

Article

Human Activities and Climate Jointly Shape the Old-Tree Diversity in Human-Dominated Landscapes of the Yellow River Basin, China

Xin Wang ¹ , Jinfen Han ¹, Pengcheng Liu ², Donggang Guo ³ and Meichen Jiang ^{4,*}

¹ College of Architecture and Design, Shanxi Vocational University of Engineering Science and Technology, Jinzhong 030619, China; wangxin_2016@foxmail.com (X.W.)

² School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

³ School of Environmental & Resource Sciences, Shanxi University, Taiyuan 030006, China

⁴ College of Information Technology, Shanghai Jian Qiao University, Shanghai 201306, China

* Correspondence: jmc0713@163.com

Abstract

Old trees function as enduring ecological legacies that preserve historical biodiversity within intensively human-modified landscapes, yet the relative influence of environmental versus anthropogenic drivers on their diversity remains unclear. Here, we aim to disentangle the joint effects of climate, urbanization intensity and cultural preservation on old-tree density and community composition. We analyzed a province-wide census of 21,733 old-tree individuals across 115 counties in Shanxi Province, China, encompassing species origin (native vs. nonnative) and growth form (trees vs. shrubs). Old-tree density was assessed using spatial simultaneous autoregressive error models, while compositional dissimilarity was quantified using generalized dissimilarity modeling. In total, 131 species were recorded, with four dominant species comprising more than 75% of all individuals. Old-tree density increased with mean annual temperature, human population density, and cultural heritage abundance, but declined sharply with cropland coverage. Driver importance varied among groups: native species were primarily governed by climatic conditions, nonnative species by land-use intensity, and tree-form old trees were positively associated with cultural heritage abundance, an effect absent in shrub-form old trees. Compositional dissimilarity was driven mainly by climatic gradients and spatial distance, with additional contributions from human-related variables, particularly for nonnative assemblages. Our findings demonstrate that climate and spatial processes establish the regional framework of old-tree community composition, while cultural and demographic contexts promote local retention of old trees. By explicitly integrating ecological filters with socio-cultural drivers, this study advances old-tree research through a large-scale empirical framework, providing both scientific insight and socially relevant guidance for conservation under land-use intensification and climate warming.

Keywords: heritage tree; cultural activity; biodiversity conservation; species origin; growth forms



Academic Editor: Panayotis Dimopoulos

Received: 11 January 2026

Revised: 9 February 2026

Accepted: 13 February 2026

Published: 15 February 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

1. Introduction

Old trees represent a distinctive form of natural-cultural heritage, acting as long-lived biological legacies that link ecological processes with human history [1]. Because of their exceptional size and longevity, they contribute disproportionately to biodiversity

maintenance and ecosystem functioning by providing specialized habitats, buffering micro-climates, storing large carbon pools, and conserving irreplaceable genetic resources [2–4]. Beyond these ecological functions, old trees play a central role in landscape aesthetics, particularly when composed of indigenous, slow-growing species that are culturally familiar, visually distinctive, and symbolically valued within local landscapes [5]. Old trees are also deeply embedded in religious, ethnological, and anthropological traditions worldwide [6,7]. Sacred groves, temple trees, churchyard trees, and commemorative plantings have been documented across Asia, Europe, Africa, and the Americas, reflecting shared human practices of attributing spiritual, social, and historical meaning to long-lived trees [8–11]. Despite this combined ecological, aesthetic and cultural importance, old trees are declining worldwide due to climate change, urban expansion, logging, and other anthropogenic pressures [12]. Clarifying the drivers underlying their diversity and compositional patterns is therefore essential.

Old trees are commonly found within human-dominated landscapes such as cities, villages, and agricultural mosaics [13,14]. A growing body of evidence shows that both environmental conditions and human activities shape their spatial distribution and diversity by regulating fundamental biological processes, including growth rates, lifespan, stress tolerance, and resilience to disturbance [1,15]. Climate is a key determinant, with mean annual precipitation strongly influencing old-tree abundance and wetter regions generally supporting higher densities [16]. Edaphic and topographic constraints further limit persistence: flat terrain with deep, fertile soils typically sustains more old trees than shallow or rugged landscapes, underscoring the importance of soil depth and nutrient availability [17,18]. In addition, long-lived tree species are often associated with higher elevations, where reduced disturbance and cooler conditions with lower metabolic rates may favor longevity [19]. Together, these patterns highlight the dominant role of environmental filtering at broad spatial scales.

Human activities impose additional and often decisive influences on old-tree dynamics. Logging, agricultural expansion, habitat fragmentation, biological invasions, and anthropogenic climate change have driven widespread losses of large and old trees worldwide [12]. For instance, intensive harvesting has markedly reduced large trees in managed and semi-natural forests across Europe [20]. Beyond external disturbances, physiological aging and accumulated structural damage increase old trees' susceptibility to pathogens and pests, often amplifying the effects of human disturbances [21]. However, human impacts are strongly context dependent. In culturally significant settings, old trees associated with temples, ancestral halls, or sacred sites benefit from long-term protection and active management, including watering, pruning, and disease monitoring, pest control, and legal protection of veteran or monumental trees, which can substantially enhance survival and longevity [22–24].

These contrasting outcomes highlight the importance of cultural heritage as a mediating pathway linking human activities to ecological processes [25,26]. In long-settled landscapes, cultural heritage shapes old-tree persistence by influencing human behavior, including selective retention, disturbance suppression, and sustained management across generations [27]. Tangible cultural heritage, such as immovable cultural relics, may serve as stable spatial refugia for old trees, while intangible cultural heritage, including beliefs and ritual practices, can influence planting, retention, and disturbance regimes through intergenerational transmission [24,28]. Species traits are likely to mediate these effects [29]. Native species often exhibit stronger cultural recognition, aesthetic appreciation, and ecological compatibility with local environments, whereas non-native species may be constrained by management intensity, lower cultural attachment, or invasive potential [30]. Similarly, long-lived tree species generally differ from shrubs or fast-growing taxa in their

sensitivity to disturbance, longevity, and cultural symbolism [31]. Integrating climatic constraints, urbanization intensity, indicators of cultural heritage with species origin and growth form therefore provides a robust framework for disentangling the relative roles of ecological filters and socio-cultural preferences in shaping old-tree diversity, density, and composition.

Located in the Yellow River Basin of China, Shanxi Province contains an exceptional concentration of cultural heritage sites and a long history of old-tree preservation [32]. The persistence of millennia-old cypress trees (*Platycladus orientalis*) planted during the Zhou Dynasty exemplifies the deep coupling between cultural continuity and old-tree survival, making the region an ideal natural laboratory to examine how environmental constraints, human pressures, and cultural protection jointly shape old-tree assemblages at regional scales [33]. Drawing on a comprehensive census of old trees across 115 counties, together with environmental variables and anthropogenic indicators representing both destructive and protective forces, we addressed three questions: (a) how does old-tree dominance structure vary among counties? We hypothesized that a small number of dominant species are widely distributed across counties, due to the similar cultural identity among people within the province [27]. (b) How do environmental and anthropogenic factors jointly regulate spatial variation in old-tree density across species origins and growth forms? We hypothesized that cultural protection activities exert a positive mediating effect on old-tree density, particularly for native species and tree-form old trees that hold strong cultural significance [34]. (c) To what extent do climatic gradients and spatial distance establish the regional framework of old-tree compositional dissimilarity, and how do human-related factors further modify these patterns? We expected that climatic gradients and spatial distance would define the primary structure of compositional dissimilarity at the regional scale [35]. By integrating ecological, cultural, and trait-based perspectives, this study advances a more holistic understanding of old-tree persistence in human-dominated landscapes.

