda et al.,
388 2017), carbon dioxide fertilization, trends in ultraviolet radiation, and the deposition of air
389 pollutants.

390 The high-elevation bioclimatic belt, where the oldest trees were found, is mainly limited by
391 low temperature, as expected in subalpine forests worldwide (e.g. Salzer et al. 2009, Silva et al.
392 2016, but see Sigdel et al. 2018 for the relevant role of precipitation in arid climates). Both the
393 significant variables in bootstrapped correlation functions and the growth variability agreement
394 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.,

419 2016 for a discussion). In the last two centuries the predictive power of DBH and age on stem
420 increment showed a decreasing trend. At the same time, older trees had lower BAI compared to
421 younger ones of similar dimension. This growth pattern is unique during the last 700 years,
422 suggesting that younger trees may have become more productive in a warming climate (e.g.
423 Camarero et al., 2015). However, since mature trees are more resilient than saplings to global
424 warming (e.g. Zhang et al., 2015), the acclimation capacity of the new cohort is uncertain.

425

426 *Conservation management implications*

427 Pollino National Park is the largest protected natural area in Italy, and our study has shown that
428 the Park harbors a unique concentration of old-growth stands, with several trees either older than
429 900 years or likely to reach that advanced age. Current conservation policies in the Park ensure the
430 preservation of this majestic and primeval tree population within strict reserves using an approach
431 that is landscape-scale and longstanding. Additional social and cultural benefits (Blicharska and
432 Mikusiński, 2014) derive from the fact that Heldreich's pine is an iconic species for biological
433 conservation in mountains of the northern Mediterranean Basin. Reconstructing the growth history
434 of the oldest trees therefore helps consolidating the territorial identity and collective well-being of
435 the local people, which need to be directly involved in order to guarantee the wilderness status of
436 the protected areas. Raising public awareness of the importance to preserve these old-growth
437 stands while maintaining a sustainable development has in fact allowed the Park to become locally
438 accepted and cherished, after being initially met with opposition at the time of its creation in the
439 1990s, which led to the torching of the "Zi Peppe" tree, a symbol for the newly designated Park.

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

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

453

454 **Conclusion**

455 Millennium-old trees and their growth trends are emblematic and unique environmental indicators
456 in this age of global changes. Old Heldreich's pines escaped medieval human impacts in remote
457 cliff sites of the Pollino massif, then a wave of pine stands established after a human demographic
458 crisis during the late 14th and 16th centuries, further intertwined with the late 15th century
459 establishment of small rural communities by people coming from Albania (Arbësh). Remote
460 mountains and cliff habitat confirmed to be long-term stable refugia for wildlife conservation
461 (Larson et al. 2000b; Pimm 2008; Tang et al. 2018), especially Heldreich's pine, as in the case of
462 other relict plants from the Tertiary era in different ecoregions (e.g., Tang et al., 2015; Qian et al.,
463 2016; White et al., 2016). These unique environments are understudied (Covy et al., 2019), but
464 cliffs can protect a wide range of organisms during periods of land exploitation, hence they
465 become stepping stones during rewilding phases of the landscape. Modern land abandonment from
466 the collapse of sheep-herding and climate warming have generated a new pulse of tree

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

472 When considering *Italus*, its establishment occurred within the cold period of the Dark Age
473 (400 – 865 CE; Helama et al., 2017). The oldest trees have then survived through the Medieval
474 Warm period, the Little Ice Age, and the recent warming, which corresponds to a renewed
475 increase in stem growth. Trees capable of long life and of tolerating climatic changes are
476 particularly relevant to management strategies aimed at increasing carbon storage in forested
477 landscapes over long time periods (Körner, 2017; Musavi et al. 2017). Further studies should be
478 aimed at determining if just the oldest trees or rather the entire Heldreich's pine population has
479 peculiar genetic features or simply a plastic response to climatic shifts.

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

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

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

502
503
504

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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.

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.

36

37

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

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

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

77 Slow, continuous stem growth is usually a premise for tree longevity (Bigler and Veblen,
78 2009; Johnson and Abrams, 2009; Piovesan et al., in review). Smaller tree-ring size and higher
79 wood density may improve vascular plasticity to withstand climate stress and enhance resilience to
80 recurrent canopy disturbance events throughout exceptionally long lifetimes (Di Filippo et al.,
81 2012). Some species, such as European beech (*Fagus sylvatica* L.), seem negligibly affected by
82 the progressive deterioration of physiological functions associated with age (Mencuccini et al.,
83 2005; Peñuelas and Munné- Bosch, 2010; Mencuccini, 2014), confirming the existence of
84 “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 (Könter 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

109 environmental change. After locating some Heldreich's pines of great longevity, we investigated
110 how old trees in this high-elevation Mediterranean environment survived land use changes and
111 long-lasting climatic episodes such as the Medieval warm period, the Little Ice Age, and lately
112 global change. Considering the temporal, environmental and cultural contexts that influenced the
113 stem growth histories of this old pine population expands our knowledge on ecological history and
114 lays a foundation for nature conservation policy in mountain landscapes (Gillson and Marchant
115 2015).

116

117 **MATERIALS AND METHODS**

118

119 *Study area*

120 Heldreich's pine forests are protected habitat in southern Europe under the Natura 2000 Directive
121 (95A0 High Oro-Mediterranean pine forests). This open forest habitat is restricted to mountains of
122 the southern Balkans, northern Greece, and southern Italy, where it characterizes the timberline
123 environment with limited undergrowth formed by sparse grasslands on often stony or rocky soils
124 (Fig. 1). Sampled trees were selected during a three-year research campaign aimed at clarifying
125 the biology and ecology of Heldreich's pine stands distributed throughout the Pollino massif (Fig.
126 2). Several rugged peaks (Pollino, Pollinello, Serra Dolcedorme, Serra delle Ciavole and Serra di
127 Crispo) occur at elevations between 1675 and 2267 m a.s.l., aligned in an amphitheater formation
128 covering about 12 km² of high mountain landscapes (Todaro et al., 2007). Our field collections
129 uncovered the oldest tree in Europe (Piovesan et al., 2018a), which we named *Italus* and was
130 shown to be 1230-years old by a combination of tree-ring and radiocarbon dating applied to stem
131 and root cores (Piovesan et. al., 2018b).

132

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

157 individual series, and the Atlantic Multidecadal Oscillation (AMO) time series at annual resolution
158 (Enfield et al., 2001; <https://www.esrl.noaa.gov/psd/data/timeseries/AMO/>), were smoothed using
159 the Gaussian function of the Past software (Hammer et al., 2001). Wavelet transform was used for
160 inspection of BAI chronologies at different scales using the Morlet function, and the significance
161 level (p-value <0.05) was plotted as a contour (chi-squared test according to Torrence and Compo,
162 1998) using a red-noise model with the estimated first order moving average autocorrelation
163 coefficient.

