



The oldest trees of the Mediterranean

Jan Esper ^{(a)(b)(*)} - Gianluca Piovesan ^(c) - Marco Carrer ^(d) - Max C.A. Torbenson ^(e)
Ulf Büntgen ^{(b)(f)(g)}

^(a) Department of Geography, Johannes Gutenberg University, Johann-Joachim-Becher-Weg 21 - 55099 Mainz, Germany.

^(b) Global Change Research Institute of the Czech Academy of Sciences, Bělidla 986/4a - 60300 Brno, Czech Republic.

^(c) Department of Ecological and Biological Sciences, University of Tuscia, largo dell'Università snc - 01100 Viterbo, Italy.

^(d) Department of Land Environment Agriculture and Forestry, University of Padova, viale dell'Università 16 - 35020 Legnaro (PD), Italy.

^(e) Department of Geography, Texas A&M University, 377 Houston Street, College Station - TX 77843-3357, USA.

^(f) Department of Geography, University of Cambridge, Downing Place - Cambridge CB2 3EN, UK.

^(g) Department of Geography, Faculty of Science, Masaryk University, Kotlářská 2 - 61300 Brno, Czech Republic.

^(*) Corresponding Author; esper@uni-mainz.de

Abstract: The Mediterranean region hosts some of the oldest trees in Europe growing in high-elevation environments and reaching ages well beyond 800 years. We here present eight of these sites from the Atlas Mountains in the west to the Taurus Mountains in the east and discuss their potential for high-resolution climate reconstruction using dendrochronological techniques. Evidence from ancient trees plays a key role in placing the current temperature and precipitation dynamics into a long-term context and thereby providing a foundation of naturally forced climate variability that is needed to validate model-based 21st century projections. This is demonstrated in a case study using maximum latewood density measurements from *Pinus heldreichii* in northern Greece to reconstruct July-September temperatures back to 730 CE. While permission for sampling increment cores from ancient trees must be granted for scientists, we argue that these sites must be sheltered from any non-scientific use to keep these treasures of nature and life protected.

Key words: old growth forests; ancient tree; tree rings; dendrochronology; Mediterranean basin; climate change.

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1. ANCIENT MEDITERRANEAN TREE SITES AND LONGEVITY

The oldest trees in Europe occur in remote, upper treeline ecotones where logging and transport are impractical and natural disturbances

such as pathogens and fires are rare (Liu et al., 2022). Trees growing under these conditions in elevations typically above 2000 m a.s.l. are characterized by reduced stem growth $< 0.5 \text{ mm yr}^{-1}$ in response to low temperatures and short vegetation periods (Gao et al., 2025). Limited