2. Materials and Methods

2.1. Old Trees Collection

In the literature, trees of exceptional age, size, or cultural significance are referred to as old trees, ancient trees, large old trees, heritage trees, or monumental trees [1,4,9,14,34]. In this study, old trees were defined as woody individuals older than 100 years, following the Regulations on the Protection of Old and Famous Trees issued by the National Forestry and Grassland Administration of China. This threshold represents an administrative and conservation-based definition rather than a biological lifespan criterion, and has been widely applied in national surveys, management practices, and scientific studies in China [34,36]. Although tree longevity varies greatly among species and regions, trees meeting this criterion generally function as long-term ecological legacies and carriers of cultural heritage, which is conceptually comparable to heritage or monumental trees recognized in other countries, despite differences in specific age thresholds. Since 2001, nationwide censuses of old and famous trees have been conducted every ten years in accordance with the Specifications for the Identification of Old and Famous Trees and the Technical Specifications for the Census of Old and Famous Trees. These surveys focus on areas outside nature reserves and forest regions, documenting scattered old trees and recording their species identity, estimated age, tree height, diameter at breast height (DBH), crown width, and geographic location (see details in Appendix A). To ensure data reliability, all records undergo multi-level quality control at county, provincial, and national levels, followed by data collation, verification, and expert review. Finalized datasets are released through official platforms or published volumes. In this study, we used data from the

2018 old-tree census in Shanxi Province, covering 118 counties and representing the most comprehensive and standardized dataset currently available for the region.

To ensure data completeness, counties with fewer than five old-tree individuals were excluded, yielding a final dataset comprising 115 counties. Latin names of species were standardized using the Leipzig Catalogue of Vascular Plants [37] and the Flora of China (<http://www.iplant.cn>) (accessed on 26 June 2025). Provincial-level species origins were identified based on the Flora of China. Species recorded outside their native provincial ranges were classified as nonnative [38]. To assess whether distribution mechanisms differed by growth form, species were further categorized as trees or shrubs according to descriptions in the Flora of China and related studies. For analyses involving species origin or growth form, counties containing only native species or only tree species were excluded to maintain comparability. This resulted in 93 counties for origin-based analyses and 72 counties for growth-form analyses. Hereafter, “old trees” refers to all qualifying woody individuals, whereas “trees” and “shrubs” denote tree-form and shrub-form old trees, respectively.

2.2. Explanatory Variables

To explain spatial variation in old-tree diversity and composition, explanatory variables were grouped into natural environmental and human activity categories. Environmental variables included mean annual temperature (MAT), temperature seasonality (TEMP_Season), mean annual precipitation (MAP), precipitation seasonality (PREC_Season), mean elevation (EleM), and elevation range (EleR). Bioclimatic data were obtained from WorldClim v2.0 at 30 arc-second resolution (<http://www.worldclim.org/>) (accessed on 28 June 2025). Elevation metrics were derived from the EarthEnv-DEM90 digital elevation model [39], with mean elevation and elevation range calculated for each county. Spatial averages of environmental variables were computed using 1 km grid cells within county boundaries [40].

Human activity variables represented both urbanization intensity and cultural preservation. Urbanization indicators included human population density (HPD), gross domestic product (GDP), and cropland coverage (CLC), and they were all extracted from the Shanxi Statistical Yearbook 2018 [41]. Cultural preservation was characterized using cultural heritage abundance (CHA) and intangible cultural heritage abundance (ICHA). CHA was compiled from 1105 national- and provincial-level key cultural relic protection units listed by the Shanxi Provincial Cultural Relics Bureau, encompassing ancient buildings, sites, tombs, grottoes, and stone carvings. ICHA included 1306 nationally and provincially recognized intangible cultural heritage items released by the Chinese State Council and the Shanxi Provincial Government, covering folk literature, traditional music, dance, drama, fine arts, crafts, medicine, and folk customs.

To reduce multicollinearity, variables with Pearson correlation coefficients exceeding $|0.7|$ were excluded prior to analysis [42]. The final set of predictors comprised three environmental variables (MAT, MAP, EleR) and four anthropogenic variables (CLC, HPD, CHA, ICHA).

2.3. Response Variables

County-level diversity was quantified using old-tree density, calculated as the number of individuals divided by county area (trees per ha), and compositional dissimilarity, measured using the Bray–Curtis index (d_{jk}) based on species abundance. For counties j and k , the contribution of species i to Bray–Curtis dissimilarity is defined as:

$$d_{ijk} = \frac{|X_{ij} - X_{ik}|}{\sum_{i=1}^S (X_{ij} + X_{ik})} \quad (1)$$

where x denotes the abundance of species i in counties j and k . Overall dissimilarity is calculated as $d_{jk} = \sum_{i=1}^S d_{ijk}$ where S is the total number of species [43]. Values range from 0 to 1, with lower values indicating greater compositional similarity. Compositional similarity was expressed as $1 - d_{jk}$.

2.4. Statistical Analysis

To account for potential spatial autocorrelation in old-tree density across counties, we applied spatial simultaneous autoregressive error models (SARs), which explicitly model spatially structured residuals and thereby ensure unbiased parameter estimates in the presence of spatial dependence that violates the independence assumption of ordinary least squares (OLS) [44]. Moran's I was calculated before and after model fitting to evaluate the presence and reduction in spatial autocorrelation [45]. For each dataset, all possible combinations of predictor variables were fitted, and Akaike weights (w) were computed to assess the relative importance of individual predictors across all model combinations [46]. Model selection was based on minimizing Akaike's Information Criterion (AIC) [47]. To improve normality and linearity, old-tree density, CLC, and HPD were log-transformed prior to analysis. All predictors were standardized to zero mean and unit variance.

Generalized additive models (GAMs), which can flexibly capture non-linear relationships, were used to examine relationships between pairwise community similarity and geographic distance by using the R package *mgcv*, allowing comparisons of distance–decay patterns among old trees differing in species origin and growth form [48]. Geographic distance was calculated as the Euclidean distance between counties based on latitude and longitude [49].

To quantify the relative contributions of environmental and spatial gradients to variation in old-tree community composition, we applied generalized dissimilarity modeling (GDM) using the *gdm* package in R. GDM is a nonlinear matrix-regression framework developed for β -diversity analyses that accommodates nonlinear relationships between compositional dissimilarity and predictor gradients [50]. Models were fitted using the default three I-spline basis functions, whose shapes describe rates of compositional turnover along each gradient. The summed I-spline coefficients indicate the magnitude of each predictor's contribution to β diversity and correspond to the maximum height of the spline curve [51]. To facilitate comparison, coefficients were rescaled so that their sum equaled the deviance explained by the model [52]. Predictor significance was evaluated using Monte Carlo permutation tests with stepwise backward elimination implemented via the function *gdm.varImp*. All analyses were conducted in R v4.5 [53].

3. Results

3.1. Diversity Distribution Patterns of Old Trees

We assembled a comprehensive inventory of 21,733 old-tree individuals representing 131 species across 115 counties in Shanxi Province, spanning 71 genera and 34 families. The dataset comprised 103 tree species and 28 shrub species, including 90 native and 41 nonnative taxa at the provincial scale. Old trees were unevenly distributed, with pronounced concentration in central and southeastern Shanxi. Fifteen counties supported more than 20 species (Figure 1a), 13 counties contained over 400 individuals (Figure 1b), and 11 centrally located counties exhibited densities exceeding 50 individuals per hectare (Figure 1c).

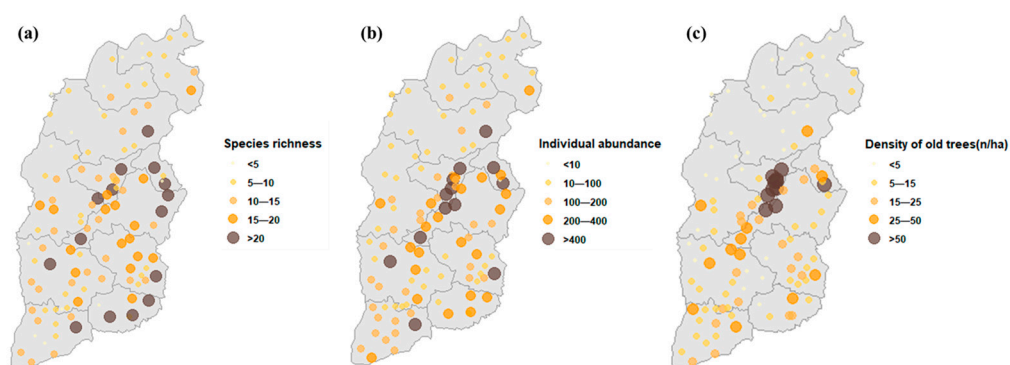


Figure 1. Spatial patterns of (a) old-tree species richness, (b) individual abundance, and (c) density across 115 counties in Shanxi Province.