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

168

169 *Spatial analysis*

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

179

180

181 RESULTS

182

183 *Tree establishment, climate, and anthropogenic impacts*

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

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

195 Sampled trees were spatially clustered (Clark-Evans test: $R = 0.27$, p-value < 0.001). These
196 forest stands are located near treeline up to 2200 m elevation, above which the dominant plant
197 species are shrubs or grasses (Fig. 5). Trees whose age was less than 600 years were less spatially
198 clustered (Clark-Evans test: $R = 0.32$, p-value < 0.001) than older trees (Clark-Evans test: $R =$
199 0.19 , p-value < 0.001), which were typically found in few cliff sites. Millennium-old trees, i.e.
200 individuals older than 900 years, were not randomly distributed over the landscape, as they
201 concentrated in the most remote and topographically complex areas. Most of the oldest trees were
202 located on west-facing summit cliffs between 2000 and 2100 m elevation. The oldest pine, named
203 *Italus* (Piovesan et al., 2018a), however, was located at lower elevation (1850 m) and on a very

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

206

207 *Growth variability in time*

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

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

228 high correlations were also found with the *Pinus heldreichii* chronology from Albania (Seim et al.,
229 2012), clearly suggesting that the Pollino and Albania mountains experience similar climatic
230 variability. Lower, but still 99.9% significant, correlations were observed between *Italus* and the
231 oldest trees (age > 900 years), of which three were discovered during the recent sampling
232 campaign (Fig. S2b, Table S1b).

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

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

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

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

257

258 **DISCUSSION**

259

260 *Old tree ecology*

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

276 Overall, tree-ring series of old Heldreich's pines are characterized by relatively large tree-
277 ring widths in the first cambial years, followed by a drop towards a very long sequence of
278 extremely small rings, a typical growth pattern of isolated trees (Fritts, 1976; Biondi and Qeadan,
279 2008). Given the stringent limits to wood growth imposed by site conditions, sensitivity to climate
280 is high (see also bootstrapped correlation functions in Fig. S5), thereby facilitating tree-ring dating
281 even for the oldest samples. The growth trajectory of most Heldreich's pines younger than 600
282 years resembles that of millennium-old individuals, but trees of intermediate ages (600-900 years)
283 experienced on average lower annual increments. Since the *Italus* growth trajectory is replicated
284 by those of other millennium-old trees in the same area, we expect a relevant pool of actually
285 smaller (DBH < 90 cm) - and younger - Heldreich's pines in the Pollino massif to continue
286 growing, provided they can survive potential future threats caused by Anthropocene changes.

287 Tree longevity is commonly assumed to be inversely proportional with growth vigor (Fig.
288 1 in Black et al., 2008; Fig. 5.5 of Briffa and Melvin, 2011; Fig. 3 in Seim et al., 2012; Di Filippo
289 et al., 2017; Piovesan et al. in press). When examining the growth trajectories of Heldreich's pine
290 in the Pollino area, most of the millennium-old individuals occupy the middle-lower portion of the
291 graph, suggesting both that extreme tree longevity requires slow growth and that extremely harsh
292 conditions are detrimental to long life. Our dataset also showed that millennium-old Heldreich's
293 pines in the Pollino area have maintained similar growth patterns regardless of appreciable
294 differences in tree age. In temperate closed old-growth forests, tree diameter has generally no
295 connection with age because of the very complex growth histories of older trees, characterized by
296 slow growth and by suppression and release periods (Di Filippo et al., 2017). Instead, in the open
297 pine stands we sampled, located above the high-mountain beech belt, larger individuals were
298 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). Anthropogenic 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

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

375

376 *Growth variability, temperature, and AMO trends*

377 *Italus* and the majority of Heldreich's pines on the Pollino Massif have shown a growth increase
378 in recent decades (Figs. 9 and 11). Such pattern – also found in bristlecone pine (Salzer et al.
379 2009) – contradicts the growth decline of tree-ring width that typically occurs as cambial age
380 increases (Fritts 1976; Biondi and Qeadan, 2008), and it does not match the widespread growth
381 decline and tree dieback that various Mediterranean ecosystems have recently experienced
382 (Dorado-Liñán et al., 2017). Our research is only a first step towards uncovering how growth
383 history of these old pines is influenced by complex non-linear processes linked to human impacts
384 in a changing environment, such as local land use (see Todaro et al., 2007; Vitali et al. 2019),
385 global increases in greenhouse gases, and regional changes in atmospheric pollution. Further
386 studies on the driving factors behind the resumed growth since the 1980s should therefore
387 consider as possibilities higher air temperature under non-limiting water stress (Granda et al.,
388 2017), carbon dioxide fertilization, trends in ultraviolet radiation, and the deposition of air
389 pollutants.

390 The high-elevation bioclimatic belt, where the oldest trees were found, is mainly limited by
391 low temperature, as expected in subalpine forests worldwide (e.g. Salzer et al. 2009, Silva et al.
392 2016, but see Sigdel et al. 2018 for the relevant role of precipitation in arid climates). Both the
393 significant variables in bootstrapped correlation functions and the growth variability agreement
394 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.,

419 2016 for a discussion). In the last two centuries the predictive power of DBH and age on stem
420 increment showed a decreasing trend. At the same time, older trees had lower BAI compared to
421 younger ones of similar dimension. This growth pattern is unique during the last 700 years,
422 suggesting that younger trees may have become more productive in a warming climate (e.g.
423 Camarero et al., 2015). However, since mature trees are more resilient than saplings to global
424 warming (e.g. Zhang et al., 2015), the acclimation capacity of the new cohort is uncertain.

425

426 *Conservation management implications*

427 Pollino National Park is the largest protected natural area in Italy, and our study has shown that
428 the Park harbors a unique concentration of old-growth stands, with several trees either older than
429 900 years or likely to reach that advanced age. Current conservation policies in the Park ensure the
430 preservation of this majestic and primeval tree population within strict reserves using an approach
431 that is landscape-scale and longstanding. Additional social and cultural benefits (Blicharska and
432 Mikusiński, 2014) derive from the fact that Heldreich's pine is an iconic species for biological
433 conservation in mountains of the northern Mediterranean Basin. Reconstructing the growth history
434 of the oldest trees therefore helps consolidating the territorial identity and collective well-being of
435 the local people, which need to be directly involved in order to guarantee the wilderness status of
436 the protected areas. Raising public awareness of the importance to preserve these old-growth
437 stands while maintaining a sustainable development has in fact allowed the Park to become locally
438 accepted and cherished, after being initially met with opposition at the time of its creation in the
439 1990s, which led to the torching of the "Zi Peppe" tree, a symbol for the newly designated Park.

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

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

453

454 **Conclusion**

455 Millennium-old trees and their growth trends are emblematic and unique environmental indicators
456 in this age of global changes. Old Heldreich's pines escaped medieval human impacts in remote
457 cliff sites, then a wave of pine stands established after a human demographic crisis during the late
458 14th and 16th centuries, further intertwined with the late 15th century establishment of small rural
459 communities by people coming from Albania (Arbësh). Remote mountains and cliff habitat
460 confirmed to be long-term stable refugia for wildlife conservation (Larson et al. 2000b;
461 Pimm2008; Tang et al. 2018), especially Heldreich's pine, as in the case of other relict plants from
462 the Tertiary era in different ecoregions (e.g., Tang et al., 2015; Qian et al., 2016; White et al.,
463 2016). These unique environments are understudied (Covy et al., 2019), but cliffs can protect a
464 wide range of organisms during periods of land exploitation, hence they become stepping stones
465 during rewilding phases of the landscape. Modern land abandonment from the collapse of sheep-
466 herding and climate warming have generated a new pulse of tree recruitment, leading to a high-

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

472 When considering *Italus*, its establishment occurred within the cold period of the Dark Age
473 (400 – 865 CE; Helama et al., 2017). The oldest trees have then survived through the Medieval
474 Warm period, the Little Ice Age, and the recent warming, which corresponds to a renewed
475 increase in stem growth. Trees capable of long life and of tolerating climatic changes are
476 particularly relevant to management strategies aimed at increasing carbon storage in forested
477 landscapes over long time periods (Körner, 2017; Musavi et al. 2017). Further studies should be
478 aimed at determining if just the oldest trees or rather the entire Heldreich’s pine population has
479 peculiar genetic features or simply a plastic response to climatic shifts.

