Conservation Biology

CONTRIBUTED PAPER

Age and spatial distribution of the world's oldest trees

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Article impact statement: Species (e.g, endangered caribou) may be less resilient to environmental change if habitat selection is reinforced by genetic determination.

Abstract

Extremely old trees have important roles in providing insights about historical climatic events and supporting cultural values, yet there has been limited work on their global distribution and conservation. We extracted information on 197,855 tree cores from 4854 sites and combined it with other tree age (e.g., the OLDLIST) data from a further 156 sites to determine the age of the world's oldest trees and quantify the factors influencing their global distribution. We found that extremely old trees >1000 years were rare. Among 30 individual trees that exceeded 2000 years old, 27 occurred in high mountains. We modeled maximum tree age with climatic, soil topographic, and anthropogenic variables, and our regression models demonstrated that elevation, human population density, soil carbon content, and mean annual temperature were key determinants of the distribution of the world's oldest trees. Specifically, our model predicted that many of the oldest trees will occur in high-elevation, cold, and arid mountains with limited human disturbance. This pattern was markedly different from that of the tallest trees, which were more likely to occur in relatively more mesic and productive locations. Global warming and expansion of human activities may induce rapid population declines of extremely old trees. New strategies, including targeted establishment of conservation reserves in remote regions, especially those in western parts of China and the United States, are required to protect these trees.

KEYWORDS
global distribution, large old trees, longevity, tallest trees, tree ring

Edad y Distribución Espacial de los Árboles Más Viejos del Mundo
Resumen: A pesar de que los árboles extremadamente viejos son importantes para proporcionar información sobre eventos climáticos históricos y sustentar los valores culturales, se han realizado pocos estudios sobre su distribución y conservación mundial.

Extrajimos información de 197,855 núcleos de árboles en 4,854 sitios y la combinamos con datos (p. ej.: la OLDLIST) de otros 156 sitios para determinar la edad de los árboles más viejos del mundo y cuantificar los factores que influyen sobre su distribución mundial. Descubrimos que los árboles extremadamente viejos, mayores a mil años, son raros. De entre 30 árboles individuales que excedían los dos mil años, 27 se encontraban en la alta montaña. Modelamos la edad máxima de los árboles con variables climáticas, topográficas del suelo y antropogénicas y nuestros modelos de regresión demostraron que la elevación, la densidad poblacional humana, el contenido de carbono en el suelo y la temperatura media anual son determinantes clave de la distribución de los árboles más longevos. Específicamente, nuestro modelo pronosticó que muchos de estos árboles se encontrarán en montañas áridas y frías de alta elevación con una alteración humana limitada. Este patrón fue significativamente diferente de aquél para los árboles más altos, que tienen la probabilidad de ocurrir en localidades relativamente más productivas y de mesohábitats. El cambio climático y la expansión de la actividad humana puede inducir una rápida declinación poblacional de los árboles extremadamente viejos. Se requieren estrategias novedosas para proteger a estos árboles, incluyendo el establecimiento enfocado de reservas de conservación en regiones remotas, especialmente aquellas en la parte occidental de China y de los Estados Unidos.

PALABRAS CLAVE
anillo de árbol, árboles más altos, árboles viejos grandes, distribución mundial, longevidad

全球最老古树的年龄和空间分布摘要

古树在记录历史气候事件和支撑文化服务等方面有着重要地位。然而, 有关古树的全球分布及其保护的工作却较为缺乏。基于此, 本研究通过收集国际树轮数据库4854个地点197855棵古树的年龄数据, 并结合另外156个有最老古树分布地点的数据 (如OLDLIST) , 来探索全球最老古树的年龄和影响其分布的关键因子。基于这些数据, 我们发现超过1000年的古树其实很少, 超过2000年的古树有30棵, 其中有27棵分布在高海拔山区。通过结合气候、土壤、地形和人类活动因素构建最老古树分布模型, 我们发现海拔、人口密度、土壤碳含量和年均温等是决定最老古树分布的关键因子。具体而言, 最老古树大多分布在高海拔、干冷、受人类活动干扰较少的山区。这一结论与最高的树的分布规律显著不同:它们主要分布在更湿润和高产的区域。因此, 考虑到全球变暖和人类活动扩张会诱发古树种群快速下降, 针对古树保护的专门措施就显得极为重要, 我们建议在中国和美国的西部偏远地区为当地古树设立保护区。

关键词: 古树, 全球分布, 最高的树, 寿命, 年轮

INTRODUCTION

Extremely old trees are natural features that have important roles, such as generating insights about historical climatic events (Di Filippo et al., 2012; Yang et al., 2014), maintaining biodiversity and ecosystem function (Lindenmayer & Laurance, 2017; Stephenson et al., 2014), and providing social and cultural benefits to people (Blicharska & Mikusiński, 2014). For example, the tree rings of extremely old trees contain information about changes in climate over several thousand years, which is critical for reliable reconstruction of past climatic conditions (Yang et al., 2014). Old trees are important reservoirs of genetic diversity and often have high reproductive fitness (Hanlon et al., 2019; Mosseler et al., 2002). These trees are also often a focus of public attention, for example, because of their cultural importance in religions and sacred practices (e.g., where children were born and people are buried) (Blicharska & Mikusiński, 2014; Lindenmayer & Laurance, 2017).