Species occurrence was highly skewed. Six species—*Styphnolobium japonicum*, *Platycladus orientalis*, *Ulmus pumila*, *Pinus tabulaeformis*, *Salix matsudana*, and *Gleditsia sinensis*—were widespread, each occurring in more than half of all counties, whereas 45 species were restricted to a single county (Figure 2a). Abundance patterns were similarly uneven: four dominant species, each characterized by distinct geographic distributions, exceeded 1000 individuals and together accounted for more than 75% of all recorded old trees. In contrast, 61 species were represented by fewer than five individuals, including 26 singletons (Figures 2b and A1).

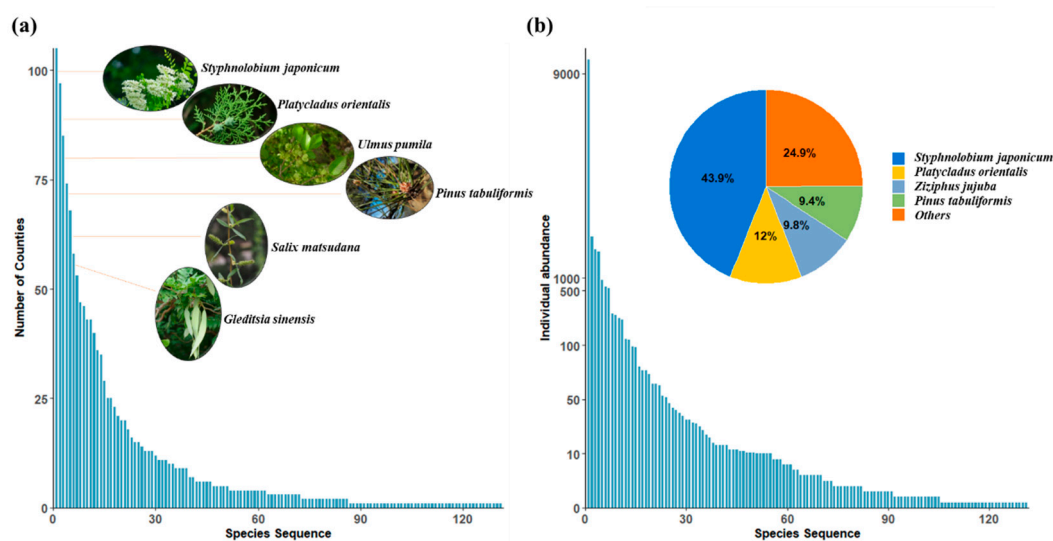


Figure 2. Frequency distributions of old trees across species by (a) number of counties and (b) individual abundance.

3.2. Factors Influencing the Density of Old Trees

Old-tree density was shaped by both environmental and anthropogenic drivers, with effects differing in magnitude and direction (Table 1). Across all old trees, human population density (HPD) and mean annual temperature (MAT) exerted the strongest positive influences, followed by cultural heritage abundance (CHA), whereas cropland coverage (CLC) showed a significant negative association. Native and nonnative species responded similarly overall but differed in dominant controls: MAT was the strongest driver for native species, while CLC imposed a stronger constraint on nonnative species. Growth forms also diverged markedly. For trees, CHA emerged as the primary positive predictor, whereas no significant effects were detected for shrubs. Instead, shrub density was mainly associated with HPD, with MAT showing comparatively weak relationships.

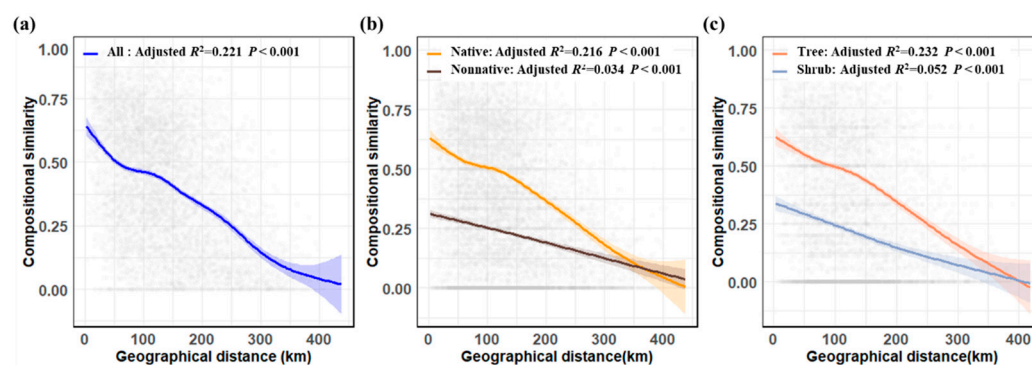
Table 1. Spatial simultaneous autoregressive (SAR) models evaluating the effects of environmental and human-activity variables on old-tree density across origins and growth forms.

Density	All		Origins				Growth Forms			
			Native		Nonnative		Trees		Shrubs	
	⁴ Variables	¹ coef.	² w	coef.	w	coef.	w	coef.	w	
	MAT	0.299 *	0.669	0.716 ***	0.996	0.464 ***	0.980	0.438 **	0.912	0.301 **
	MAP		0.287	−0.334 **	0.670	−0.490 ***	0.988	−0.271 *	0.535	0.363
	EleR		0.393		0.301		0.380		0.276	0.333
	CLC	−0.158 *	0.549	−0.430 ***	0.987	−0.650 ***	1.000	−0.389 ***	0.980	−0.215 *
	HPD	0.250 ***	0.975		0.633		0.300	0.426 ***	0.997	0.447 ***
	CHA	0.152 *	0.636	0.190 *	0.696	0.346 ***	0.989	0.255 *	0.656	0.403
	ICHA		0.391	0.184 *	0.644	0.169	0.588		0.316	0.294
	³ Pseudo r ²	0.642		0.554		0.452		0.596		0.382

¹ Values are standardized coefficients (coef.) from the best-supported model based on Akaike's Information Criterion. ² Akaike weights (w) indicate the relative importance of predictors derived from all model combinations. ³ Pseudo r² values are presented to indicate the explanatory power of the models. ⁴ MAT, mean annual temperature; MAP, mean annual precipitation; EleR, elevation range; CLC, cropland coverage; CHA, cultural heritage abundance; ICHA, intangible cultural heritage abundance; HPD, human population density. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

3.3. Compositional Similarity of Old Trees Among Counties

Old-tree assemblages exhibited a clear distance–decay pattern, with compositional similarity declining significantly with increasing geographic distance (Adjusted $R^2 = 0.221$, $p < 0.001$; Figure 3a). The magnitude of spatial turnover varied among groups. Native assemblages showed a steeper and more pronounced decay than nonnative assemblages, while maintaining higher overall similarity across distances (Figures 3b and A2a). A comparable contrast was observed between growth forms: trees displayed stronger distance–decay relationships and higher compositional similarity than shrubs (Figures 3c and A2b).

**Figure 3.** Distance–decay relationships of compositional similarity for old trees: (a) all species, (b) by origin, and (c) by growth form. Curves were fitted using generalized additive models (GAMs); shaded bands denote 95% confidence intervals. Colors represent different groups.