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

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

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

502

503

504

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Acknowledgments

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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

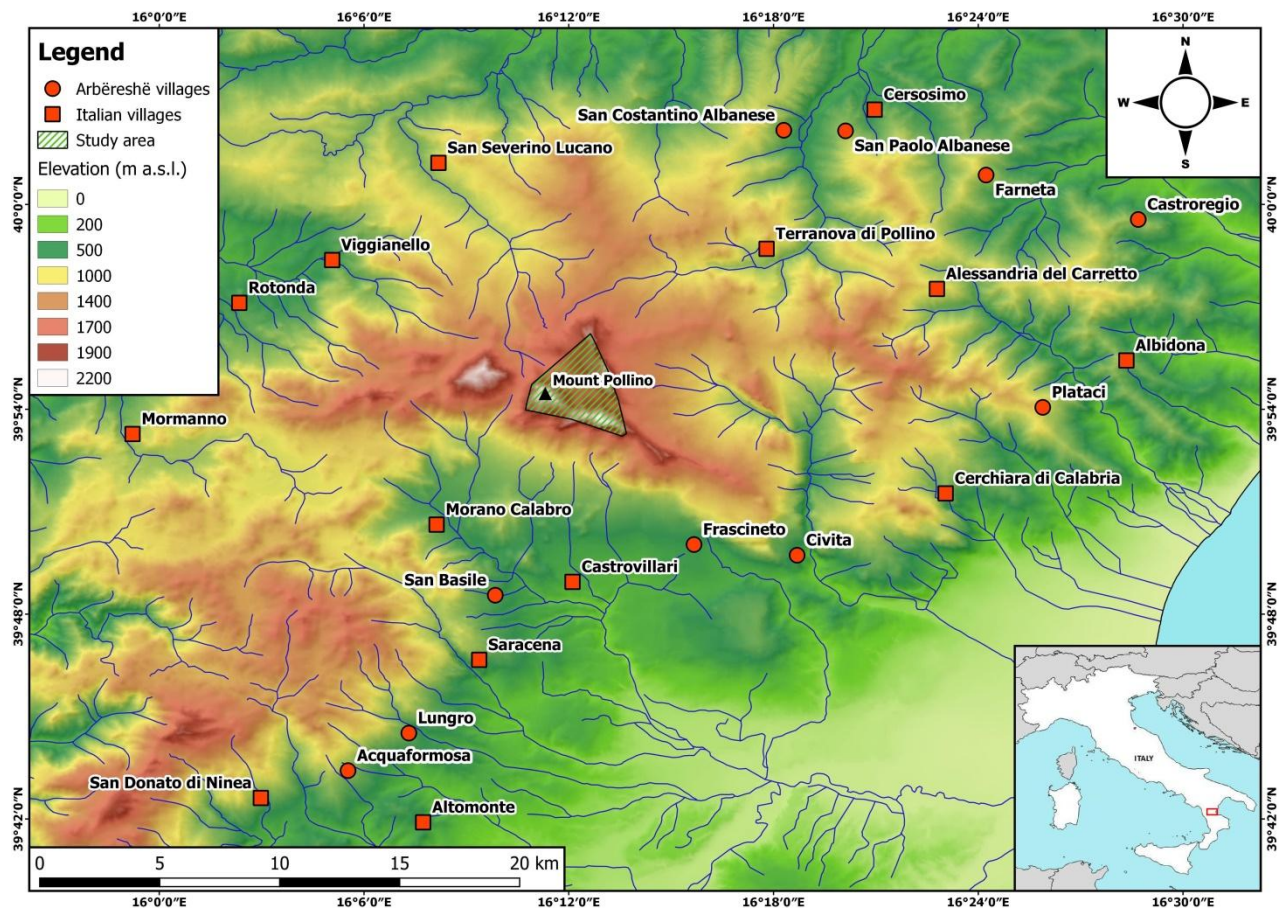


Fig. 2

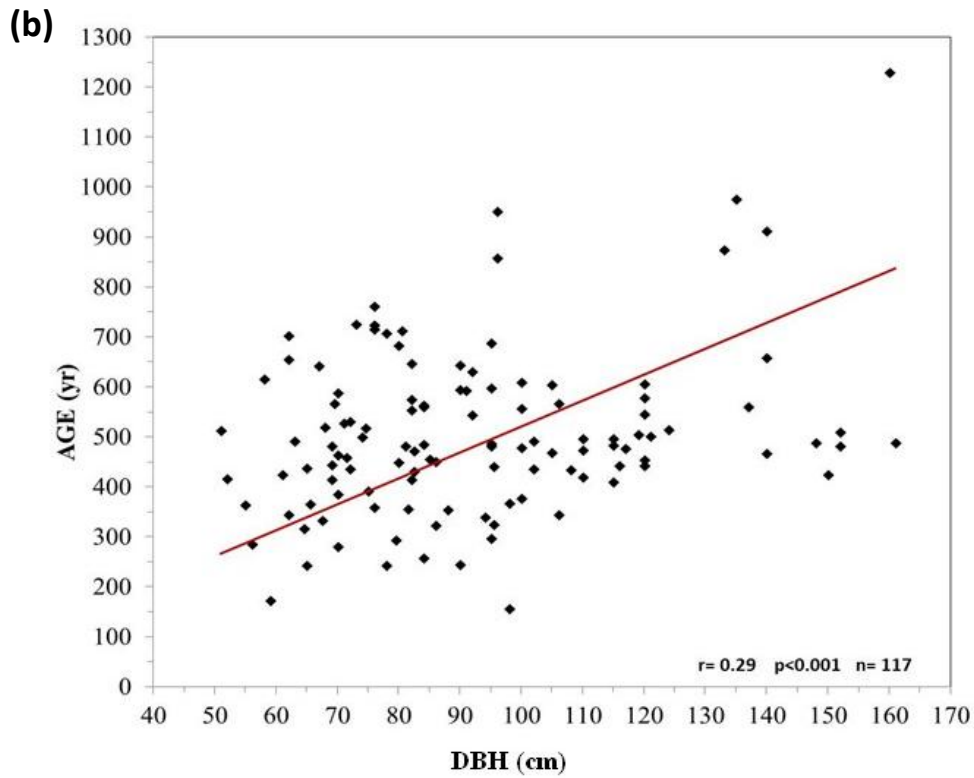
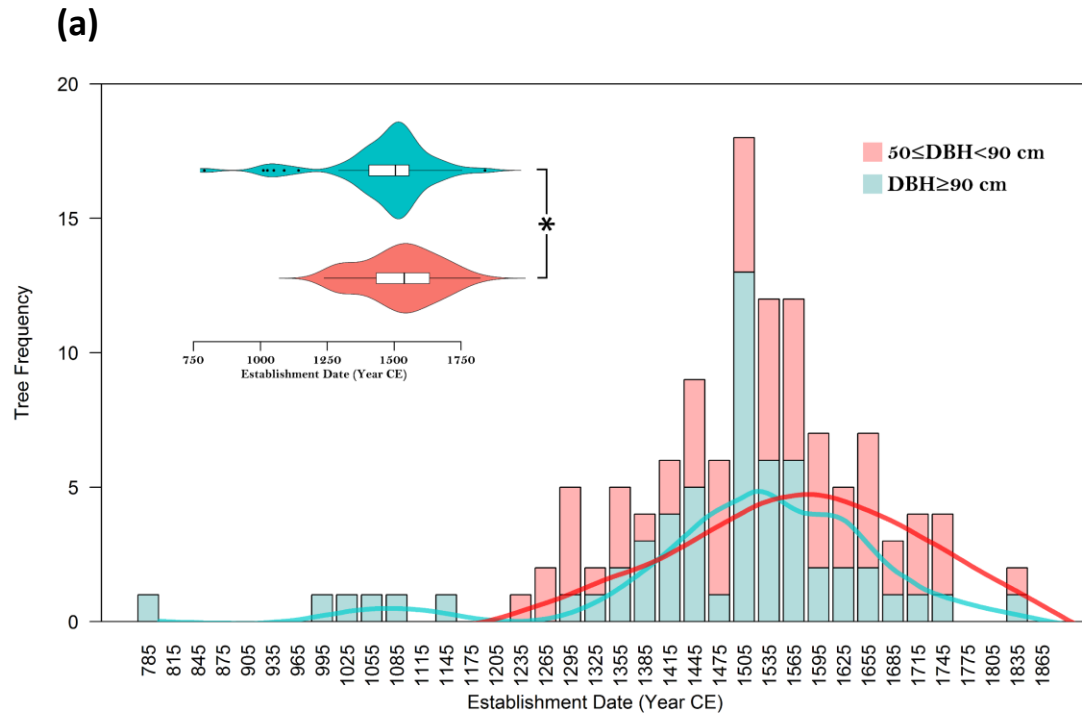