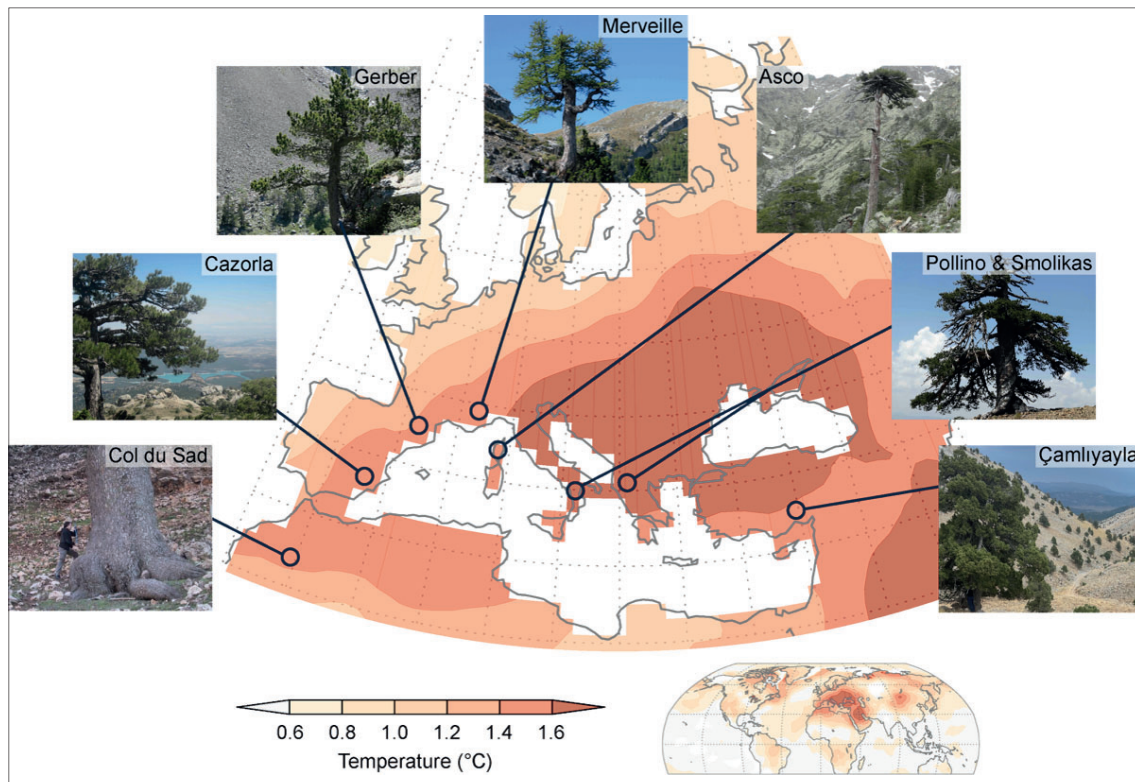


Figure 1 - Old tree sites in the Mediterranean including Col du Sad (*Cedrus atlantica*) in Morocco, Cazorla (*Pinus nigra*) and Gerber (*Pinus uncinata*) in Spain, Merveilles (*Larix decidua*) and Asco (*Pinus nigra*) in France, Pollino (*Pinus heldreichii*) in Italy, Smolikas (*Pinus heldreichii*) in Greece, and Camliyayla (*Juniperus excelsa*) in Turkey. Background colors show June-August mean temperature changes from 1965-1994 to 1995-2024 CE.

growth is one of the pre-conditions for trees to reach ages > 800 years (Büntgen et al., 2019; Schulman, 1954), as otherwise mechanical and physiological stresses constrain plant lifespans (Ziaco et al., 2016). The overall size and habit of trees, however, varies broadly among Mediterranean treelines, i.e. include rather small *Juniperus excelsa* up to 10 m height in the Taurus Mountains of Turkey and > 30 m tall *Cedrus atlantica* in the Middle Atlas of Morocco (Figure 1). While the community structure of old growth treeline forests is generally loose, the *Juniperus excelsa*, *Cedrus atlantica*, and *Pinus heldreichii* (Greece and Italy) stands are particularly open with distances frequently exceeding 10 m and more between trees.

Old tree genera and species exhibit a re-

silient life strategy including the capacity to survive persistent climate fluctuations, such as recorded throughout the past millennium (Esper et al., 2024). Growing in montane and sub-alpine Mediterranean environments, ancient trees develop growth habits characterized by low gravity centers and gnarled morphologies capable of withstanding extreme winds and ice storms, and resilient to lightning strikes. High levels of secondary compounds and dense wood support surviving disease and insect outbreaks, even in genera that lack constitutive resin canals such as *Cedrus* and *Juniperus*.

Ancient tree species evolved from distant evolutionary lineages of conifers derived from ancestral radiations. The divergence of pines, larches, and cedars within the Pinaceae fami-

Table 1 - Old tree sites in the Mediterranean. Growth refers to the average ring width of the oldest trees in a site.

Site	Region	Location	Elevation (m a.s.l.)	Species	Height (m)	Growth (mm)	Age (yrs.)
Col du Sad	Atlas Mt.	32°58'N 5°04'E	2200	<i>Cedrus atlantica</i>	35	0.45	1100
Cazorla	Cazorla	37°48'N 2°57'W	2000	<i>Pinus nigra</i>	15	0.31	800
Gerber	Pyrenees	42°38'N 1°06'E	2300	<i>Pinus uncinata</i>	15	0.42	800
Merveille	Alps	44°03'N 7°27'E	2200	<i>Larix decidua</i>	15	0.33	900
Asco	Corsica	42°23'N 8°55'E	1600	<i>Pinus nigra</i>	20	0.44	850
Pollino	Apennines	39°53'N 16°9'E	2100	<i>Pinus heldreichii</i>	20	0.40	1100
Smolikas	Pindus Mt.	40°17'N 29°3'E	2100	<i>Pinus heldreichii</i>	20	0.42	1100
Camliyayla	Taurus Mt.	37°13'N 34°35'E	2100	<i>Juniperus excelsa</i>	10	0.39	1000

