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Size-focused conservation may fail to protect the world's oldest trees

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SUMMARY

Old trees are irreplaceable natural resources that provide multifaceted benefits to humans. Current conservation strategies focus primarily on large-sized trees that were often considered old. However, some studies have demonstrated that small trees can be more than thousands of years old, suggesting that conventional size-focused perceptions may hamper the efficiency of current conservation strategies for old trees. Here, we compiled paired age and diameter data using tree-ring records sampled from 121,918 trees from 269 species around the world to detect whether tree size is a strong predictor of age for old trees and whether the spatial distribution of small old trees differs from that of large old trees. We found that tree size was a weak predictor of age for old trees, and diameter explained only 10% of the total age variance of old trees. Unlike large-sized trees that are mainly in warm, wet environments and protected, small old trees are predominantly in cold, dry environments and mostly unprotected, indicating that size-focused conservation failed to protect some of the oldest trees. To conserve old trees, comprehensive old-tree recognition systems are needed that consider not only tree size but also age and external characteristics. Protected areas designed for small old trees are urgently needed.

INTRODUCTION

Old trees are irreplaceable conservation resources with a wide range of key ecological, evolutionary, and cultural values.[1–3] Old trees provide critical habitat for many animal and plant species.[4] They are also vital evolutionary resources that can have long-term adaptive capacity in environments subject to rapid change.[5] Old trees have numerous social-cultural material, aesthetic, and religious values for humans.[6] However, environmental changes are driving a widespread loss of old trees and there is an urgent need to protect them.[7–9]

Current conservation efforts for old trees are focused primarily on large old trees.[10,11] Tree age is often positively correlated with diameter, especially within a particular ecosystem type[12]; large old trees are generally defined as trees with an extremely large diameter, such as trees with a diameter at breast height (DBH) $\geq$50 cm. Therefore, most old trees of conservation concern are large-sized, such as mountain ash (*Eucalyptus regnans*), which typically occurs in productive parts of landscapes.[13] However, large trees are not necessarily the oldest trees, and some large trees are not particularly old. For example, many mountain ash trees exceed 500 cm in DBH, but most of them are less than 500 years old.[14] Conversely, many ancient trees are small.[15,16] A 1,140-year-old Phoenician juniper (*Juniperus phoenicea*) in the Verdon Gorge of France is only 8 cm in DBH and 1.5 m in height.[17] A 1,032-year-old eastern white cedar (*Thuja occidentalis*) in the Niagara Escarpment of Canada is only 30 cm in diameter.[18] The oldest tree species in China, a Qilian juniper (*Juniperus przewalskii*) living in the northeast Tibetan Plateau, may exceed 3,000 years old[19] but has a maximum tree height of only 12 m. Such small but long-living trees, which we term "small old trees," are at risk of being overlooked because of their inconspicuous size.

Small old trees can be common as predicted by growth-lifespan trade-offs in which trees with a slow growth rate tend to be small and have a long lifespan.[15,20] Low investment in stem growth allows small trees to invest more energy and resources in survival. For example, to improve drought resistance, trees may develop small xylem conduits,[21] incorporate new assimilates into storage pools, and invest more in root establishment at the expense of stem growth.[22] To adapt to resource-poor environments, pine trees would grow more slowly and invest more in chemical and anatomical defenses, such as higher density of constitutive resin canals[23] and inducibility of foliar phenolic compounds[24] to defend against pests and pathogens, than trees living in resource-rich environments.[25] Such investment enhances stress tolerance and promotes the longevity of small-sized trees. In contrast, large trees are usually vulnerable to

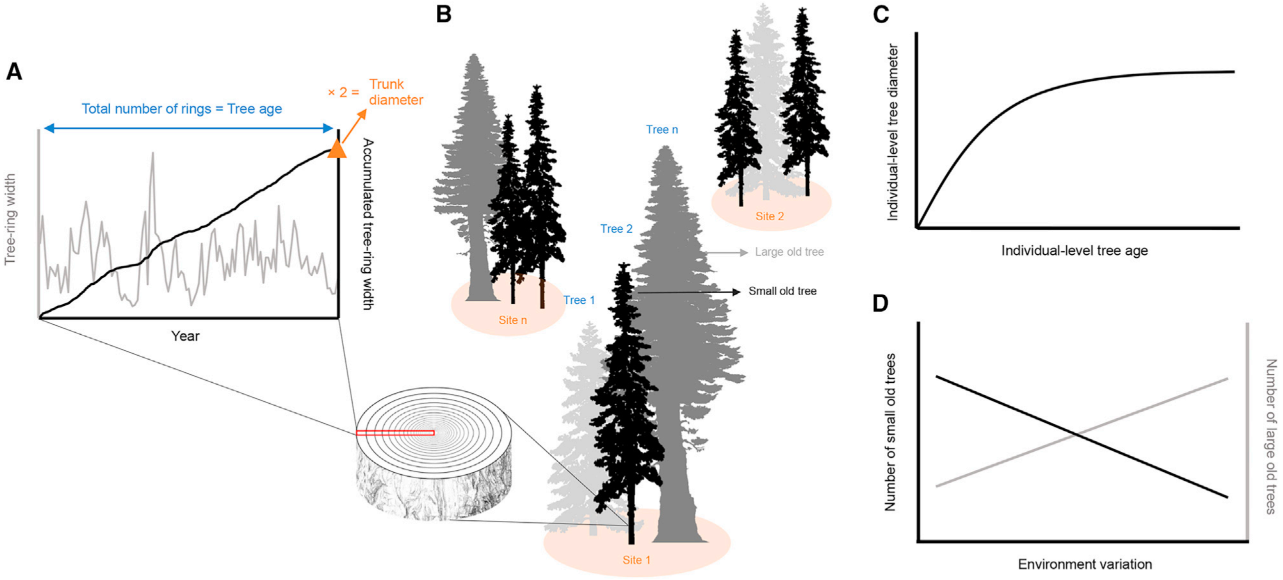

Figure 1. Flow chart for assessing tree age-diameter relationship and exploring the influencing factors for the distribution of small and large old trees

(A) Estimation of tree age and trunk diameter from time series data on annual tree-ring width (tree-ring series).

