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Vertical cliffs harbor millennia-old junipers in the Canary Islands

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The ability of trees to endure for millennia, surpassing human lifetimes, and survive the most destructive human and natural hazards is astonishing. But what is the ecological role of tree longevity? Are old trees more than impressive nature wonders? Can ancient trees become effective genetic reservoirs able to recover bygone ecosystems? Oceanic islands are ideal ecosystems to address these questions, as they have experienced recent and intense human-induced environmental changes. In the Canary Islands in the northeastern Atlantic Ocean, human colonization since the fifth century BCE (Rodríguez-Varela et al., 2017) added logging, fire, and grazing pressure to a territory already experiencing regular volcanic activity. Tenerife Island is the most populated island of the Canary Islands archipelago and harbors the largest subalpine ecosystems in the entire Macaronesian Biogeographic Region. Woodlands in the Tenerife subalpine environment were once formed by the Canary Island juniper (*Juniperus cedrus* Webb. & Berthel.; hereafter juniper; Machado & Galván, 2012, García-Cervigón et al., 2019), but historical human pressure restricted its distribution to inaccessible spots, away from human activity, such as cliffs.

Identifying these primeval junipers and establishing their age is paramount to preserving existing populations and restoring this vulnerable ecosystem, but also to advancing the historical ecology of the Canary Islands. Thus, after discovering the 1100-years-old "Patriarch" juniper in the subalpine plain of Tenerife (García-Cervigón et al., 2019), we looked up to the inaccessible cliffs with the purpose of studying the most extensive populations of junipers. Our aim was to find out whether the junipers in cliffs were also old despite the great