Fig.3

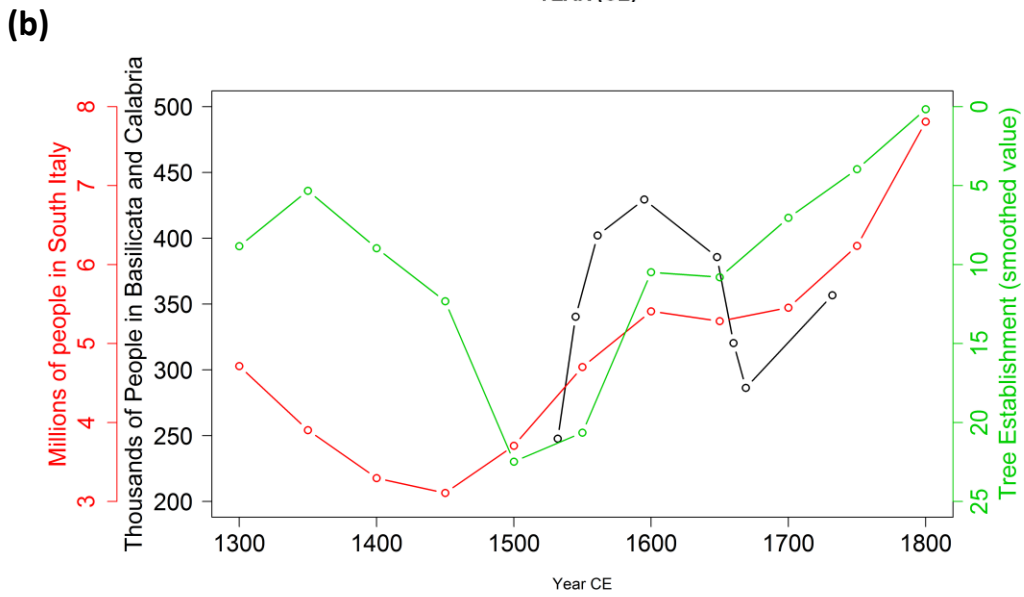
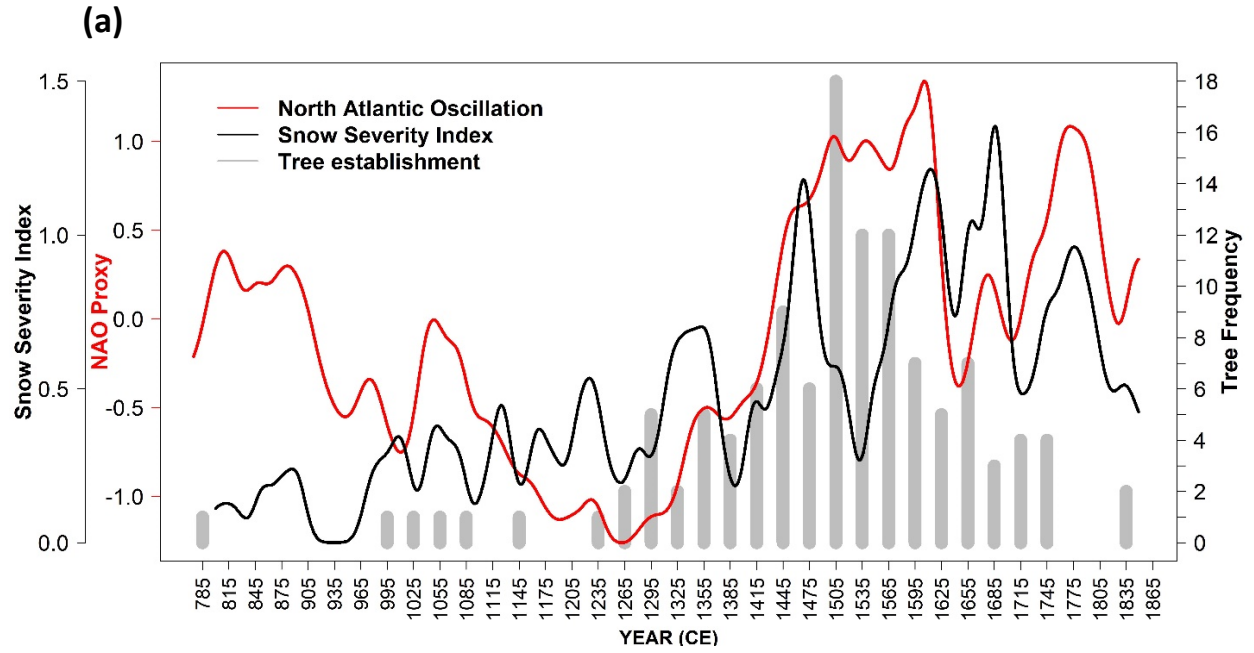