(B) Three cases of forest sites, each integrated by multiple tree-ring series sampled from at least 20 individuals.

(C) Conceptual relationship between tree age and diameter at the individual level.

(D) Hypothetical effects of environmental variables on the number of small and large old trees, respectively. Silhouette credit: Yiping Wang.

See also Table S2.

hydraulic stress owing to the high demand for sunlight and water, and the tall height of their canopy that exacerbates hydraulic stresses and xylem cavitation.[26] An advantage of high stress tolerance is that small old trees have been reported to occur in both productive areas such as in understory layers of tropical wet forests,[27] as well as in less fertile locations like vertical cliffs[17] and high-mountain zones.[15,28] However, there is a lack of data that pairs age and tree size for old trees at a global scale, limiting our understanding of the distribution and conservation status of small old trees.

The International Tree Ring Data Bank is the largest and most comprehensive tree-ring database globally. It provides individual-level time series data on annual tree-ring width. This can be used to simultaneously estimate tree age and trunk diameter by counting total rings for each individual and by accumulating annual tree-ring widths of each series, respectively.[29] Although this database has relatively few trees from tropical regions with modest seasonality (as indistinct seasonality prohibits tree-ring formation), it has been used to explore the distribution patterns of the oldest known trees in the world.[30] Here, we collected data from 121,918 trees sampled from 5,162 sites from the International Tree Ring Data Bank (Data S1A) covering a geographical range from 163.7°W to 177.2°E and from 54.9°S to 72.5°N, with elevations ranging from 1 m to 4,500 m above sea level (a.s.l.) (Figure S1). We coupled individual-level data on tree age with corresponding trunk diameter and asked: (1) is size a strong predictor of age for old trees? (2) What are the distribution patterns of small and large old trees? (3) What factors influence the distribution patterns of small and large old trees? To answer these questions, we used generalized linear mixed models to fit the age-diameter relationships for different age classes with species and sites included as random effects. We identified the environmental factors that determine the occurrence of small old trees as well as large old trees (Figure 1). Our work will provide a detailed understanding of old trees and guide the design of more effective conservation strategies.

RESULTS

Size is a weak indicator of age for old trees

We found that tree age increased with diameter for trees across all age classes (slope = 0.49, SE = 0.01, $p < 0.001$, $R^2 = 0.18$, n = 121,918) (Figure 2A; Table 1). However, when analyzing this relationship in each age class, the explanatory power of diameter on age decreased from young trees (<104 years old, slope = 0.24, SE = 0.01, $p < 0.001$, $R^2 = 0.18$, n = 30,269), to middle-aged trees (104∼264 years old, slope = 0.19, SE = 0.01, $p < 0.001$, $R^2 = 0.11$, n = 61,094) and old trees (≥264 years old, slope = 0.20, SE = 0.02, $p < 0.001$, $R^2 = 0.10$, n = 30,555) (Table 1). The diameter density distribution of old trees was left-skewed, with the average diameter of old trees being 45.7 cm (Figure 2B). More than 64%, 25%, and 9% of old trees (n = 30,555) had a diameter of <50, 30, and 20 cm, respectively. Less than 2% of old trees had a diameter ≥100 cm, demonstrating that many old trees were small and that tree size was a weak predictor of age for old trees. In addition, we found that species-level maximum tree age was not associated with tree maximum height (Figure 2C; slope = -1.65×10^{-5}, SE = 2.66×10^{-3}, p = 0.99, n = 120).