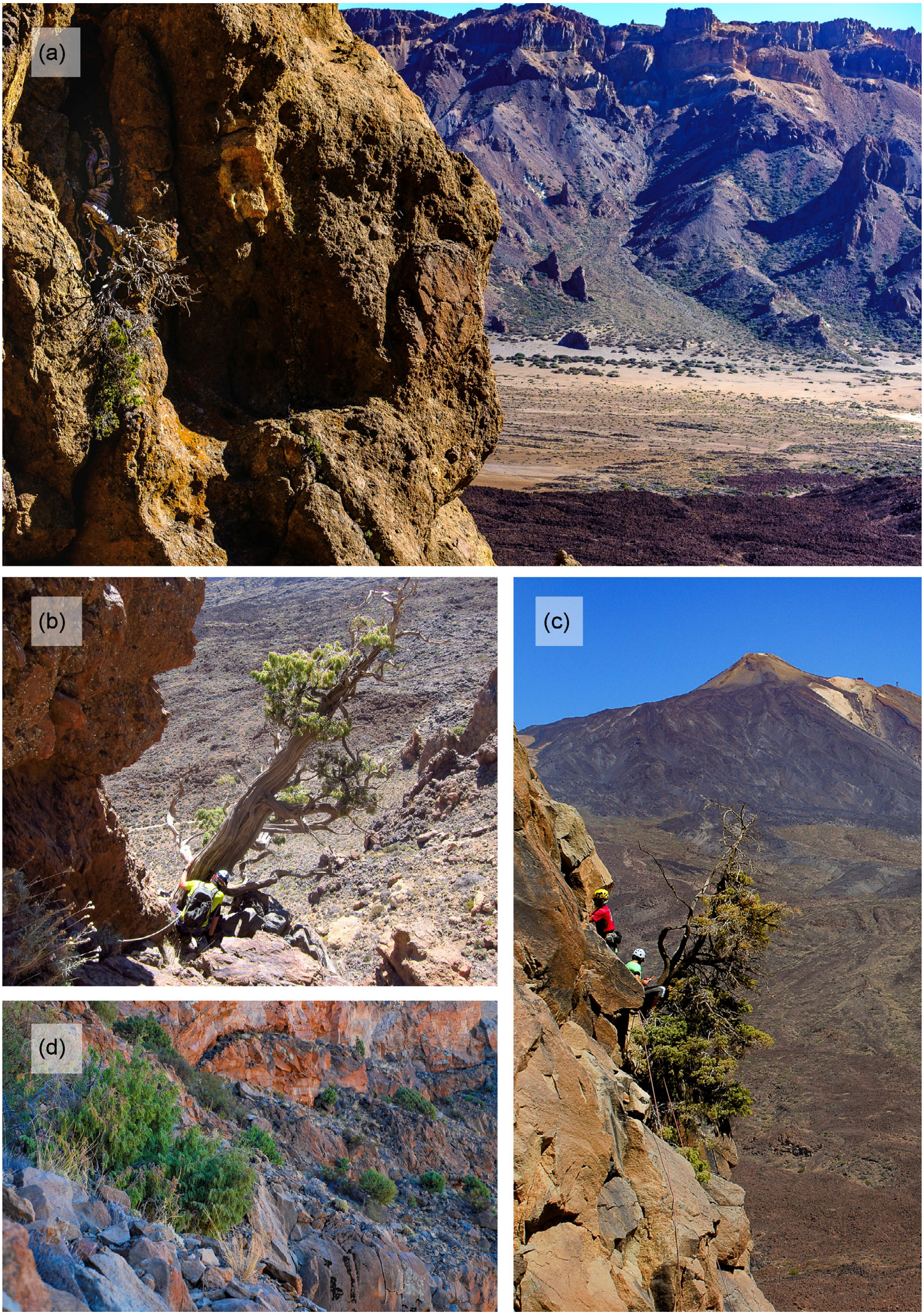

FIGURE 1 *Juniperus cedrus* can reach impressive ages on the cliffs of the Teide National Park in Tenerife, Canary Islands. (a) The oldest juniper is at least 1481 years old and has a twisted and inverted stem, while (b) its neighbor is 1236 years old. (c) Reaching these ancient junipers is not easy, and hence, the use of advanced climbing techniques was essential. (d) As a result of the conservation measures of the Teide National Park, and of the seeds produced by these ancient junipers, the species is beginning to regain its past presence

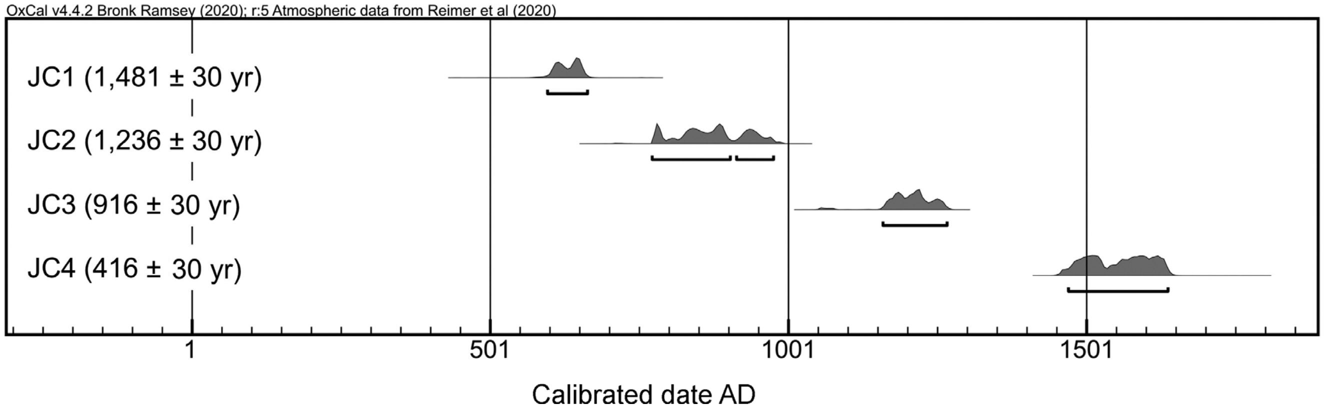

FIGURE 2 Radiocarbon dating for the selected *Juniperus cedrus* individuals (JC1–JC4) growing on cliffs in the Teide National Park in Tenerife, Canary Islands. Dating was corrected considering the atmospheric $\delta^{14}C$ variations during the last millennium, and uncertainty in dating was estimated accordingly

limitations imposed by their marginal habitat, and whether cliff-confined junipers were effective seed sources to bring juniper woodlands back from the past.

With these goals in mind, we undertook two climbing campaigns in 2019 and 2020. Cliff-confined junipers are growing in minimal amounts of soil, and the weather conditions do not help them thrive (~400 mm of annual precipitation with a 5-month drought and a mean temperature of 10.0°C; Appendix S1: Figure S1). We approached the junipers (Figure 1) to collect information on their diameter, age, sex, and fruit production. Climbing vertical cliffs is never an easy job, but the challenge increases exponentially in volcanic terrain where the risk of rock instability is always present. We used advanced climbing techniques to access to a total of 61 individuals (62.9% males and 37.1% females) between altitudes 2100 and 2600 m above sea level, and we took 1–2 wood cores from each to evaluate their growth history. To get a first estimate of their age, we counted tree rings on the well-preserved outer portion of wood cores, cross-dating them in most of the cases, resulting in an average of 198 $\pm$ 10 years (maximum 548 years). This contrasted with the rest of junipers growing at the foothills that were extremely young (39 $\pm$ 2 years, $n = 30$; García-Cervigón et al., 2019). This result indicates that junipers established in the most accessible areas only after the designation of the site as National Park in 1954, when the species was protected from the pressure of goats' teeth and human axes.