3.4. Drivers of Species Compositional Patterns

Determinants of compositional dissimilarity differed markedly among groups, although climatic and spatial variables consistently dominated. For all old trees, mean annual temperature (MAT), geographic distance (DIS), and mean annual precipitation (MAP) were the principal predictors, while human-activity variables contributed little, with only HPD showing a weak but significant effect. Native species closely mirrored the overall pattern, with dissimilarity structured primarily by climate gradients and spatial separation. In contrast, nonnative species exhibited low explanatory power and weak spatial structuring, with HPD emerging as a relatively main driver. Among growth forms, trees showed strong climate- and space-driven compositional turnover, whereas shrubs

displayed low explained deviance and responded mainly to climatic variables (Figure 4; Table A1).

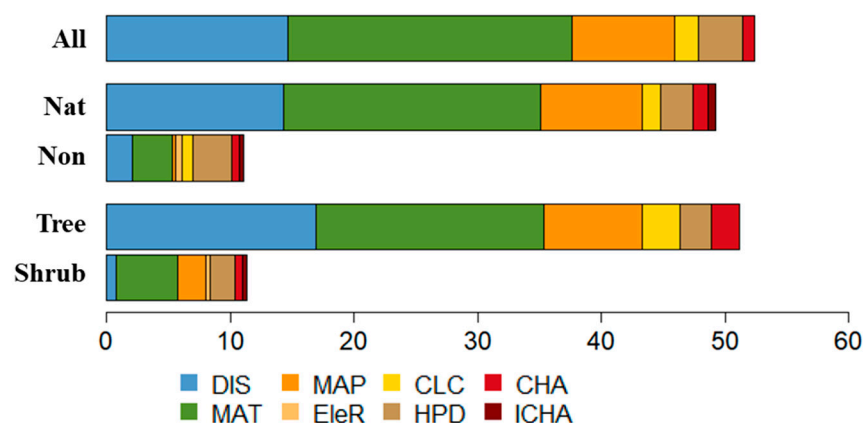


Figure 4. Relative contributions of spatial, environmental, and human-activity predictors to explained deviance in compositional dissimilarity based on generalized dissimilarity modeling (GDM). Analyses were conducted for all species (All), native (Nat) and nonnative species (Non), and tree and shrub groups. Predictor importance is indicated by the maximum height of GDM transformation functions. Bar colors denote predictors; definitions are provided in Table 1.

4. Discussion

4.1. Dominance Structure of Old Tree Diversity

Our province-wide census of 21,733 old-tree individuals spanning 131 species across 115 counties in Shanxi Province demonstrates that, although old trees constitute only a small fraction of regional tree resources, they represent more than 25% of the naturally occurring woody plant species pool [54]. This marked overrepresentation highlights old trees as long-lived legacy elements that retain historical vegetation signals and safeguard a substantial share of regional biodiversity within increasingly human-dominated landscapes [4].

Consistent with hypothesis, old-tree assemblages in Shanxi exhibit a pronouncedly uneven dominance structure, with a few widespread and abundant species co-occurring alongside many rare and geographically restricted taxa, consistent with patterns reported for Taiyuan city of Shanxi province [33]. The prominence of dominant species likely reflects the relationship between broad ecological tolerance, sustained utilitarian value, and long-term cultural selection [27]. Species such as *Ulmus pumila* and *Gleditsia sinensis* combine strong adaptation to regional environments with repeated human preference for medicinal and edible uses [55,56]. Beyond utilitarian functions, culturally revered species—exemplified by *Styphnolobium japonicum*—have been intentionally conserved because of their symbolic importance in historical narratives, collective memory, and place-based identity [57]. The Big Pagoda Tree (*Styphnolobium japonicum*) in Hongdong County of Shanxi, which served as a major gathering site for migrants during the early Ming Dynasty and remains a potent symbol of ancestral origin for millions of descendants, illustrates this process vividly [58]. Together, these examples underscore the central role of biocultural processes in structuring contemporary old-tree diversity [59,60].

Accordingly, dominant old-tree species can be viewed as “winners” of long-term anthropogenic filtering, possessing traits that enable persistence under sustained disturbance and management and thus being preferentially retained in settlements, cultural landscapes, and restoration settings [2,61]. Conversely, the high proportion of low-abundance and single-county species indicates substantial regional vulnerability, as stochastic losses of rare old trees may disproportionately erode compositional diversity [62,63]. Many endangered and relict taxa, including *Ginkgo biloba*, persist primarily as isolated old individuals within

human settlements, where they function as irreplaceable reservoirs of genetic diversity and evolutionary history [4]. Thus, recognizing such dominance patterns may help prioritize keystone species for protection in culturally important landscapes, where their loss would disproportionately affect both ecological functions and cultural identity [64]. Collectively, these patterns emphasize the dual role of old trees as archives of long-term human–environment interactions and as priority conservation targets, underscoring their importance for biodiversity conservation, cultural heritage preservation, and the maintenance of evolutionary potential in modified landscapes [1].

4.2. Environmental and Anthropogenic Controls on Old Tree Density

The significant effects of anthropogenic and climatic predictors on old-tree density also reflect the joint influence of human-mediated selection and long-term environmental filtering [65]. The strong positive relationship between human population density and old-tree density across all groups indicates preferential retention of old trees in densely inhabited areas. This pattern is consistent with evidence from both provincial [66] and national scales [36] and suggests that human presence does not inherently translate into old-tree loss. Instead, densely populated regions often coincide with greater economic resources and institutional capacity, facilitating conservation infrastructure, management inputs, and legal protection that promote old-tree persistence. Such stewardship commonly involves active management (e.g., watering, pruning, pest control) and deliberate protection driven by cultural, religious, and symbolic values [1].

The positive association with cultural heritage abundance suggests that cultural heritage mediates human–tree interactions that heritage-rich counties tend to support reduced tree removal and sustained stewardship, allowing temples, monuments, and other immovable heritage sites to function as long-term refugia for old trees in human-dominated landscapes [24]. Consistently, Zhang and Grose (2025) found that 62% of large old trees in Zhoukou city were located within or directly associated with temples [28]. By contrast, the strong negative effect of cropland coverage highlights the enduring tension between intensive agriculture and old-tree persistence, as agricultural expansion and mechanization have historically necessitated tree removal and limited opportunities for long-term survival [67]. Together, these opposing influences show that old-tree density in anthropogenic landscapes reflects a balance between culturally driven protection and land-use intensification. By comparison, old trees occurring in managed forests are subject to a different set of constraints. Silvicultural practices such as rotation-based harvesting, thinning, and timber-oriented management often limit the persistence of very old individuals, regardless of surrounding population density or cultural context [12,68]. As a result, the positive associations between human presence, cultural heritage, and old-tree density documented in human-dominated landscapes may be reduced or absent in managed forest systems [69].

For different species of origin, the influences of climate and anthropogenic factors on old-tree density varied markedly. For example, native old-tree density was most strongly associated with temperature, indicating that the current distribution of native legacy individuals continues to reflect long-term climatic filtering and historical climate–vegetation equilibria [2,70]. Having persisted through centuries of environmental variability, these native old trees remain tightly linked to regional thermal regimes, suggesting climatic filtering over extended timescales and a potential sensitivity to ongoing climate change [71,72]. By contrast, nonnative old-tree density was more strongly constrained by the cropland coverage, suggesting that land-use intensity outweighs macroclimatic controls on their persistence. This pattern likely reflects anthropogenic introduction and management pathways, whereby establishment and survival are shaped more by land-use context and human decision-making than by climatic suitability alone [73].

Growth forms further modulated these relationships. Cultural activity exerted a much stronger influence on tree density than on shrub density, indicating that trees are more likely to be preserved and actively managed in culturally rich regions. This disparity is plausibly linked to tree stature: greater height, biomass, and longevity increase visibility and the likelihood of acquiring symbolic, historical, or spiritual significance [5]. Supporting this interpretation, Huang et al. (2023) showed that old-tree species with greater potential height have a higher probability of long-term persistence [34]. In contrast, density of shrub-form old trees was driven primarily by human population density, with climatic variables playing a secondary role, suggesting that smaller, more disturbance-tolerant shrubs are more tightly coupled to local management regimes than to broad-scale climate gradients.