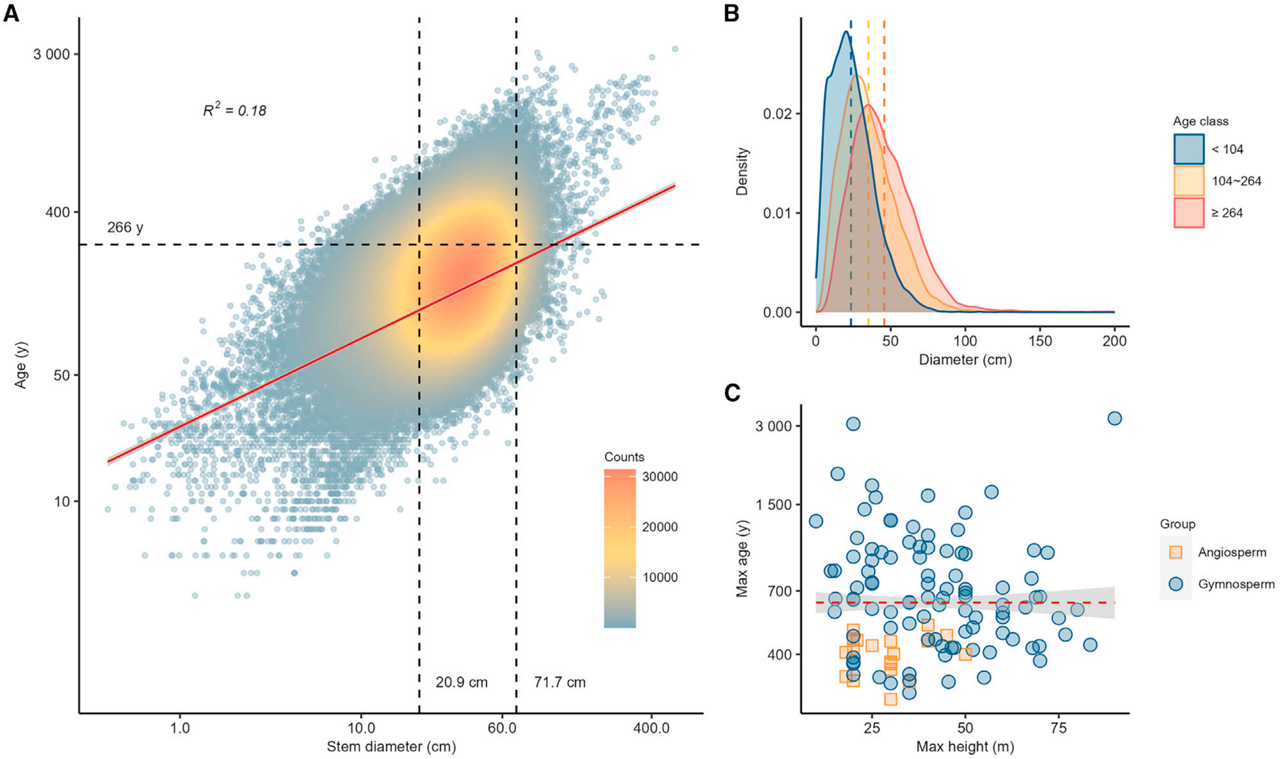

Figure 2. Relationship between tree age and stem diameter

(A) Fit of a generalized linear mixed model between age and diameter for all 121,918 trees (for more detail, see Table 1).

(B) Distribution of tree diameters of three age classes categorized by quartile. Dashed lines mark the average diameter of each age class (from left to right: 24.3, 35.1, and 45.7 cm).

(C) Relationship between maximum height and maximum age of species with three sample sites at least and a maximum age ≥264 years old. Red dashed line fitted by a linear model.

Gray shades in (A) and (C) are bands of 95% confidence interval.

See also Figures S2 and S4 and Data S1.

The distribution pattern of small old trees is different from that of large old trees

We found that 77 species were characterized as small old trees and 106 species were characterized as large old trees. About 92% of species with small old trees and 85% of species with large old trees were gymnosperms (Figure S2). There were no significant differences in wood density and seed mass between species with small old trees and species with large old trees, except for tree height that was lower in the former than in the latter ($p = 0.04$) (Figure S2).

The number of small old trees at a forest site decreased with annual mean temperature (slope = −0.13, SE = 0.01, $p < 0.001$), total precipitation (slope = -7×10^{-4}, SE = 1×10^{-4}, $p < 0.001$), altitude (slope = -2×10^{-4}, SE = 1×10^{-4}, $p < 0.001$), and soil fertility (slope = −0.1, SE = 0.03, $p < 0.001$) (Figures 3B and S3; Table S1). In contrast, the number of large old trees at each site increased with annual mean temperature (slope = 0.02, SE = 0.01, $p = 0.006$), total precipitation (slope = 6×10^{-4}, SE = 1×10^{-4}, $p < 0.001$), and altitude (slope = 3×10^{-4}, SE = 1×10^{-4}, $p < 0.001$) (Figures 3D and S3; Table S1). The intensity of human activities had a significant negative effect on the number of large old trees (slope = −1.22, SE = 0.28, $p < 0.001$), but not small old trees (slope = −0.66, SE = 0.39, $p = 0.09$) (Figure 3; Table S1). Finally, 45% of large old trees (total trees = 3,060) were in nature reserves, whereas 29% of small old trees (total trees = 3,064) occurred in protected areas (Figure 4).

DISCUSSION

Based on paired age and diameter data for 121,918 trees of 269 species around the world from the International Tree Ring Data Bank database, we found that tree size was a statistically significant indicator of tree age. However, the ability to predict age from size was weak for old trees, explaining only 10% of the age variance among individuals (≥264 years old) across various species at a global scale (Table 1). Moreover, more than 64% of individual old trees were smaller than 50 cm in diameter, indicating that many old trees are small in size. Considering that small old trees have different distribution patterns relative to large old trees, current conservation strategies are biased toward large-sized trees and may fail to conserve some of the world's oldest trees.

Current recognition of old trees was size-focused due to the difficulty of acquiring reliable tree age as tree coring involves intensive field and laboratory work that is expensive and time consuming.[10] In the UK, diameter was considered to be an

Table 1. The results of the generalized linear mixed models for fitting the relationship between age and diameter of individual trees for different age classes

Groups	Intercept (SE)	Slope (SE)	DF	p value	Marginal R^2
All trees	3.25 (0.05)	0.49 (0.01)	116,757	<0.001	0.18
Trees <104 years	3.55 (0.05)	0.24 (0.01)	27,515	<0.001	0.18
Trees 104∼264 years	4.42 (0.03)	0.19 (0.01)	56,445	<0.001	0.11
Trees ≥264 years	5.07 (0.06)	0.20 (0.02)	27,720	<0.001	0.10

$\log_e$-transformed tree age and diameter were respectively treated as a response and predictor variable. All models treated site nested within species as a random intercept in all models, and diameter depending on site nested within species as a random slope. Marginal R^2 was used to quantify the variance of tree age explained only by diameter. See also Figure S4.