Fig. 4

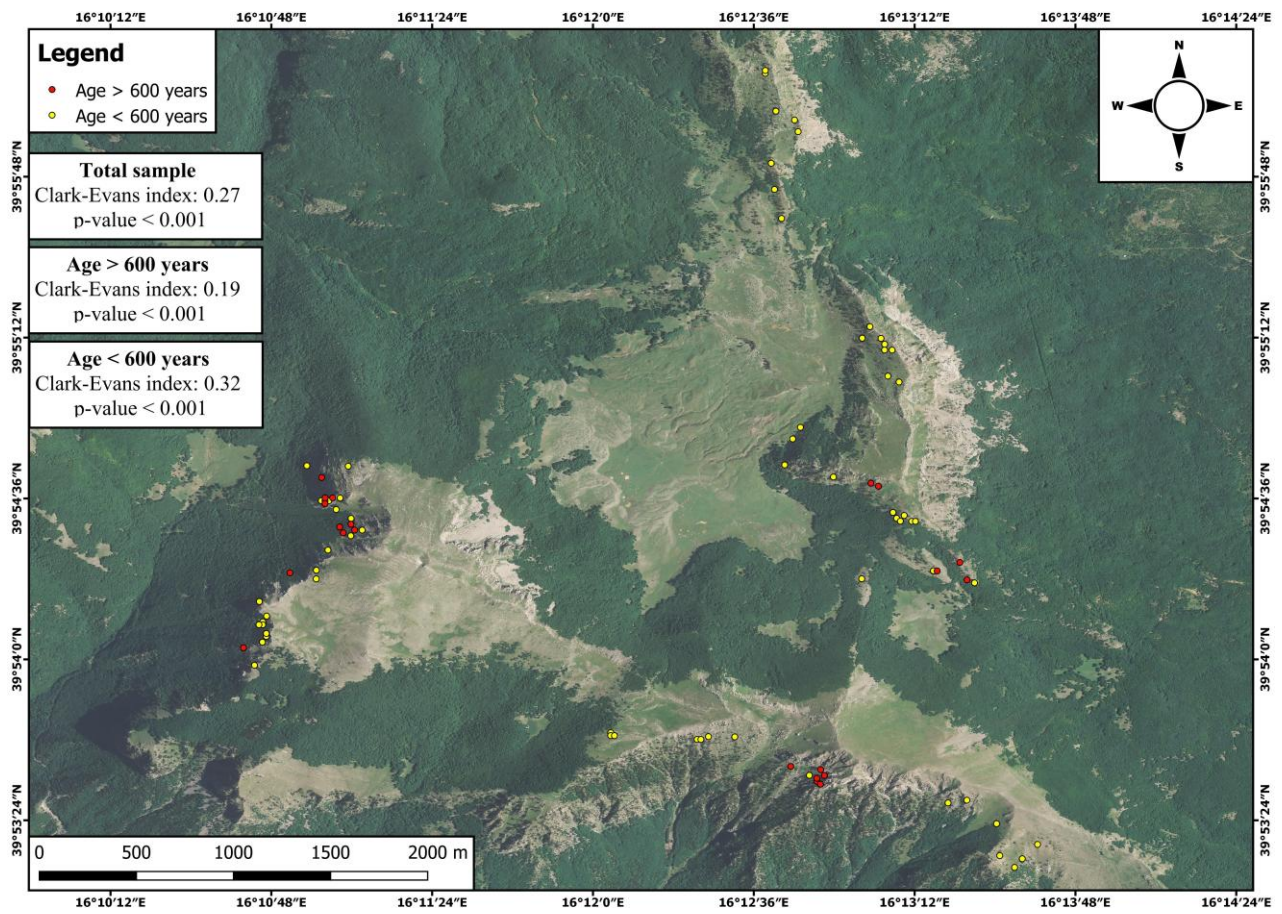


Fig. 5

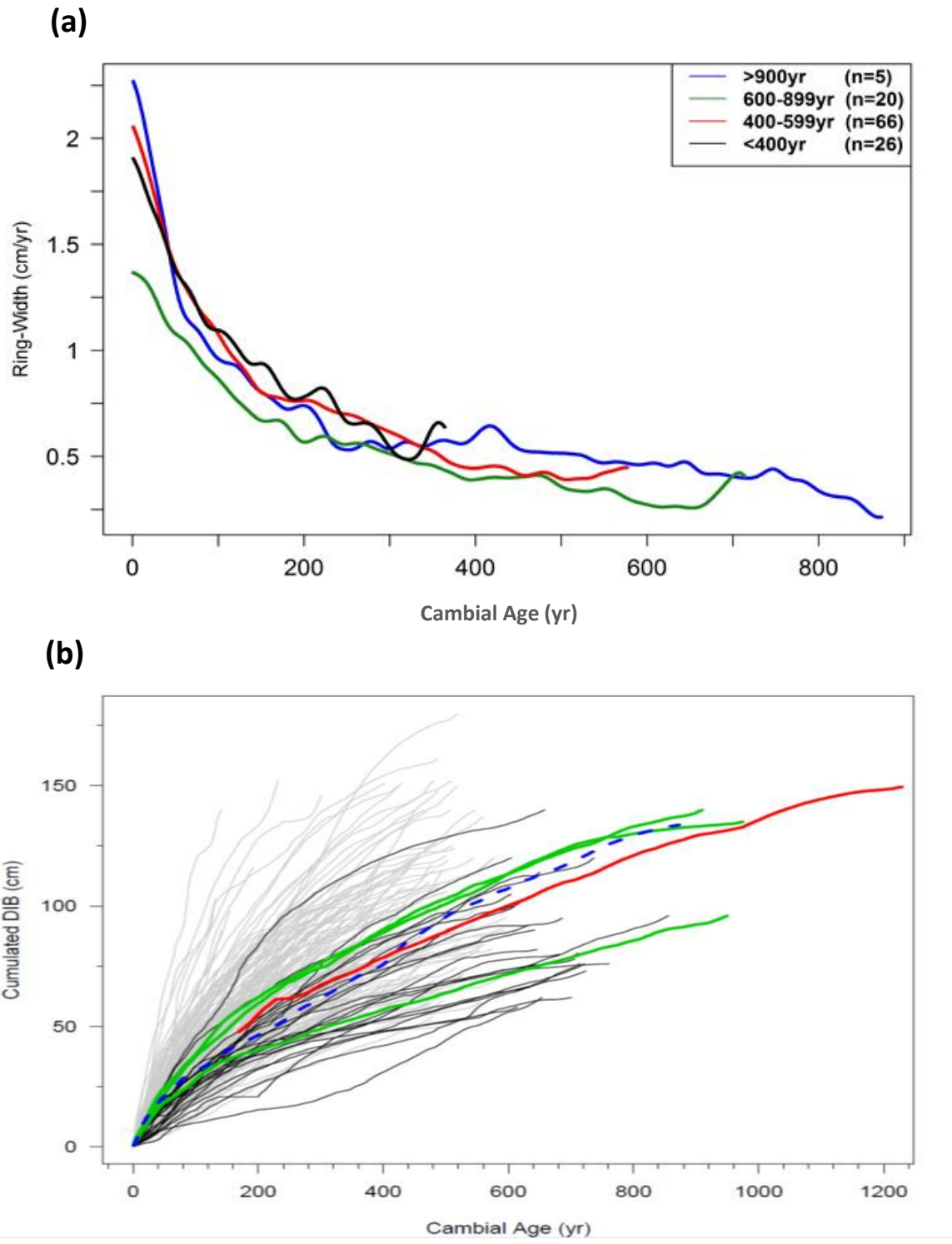


Fig. 6

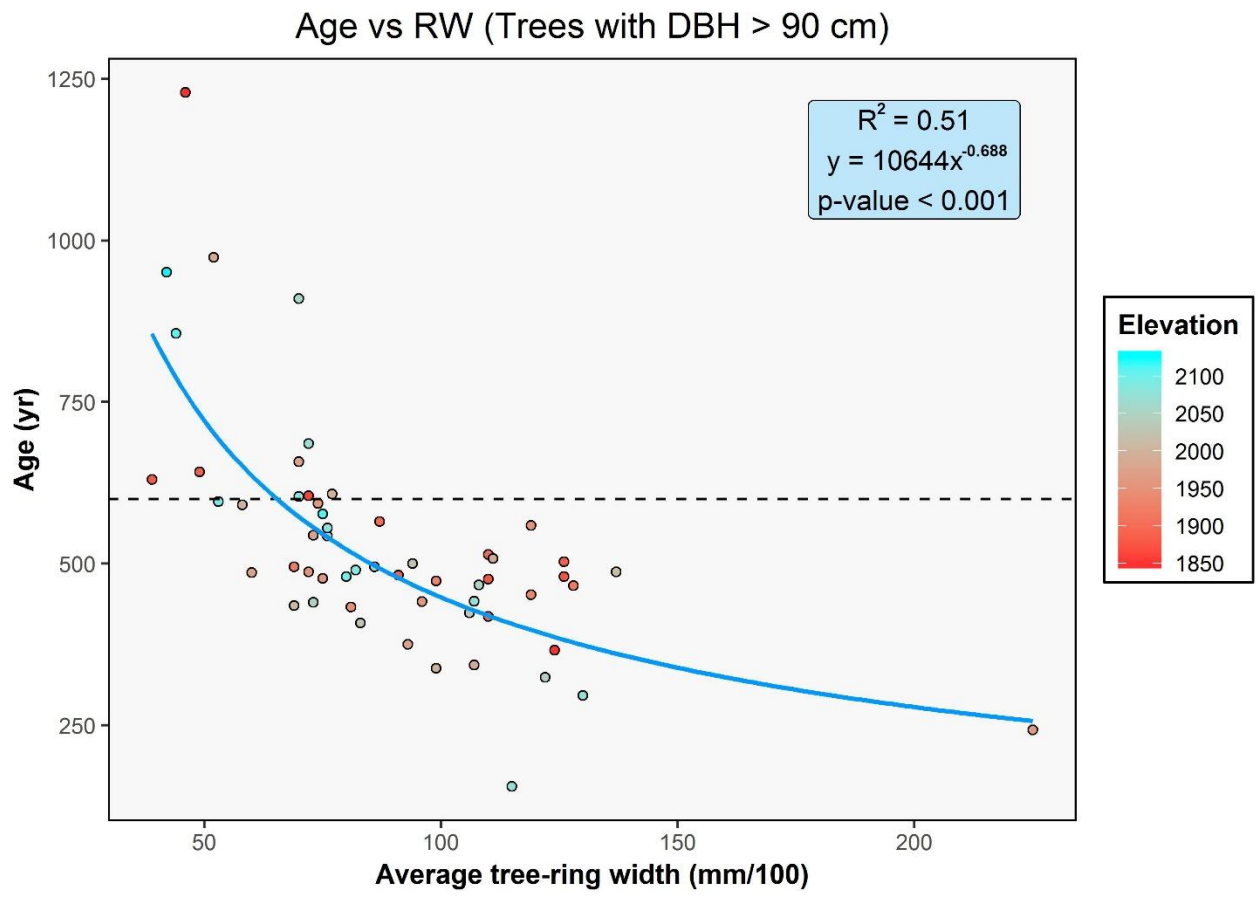


Fig. 7

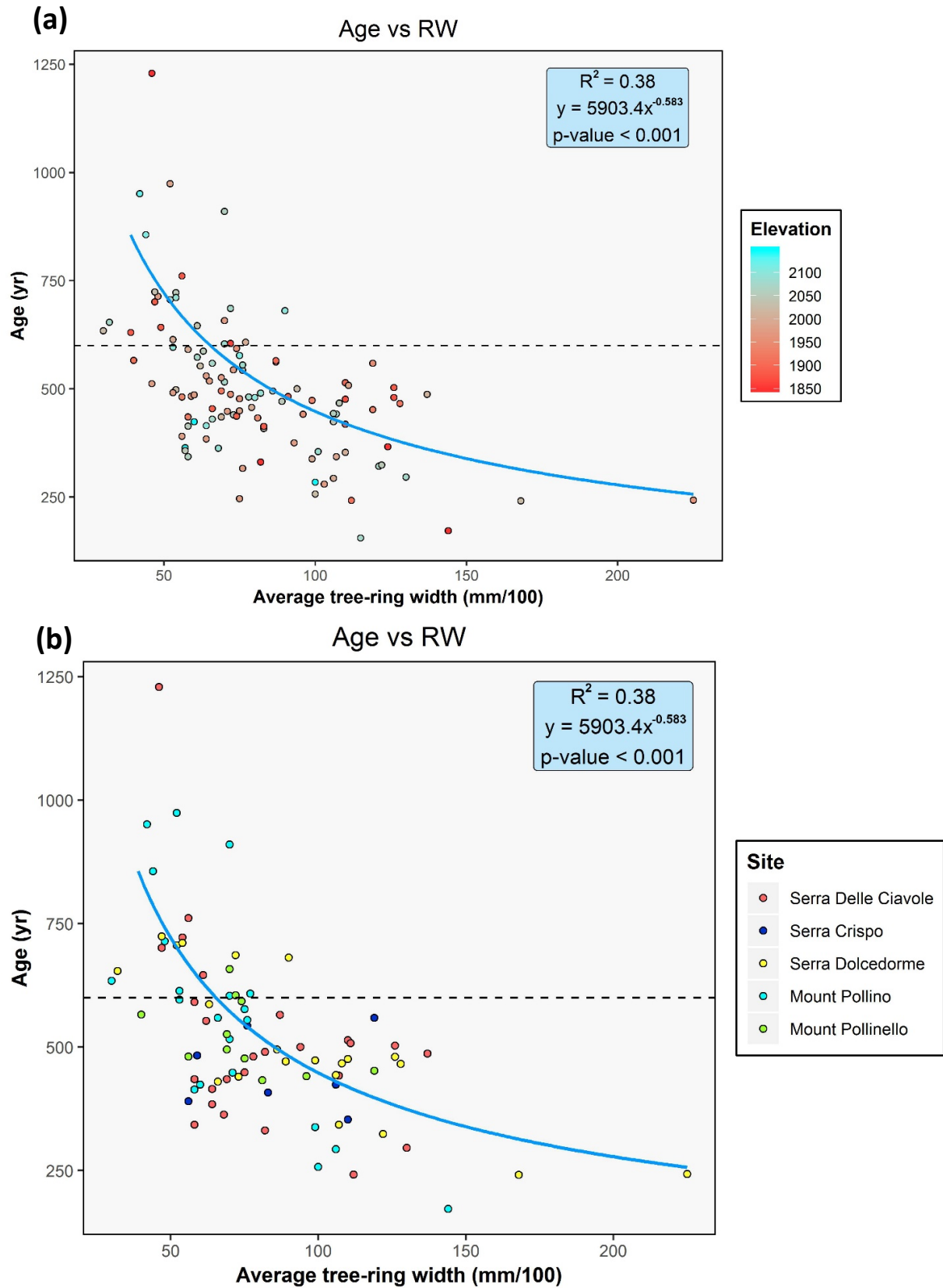