Collectively, these findings indicate that urban and village landscapes can sustain high densities of old trees when long-term protection and active stewardship are in place, particularly where cultural heritage reinforces tree retention. Integrating old-tree conservation into cultural heritage management, urban green infrastructure, and village-level land-use planning may therefore enhance persistence, whereas intensively farmed regions require targeted retention and buffering strategies. Conservation planning should further account for differences in species origin and growth form, as these traits mediate sensitivity to land-use intensity and management regimes.

4.3. Drivers of Compositional Dissimilarity Across Species Groups

The pronounced distance–decay relationships among counties indicate that old-tree assemblages remain strongly spatially structured at the regional scale, with compositional similarity declining with increasing geographic distance. This pattern reflects persistent spatial processes, including dispersal limitation and historical contingencies associated with past land use and cultural practices, that continue to shape old-tree community composition [27,29]. Steeper distance–decay slopes for native species and tree growth forms indicate stronger spatial turnover and regional differentiation, consistent with a greater imprint of long-term biogeographic processes and enduring environmental filtering than observed for nonnative species and shrubs [74]. Notably, native old trees and tree-form assemblages also exhibited consistently higher overall compositional similarity than nonnative species and shrubs. This seemingly counterintuitive pattern likely arises from the dominance of a small set of widespread native tree species that combine broad geographic distributions with high local abundance. The disproportionate contribution of these ecologically tolerant and historically favored taxa elevates compositional overlap among counties, increasing regional similarity despite marked spatial turnover. Together, these results suggest that native old-tree composition is governed not only by climate and spatial constraints but also by uneven species contributions resulting from long-term ecological suitability and selective persistence under human influence [29].

In contrast, nonnative old trees displayed weaker distance–decay relationships and low model explanatory power, with species composition showing only marginal responses to climatic and spatial gradients. Instead, human population density emerged as the relatively stronger predictor, indicating that nonnative old-tree assemblages are largely decoupled from natural biogeographic constraints. This spatial homogenization is consistent with human-mediated introduction, cultivation, and repeated planting of a limited set of favored species across broad areas, which reduces spatial differentiation and dampens environmental signals [35,75].

These patterns were also modulated by growth form. Tree-form old trees exhibited strong climate- and space-driven compositional differentiation, indicating that long-lived, large-stature woody species integrate cumulative effects of environmental filtering and historical dispersal constraints over extended timescales [76,77]. Similar dynamics have been

reported in old-growth and mature forest systems, where canopy-dominant assemblages remain tightly aligned with macroclimatic and spatial gradients despite local disturbances at large spatial scales [78]. The relatively weak imprint of contemporary human activity on old-tree composition may reflect historical reliance on locally adapted species in plantings or the persistence of remnant individuals following past disturbances, both of which reinforce congruence with regional environmental conditions [79]. Although the widespread occurrence of a few dominant species increases compositional similarity among counties, recent population movements and economic activity do not appear to have led to strong regional homogenization. In contrast, shrub-forming old trees—occupying lower vertical strata and characterized by high tolerance to disturbance, pruning, and resprouting—showed weak spatial structuring and low explained deviance, suggesting that their assemblages are shaped primarily by local-scale processes such as microhabitat heterogeneity and localized human disturbance, with regional climatic and spatial signals largely attenuated. In addition, low explained deviance of shrubs would be related to the unevenly distributed and comparatively sparse across counties, which can reduce statistical power at broad spatial scales [80].

Collectively, old-tree compositional patterns were shaped by the joint influence of long-term climatic filtering, spatial constraints, and human-mediated selection. Origins and growth forms modulate the balance between regional-scale environmental filtering and local-scale anthropogenic and ecological processes within old woody assemblages. Although anthropogenic variables did not dominate compositional patterns at the regional scale, their effects may be partly obscured by unaccounted interspecific differences in cultural significance and utilitarian value [34]. The context-dependent effects observed across species origins and growth forms further suggest that conservation and landscape management should adopt differentiated strategies, aligning species traits and cultural values with local environmental and socio-economic contexts.

4.4. Implications and Limitations

Our results highlight that old-tree conservation in human-dominated landscapes cannot rely solely on protected areas but must be embedded within cultural heritage planning, urban green-space design, and agricultural land-use management. By identifying the contrasting roles of cultural protection and land-use intensification, this study provides a spatial framework for prioritizing areas where old-tree persistence can be most effectively supported.

Several limitations should be acknowledged. First, this study focused on regional-scale patterns and did not incorporate site-level attributes such as aesthetic value and tree vitality, or health status. These attributes are important dimensions for evaluating the condition, visibility, and social perception of individual old trees, and may strongly influence local conservation decisions and management priorities in human-dominated landscapes. Future studies could adopt multi-scale approaches that integrate regional analyses with site-level assessments based on field surveys, expert evaluations, or standardized health and aesthetic indicators. Second, causal mechanisms underlying human–tree relationships cannot be fully resolved using correlative approaches. Future work that integrates site-level assessments of vitality and aesthetic or cultural valuation with long-term management histories would help resolve how human preferences interact with ecological processes to shape the biogeography of old-tree communities. Third, the administrative 100-year threshold may differentially represent ecological age across fast- and slow-growing species, a limitation that warrants refinement using species-specific longevity metrics in future studies.

5. Conclusions

This province-wide analysis shows that regional patterns of old-tree diversity arise from the coupled effects of species dominance, climatic filtering, spatial constraints, and differentiated human influences. A small number of widespread, abundant species—favored by broad environmental tolerance and long-term cultural and utilitarian selection—dominate old-tree assemblages and elevate compositional similarity across space. Old-tree density is jointly promoted by climatic suitability and human presence, whereas intensive agriculture consistently undermines persistence, highlighting the contrasting roles of settlement and land-use intensification. At the compositional level, strong distance–decay relationships indicate that native and tree-form old trees remain structured by long-term biogeographic processes, while nonnative and shrub assemblages are increasingly homogenized through human-mediated management. Beyond the regional context, our findings provide a general framework for understanding how ecological filters and socio-cultural preferences jointly shape old-tree assemblages in human-dominated landscapes worldwide. We demonstrate that conserving old trees requires context-specific strategies, including reducing intensive agricultural expansion in culturally valued areas and applying buffer zones, incentive-based protection, and landscape integration in intensively farmed regions. Recognizing old trees as both ecological assets and cultural heritage can align biodiversity conservation with spatial planning and community engagement.

Author Contributions: X.W.: Conceptualization, Data curation, Formal analysis, Writing—original draft. J.H.: Data curation, Writing—review and editing. P.L.: Writing—review and editing. D.G.: Data curation. M.J.: Writing—review and editing, funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Natural Science Foundation of China (Grant No. 32300175), the Fundamental Research Program of Shanxi Province (Grant No. 202303021222281 and 202303021222287), and the Doctoral Start-up Research Fund (BBYQ202416) provided by Shanghai Jian Qiao University.

Data Availability Statement: The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Acknowledgments: We gratefully acknowledge the Shanxi Forestry and Grassland Bureau for providing access to the census data of large old trees used in this study.

Conflicts of Interest: The authors declare no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Appendix A

Old trees data

These scattered old trees were recorded in terms of their species identity, estimated age, tree height, diameter at breast height (DBH), crown width, and geographic location. Tree age was estimated using a non-destructive, integrative approach commonly applied in old-tree surveys, including literature-based tracing, interview-based estimation with residents or managers, and indirect inference from morphological characteristics such as trunk diameter and growth form. Where applicable, age estimation was informed by empirical relationships between tree-ring data and diameter reported in previous studies. Tree height was measured in the field using a hypsometer or laser rangefinder; in cases where instrument-based measurement was constrained, tape-and-pole methods were applied as supplementary approaches. Diameter at breast height (DBH) was measured at 1.3 m above ground using a standard diameter tape. Crown width was determined using the cross method, by measuring crown diameters along two perpendicular directions and

calculating their average. Geographic coordinates were recorded in situ using handheld GPS devices.