important proxy for old trees which generally have girth >600 cm.[31] Similarly, technical guidelines to document old trees in China used trunk diameter as a proxy for old trees.[32] In Qinghai province, for instance, old trees were identified as trees with trunk diameters >150 cm.[32] In the western US, forests dominated by trees with large girth, usually >100 cm, were identified as old growth.[33] These size-focused conservation policies led to large old trees attracting considerable scientific research and conservation efforts.[6,34] However, we found the relationships between tree size and age varied among age classes: tree size explained 18% of the variance in age for young trees, but 10% for old trees (Table 1). Tree size tends to increase with age before plateauing for a prolonged period (Figure S4). For example, a study of four common species in North America showed that the diameter of all species linearly increased with age at a relatively young age, and reached its largest value at ∼200 years old for eastern hemlock (*Tsuga canadensis*) and ∼300 years old for Douglas fir (*Pseudotsuga menziesii*).[35] As trees age, the slope of such linear relationships becomes shallower (Figure S4) and tree size lessens as an indicator of age, especially for the oldest trees. In a forest of *Polylepis rodolfo-vasquezii* in central Peru, the explanatory power of tree size to predict the total variance of age decreased from 60% for a young tree population to less than 2% for an old tree population.[36] A study in Manaus, Brazil showed that tree size does not predict the age of the oldest trees, because trees over 1,100 years old have diameters that are half those of the largest trees.[37] Among the 30,555 old trees ≥264 years in our dataset, 64% of individuals had diameters <50 cm, and 25% had a diameter <30 cm (Figure 2), confirming that many old trees are small.

Several processes may explain why many old trees are small. First, there is a "growth-lifespan trade-off," in which trees have increased stress resistance capacity that extends lifespan at the cost of growth.[20] This is a main driver for the long-term survival of old trees. For example, trees were prone to form narrow xylem conduits to increase drought resistance in arid areas at the cost of stem growth.[21] In cold environments, narrow xylem conduits can also reduce the risk of freeze-thaw-induced embolism that causes tree hydraulic failure during the early growing season.[38] Therefore, many old trees are small yet persist in stressful environments that are cold and dry, as well as in high-mountain areas with poor soil, as demonstrated by previous studies.[17,28] In contrast, numerous large tall trees are vulnerable to drought due to their requirement for wider xylem conduits to acquire an adequate water supply which increases the risk of embolism-induced hydraulic failure.[26] Second, stressful environments protected small old trees from disturbances caused by natural enemies.[39] For example, native leaf beetles (*Chrysomela aeneicollis*) in the eastern Sierra Nevada Mountains of California have lower mean fecundity in high-mountain areas due to hypoxia and the cold environment and showed decreased abundance.[40] In the French Alps, trees living in high-mountain regions with a cold climate experienced lower levels of herbivory than trees in lower-elevation regions.[41] Unlike small old trees, large old trees primarily occur in warm and moist environments, conditions that also favor natural enemies.[42] For example, herbivory rates in humid tropical forests (11.1%) are significantly higher than in temperate broad-leaved forests (7.1%).[43] Compared to high-mountain regions, mountain pine beetles (*Dendroctonus ponderosae*) in the western United States and Canada exhibit higher rates of herbivory in coastal regions and other low-elevation forests.[44] Third, small old trees are often of limited use as timber for humans because they are frequently short-statured, with twisted and knotted stems, and consequently less suitable for logging. In addition, small old trees often occur in areas inaccessible to humans such as cliffs and high-mountain areas,[17,28] increasing the transportation costs for timber from small old trees. Conversely, humans prefer to log large old trees for their large size and knot-free stems. In tropical forests, logging operations have targeted the largest trees, causing a widespread and disproportionate loss of large old trees.[45] Notably, our findings showed that human disturbance had negative effects on large old trees but not small old trees (Figure 3).

Although small old trees have strong stress resistance and are less susceptible to threats from natural enemies and human activities, they are at increasing risk of population decline due to land-use change, climate warming, and possibly new pathogens.[8] Global warming may allow insect herbivores and new pathogens to occupy high-latitude and mountainous areas that were previously refugia for small old trees.[15] As a result, billions of coniferous trees living in forests ranging from Mexico to Alaska have been killed by warming-induced native bark beetle outbreaks[44] and pathogens.[46] Given that small old trees are irreplaceable features of forest ecosystems, it is vital to ensure their conservation.

In our study, ∼71% of small old trees occurred outside protected areas, a higher proportion than large old trees (55%; Figure 4). Small old trees were more prone to occur in stressful environments that are cold, arid, and have low levels of fertility (Figures 3 and S3). These places are characterized by low levels of biodiversity and are less likely to be protected. For example, Qilian juniper, an extremely old tree species that can exceed 3,000 years old and reach a maximum plant height of 12 m, is found primarily in unprotected forests on the Tibetan Plateau.[19] In contrast, large old trees are frequently found in biodiverse environments that are already protected. For example, the tallest tree in Asia, *Shorea faguetiana*, was found in a protected