Effective conservation of very old trees requires a basic understanding of their global distribution patterns because they are likely to be threatened by climate change, habitat loss, and habitat fragmentation (Bennett et al., 2015; Lindenmayer & Laurance, 2017; Patrut et al., 2018). Many continents and countries have documented the occurrence of their oldest trees, including the oldest dated trees in Europe (Piovesan et al., 2018), China (Liu et al., 2019b), Africa (Patrut et al., 2018), South America (Lara & Villalba, 1993), and the United States (Ferguson, 1968). However, current studies on old trees have been conducted primarily at the regional level, and the spatial distribution of old trees at a global scale has not yet been quantified. This is an important knowledge gap for the practical conservation of these trees.

The oldest trees in a given region tend to occur in relatively cold (Currey, 1965; Liu et al., 2019b; Piovesan et al., 2018), dry (Locosselli et al., 2020), less fertile (Di Filippo et al., 2015; Larson, 2001), and steep topographical environments (Liu et al., 2019b) with limited anthropogenic disturbance (Lindenmayer et al., 2012). For example, tree species in temperate regions were frequently reported to exceed 1000 years old (Currey, 1965; Liu et al., 2019b; Piovesan et al., 2018; Schulman, 1954), whereas tree species in tropical regions rarely exceed 600 years (Di Filippo et al., 2015; Schöngart et al., 2017) (but see Patrut et al. [2018]). The underlying mechanism for this pattern may be slow growth rates in cold areas, which, based on metabolic theory, would promote longevity (Büntgen et al., 2019). Moreover, the oldest trees tend to occur in harsh edaphic environments (Di Filippo et al., 2015; Schulman, 1954). For example, the oldest tree in Europe was found on a steep and rocky slope in the mountains of Pollino National Park (Piovesan et al., 2018), and the oldest trees in China are located on steep slopes with stony soils in high mountains (Liu et al., 2019b). In the central United States, the oldest trees are found on steep slopes with infertile soils (Therrell & Stahle, 1998). Some of the oldest trees growing in Mediterranean environments are on cliffs (Mathaux et al., 2016). Larson (2001) found that *Thuja occidentalis* can be over 1500 years old on cliffs, whereas its maximum age on fertile sites is 400 years. Finally, although certain old trees have been worshiped and safeguarded by local communities (Blicharska & Mikusiński, 2014; Lindenmayer & Laurance, 2017), human activities, such as land clearing, logging, and agricultural expansion, are major threats to large old trees (Lindenmayer et al., 2012). As such, the oldest trees are more likely to persist in regions with limited human disturbance, such as those with low human population density (Liu et al., 2019a).

Quantification of the age of the oldest trees is challenging. Some researchers have used tree size to estimate the age of the oldest trees (Black et al., 2018; Liu et al., 2019a). However, large diameter does not always correspond to old age (Lindenmayer & Laurance, 2017). For example, small understory trees in Congolese rainforest can be older than large-diameter canopy trees (Hubau et al., 2019). Therefore, although measurements of diameter provide basic information on broad-scale patterns of large old trees, they do not provide accurate information on the oldest trees. Radiocarbon dating and tree ring analyses have provided more accurate estimates of tree age (Ferguson, 1968; Lara & Villalba, 1993; Liu et al., 2019b; Piovesan et al., 2018). However, most such studies focused primarily on climate reconstructions and tree growth and provided limited information on the distribution patterns of the oldest trees at regional or larger scales.

Fortunately, data on tree ages are accumulating rapidly thanks to the development of the International Tree Ring Data Bank (ITRDB), which is the most comprehensive existing database on global tree ring studies (Zhao et al., 2019). Meanwhile, there are increasing resources specifically designated for studying old trees and numerous studies documenting the oldest trees in a particular region (Ferguson, 1968; García-Cervigón et al., 2019; Lara & Villalba, 1993; Liu et al., 2019b; Piovesan et al., 2018;

Stahle et al., 2019). Together, these data and resources make it possible to map the global distribution of the oldest trees. We documented the age of the world's oldest trees and then constructed models of the factors influencing the global distribution of these trees, including topographic, climatic, edaphic, and anthropogenic drivers. Specifically, we aimed to determine where the oldest trees occur and what species are they and the key determinants of their occurrence.

