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Rediscovering Montecristo's treasure: The island's holm oaks reveal exceptional longevity

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The rugged, uninhabited Montecristo Island (Italy), halfway between mainland Tuscany and Corsica in the Mediterranean Sea, was made famous by the A. Dumas novel *The Count of Monte Cristo* (1844) as the place hiding an incredibly rich treasure. Since 1971, the island (10.4 km^2) has been a state-owned strictly protected area, accessible only to scientists and to a limited number of visitors on guided ecotourism activities. The plant communities of the island are not very species rich, because of geographical isolation and uniform substrate, but biogeographically important species are present (Chiarucci et al., 2021). Montecristo hosts an isolated population of ~200 large individuals of the holm oak (*Quercus ilex* L.), remnants of a forest covering the island in the past (Crudele et al., 2005). Most of them are of impressive diameter, and the occurrence of "holm oaks of a huge size" had been already mentioned in the late 16th century (Ferruzzi, 2017). However, the most well known biological feature of the island is a population of feral goats, whose age of introduction, origin and conservation value are hotly debated (e.g., Gippoliti, 2015; Somenzi et al., 2022). Since the establishment of the island as a strictly protected area, the goat population underwent an increase due to the cessation of hunting (Spagnesi et al., 1986). Probably as a consequence of increased goat browsing, juvenile holm oaks are now extremely rare, while the old, gnarled trees are surviving as sparse individuals within the *Erica scoparia* and *E. arborea* low shrubland, or even emerging from cracks in the barren granite (Figure 1; Video S1).

In the Mediterranean Basin, mountain ecosystems have been found to host very long-lived trees, both evergreen conifers and deciduous broadleaved species

FIGURE 1 One of the old holm oaks of Montecristo during wood sampling aimed at radiocarbon dating (photograph by Goffredo Filibeck, 27 June 2018). This was the individual with the largest diameter (185 cm), but not the oldest age (cf. Figure 2).

(Piovesan & Biondi, 2021). Conversely, long-aged trees are extremely rare in coastal Mediterranean ecosystems, because of the long history of coppicing, burning and other types of anthropogenic disturbance. Moreover, dating evergreen warm-temperate trees (the dominant species in the coastal vegetation belt) is a complex task due to the plasticity of intra-annual growth patterns (Campelo et al., 2021) and rotted or hollow trunks.

Although some shrubby conifers of the Mediterranean coast have been shown to be exceptionally long living (*Juniperus phoenicea* from southern France provided radiocarbon dates of 2500 years BP: Mathaux et al., 2016), evergreen broadleaved trees have been rarely dated on a rigorous basis. Claims of an age of "many thousand years" for Mediterranean olive trees (*Olea europaea*), for instance, are mostly based on trunk size. Recent radiocarbon dating has challenged this myth, with monumental olive trees in Spain found to have maximum estimated ages of 300–500 years (Camarero et al., 2021), and the olive trees in the Garden of Gethsemane (Israel) were probably planted in the 12th century CE (i.e., Common Era; Bernabei, 2015).

Surprisingly, very little data are available on the longevity of *Quercus ilex*, the evergreen tree dominating most forest vegetation along the Mediterranean coasts and playing a major role as a foundation species (sensu Ellison, 2019). An estimate of natural mortality age in a *Q. ilex* mature forest in Corsica (based on tree rings and stem diameters) has provided a maximum lifespan of ~170 years (Panaïotis et al., 1997). Dead holm oaks in open wood pastures in Spain were found to have ages at the time of death of between 38 and 230 years (Gea-Izquierdo et al., 2021). However, indirect historical evidence, such as old planted trees in Renaissance gardens (Piovesan, 1994), has suggested the possibility for this species to attain ages of >500 years.