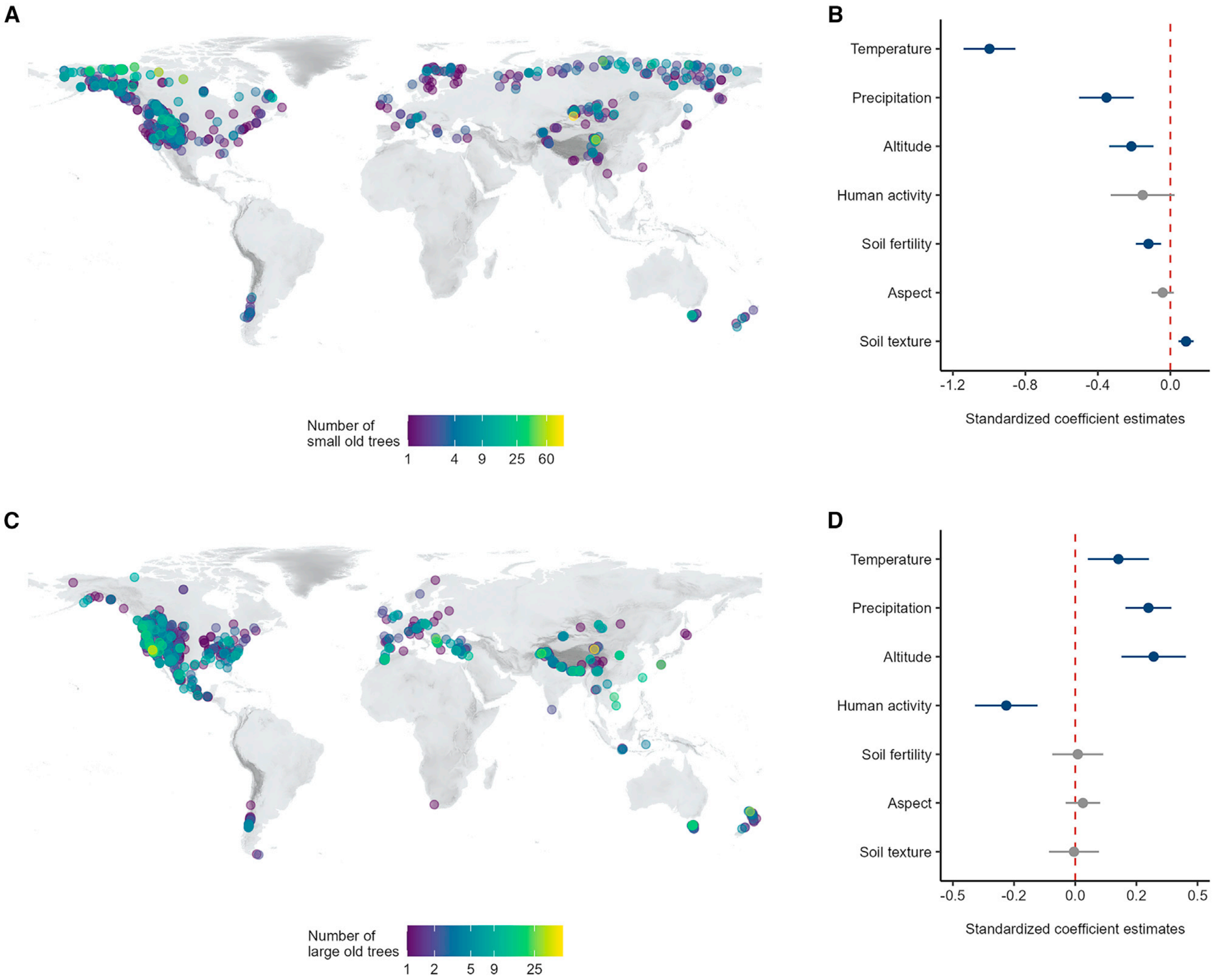

Figure 3. Distribution pattern of small and large old trees and their associated environmental covariates

(A and C) Location of forest sites with small (A) and large (C) old trees. The dots' color gradient from blue to yellow indicates the lowest to the highest number of small or large old trees across sites.

(B and D) Relative effects of environmental variables on the number of small (B) and large (D) old trees for each site. Dots represent standardized coefficients, and bars represent 95% credible intervals from generalized linear mixed models (Table S1). Dark blue dots mark estimates with a probability greater than 95%, and light gray dots mark estimates with a probability lower than 95%.

See also Figure S3, Table S1, and Data S1.

rainforest in Sabah, Malaysia.[47] Because current conservation efforts are often biased toward large old trees, size-focused conservation strategies may fail to conserve the world's oldest trees. We found that ∼93% of small old trees analyzed were outside protected areas supporting large old trees (Data S1B). Our results are consistent with previous studies, as old-growth forests at the southernmost forest edge of the Brazilian Atlantic supporting old trees with a diameter <40 cm were rarely protected,[48] and small old trees in Finland and Sweden often occurred in unprotected areas.[49]

Our results have important implications for the conservation of old trees. First, it is essential to acknowledge that large trees are not always old. Because tree size is a weak predictor of age for old trees, we suggest that the recognition of old trees should consider not only size but also other characteristics of old trees. For example, some special external characteristics could help to guide the recognition of old trees. These include hollowing trunks, large holes and cavities, spiral grain, crown dieback, and the presence of fungi, invertebrates, and other saproxylic organisms (Table S2). A 250-year-old ponderosa pine, for instance, usually has colorful bark plates with maximum plate width between fissures >25 cm, and no visible knot or whorl indicators on the main trunk below the crown.[50] Second, many gymnosperm species, particularly species from the pine and cypress families, can be extremely old but small in size. The oldest known tree species in the world, bristlecone pine, and the oldest tree species in China, Qilian juniper, are only ∼16 and ∼12 m in maximum height, respectively.[15] Thus, conifer species with low maximum tree height and notable external characteristics are worthy of more conservation attention. Third, our study on the