METHODS

Tree data

We compiled detailed information on scientifically dated trees from around the world. First, we extracted all tree ring records from the ITRDB (Appendix S1). Many of these studies have cored old trees in undisturbed regions and contain accurate information on tree ages. From this database, we extracted information on the location, species, age, and elevation of all 197,855 tree cores from >230 species at 4854 sites. Second, we collected data from recently published studies that were not at the time included in the ITRDB and that were recommended by tree ring experts. Tree ring sampling is biased toward conifer species because their rings are easily counted (Zhao et al., 2019), and there are few tree ring studies in the ITRDB from tropical regions because many tropical trees do not produce easily recognizable annual growth rings (Zuidema et al., 2012). To close this gap in data coverage, we expanded our literature and data search by using the keyword phrase *the oldest trees* and focused on old trees in tropical regions relative to a combination of radiocarbon dating and tree ring-based approaches (Liu et al., 2019b; Patrut et al., 2018).

To maximize hardwood species in our database, we requested information from experts working on tropical tree rings through emails and personal communication (e.g., A. Di Filippo & A. Patrut). The records obtained from tropical areas are primarily from dendroclimatological studies, and some of the tree cores used had rotten sections. As such, it is likely that these records are underestimates. Nevertheless, these data provided an opportunity to map the global distribution pattern of the oldest trees based on the same criteria.

To avoid potential problems with spatial dependence, we focused only on the oldest tree species at a given site from all the data sets compiled when modeling the distribution pattern of maximum tree age. We included information from reliable databases and peer-reviewed articles that documented the oldest trees in given regions, such as the OLDLIST, a database of the oldest scientifically dated trees in the world (Brown, 1996) (Appendix S2). We extracted species, latitude, longitude, and elevation data from each of the original studies in our data sets. In total, we collected data from 156 sites in addition to the 4854 sites in the ITRDB (Figure 1 & Appendix S2). To determine whether the oldest tree species were also those with the largest maximum tree height at the global scale, we extracted tree maximum height information from local floras and reliable databases, such as the Gymnosperm Database (https://www.conifers.org/) (Appendix S3). To model the global distribution
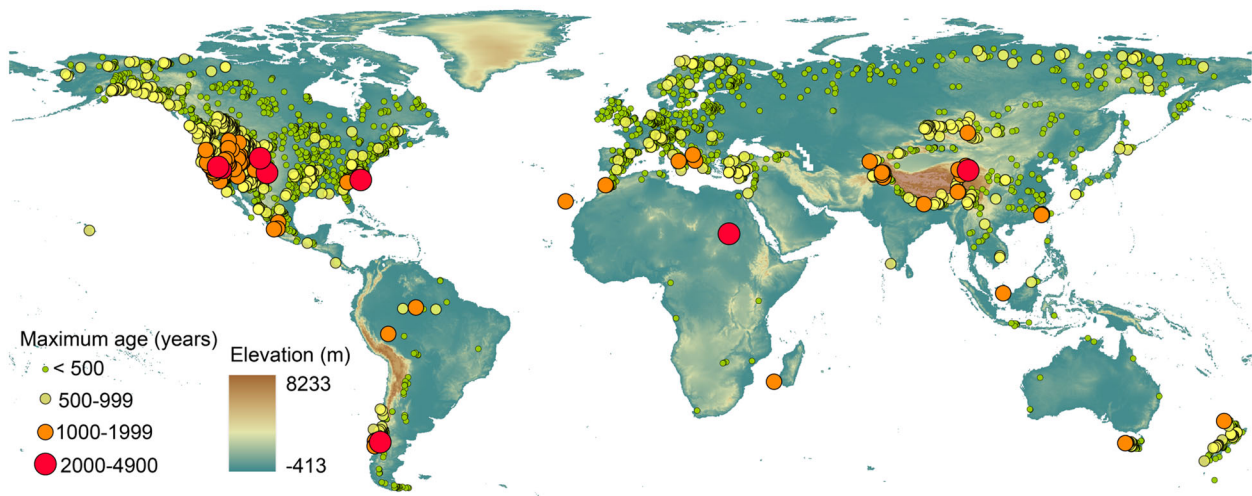
FIGURE 1 Global distribution of the oldest tree recorded at each site, including 4854 sites from the International Tree Ring Data Bank and 156 sites from other scientifically dated resources (see text for details)

pattern of maximum tree age (age of the oldest tree at a given site), we included only living trees that were ≥ 100 years old in the ITRDB (most sites have trees exceeding 100 years old) (Liu et al., 2019a).