ly occurred during the Late Triassic and Early Jurassic (Ran et al., 2018). It remains unclear, however, whether tree longevity facilitated the survival of these taxa across geological eras. Yet the oldest trees of the Mediterranean suggest that longevity is an adaptive trait that evolved over millions of years in harsh mountainous environments near the upper forest limit. The inability of angiosperms to evolve comparable longevity in such extreme environments underscores the conservation value of millennial-age conifers serving as living fossils and unique source for paleoclimate research and climate action (Büntgen & Esper, 2025; Büntgen et al., 2025).

While many old tree sites have been described in individual papers detailing tree-ring and other findings (Biondi, 1992; Büntgen et al., 2008, 2017, 2024; Esper et al., 2020a, 2021, 2022; Klippel et al., 2018; Römer et al., 2021; Serre-Bachet, 1985, 1994), a systematic overview and comparison of the oldest trees in the Mediterranean is missing. We here present such an overview and provide detail on the age, size, and growth rates of *Cedrus atlantica* in the Atlas Mountains (Morocco), *Pinus nigra* in the Cazorla Mountains (Spain), *Pinus uncinata* in the Pyrenees (Spain), *Larix decidua* in the Maritime Alps (France), *Pinus nigra* on Corsica (France), *Pinus heldreichii* in the southern

Apennines (Italy), *Pinus heldreichii* in the Pindus Mountains (Greece), and *Juniperus excelsa* in the Taurus Mountains (Turkey) (Table 1).

Tree ages reach a maximum in the gigantic *Cedrus atlantica* in Morocco, and massive *Pinus heldreichii* in Italy and Greece where single individuals live for 1100 years and more (Esper et al., 2007; Konter et al., 2017; Piovesan et al., 2018). The two pine sites also contain ample dead wood on the ground that allowed the development of even longer chronologies using the crossdating technique (Holmes, 1983) (see section 3 below). The lowest growth rate (0.31 mm per year) is reached in *Pinus nigra* in southern Spain, though estimating representative minimum values at a given site is somewhat challenging. This is because the oldest tree in a stand does not necessarily display the lowest growth rate of all trees. The values reported here should therefore be understood as rough estimates of minimum growth rates at a particular site, even though the values are derived from highly precise tree-ring width measurements (see the section 2).

2. CLIMATE INFORMATION FROM OLD TREES

The old tree sites are located in a region that has warmed by more than 1.4 °C considering

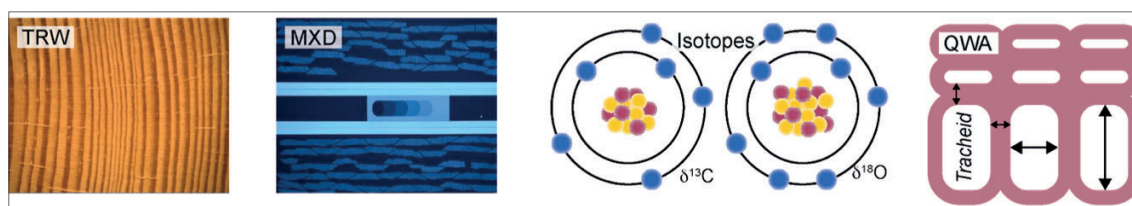


Figure 2 - Tree-ring proxies used for climate reconstruction. Tree-ring width (TRW) and maximum latewood density (MXD) are classic growth parameters. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are the most commonly used stable isotopes, and quantitative wood anatomy (QWA) represents a whole chain of microscopic features including cell wall and lumen size measurements.

mean June-August temperatures between two 30-year periods from 1965-1994 and 1995-2024 CE (see the color scheme and insert map in Figure 1). The Mediterranean thereby stands out as one of most rapidly warming areas north of 30° south (Marcos et al., 2025; Tejedor et al., 2024). Rapid warming also triggers evapotranspiration to increase and additionally forces trees to take in more water through their roots and close their stomata to prevent dehydration. All these processes are in some way archived in the rings of old trees and quantified by dendrochronologists when measuring tree-ring (i) width; (ii) density; (iii) stable isotopes, and (iv) wood anatomical traits (Figure 2).