Fig. 8

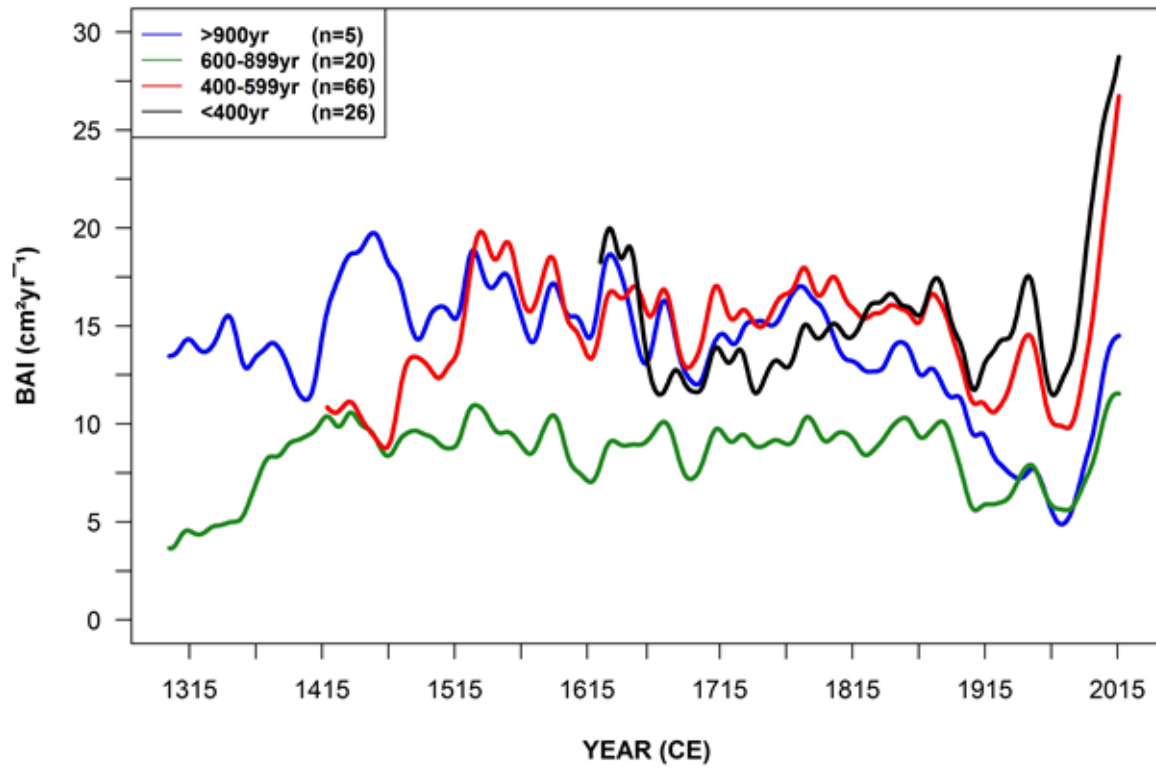


Fig. 9

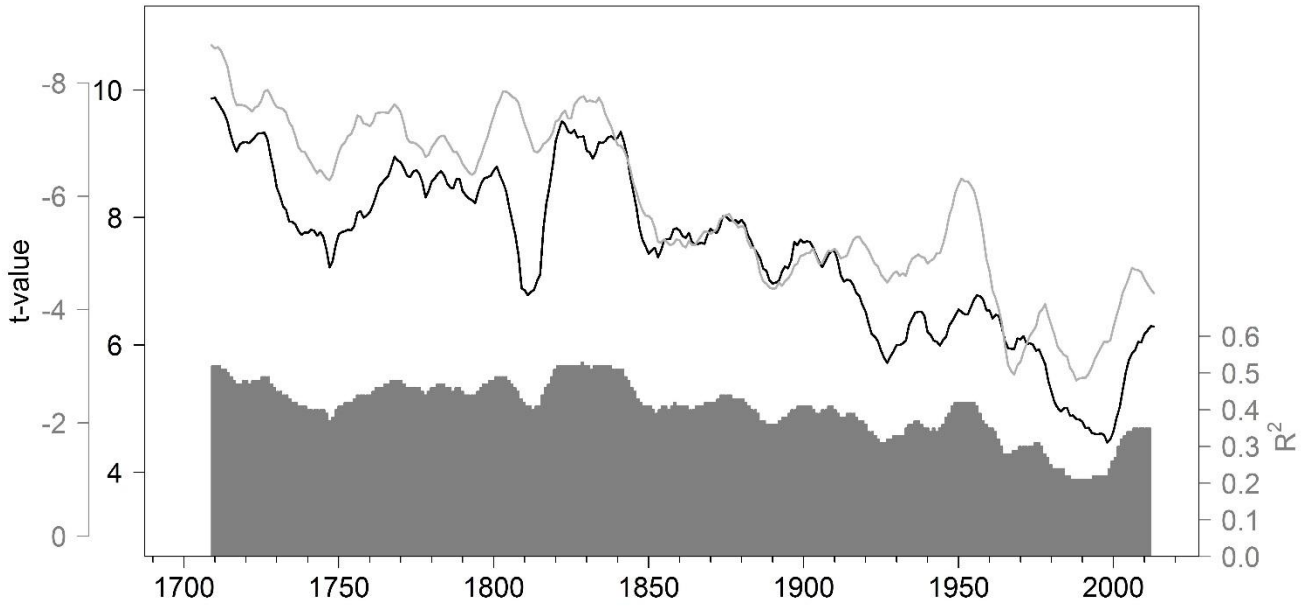


Fig. 10

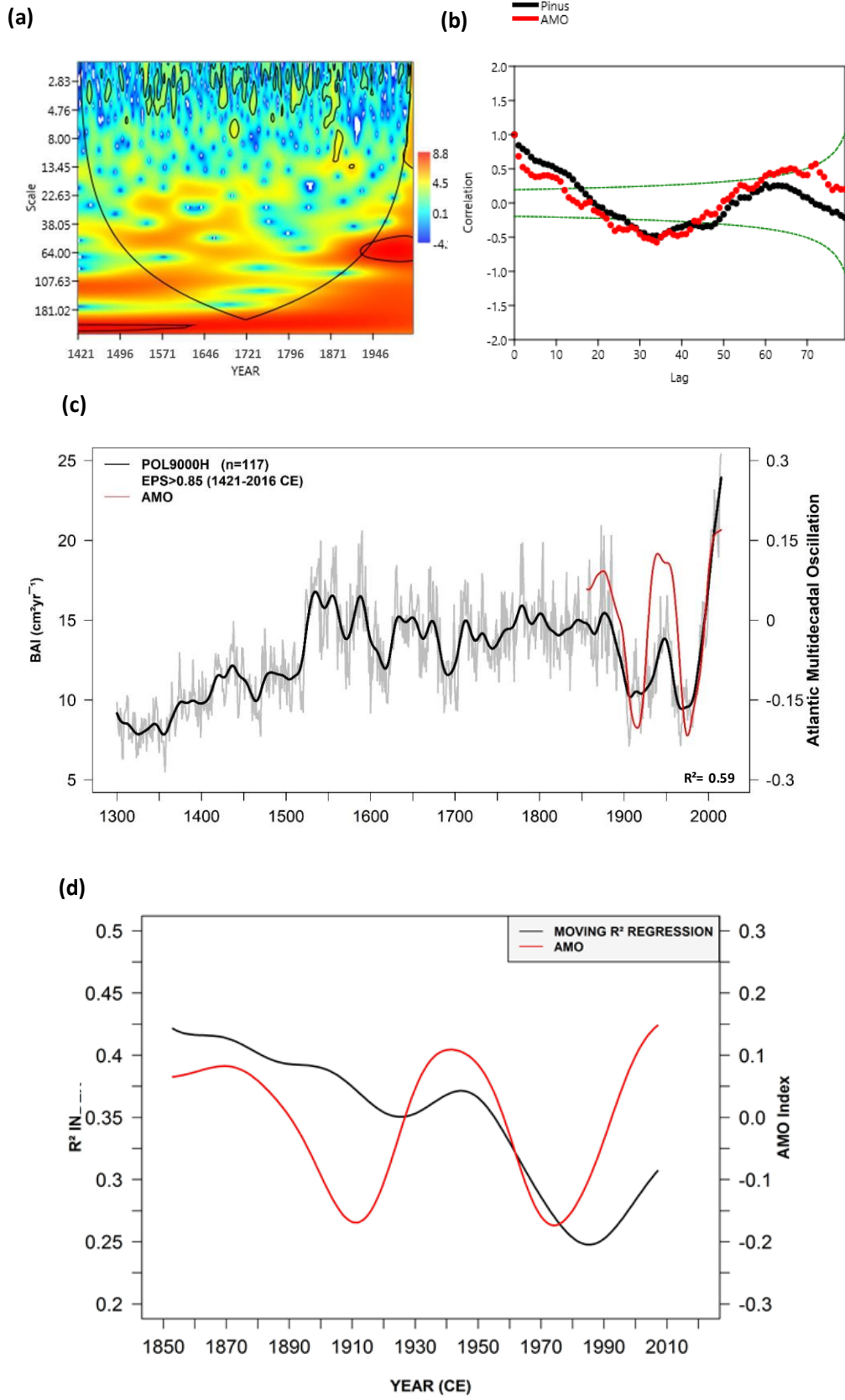


Fig. 11