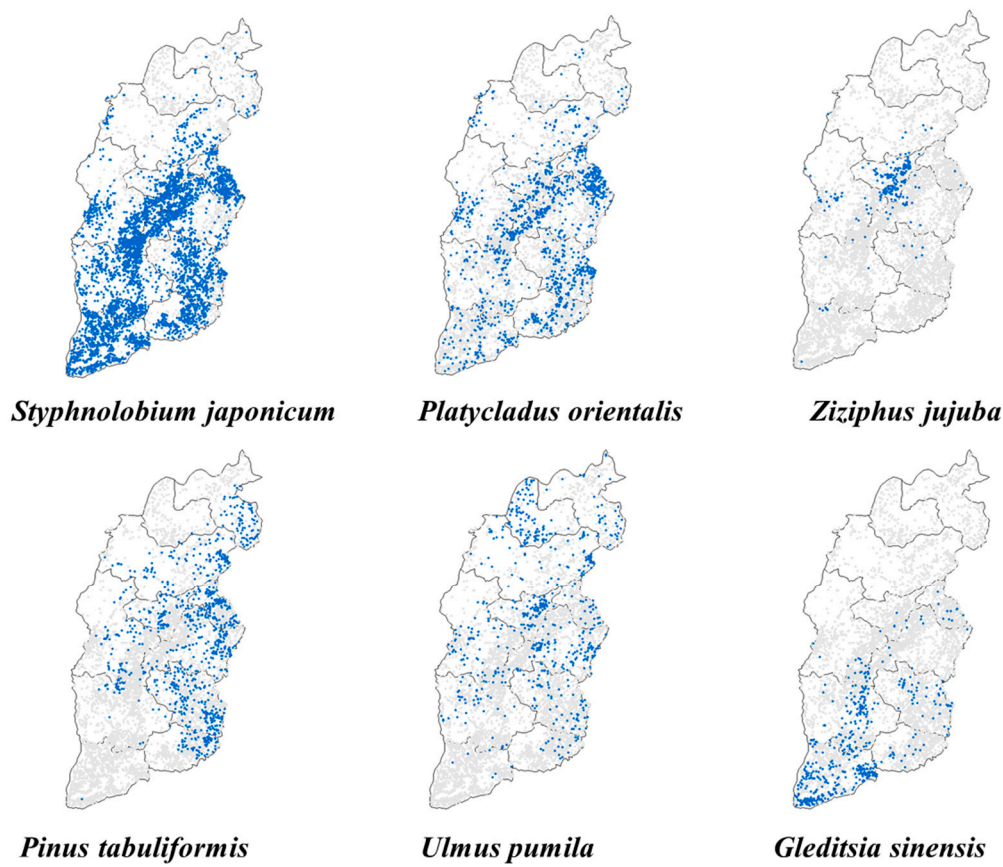


Figure A1. Geographic distributions of the six most abundant species based on individual counts. Each dot represents the occurrence of an individual tree of the corresponding species.

Table A1. Results of generalized dissimilarity models (GDMs). Values represent the summed I-spline coefficients (maximum spline height) for each predictor. Predictors with zero I-spline sums were excluded a priori. Statistically significant predictors are shown in bold ($p < 0.05$). Total deviance explained indicates the proportion of compositional dissimilarity accounted for by all predictors in each model.

Variables	All	Nat	Non	Tree	Shrub
DIS	14.634	14.295	2.083	16.927	0.765
MAT	22.983	20.786	3.272	18.426	5.018
MAP	8.321	8.195	0.223	8.000	2.241
EleR			0.509		0.310
CLC	1.873	1.525	0.915	3.025	
HPD	3.598	2.641	3.127	2.552	2.050
CHA	1.004	1.200	0.561	2.242	0.655
ICHA		0.572	0.368		0.281
Percent deviance explained	52.413	49.215	11.059	51.172	11.320

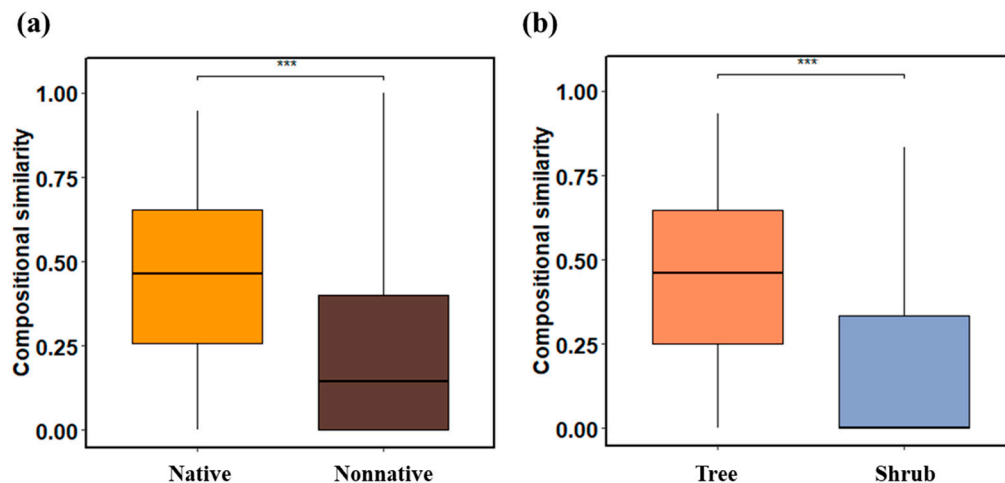


Figure A2. Compositional similarity of old trees among counties: (a) native versus nonnative species; (b) trees versus shrubs. Group differences were assessed using the Wilcoxon rank-sum test. *** $p < 0.001$.

References

1. Lindenmayer, D.B.; Laurance, W.F. The ecology, distribution, conservation and management of large old trees. *Biol. Rev.* **2017**, *92*, 1434–1458. [\[CrossRef\]](#)
2. Cannon, C.H.; Piovesan, G.; Munné-Bosch, S. Old and ancient trees are life history lottery winners and vital evolutionary resources for long-term adaptive capacity. *Nat. Plants* **2022**, *8*, 136–145. [\[CrossRef\]](#)
3. Slik, J.W.F.; Paoli, G.; McGuire, K.; Amaral, I.; Barroso, J.; Bastian, M.; Blanc, L.; Bongers, F.; Boundja, P.; Clark, C.; et al. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Glob. Ecol. Biogeogr.* **2013**, *22*, 1261–1271. [\[CrossRef\]](#)
4. Piovesan, G.; Cannon, C.H.; Liu, J.; Munné-Bosch, S. Ancient trees: Irreplaceable conservation resource for ecosystem restoration. *Trends Ecol. Evol.* **2022**, *37*, 1025–1028. [\[CrossRef\]](#)
5. Blicharska, M.; Mikusiński, G. Incorporating social and cultural significance of large old trees in conservation policy. *Conserv. Biol.* **2014**, *28*, 1558–1567. [\[CrossRef\]](#) [\[PubMed\]](#)
6. Turner, N.J.; Ari, Y.; Berkes, F.; Davidson-Hunt, I.; Ertug, Z.F.; Miller, A. Cultural Management of Living Trees: An International Perspective. *J. Ethnobiol.* **2023**, *29*, 237–270. [\[CrossRef\]](#)
7. Ogwu, M.C.; Osawaru, M.E. Traditional Methods of Plant Conservation for Sustainable Utilization and Development. In *Biodiversity in Africa: Potentials, Threats and Conservation*; Izah, S.C., Ed.; Sustainable Development and Biodiversity; Springer: Singapore, 2022; Volume 29, pp. 451–472. [\[CrossRef\]](#)
8. Kandari, L.S.; Bisht, V.K.; Bhardwaj, M.; Thakur, A.K. Conservation and management of sacred groves, myths and beliefs of tribal communities: A case study from north-India. *Environ. Syst. Res.* **2014**, *3*, 16. [\[CrossRef\]](#)
9. Zapponi, L.; Mazza, G.; Farina, A.; Fedrigoli, L.; Mazzocchi, F.; Roversi, P.F.; Peverieri, G.S.; Mason, F. The role of monumental trees for the preservation of saproxylic biodiversity: Re-thinking their management in cultural landscapes. *Nat. Conserv.* **2017**, *19*, 231–243. [\[CrossRef\]](#)
10. Alders, W.; Lim, J.S.; Brunner, L. Detecting baobab trees (*Adansonia digitata*) in drone imagery and evaluating their anthropogenic legacy in eastern Africa. *J. Archaeol. Sci.* **2025**, *180*, 106280. [\[CrossRef\]](#)
11. Rashford, J. A Historically Contextualized Account of the Baobab Trees (*Adansonia digitata* L.) of Tobago. *Econ. Bot.* **2022**, *76*, 127–157. [\[CrossRef\]](#)
12. Lindenmayer, D.B.; Laurance, W.F.; Franklin, J.F. Global decline in large old trees. *Science* **2012**, *338*, 1305–1306. [\[CrossRef\]](#)
13. Gibbons, P.; Lindenmayer, D.B.; Fischer, J.; Manning, A.D.; Weinberg, A.; Seddon, J.; Ryan, P.; Barrett, G. The future of scattered trees in agricultural landscapes. *Conserv. Biol.* **2008**, *22*, 1309–1319. [\[CrossRef\]](#)
14. Vargas-Gaete, R.; Salas-Eljatib, C.; Fernández-Urrutia, C.; Fuentes-Ramírez, A.; Almonacid, L. Heritage trees: Getting to know the oldest inhabitants of a city in southern Chile. *Urban For. Urban Green.* **2025**, *112*, 128916. [\[CrossRef\]](#)
15. Liu, S.; Xu, H.; Wang, G.; Jin, B.; Cao, F.; Wang, L. Tree longevity: Multifaceted genetic strategies and beyond. *Plant Cell Environ.* **2025**, *48*, 244–259. [\[CrossRef\]](#)
16. Bennett, A.C.; McDowell, N.G.; Allen, C.D.; Anderson-Teixeira, K.J. Larger trees suffer most during drought in forests worldwide. *Nat. Plants* **2015**, *1*, 15139. [\[CrossRef\]](#)