Tree-ring width (TRW) is by far the most common parameter, used in ~99% of all dendrochronological studies. It can easily be quantified using a measurement table connected to a computer to produce annually resolved timeseries at 1/100 mm resolution. TRW is a particularly strong hydroclimatic proxy in warm-dry environments, but signal strength is limited in cold-moist environments such as the Mediterranean treeline ecotones hosting the oldest trees. Strong hydroclimate signals are recorded in the TRW data from the southern sites of the network (i.e., Col du Sad in Morocco and Camliyayla in Turkey), where the environment near the treeline is expected to be drier (Esper et al., 2007). At the heart of the Mediterranean basin, *Pinus heldreichii* growth

on the Pollino Massif has shown multidecadal synchrony with the Atlantic Multidecadal Oscillation (AMO) since 1850 (Piovesan et al., 2019). TRW hydroclimatic signals diminish towards the northern sites, particularly in the Merveille *Larix decidua* stand of the French Maritime Alps (Büntgen et al., 2012), from where - on the other hand - a stronger temperature signal in maximum latewood density (MXD) has been reported (Esper et al., 2025). MXD is an estimate of the size of the thickest cell wall toward the end of each tree ring and is much more complex and expensive to measure compared to TRW (Schweingruber, 1983). However, the proxy provides robust estimates of summer temperature variability in northern Mediterranean sites including Merveille (Alps), Gerber (Pyrenees), Asco (Corsica), and Smolikas (Pindus), but the signal fades towards the south in Cazorla (Sierra de Cazorla), Camliyayla (Taurus), and Col du Sad (Atlas).

Similar relationships between site conditions and signal strength, such as detailed for TRW and MXD, do not exist for tree-ring stable isotopes, of which $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are the most common (Esper et al., 2018). Measuring stable isotopes is even more expensive than MXD, yet the interannual variance is highly common among single trees, and skillful reconstructions of both temperature and precipitation can be derived from these data in high elevation Mediterranean sites (Heinrich et al., 2013; Lukač et al., 2021). Finally, the climat-