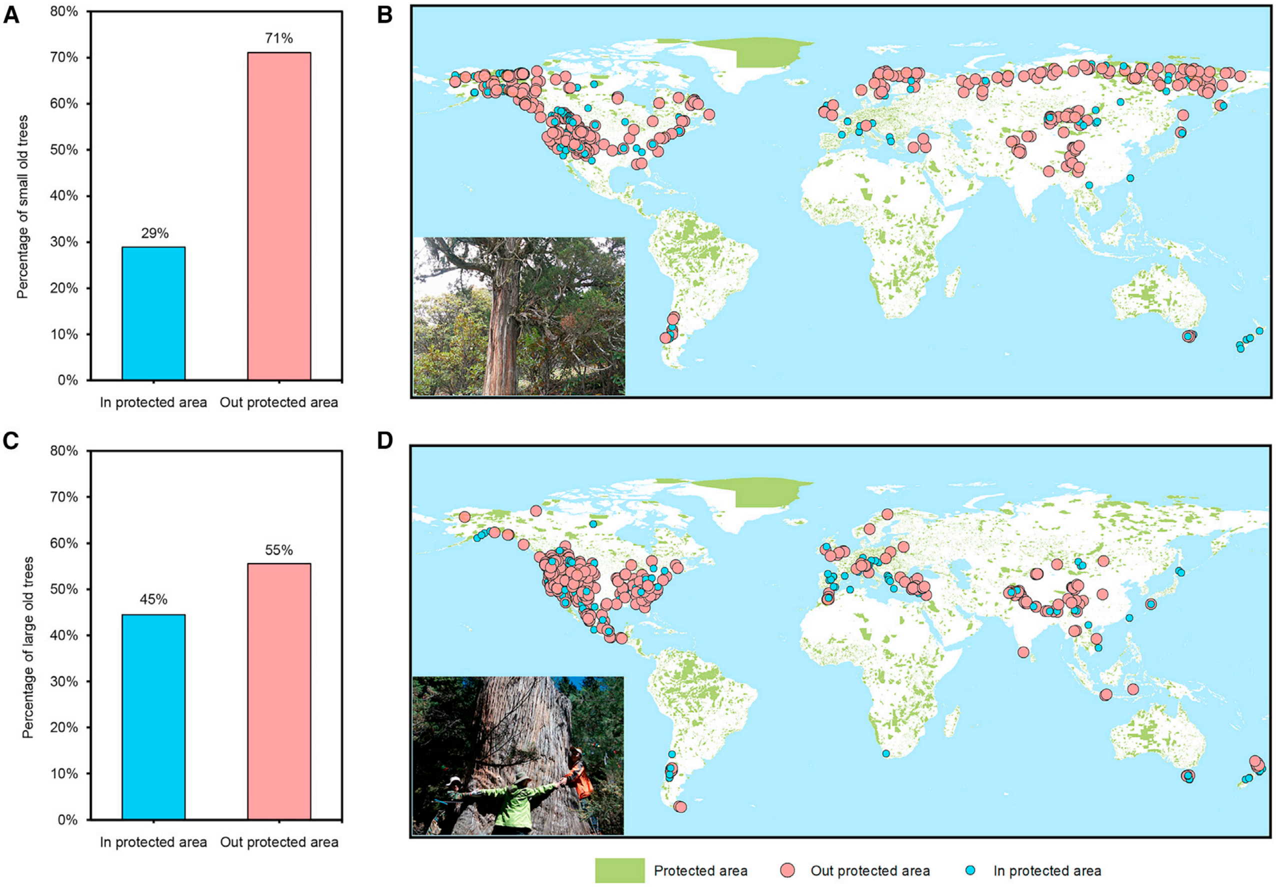

Figure 4. Protected status of small and large old trees

(A and C) Percentage of small (A, total trees = 3,064) and large (C, total trees = 3,060) old trees in and out of protected areas.

(B and D) Location of sites with small (B) and large (D) old trees, where large, pink and small, blue circles separately mark sites outside and in protected areas, and green areas show the world's protected areas. Pictures depict a small old tree with an age >900 years and a diameter of approximately 20 cm living in a high-mountain location (B) and a large old tree ~400 years old with a diameter of around 200 cm growing in a mountain with lower elevation on the West Sichuan Plateau (D). Photo credit: Xuehan Cheng.

See also Data S1.

distribution of small old trees identified several hotspots that are important to protect. In boreal forests in northern Canada and Alaska, there are many small old trees, such as dwarf white spruce (*Picea glauca*) that exceed 300 years old and have a diameter <20 cm (Data S1A). Some small old trees occur in hotspots for large old trees. In the Rocky Mountains, many Douglas fir exceed 360 years old and have a diameter <20 cm but are facing a high risk of logging for woody products and Christmas trees.[51] Finally, there is a limited ability to map small old trees in tropical areas due to a lack of tree-ring data from these areas. In a tropical forest in the Congo, small understory trees with a mean DBH of 16.1 cm (mean age of 262 years old) were much older than larger canopy trees with a mean DBH of 43.5 cm (194 years old).[27] In addition, the lack of large-scale investigations of characteristics of old trees such as tree height, bark, and canopy traits, also limits our ability to build models to predict the age of old trees. Therefore, maps of key areas for small old trees around the world will require more tree-ring studies spanning a range of environmental conditions and taxonomic groups.

Conclusions

By using paired tree age and diameter data from a global tree-ring database from 269 species, we found that tree size was a weak predictor of age for old trees, challenging the conventional perceptions that larger trees are older. As small old trees occur primarily in habitats that are different from large old trees, current tree size-focused conservation and management policies have failed to protect small old trees. We call for comprehensive old-tree recognition systems to identify hotspots for small old trees and establish protected areas designed for extremely old trees with small sizes.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2023.09.046.