17. Piovesan, G.; Biondi, F.; Baliva, M.; Dinella, A.; Di Fiore, L.; Marchiano, V.; Presutti Saba, E.; De Vivo, G.; Schettino, A.; Di Filippo, A. Tree growth patterns associated with extreme longevity: Implications for the ecology and conservation of primeval trees in Mediterranean mountains. *Anthropocene* **2019**, *26*, 100199. [\[CrossRef\]](#)
18. Poulsen, J.R.; Medjibe, V.P.; White, L.J.T.; Miao, Z.; Banak-Ngok, L.; Beirne, C.; Clark, C.J.; Cuni-Sanchez, A.; Disney, M.; Doucet, J.-L.; et al. Old growth Afrotropical forests critical for maintaining forest carbon. *Glob. Ecol. Biogeogr.* **2020**, *29*, 1785–1798. [\[CrossRef\]](#)
19. Liu, J.; Yang, B.; Lindenmayer, D.B. The oldest trees in China and where to find them. *Front. Ecol. Environ.* **2019**, *17*, 319–322. [\[CrossRef\]](#)
20. Jönsson, M.T.; Fraver, S.; Jonsson, B.G. Forest history and the development of old-growth characteristics in fragmented boreal forests. *J. Veg. Sci.* **2009**, *20*, 91–106. [\[CrossRef\]](#)
21. Takács, M.; Szénási, Á.; Malatinszky, Á. Polypores, Agrobacterium and ivy damage on Hungarian ancient trees. *Nat. Conserv.* **2020**, *40*, 1–38. [\[CrossRef\]](#)
22. Nolan, V.; Reader, T.; Gilbert, F.; Atkinson, N. The Ancient Tree Inventory: A summary of the results of a 15 year citizen science project recording ancient, veteran and notable trees across the UK. *Biodivers. Conserv.* **2020**, *29*, 3103–3129. [\[CrossRef\]](#)
23. Wonglangka, W.; Han, F. Green heritage and Lanna urban identity: A study of temples in Chiang Mai Old City. *Sustainability* **2024**, *16*, 6574. [\[CrossRef\]](#)
24. Huang, L.; Tian, L.; Huang, L.; Jin, C.; Hu, S.; Zhang, Z.; Yan, E.; Jim, C.Y.; Yang, Y.; Lindenmayer, D.B.; et al. Religious temples are long-term refuges for old trees in human-dominated landscapes in China. *Curr. Biol.* **2025**, *35*, 2994–3000.e3. [\[CrossRef\]](#)
25. Bridgewater, P.; Rotherham, I.D. A critical perspective on the concept of biocultural diversity and its emerging role in nature and heritage conservation. *People Nat.* **2019**, *1*, 291–304. [\[CrossRef\]](#)
26. Cheng, Z.; Lu, X.; Fan, Y.; Cui, Q.; Hu, X.; Long, C. Traditional knowledge promotes the protection of large old trees: A case from China's richest biocultural diversity area. *People Nat.* **2025**, *7*, 2700–2713. [\[CrossRef\]](#)
27. Huang, L.; Tian, L.; Zhou, L.; Jin, C.; Qian, S.; Jim, C.Y.; Lin, D.; Zhao, L.; Minor, J.; Coggins, C.; et al. Local cultural beliefs and practices promote conservation of large old trees in an ethnic minority region in southwestern China. *Urban For. Urban Green.* **2020**, *49*, 126584. [\[CrossRef\]](#)
28. Zhang, A.; Grose, M.J. Where to find large old trees in China?—Temples as the refuge for large old trees in Chinese cities. *Arboric. J.* **2025**, *47*, 250–269. [\[CrossRef\]](#)
29. Jin, C.; Zheng, M.; Huang, L.; Qian, S.; Jim, C.Y.; Lin, D.; Zhao, L.; Minor, J.; Coggins, C.; Chen, B.; et al. Co-existence between humans and nature: Heritage trees in China's yangtze River region. *Urban For. Urban Green.* **2020**, *54*, 126748. [\[CrossRef\]](#)
30. Vilà, M.; Espinar, J.L.; Hejda, M.; Hulme, P.E.; Jarošík, V.; Maron, J.L.; Pergl, J.; Schaffner, U.; Sun, Y.; Pyšek, P. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* **2011**, *14*, 702–708. [\[CrossRef\]](#) [\[PubMed\]](#)
31. Díaz, S.; Kattge, J.; Cornelissen, J.H.C.; Wright, I.J.; Lavorel, S.; Dray, S.; Reu, B.; Kleyer, M.; Wirth, C.; Colin Prentice, I.; et al. The global spectrum of plant form and function. *Nature* **2016**, *529*, 167–171. [\[CrossRef\]](#)
32. Zhang, J.T. A study on relations of vegetation, climate and soils in Shanxi province, China. *Plant Ecol.* **2002**, *162*, 23–31. [\[CrossRef\]](#)
33. Pan, Y.; Wang, S.; Xie, C.; Jim, C.Y. Species diversity and spatial pattern of heritage trees in Taiyuan. *Sci. Rep.* **2025**, *15*, 17584. [\[CrossRef\]](#)
34. Huang, L.; Jin, C.; Pan, Y.; Zhou, L.; Hu, S.; Guo, Y.; Meng, Y.; Song, K.; Pang, M.; Li, H.; et al. Human activities and species biological traits drive the long-term persistence of old trees in human-dominated landscapes. *Nat. Plants* **2023**, *9*, 898–907. [\[CrossRef\]](#)
35. Wang, X.; Svenning, J.-C.; Liu, J.; Zhao, Z.; Zhang, Z.; Feng, G.; Si, X.; Zhang, J. Regional effects of plant diversity and biotic homogenization in urban greenspace—The case of university campuses across China. *Urban For. Urban Green.* **2021**, *62*, 127170. [\[CrossRef\]](#)
36. Liu, J.; Lindenmayer, D.B.; Yang, W.; Ren, Y.; Campbell, M.J.; Wu, C.; Luo, Y.; Zhong, L.; Yu, M. Diversity and density patterns of large old trees in China. *Sci. Total Environ.* **2019**, *655*, 255–262. [\[CrossRef\]](#)
37. Freiberg, M.; Winter, M.; Gentile, A.; Zizka, A.; Muellner-Riehl, A.N.; Weigelt, A.; Wirth, C. LCVP, The Leipzig catalogue of vascular plants, a new taxonomic reference list for all known vascular plants. *Sci. Data* **2020**, *7*, 416. [\[CrossRef\]](#)
38. Padullés Cubino, J.; Cavender-Bares, J.; Hobbie, S.E.; Hall, S.J.; Trammell, T.L.E.; Neill, C.; Avolio, M.L.; Darling, L.E.; Groffman, P.M. Contribution of non-native plants to the phylogenetic homogenization of U.S. yard floras. *Ecosphere* **2019**, *10*, e02638. [\[CrossRef\]](#)
39. Robinson, N.; Regetz, J.; Guralnick, R.P. EarthEnv-DEM90: A nearly-global, void-free, multi-scale smoothed, 90m digital elevation model from fused ASTER and SRTM data. *ISPRS J. Photogramm. Remote Sens.* **2014**, *87*, 57–67. [\[CrossRef\]](#)
40. Yang, W.; Ma, K.; Kreft, H. Environmental and socio-economic factors shaping the geography of floristic collections in China. *Glob. Ecol. Biogeogr.* **2014**, *23*, 1284–1292. [\[CrossRef\]](#)