Our curiosity went even further, because some trees stood out for their extremely old appearance (Figure 1): twisted horizontal or inverted stems, low crown cover, and very large dead portions with inner wood rot. Given their complex morphology and the abundance of dead wood, we were unable to take complete pith-to-bark cores from these specimens. Consequently, we took a small piece of intact wood from the exposed central part of the base of the main stem from four potentially old junipers to determine their age as exactly as possible by using ^{14}C. The results were impressive: two out of four junipers were older than 1000 years (Poznan Radiocarbon Laboratory, Poland; Figure 2; Appendix S1: Figure S2); more specifically, a female reached at least 1410 $\pm$ 30 years BP (before 1950) and a male 1165 $\pm$ 30 years BP, while the other two reached 845 $\pm$ 30 (male) and 345 $\pm$ 30 years BP (female). In other words, these junipers are 1481 $\pm$ 30, 1236 $\pm$ 30, 916 $\pm$ 30, and 416 $\pm$ 30 years old, respectively, which means that at least two junipers on the cliffs of Teide National Park are older than "The Patriarch." In addition, the multiple-age cohorts of these trees suggest that the establishment of junipers on cliffs has been sustained over long periods of time.

The 1481-years-old juniper is older than other scientifically dated millennial conifers in continental Europe (Camarero & Ortega-Martínez, 2019, Konter et al., 2017, Piovesan et al., 2018). Older trunks of dead junipers have been described in cliffs in southern France (Mandin, 2005; Mathaux et al., 2016). To our knowledge, if we consider this juniper as an inverted tree (Figure 1a), it represents the oldest known living tree in the European Union, although junipers in other regions (e.g., *Juniperus przewalskii* Kom. in the Tibet) can exceed this age in remote, high-elevation areas under extreme cold and arid climate conditions (Liu et al., 2019). All these studies confirm that the genus *Juniperus* can achieve outstanding ages in extreme environments (Piovesan & Biondi, 2021), and that very old junipers are found in locations with absence of human disturbances regardless of habitat suitability.

Cliff habitats in the Tenerife subalpine area played a primordial role as refuges for junipers conservation during the most intensive land use periods (Larson et al., 1999). Despite the extreme constraints including rockfalls, limited root space or low water storage capacity, cliff-confined junipers have reached maximum ages for the species and latitude (Piovesan & Biondi, 2021). These trees have survived long-lasting climatic reversals, showing a great resilience to profound droughts and extreme conditions derived from volcanic eruptions. The very low growth rates observed for these trees (e.g., the 1481-years-old juniper has a trunk diameter of just 79 cm; an average increment rate of 0.29 mm/year) can be attributed to the abiotic limitations they are subject to and may have increased the probability of reaching long tree lifespans (Brienen et al., 2020). Finally, the peculiar growth form of this species, which can show a great variability of forms, underlines the extreme plasticity of *J. cedrus* to reach such advanced ages.

The 1481-years-old juniper as well as "The Patriarch" are both females and they are still producing viable fruits, suggesting that there are no age limitations to fruit production. The fruits of these millenary junipers are dispersed by frugivorous birds (Rumeu et al., 2011) and are recovering the vanished populations in flat accessible areas (García-Cervigón et al., 2019; Machado & Galván, 2012; Nogales et al., 2014). Conservation measures implemented by the National Park, in particular the enhancement of frugivorous birds' habitats and the control of introduced herbivores populations (Martín-Esquivel et al., 2020), are critical to sustain new pulses of juniper recruitment. Our results show that junipers have been growing in the escarpments for centuries and even for more than a millennium until a window of opportunity (protection after the establishment of the Teide National Park) enabled them to return to the flatlands. These ancient trees therefore represent both the past and the future of the species. Further research should (a) study the genetic diversity of isolated junipers and their kinship relations with flatlands junipers, (b) evaluate the potentiality of cliff-confined junipers for long-term climate reconstructions, and (c) evaluate the impact of climate warming and introduced herbivores pressure on juniper establishment.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Sangüesa-Barreda, 2021) are available on Figshare at https://doi.org/10.6084/m9.figshare.16823014.v2.

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