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AUTHOR CONTRIBUTIONS

Y.M. and J.L. conceived the idea. Y.M. collected the data and performed the analysis. J.L., D.L., S.Z., and D.W. provided scientific and statistical advice. Y.M. and J.L. wrote the first draft of the manuscript. All authors revised the text and provided critical feedback.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data S1: Data supported the key findings in this study.	This study	Data S1
Software and algorithms		
R version 4.3.1	R Core Team[52]	https://www.r-project.org/
stats version 4.3.1	R Core Team[52]	https://www.r-project.org/
nlme version 3.1-162	Pinheiro et al.[53]	https://CRAN.R-project.org/package=nlme
V.PhyloMaker version 0.1.0	Jin and Qian[54]	https://github.com/jinyizju/V.PhyloMaker
MASS version 7.3-60	Venables and Ripley[55]	https://www.stats.ox.ac.uk/pub/MASS4/
Other		
Tree-ring dataset	International Tree Ring Data Bank	https://www.ncei.noaa.gov/pub/data/paleo/treering/
Tree-ring dataset with diameter at breast height	DendroEcological Network	https://www.uvm.edu/femc/dendro#data
TRY Plant Trait Database	Kattge et al.[56]	https://www.try-db.org/TryWeb/Home.php
Climatic Research Unit (CRU) 4.05 dataset	Harris and Osborn[57]	https://crudata.uea.ac.uk/cru/data/hrg/
ETOPO1 Dataset	ETOPO Global Relief Model	https://www.ngdc.noaa.gov/mgg/global/
The Regridded Harmonized World Soil Database v.1.2	Wieder et al.[58]	https://daac.ornl.gov/SOILS/guides/HWSD.html.
Global Human Modification of Terrestrial Systems, v1	Kennedy et al.[59]	https://sedac.ciesin.columbia.edu/data/set/lulc-human-modification-terrestrial-systems
The World Database on Protected Areas	Protected planet	http://www.protectedplanet.net/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Jiajia Liu (liujiajia@fudan.edu.cn).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data on tree age and diameter, site-level environmental variables, and species-level plant traits used in the statistical analysis of this study are available as supplemental Excel spreadsheets. The tree-ring, environmental variables, global tree density, and protected areas datasets are publicly available. DOIs are listed in the key resources table.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Tree age and diameter data were estimated using tree-ring time series of 121,918 trees from 269 species that were downloaded from the International Tree Ring Data Bank. Site-level climatic data was extracted from the Climatic Research Unit dataset.[57] Aspect data were extracted from the ETOPO1 Global Relief Model. Soil parameters datasets were downloaded from the Regridded Harmonized World Soil Database.[58] The dataset of human activity intensity was derived from Global Human Modification of Terrestrial System.[59] The world database on protected areas was downloaded from Protected Planet.

METHOD DETAILS

Tree-ring data

To estimate data on tree age and their corresponding diameter from individual-level time series data on annual tree-ring width (hereafter, tree-ring series), we downloaded 218,413 tree-ring series sampled from 5,173 forest sites around the world from the global tree-ring database, the International Tree Ring Data Bank: https://www.ncei.noaa.gov/pub/data/paleo/treering/ (accessed on 28 September 2021). Each forest site represented an independent tree population that was selected to reconstruct past climate information. At least 20 trees were sampled per site and two samples per tree were extracted using a 5 mm-diameter hand-held increment borer along the radius of a tree usually at breast height (~1.3 m). Many large trees in the tropics have buttresses, and such trees were cored above any buttress to have accurate tree age information.

To ensure the accuracy of tree age and diameter estimation, we manually checked formatting issues of all downloaded tree-ring series, including mismatched measurement accuracy, broken sequences, and repeated cores with the following steps. First, we manually checked the measurement accuracy of tree-ring series with abnormal tree-ring width (TRW) values, particularly the outlier series with median TRW beyond three standard deviations from the mean TRW for the same species. We corrected measurement accuracy referring to the other correct tree-ring series from the same site and the same species, as well as the detailed measuring information provided by earlier publications. Second, to minimize underestimation of tree diameter, we excluded broken tree-ring series that had non-consecutive calendar years, or which had consecutive repeated TRW values for decades. Third, for a tree with more than one tree-ring series, we retained the one with the maximal number of total rings to minimize the underestimation of tree age. In total, we collected tree-ring series for 121,918 trees from 5,162 forest sites (Data S1A and S1B) covering a geographical range from 163.7°W to 177.2°E and from 54.9°S to 72.5°N (Figure 1). This dataset includes 269 tree species of 82 genera from 35 families, of which 104 species are angiosperms and 165 species are gymnosperms (Data S1C). See also Figures S1 and S2.

Estimate tree age and diameter

We summed the total number of tree rings from each tree-ring series to estimate tree age (Figure 1) because tree-ring samples are generally extracted as close to the pith as possible for each tree. Although this approach might underestimate tree age because of missing rings from hollow trees and the number of years to reach sample height, the risk of underestimation is the same for all individuals and has no directional impact on our core results. To obtain tree diameter data, we summed annual TRWs and multiplied the value by two for each tree-ring series. Such accumulation of TRWs is a reliable measurement of tree diameter because tree-ring samples were generally extracted along the radius of the trunk, and recorded annual increments of tree radial growth over their lifespan. To test whether summed TRWs could predict realistic tree diameter, we collected tree-ring series of 562 trees which recorded realistic DBH, from the DendroEcological Network: https://www.uvm.edu/femc/dendro#data. We fitted the relationship between the estimated and observed diameter using linear models using "*stats*" package in R version 4.3.1.[52] Results showed that summed TRWs and observed DBH were essentially identical (Slope = 0.94, SE = 0.02, adjusted $R^2 = 0.76$, $P < 0.001$) (Figure S4C), and thus we used summed TRWs as reliable estimates of tree diameters in this study. In total, we obtained paired age and diameter data for 121,918 trees with an age ranging from 3 to 3,205 years old (mean age of 207 years old), and tree diameter ranging from 0.40 to 538.89 cm (mean diameter of 35.09 cm) (Data S1A).