To identify the best predictors of maximum tree age at a given site, we extracted four types of environmental variables that are likely linked to the presence of old trees: climate (Di Filippo et al., 2012), soil (Larson, 2001), topography (Liu et al., 2019b), and human population density (Lindenmayer et al., 2012; Liu et al., 2019a). We extracted nine climatic variables from the WorldClim2 database at 1-km spatial resolution (Fick & Hijmans, 2017), three anthropogenic variables data from the HYDE 3.2 database (Goldewijk et al., 2017), and three soil variables from the Soilgrids database at 250-m spatial resolution (Hengl et al., 2017). These variables are commonly used in macroecological studies (e.g., modeling the global pattern of canopy height [Zhang et al., 2016]). Our preliminary analyses revealed that many of these predictor variables, including historical climatic variables, were highly correlated (Spearman's rank correlation). Thus, we excluded them from the analyses (Appendix S4).

Model of spatial distribution of the world's oldest trees

We modeled seven ecologically meaningful variables, including three climatic variables (mean annual temperature, precipitation of driest quarter, and precipitation of warmest quarter), one soil variable (soil organic carbon content in layer 1), two anthropogenic variables (global human population density and proportion of urban area), and one topographical variable (elevation) to predict maximum tree age based on different environmental predictors.

To ensure that our predictor- and response-variable data were normally distributed, we log transformed human population density and proportion of urban area. We calculated variable inflation factors (VIFs). All VIFs were below 4.1, suggesting no serious multicollinearity between explanatory variables. We used both ordinary least squares and spatial linear models to evaluate the relative importance of the predictor variables in determining patterns of maximum tree age. The response variable was log-transformed to meet the assumption of residual normality and homoscedasticity. Model residuals were checked, and we found no evidence that the residuals were correlated with predictors. To account for the effect of spatial autocorrelation and reduce the possible influence of spatial sampling bias in our data, we employed spatial simultaneous autoregressive error models (Kissling & Carl, 2008). We then used an approach that yields natural decompositions of the model R^2 in linear regression models to evaluate the relative importance of each predictor (Grömping, 2015). For both models, we calculated the overall R^2 and used Moran's I index to assess spatial autocorrelation. We conducted all analyses in R 4.0.0 (R Core Team, 2020). We used the R packages spdep, relaimpo, and spatialreg to construct spatial linear models and assess the relative importance of potential explanatory variables.

To identify the threat status of the studied tree species, we first extracted information from the International Union for the Conservation of Nature (IUCN) Red List website (https://www.iucnredlist.org/ [accessed in November 2021]) on threat category and threats for all study species that exceeded 100 years. We focused on species for which there were specimens ≥500 years old and downloaded the global protected area map from the December 2021 World Database of Protected Areas (https://www.protectedplanet.net/en). We considered sites with trees ≥500 years old priority conservation areas for extremely old trees, and we overlaid locations of these sites

TABLE 1 Worldwide distribution of trees ≥2000 years old[a]

Species	Tree age (years)	Elevation (m)	Location	References
Pinus longaeva	4900	3277	Wheeler Peak, USA	Currey (1965)
Pinus longaeva	4850	2950	White Mountains, California, USA	Brown (1996)
Fitzroya cupressoides	3622	890	Western slopes of the Andes, Chile	Lara and Villalba (1993)
Sequoiadendron giganteum	3266	1524–2133	Sierra Nevada Mountains, USA	Brown (1996)
Sequoiadendron giganteum	3220	1524–2133	Sierra Nevada Mountains, USA	Brown (1996)
Sequoiadendron giganteum	3075	1524–2133	Sierra Nevada Mountains, USA	Brown (1996)
Juniperus przewalskii	3053	4175	Zongwulong Mountain, China	Yang et al. (2014)
Sequoiadendron giganteum	3033	1524–2133	Sierra Nevada Mountains, USA	Brown (1996)
Pinus longaeva	2984	2805	White Mountains, California, USA	International Tree Ring Data Bank (ITRDB)
Juniperus przewalskii	2868	4175	Zongwulong Mountain, China	Yang et al. (2014)
Pinus longaeva	2730	2805	White Mountains, California, USA	ITRDB
Pinus longaeva	2658	2805	White Mountains, California, USA	ITRDB
Juniperus occidentalis	2675	2133	Sierra Nevada Mountains, USA	Brown (1996)
Taxodium distichum	2624	2	Black River, North Carolina, USA	Stahle et al. (2019)
Juniperus przewalskii	2582	4175	Zongwulong Mountain, China	Yang et al. (2014)
Pinus longaeva	2566	2805	White Mountains, California, USA	ITRDB
Pinus longaeva	2486	2805	White Mountains, California, USA	ITRDB
Juniperus przewalskii	2460	4175	Zongwulong Mountain, China	Yang et al. (2014)
Adansonia digitata	2450	1077	Mbuma, Zimbabwe	Patrut et al. (2018)
Pinus aristata	2435	3280–3430	Black Mountain, Colorado, USA	Brown (1996)
Juniperus przewalskii	2301	4175	Zongwulong Mountain, China	Yang et al. (2014)
Juniperus przewalskii	2289	4175	Zongwulong Mountain, China	Yang et al. (2014)
Juniperus przewalskii	2230	4175	Zongwulong Mountain, China	Yang et al. (2014)
Pinus longaeva	2193	2805	White Mountains, California, USA	ITRDB
Juniperus przewalskii	2169	4175	Zongwulong Mountain, China	Yang et al. (2014)
Juniperus przewalskii	2156	4175	Zongwulong Mountain, China	Yang et al. (2014)
Pinus balfouriana	2110	1524–2133	Sierra Nevada Mountains, USA	Brown (1996)
Taxodium distichum	2098	2	Black River, North Carolina, USA	Stahle et al. (2019)
Pinus longaeva	2042	2805	White Mountains, California, USA	ITRDB