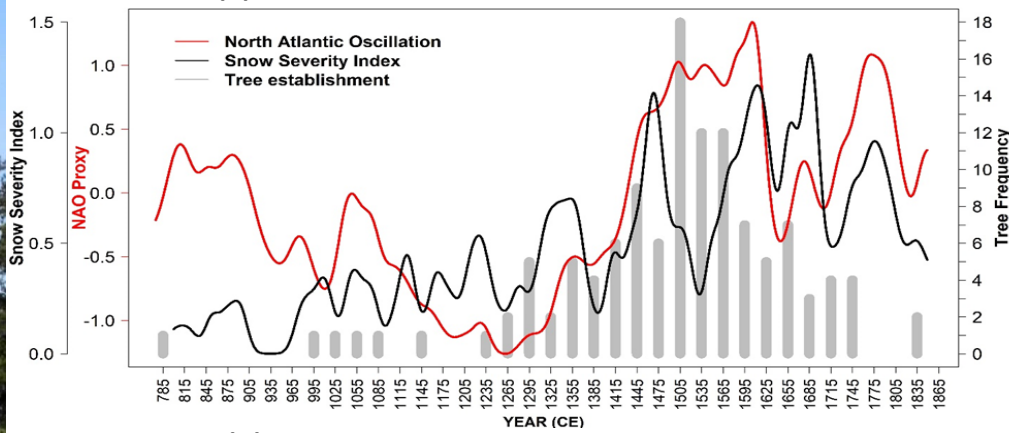


Fig. 12

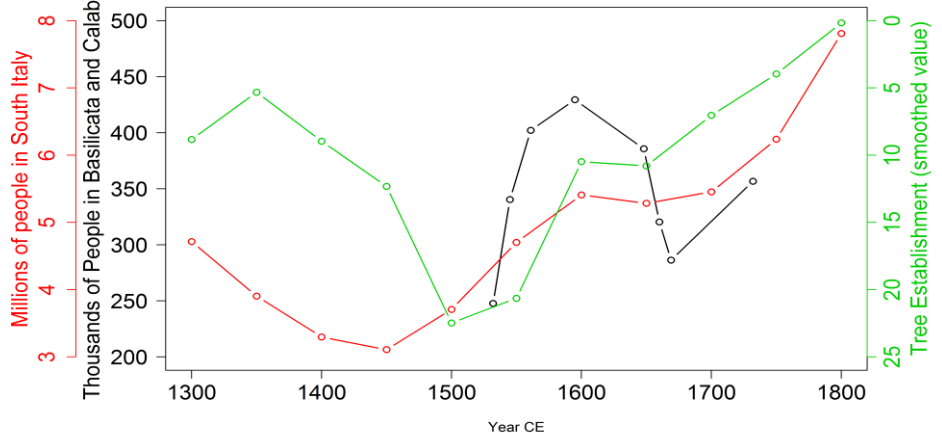


Photo edited by Gianluca Piovesan

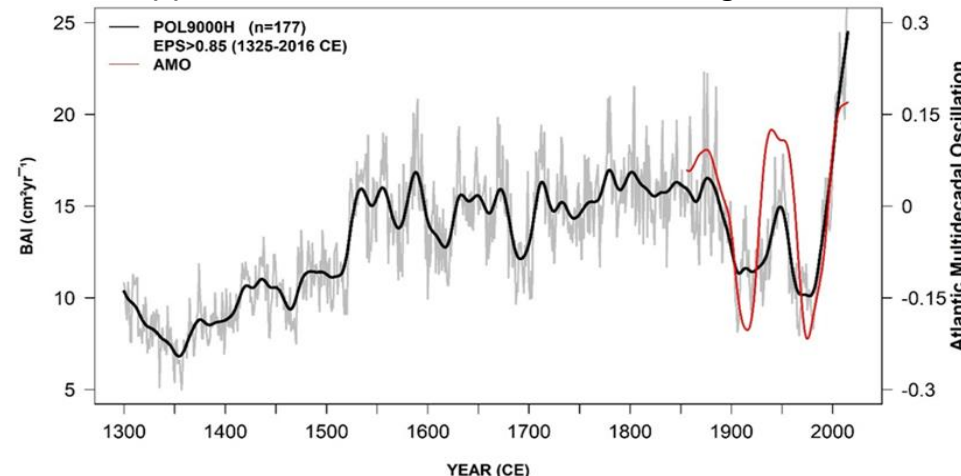
(a) Climate variations vs tree establishment



(b) Population trends vs tree establishment



(c) Atlantic multidecadal oscillation vs tree growth



Supplementary material

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