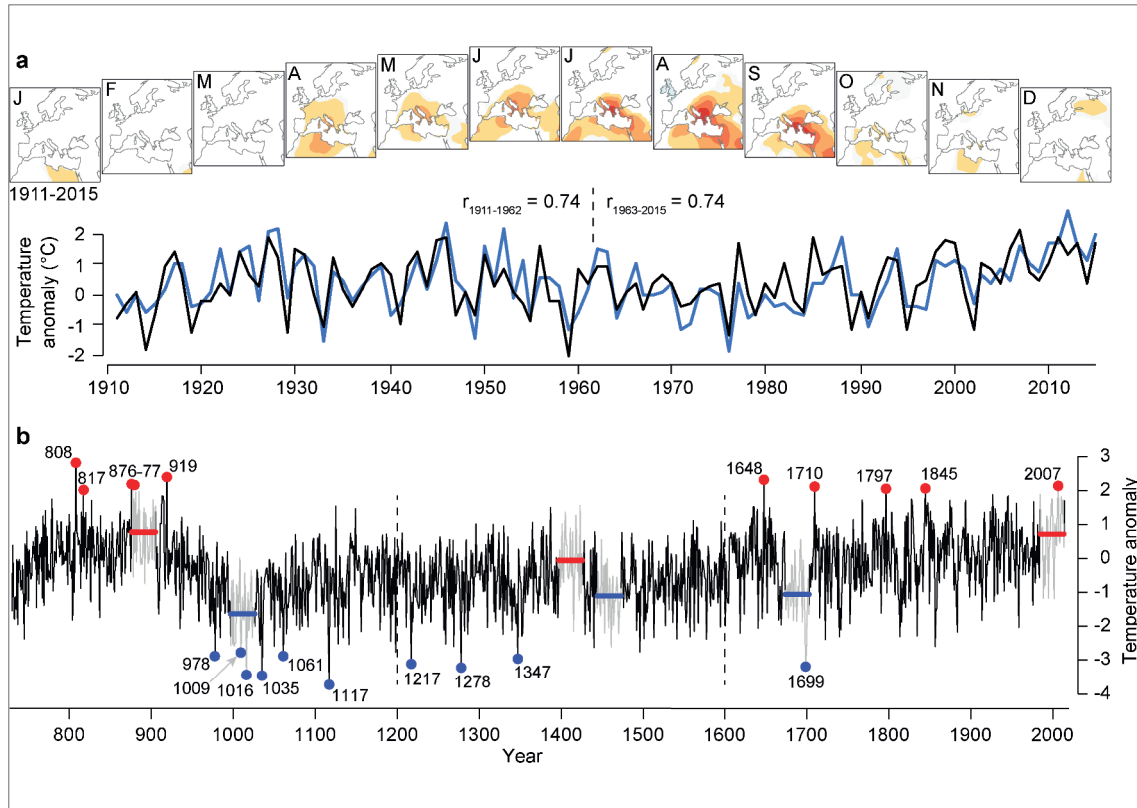


Figure 3 - Tree-ring calibration and temperature reconstruction. a) Monthly correlations of the *Pinus heldreichii* MXD chronology from Mount Smolikas against gridded instrumental temperatures (Rohde et al., 2013) from 1911-2015 CE (details on color scale in Esper et al., 2020b). Bottom curves are the MXD chronology (black) shown together with the July-September (JAS) temperature record (blue) from the station in Larissa (Greece). b) The MXD-based JAS temperature reconstruction back to 730 CE (black curve). The ten coldest and warmest years are highlighted in blue and red. Blue and red horizontal lines indicate the coldest and warmest 30-year periods before 1200 CE, from 1201-1600 CE, and after 1601. All temperatures expressed as anomalies with respect to 1961-1990 CE.

ic signals of relatively new microscopic xylem traits (Quantitative Wood Anatomy; QWA), including cell wall and lumina sizes in different orientations, are yet to be explored (Carrer et al., 2018; Frigo et al., 2024). Tracheid size measurements of old Mediterranean trees provide information on past hydroclimatic conditions as well as fundamental ecophysiological processes (Carrer et al., 2016; Mantovani et al., 2026; Pellizzari et al., 2016). The production of such data is highly labor intensive and the development of millennium-length QWA records from the Mediterranean region is still pending.

3. MILLENNIUM-LENGTH RECONSTRUCTION AND NEXT STEPS

MXD series from living *Pinus heldreichii* trees on Mount Smolikas (Greece) have been crossdated with series from relict wood on the ground to develop a millennium-length chronology starting in 730 CE. The chronology calibrates at $r = 0.74$ against remote station data from the coastal city of Larissa split over 1911-1962 and 1963-2025 CE calibration/verification periods (the blue and black curves in Figure 3a). This stationary signal has been

used to develop a June–September temperature reconstruction of unprecedented quality representing interannual to multi-decadal to multi-centennial variability. The warm conditions prior to 900 CE and millennial-scale warming trend since 1000 CE are new features that have not been shown in previous, coarser-resolution reconstructions from the Mediterranean. These features, as well as the extreme 30-year periods and extreme years (highlighted in Figure 3b), could only be detected because of the high age of living *Pinus heldreichii* and combination with relict wood, making this the longest annually resolved temperature reconstruction of the Mediterranean (Esper et al., 2020b).

The paleo-climatic (and -environmental) potential of the oldest Mediterranean tree sites has not been fully explored yet. Except for Smolikas in the Pindus Mountains and Gerber in Pyrenees, long tree-ring stable isotope chronologies are missing. Additional MXD data from the Apennines and Taurus mountains could provide skillful temperature reconstructions, though the applicability of density measurements from juniper trees needs to be explored. Beyond this, efforts to develop millennium-length QWA chronologies from old Mediterranean tree sites are recommended as these data will likely add information not only on long-term hydroclimatic dynamics but also on ecophysiological processes of wood formation in unique treeline ecotones. To accomplish these objectives, scientist must be able to access and sample these forests using harmless increment cores. Beyond this, the ancient tree sites in the Mediterranean and elsewhere need be protected from cutting and exploitation.

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