[a]Most occur in high-elevation mountainous areas.

on the global protected area network. Based on these results, we identified conservation gaps.

RESULTS

We produced the first map of the global distribution of existing old trees based on scientifically dated records (Figure 1). A *Pinus longaeva* (4900 years) in the United States was the oldest dated tree species in the world, followed by a *Fitzroya cupressoides* (3622 years) in Chile, a *Sequoiadendron giganteum* (3266 years) in the United States, and a *Juniperus przewalskii* (3053 years) in China (Table 1), all gymnosperms. There were an additional 24 gymnosperm species >1000 years old (Appendix S3). Only three angiosperm species exceeded 1000 years old: *Adansonia digitata* (~2450 years old), *Cariniana micrantha* (~1400 years old), and *Dipteryx odorata* (~1200 years old). The ages of all of these

angiosperms were determined by radiocarbon dating (Appendix S2).

We recorded 243 tree species: 82 angiosperm species and 161 gymnosperm species >100 years old. Gymnosperms had a significantly higher maximum longevity (mean 714 years old) than angiosperms (mean 334 years old) ($t = -5.96$, df = 238.97, $p<0.001$) (Figure 2a). Log-transformed species maximum longevity was only weakly correlated with species maximum height (Pearson's correlation: $p = 0.013$, 95% CI 6.34×10^{-4} to 5.31×10^{-3}) (Figure 2b). For gymnosperms, there was no significant linear relationship between species maximum longevity and maximum height (Pearson's correlation: df = 159, $p = 0.99$).

Data from ITRDB showed that 8072 of the cored trees (4.04%) were older than 500 years. There was no statistically significant evidence of a relationship between the number of cored trees and elevation ($t = 4.52$, $p = 0.11$), indicating that there was
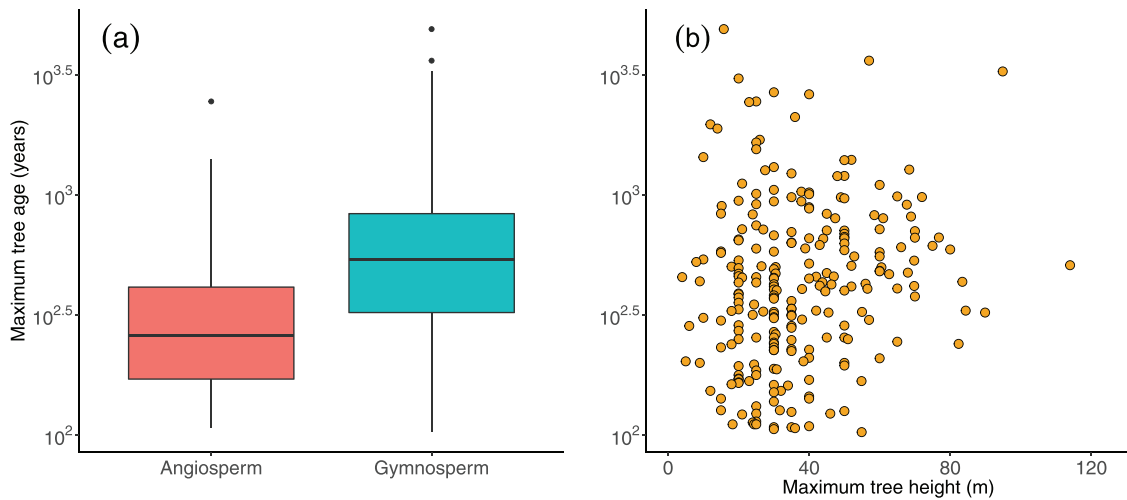
FIGURE 2 (a) Recorded maximum tree age of angiosperm and gymnosperm species and (b) relationship between maximum longevity and maximum height of 243 studied species (Pearson's test, $r=0.16$, $p=0.013$, 95% CI 6.34×10^{-4} to 5.31×10^{-3})