Tree age-diameter relationship

To explore age-diameter relationships among age classes, we first divided all trees into three age classes based on quartiles of the full dataset: young trees with age <104 years old (the 25th quantile), middle-aged trees of 104~264 years old and old trees with age ≥264 years old (the 75th quantile). In each age class, we investigated the diameter density distribution of individuals. To test whether the age-diameter relationships vary among age classes, we fitted age-diameter relationships of each age class and across all age classes using generalized linear mixed models (GLMMs) with Gaussian error distribution (identity link) separately, with "*nlme*" package[53] in R version 4.3.1.[52] For all models, tree age ($\log_e$-transformed) was treated as a response variable, with diameter ($\log_e$-transformed) as the predictor variable. To account for phylogenetic and spatial relationships among trees, site nested within species was treated as a random intercept in all models, and diameter depending on site nested within species was treated as a random slope to account for variations of age-diameter relationships across site and species. We used marginal R^2 to quantify the variance of tree age explained by diameter.[60]

To examine associations between tree age and height, another indicator of tree size, we used a linear model to fit the relationship between species lifespan (the maximum tree age of each species) and maximum height. We used the maximum tree age and maximum height at the species level because of the lack of individual-level tree height data. The linear model with maximum tree height as a predictor and age ($\log_e$-transformed) as a response variable was fitted using "*stats*" package in R version 4.3.1.[52] Maximum tree height data were collected from Liu et al.[28] and the Gymnosperm Database: https://www.conifers.org/ (Data S1C). To ensure the representative of maximum tree age, only species with a maximum age ≥ 264 years old and including at least three sample sites were included in this analysis.

Identification of small and large old trees

As tree age and size vary substantially among species and ecosystems, we identified small old trees and large old trees based on the relative age and diameter of all individuals referring to the definition of large old trees (age and DBH >75th quantile) used by Begović et al.[11] First, we defined old trees as those older than the 75th quantile of all individuals in the full dataset (264 years old). In total, 30,555 trees were defined as old trees, with diameters ranging from 3.57 to 538.89 cm. Among these old trees, we then defined their smallest 10 quantiles (old trees with a diameter $\leq$ 20.9 cm) as small old trees, and the largest 10 quantiles (old trees with a diameter $\geq$ 71.7 cm) as large old trees (Figure 2A). Based on the definition, a total of 3,064 old trees were identified as small old trees and 3,060 as large old trees. We counted the number of small old trees and large old trees separately for each forest site to explore their distribution pattern (Data S1B).

Phylogenetic differences

To assess phylogenetic differences between small and large old trees, we generated a phylogenetic framework for the studied species (n = 269) using "*V.PhyloMaker*" package[54] in R version 4.3.1.[52] The phylogenetic backbone used by "*V.PhyloMaker*" was implemented with a mega-tree derived primarily from the largest dated phylogeny for seed plants (i.e. GBOTB).[54] To determine how small and large old trees differed in plant traits at the species level, we conducted a two-way analysis of variance (ANOVA) to assess differences in plant functional traits, between species with small old trees and species with large old trees. The plant functional traits include three widely-used traits: woody density, height, and seed mass,[61] and were downloaded from the TRY Plant Trait Database: https://www.try-db.org/TryWeb/Home.php.[56] We extracted each plant trait data for each species by averaging standardized individual-level trait values by excluding the individual value with error risk exceeding three in the dataset which indicates likely mistakes in the value. See also Figure S2

Distribution pattern

To compare the distribution pattern of small old trees and large old trees, we collected seven environmental variables known to be associated with the distribution of old trees[34]: (1) annual mean temperature and (2) total precipitation extracted from the Climatic Research Unit (CRU) 4.05 dataset[57]: https://crudata.uea.ac.uk/cru/data/hrg/, (3) altitude collected from the International Tree Ring Data Bank and (4) aspect extracted from the ETOPO1 Global Relief Model: https://www.ngdc.noaa.gov/mgg/global/, (5) soil texture and (6) soil fertility clustered using principal component analysis (PCA) from nine soil characteristics downloaded from the Regridded Harmonized World Soil Database v.1.2[58]: https://daac.ornl.gov/SOILS/guides/HWSD.html (Figure S4D), and (7) human activity intensity derived from Global Human Modification of Terrestrial system[59]: https://sedac.ciesin.columbia.edu/data/set/lulc-human-modification-terrestrial-systems (Table S3). We calculated variable inflation factors (VIFs), and all VIFs were below 1.4, suggesting limited multi-collinearity between explanatory variables. See also Figure S4 and Table S3

We used GLMMs to identify the predictors that influenced the distribution of small and large old trees separately. We fitted GLMMs with quasi-poisson error distribution (identity link) with the number of small and large old trees for each forest site as response variables separately. In both models, fixed predictors included all seven environmental variables, and the total number of sampled trees at a forest site was added as a covariate to control for the bias caused by varied sampling sizes. Species identity was treated as a random intercept. Finally, we refitted both models with Z-transformed variables (standardized to zero mean and unit standard deviation) to quantify the relative importance of all predictors on the number of small and large old trees. These processes were conducted using "*MASS*" package[55] in R version 4.3.1.[52]

To detect how small and large old trees varied in different environments, we conducted a principle component analysis (PCA) to cluster forest sites with small and large old trees using "*stats*" package in R version 4.3.1.[52] These two clusters were discriminated by environmental factors that have significant effects on the variation of the number of small and large old trees among sites. We then applied a two-way ANOVA to test the statistical significance of the difference in environmental factors between sites with small and large old trees.

Protection status

To compare the protected status of small old trees and large old trees, we downloaded the global protected areas from The World Database on Protected Areas (WDPA): http://www.protectedplanet.net/. We then extracted the number of small and large old trees within protected areas versus outside protected areas.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were performed using R version 4.3.1. and the details can be found in the method details, and the legends of figures and tables. Generalized linear mixed models were used to fit the age-size relationships and explore the influencing factors of the distribution pattern of small old trees. Principle component analysis was used to cluster forest sites with small and large old trees and reduce the dimensionality of soil parameters datasets. Two-way ANOVA was used to compare differences in plant traits and environmental conditions between groups of small and old trees.