We were impressed by the imposing trees of Montecristo and thought they could help to address the fundamental question of holm oak longevity in nature using radiocarbon dating. We sampled the inner wood close to the base of six large, hollowed trees (diameter between 80 and 185 cm; see Appendix S1), located between 368 and 498 m above sea level (Figure 1). The sampled trees were chosen among those growing in the less productive topographic positions, as longevity is usually negatively related to the growth rate (Piovesan & Biondi, 2021). Methodological details about both the field sampling and radiocarbon dating are provided in Appendix S1.

The conventional radiocarbon ages measured for the analyzed trees spanned from 430 to 742 uncalibrated ^{14}C years BP (Appendix S2: Table S1). Conventional radiocarbon ages were then calibrated to calendar years (CE) using the latest accepted calibration curve INTCAL20 (Appendix S2: Table S1 and Figures S1–S7). It is to be underlined that calibration can result in a loss of chronological resolution; in particular, a poorer resolution is usually obtained for samples corresponding to periods of "plateau" of the calibration curve (Hajdas et al., 2021). Furthermore, the complex shape of the calibration curve may yield multimodal and non-Gaussian distributions of the calibrated time ranges, making the interpretation of ^{14}C data difficult, as it was found for example, for sample LTL19795 (Appendix S2: Figure S4). Some of these effects (in particular the non-Gaussian distribution) have become more relevant and common with the release of INTCAL20. This is because of the higher temporal resolution of the latest calibration curve, with less "smooth" and more "wiggly" shapes at several time intervals (Van der Plicht et al., 2020).

The difference between the calibrated ages and the year 2022 CE was then used to calculate the age of each tree: we obtained 444 ± 90 (probability 92.3%) calendar years for the youngest sampled tree and 761 ± 42 (probability 91.7%) calendar years for the oldest one (Figure 2; Appendix S2: Figures S1–S7).

These results outdate by far all the available data on the *Q. ilex* lifespan, and show that the evergreen oaks of the Mediterranean coastal habitats can reach a potential maximum lifespan of more than 700 years, that is, they are of the same magnitude recorded for the deciduous oaks from the Mediterranean mountains (Piovesan et al., 2020). Moreover, these findings place the holm oaks of Montecristo among the oldest known extratropical broadleaved trees in the world, thus expanding the biogeography of the maximum ages measured for hardwood trees beyond eastern North America (679 years in *Nyssa sylvatica*; Di Filippo et al., 2015) and Mediterranean mountains (622 years in *Fagus sylvatica* and 934 ± 65 years in *Quercus petraea*; Piovesan & Biondi, 2021) to the Mediterranean coastal areas.

The age of Montecristo's oaks is even more interesting when compared with the average maximum lifespan of a sample of 80 angiosperm tree species worldwide; that based on currently available, public-domain tree-ring data is of 229 ± 132 years (Biondi et al., 2023). Additionally, our results confirmed the lack of a relationship between trunk diameter and age (Figure 2) in old trees, highlighted by Piovesan and Biondi (2021). Finally, this study underlines how radiocarbon dating of ancient trees with rotting trunks represents an extremely interesting solution for overcoming the limitations of tree-ring methods when exploring the senescent stage of tree life (Piovesan et al., 2020; see also: http://www.rmtrr.org/oldlist.htm).