TABLE 2 The results of nonspatial (ordinary least squares [OLS]) and spatial linear regression models (SLMs) used to predict the distribution pattern of the oldest trees, with maximum tree age (log transformed) based on living trees ≥100 years old as a response variable

Predictor variables	Standardized coefficient	
	OLS	SLM
Elevation	0.3867[a]	0.4392[a]
Human population density[b]	−0.2353[a]	−0.1957[a]
Proportion of urban area[b]	0.0166	0.0165
Mean annual temperature[b]	−0.1147[a]	−0.1416[a]
Precipitation of driest quarter	0.122[a]	0.1991[a]
Precipitation of warmest quarter	−0.0674[a]	−0.0709[a]
Soil organic carbon content	−0.1288[a]	−0.1493[a]
Model R^2	0.2655	0.287
Model AIC	−1387	−1806
Errors Moran's I	0.2978	0.0809

[a] $p < 0.001$.
[b] Log transformed.

no elevational sampling bias. However, the proportion of cored trees ≥500 years old on a site was significantly and positively correlated with elevation ($t = 20.31$, $r = 0.29$, $p<0.001$, 95% CI 2.84×10^{-3} to 3.45×10^{-3}), indicating that extremely old trees were more common in high-elevation areas. There were 30 trees >2000 years old, and 27 of them occurred in high mountains (Table 1).

Our regression models demonstrated that elevation was significantly positively related to maximum tree longevity, whereas human population density had a significant negative effect (Table 2). Maximum tree longevity was also influenced by mean annual temperature and precipitation variables (Table 2). Soil variables, especially organic carbon content, had a negative effect on maximum tree longevity. Our best fitting spatial model showed that these variables explained 28.7% of the total vari-ation of the maximum tree longevity (Table 2). Among these variables, elevation had the strongest association with maximum tree age (Appendix S5).

Thirteen of 95 tree species ≥500 years old are threatened with high extinction risk (critically endangered, endangered, or vulnerable), and 18 species have decreasing populations (Appendix S3). The greatest threat to these species is resource overexploitation (biological resources use); 71.6% of the assessed species are affected. Habitat loss (35.8%), fire (32.8%), invasive species (29.9%), and climate change (23.9%) followed as lesser threats. About 37% of the sites with trees ≥500 years old were located in protected areas, mainly, North America, Eastern Europe, and New Zealand (Figure 3). However, many extremely old trees, ≥2000 years old, in western parts of China and the United States were outside protected areas (Figure 3).

DISCUSSION

Our global assessment of the existing oldest trees in the world revealed trees over 1000 years old were rare (Figure 1). According to the ITRDB database, there were 197,855 cored old trees, 620 trees (0.31%) ≥1000 years, 18 trees (0.009%) ≥2000 years, and 1 tree >3000 years old. Therefore, unlike the frequently reported extremely old trees ≥2000 years in many countries (e.g., Black et al., 2018; Liu et al., 2019a), we found that local estimates of tree ages for extremely old trees based on tree diameters or tree height are probably inaccurate. For example, at least 102 counties in China, many of which are in the eastern parts of the country with high population densities, claim to have living trees >1000 years old (Liu et al., 2019a). However, dendrochronological evidence reveals that old trees in the eastern parts of China rarely exceed 1000 years old (Liu et al., 2019b). Similarly, early European explorers in Africa claimed baobab trees were >5000 years old, but radiocarbon dating shows that the oldest ones are about 2450 years old (Patrut et al., 2007, 2018).
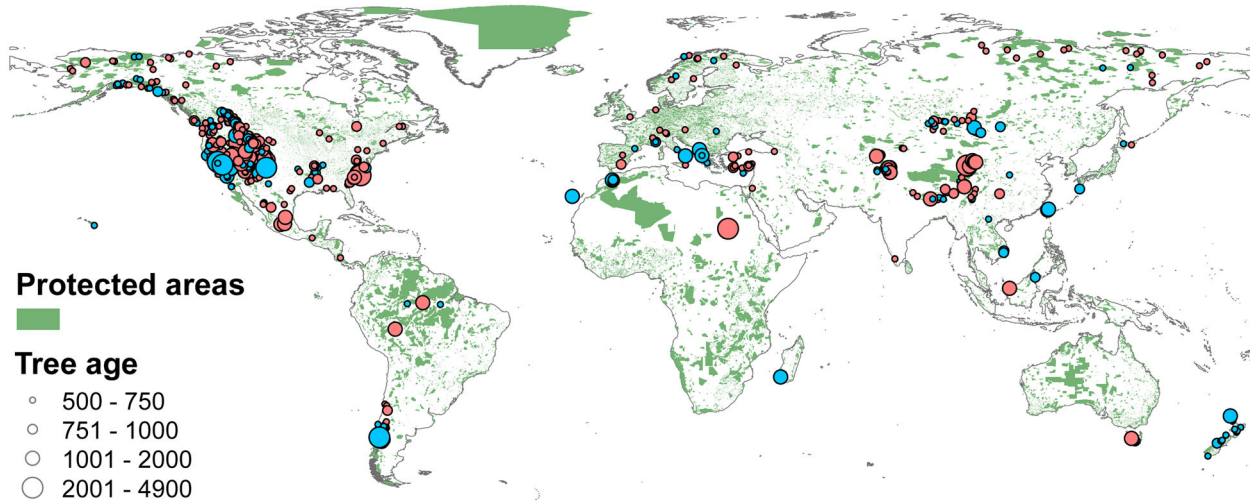
FIGURE 3 Distribution of sites with trees ≥500 years and the trees' conservation status (blue dots, sites in existing protected area network; red dots, sites outside protected areas)

Several processes may explain why especially long-lived trees (e.g., those exceeding 1000 years) are rare and are distributed primarily in mountains with stressful environmental conditions. First, biologically, only those species with specific morphological and physiological traits survive for such long periods. According to our analyses, gymnosperm species, especially pines and cypress, tend to live longer than angiosperm species, and results of a global analysis of gymnosperms showed that they generally colonize arid, boreal, and mountainous areas (Fragnière et al., 2015). This pattern may relate to their defensive traits and adaptability to drought and cold (Xu & Liu, 2022; Piovesan & Biondi, 2021). For example, high resistance to diseases and pests and high tolerance to the stressful climate conditions supporting *P. longaeva* (Appendix S6) is at least partially responsible for the longevity of this species (Bentz et al., 2017).

Second, we found that maximum tree longevity is associated with less fertile soil, dry, and cold environments (Table 2). The oldest trees are more likely to occur where resources are scarce (Munné-Bosch, 2018; Schulman, 1954). For example, there is a three-fold increase in maximum lifespan of *Fagus sylvatica* between hilly versus high-mountain sites (Di Filippo et al., 2015) and a three-fold increase for *T. occidentalis* between sites on fertile soils versus those on cliffs (Larson, 2001). Trees growing in challenging environments grow slowly and likely invest more energy in resisting severe droughts, windstorms, fire, and pathogens (Di Filippo et al., 2015; Issartel & Coiffard, 2011). Beyond these local studies, a recent global analysis confirms that climatic dryness can promote longevity of drought-tolerant trees (Xu & Liu, 2022).

Third, even if trees can grow extremely old, they are often those deliberately targeted for firewood collection or likely to be cleared for agriculture. We found that 70.6% of the studied tree species ≥500 years old are threatened by resource overexploitation. Globally, old-growth forests at lower elevations have generally been logged (Sandel & Svenning, 2013), result-

ing in a rapid decline of extremely old trees in many parts of the world (Lindenmayer et al., 2012). The remaining old trees are, therefore, more likely to persist in remote regions with limited anthropogenic disturbances, as we confirmed. In summary, we found that the current global distribution pattern of the oldest trees is a consequence of both environmental factors and human activity.

Although the oldest trees have persisted in harsh environments in the past, global change may be affecting their future survival and may induce rapid population declines of extremely old trees. Under global warming, high mountains are warming faster than low elevations (Pepin et al., 2015), and such changes can be problematic for the oldest trees because there may be an upper temperature limit for these species, and some of these trees die in response to shifts in climate (Brienen et al., 2020; McIntyre et al., 2015). For example, in Africa, nine of the oldest baobab trees died over 12 years. Their deaths may be associated, at least in part, with global climate change (Patrut et al., 2018). In addition, competitors with, and predators of, old trees have moved to higher elevations under global warming (Raffa et al., 2013). For example, *P. longaeva* and *S. giganteum* are threatened by invasive species (Appendix S3). Many extremely old trees persist in regions with limited human activity, such as in high mountains (Liu et al., 2019b; Piovesan et al., 2018), and in inaccessible places, such as cliffs and rivers (Mathaux et al., 2016; Stahle et al., 2019). Unfortunately, human activities, including deforestation and logging, are increasingly impinging on these areas. For example, hilltop forests in many areas that are not optimal for agriculture have, nevertheless, been converted into farmlands in recent decades when land at lower elevations has been fully utilized (Xiong et al., 2020). Inventory of tree ages in these regions is urgently required to protect ancient forests.