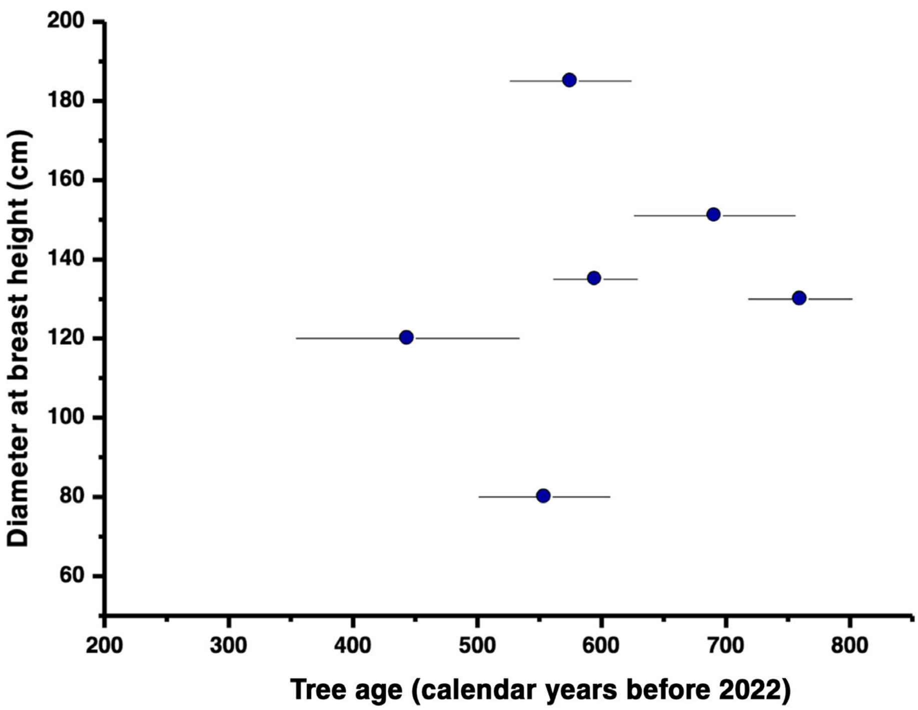

FIGURE 2 Tree ages (years before 2022) plotted against diameter at breast height of Montecristo holm oaks. Error bars correspond to 2 sigma confidence levels of calibrated radiocarbon ages. The lack of a relationship between trunk diameter and age is apparent.

Holm oak is adapted to the Mediterranean climate of Montecristo—characterized by a prolonged summer drought, strong winds and mild winter temperatures—through traits that provide resistance to wood degradation and resilience after drought disturbance. For instance, its high wood density (Giordano, 1981) ensures resistance to drought-induced embolism (Xu & Liu, 2022) and wood-decaying fungi and bacteria (Chave et al., 2009). Moreover, holm oak has an enormous ability to reiterate trunks and limbs in response to severe drought, wind damage and fires. Consistently with that already observed for the ancient (deciduous) sessile oaks (*Quercus petraea*) in the southern Italian mountains (Piovesan et al., 2020), Montecristo's holm oaks still produce large amounts of viable seeds that are regularly collected by the protected area management and grown in nurseries for ex-situ conservation (see Appendix S2: Figure S8), confirming that active reproduction capacity in trees can be maintained even during the senescent stage.

In the context of global changes, the conservation of these ancient holm oaks may bear a strategic significance, because of their unique fitness for the restoration of functional forest ecosystems (Cannon et al., 2022). However, the *Q. ilex* population of Montecristo is threatened by two alien species: the feral goat and the invasive tree *Ailanthus altissima*. The latter is highly invasive on the island: being unpalatable, it is likely to be favored by the high density of feral goats, as they suppress the otherwise strong competition operated by native shrubs and trees; this leads to the displacement of vast expansions of natural vegetation by monophytic *A. altissima* thickets. Indeed, the presence of a large population of feral goats in such a small and isolated ecosystem causes constant and extreme browsing pressure on plant communities. Currently, the demographic structure of the oak population is very worrying, because of the almost complete lack not only of saplings, but also of mature trees of intermediate age. However, in small experimental enclosures protected from goat browsing, seedlings and saplings of *Q. ilex* are readily established.

The current situation of this remote island ecosystem, with no human population and no productive activities, offers a unique opportunity for biological conservation, namely the possibility of a rewilding plan to promote the restoration of the ecological complexity of a Mediterranean landscape (Fernández et al., 2017). To this end, it may be necessary to consider the demographic control, or possibly the complete translocation, of the introduced goat population. The ancient holm oaks are the real "treasure" of Montecristo, and actions targeted at helping them in leaving a healthy, vital descendance, and at restoring natural dynamics on the island, are urgent.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The tree diameters and radiocarbon dates are reported in Appendix S2. Data (Filibeck et al., 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.7835623.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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