Our results have important implications for the conservation of large old trees. Current efforts to conserve large old trees

are based primarily on identifying trees for protection on their diameter and height (Lindenmayer & Laurance, 2017; but see Riling et al. [2019]). However, we found that the oldest trees are not necessarily the tallest or largest (Figure 2b). Therefore, conservation strategies developed for the tallest trees and trees with the largest diameters may not be appropriate for conserving the oldest trees. The tallest trees generally grow in moist productive areas with high precipitation or prolonged periods of fog (Larjavaara, 2014), including the tallest trees in Borneo and in the Amazon Basin (Gorgens et al., 2019; Shenkin et al., 2019). These extremely tall trees or trees with very large diameters are features of old forests, and their importance has been relatively well recognized. In contrast, the oldest trees are more likely to occur in cold, arid, high-elevation areas, with few people and where there may be few or no conservation programs (Figure 3). Although the current risk of loss of old trees in these regions is relatively low and the proportion of threatened species is low, in coming decades, they may be vulnerable to rapid environmental changes, including warming, habitat fragmentation, logging, and disease (Bennett et al., 2015; Lindenmayer & Laurance, 2017; Patrut et al., 2018). We, therefore, argue that new conservation strategies are urgently required to conserve the world's oldest trees. These include conservation reserves specifically established for the protection of these trees located in mountainous areas that may support limited other biodiversity because they are characterized by extreme environments. For example, as shown in Table 1, the U.S. White Mountains and Chinese Zongwulong Mountain are hotspots for the world's oldest trees and should be targeted for protection. Our results suggest that extremely old trees in the western parts of China and the United States deserve greater conservation effort (Figure 3). There are also extremely old trees growing on productive sites at moderate to low elevations, such as *F. cupressoides* on the western slopes of the Andes (Chile). Yet, these species are threatened by logging, firewood harvesting, and livestock farming according to the IUCN Red List website. As such, there may also be a need to institute bans on clearing, exotic livestock grazing, and firewood harvesting in regions where old trees occur (Lindenmayer et al., 2014). Moreover, targeted conservation strategies for these trees need to consider indigenous knowledge and contributions of local communities to improve conservation effectiveness. Finally, the location of some extremely old trees may need to be kept secret to limit the risks of them being vandalized (Lindenmayer & Scheele, 2017) or human visitation introducing pathogens and diseases that compromise tree health (Black et al., 2018).

Our data sets have several potential biases. First, although we sourced as much tree age information as possible, most of the data were obtained from the ITRDB. Unfortunately, the database is biased toward conifer species, whereas broadleaf species, especially those in the tropics, are underrepresented (Di Filippo et al., 2015; Zhao et al., 2019). Second, our study was biased toward cored trees from undisturbed areas (in many cases, mountains) to avoid anthropogenic influence on tree growth. However, there can be long-lived trees at low elevations in human-dominated landscapes, such as in ancient temples and cities and along rivers (Liu et al., 2019a; Stahle et al., 2019).

Indeed, people in many regions (including those in densely populated areas) worship old trees and protect these trees (Black et al., 2018; Blicharska & Mikusiński, 2014). However, such trees are often not scientifically dated and were rarely included in our database. Third, many old trees are hollow, and age information from the rotten parts of these trees is missing. These potential uncertainties related to hollow trees are likely to have influenced our results. These limitations of our data sets and methods may have contributed to our model explaining only 27.5% of the total variation in the distribution of the oldest trees. Indeed, many extremely old trees may have yet to be found. Therefore, old trees in tropical and human-dominated landscapes deserve more attention from a conservation perspective. To improve the predictive ability of our models, we suggest that future research targets the collection of tree longevity information on hardwood species across disturbance gradients by using advanced dating technologies.

Ours is the first global assessment of the age and spatial distribution of the oldest surviving trees in the world. We found that the world's oldest surviving trees are mostly gymnosperms. With few exceptions (e.g., Lara & Villalba, 1993; Stahle et al., 2019), they are most likely to occur at sites that are high-elevation, remote, cold, and dry with poor soils that are unsuitable for human exploitation. This spatial distribution pattern is different from that found for the tallest trees, which typically occur in high-productivity environments. The oldest trees in high mountains are at risk from climate change and increasing human disturbance, yet many of them are outside protected areas. Better conservation of these trees will require new and often targeted conservation strategies.

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