41. Shanxi Provincial Bureau of Statistics; Survey Office of the National Bureau of Statistics in Shanxi. *Shanxi Statistical Yearbook 2018*; China Statistics Press: Beijing, China, 2018.
42. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; Marquéz, J.R.G.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **2013**, *36*, 27–46. [\[CrossRef\]](#)
43. Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Wagner, H. *Vegan: Community Ecology Package*. R Package Version 2.2-0. 2014. Available online: <https://CRAN.R-project.org/package=vegan> (accessed on 10 November 2025).
44. Kissling, W.D.; Carl, G. Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob. Ecol. Biogeogr.* **2008**, *17*, 59–71. [\[CrossRef\]](#)
45. Rangel, T.F.; Diniz-Filho, J.A.F.; Bini, L.M. SAM: A comprehensive application for Spatial Analysis in Macroecology. *Ecography* **2010**, *33*, 46–50. [\[CrossRef\]](#)
46. Zhang, J.; Kissling, W.D.; He, F. Local forest structure, climate and human disturbance determine regional distribution of boreal bird species richness in Alberta, Canada. *J. Biogeogr.* **2013**, *40*, 1131–1142. [\[CrossRef\]](#)
47. Cavanaugh, J.E.; Neath, A.A. The Akaike information criterion: Background, derivation, properties, application, interpretation, and refinements. *WIREs Comput. Stat.* **2019**, *11*, e1460. [\[CrossRef\]](#)
48. Wood, S. Package 'mgcv'. The R Project for Statistical Computing. 2025. Available online: <https://CRAN.R-project.org/package=mgcv> (accessed on 14 November 2025).
49. Capinha, C.; Essl, F.; Seebens, H.; Moser, D.; Pereira, H.M. The dispersal of alien species redefines biogeography in the Anthropocene. *Science* **2015**, *348*, 1248–1251. [\[CrossRef\]](#)
50. Ferrier, S.; Manion, G.; Elith, J.; Richardson, K. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers. Distrib.* **2007**, *13*, 252–264. [\[CrossRef\]](#)
51. Fitzpatrick, M.; Mokany, K.; Manion, G.; Nieto-Lugilde, D.; Ferrier, S. *gdm: Generalized Dissimilarity Modeling* 2024. R package version 1.6. Available online: <https://github.com/fitzlab-al/gdm> (accessed on 1 December 2025).
52. König, C.; Weigelt, P.; Kreft, H. Dissecting global turnover in vascular plants. *Glob. Ecol. Biogeogr.* **2017**, *26*, 228–242. [\[CrossRef\]](#)
53. R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing: Vienna, Austria. 2025. Available online: <https://www.R-project.org/> (accessed on 10 September 2025).
54. Shanxi Forest Editorial Committee. *Forests of Shanxi*; China Forestry Publishing House: Beijing, China, 1993.
55. Gu, W.; Lan, Y.; Sun, C. Research advances and utilization development of *Gleditsia sinensis* in world. *Sci. Silvae Sin.* **2003**, *39*, 127–133. (In Chinese)
56. Xie, J.; Wang, Z.; Li, Y. Stomatal opening ratio mediates trait coordinating network adaptation to environmental gradients. *New Phytol.* **2022**, *235*, 907–922. [\[CrossRef\]](#)
57. Yue, H.; Jiang, S.; Yang, J. The evolution of *Sophora japonica*-based moralized landscapes in traditional Chinese gardens. *Chin. Landsc. Archit.* **2024**, *40*, 126–132. (In Chinese)
58. Zhao, S.Y. Ancestral memory, homeland symbolism, and ethnic history: An analysis of the Hongtong “Big Locust Tree” legend in Shanxi, China. *Hist. Res.* **2006**, *1*, 1–16. (In Chinese)
59. Teng, S.N.; Xu, C.; Teng, L.; Svenning, J.-C. Long-term effects of cultural filtering on megafauna species distributions across China. *Proc. Natl. Acad. Sci. USA* **2020**, *117*, 486–493. [\[CrossRef\]](#) [\[PubMed\]](#)
60. Zhang, M.-J.; Chen, B.; Xu, C. Cultural tree preference and its influence on tree biodiversity in urban public spaces in Nanjing city, China. *Urban For. Urban Green.* **2020**, *48*, 126568. [\[CrossRef\]](#)
61. Xu, W.-B.; Svenning, J.-C.; Chen, G.-K.; Zhang, M.-G.; Huang, J.-H.; Chen, B.; Ordonez, A.; Ma, K.-P. Human activities have opposing effects on distributions of narrow-ranged and widespread plant species in China. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 26674–26681. [\[CrossRef\]](#) [\[PubMed\]](#)
62. Lowney, C.A.; Graham, B.D.; Spetich, M.A.; Shifley, S.R.; Saunders, M.R.; Jenkins, M.A. Two decades of compositional and structural change in deciduous old-growth forests of Indiana, USA. *J. Plant Ecol.* **2015**, *9*, 256–271. [\[CrossRef\]](#)
63. Elsy, A.D.; Pfeifer, M.; Jones, I.L.; DeWalt, S.J.; Lopez, O.R.; Dent, D.H. Incomplete recovery of tree community composition and rare species after 120 years of tropical forest succession in Panama. *Biotropica* **2024**, *56*, 36–49. [\[CrossRef\]](#)
64. Cholewińska, O.; Keczyński, A.; Kusińska, B.; Jaroszewicz, B. Species identity of large trees affects the composition and the spatial structure of adjacent trees. *Forests* **2021**, *12*, 1162. [\[CrossRef\]](#)
65. Coggins, C.; Minor, J. Fengshui forests as a socio-natural reservoir in the face of climate change and environmental transformation. *Asia Pac. Perspect.* **2018**, *15*, 4–29.
66. Xie, C.; Yan, J.; Liu, D.; Jim, C.Y. Diversity and abundance of large old trees in Hainan Island: Spatial analysis and environmental correlations. *Biotropica* **2024**, *56*, e13391. [\[CrossRef\]](#)
67. Brandt, M.; Gominiski, D.; Reiner, F.; Kariryaa, A.; Guthula, V.B.; Ciais, P.; Tong, X.; Zhang, W.; Govindarajulu, D.; Ortiz-Gonzalo, D.; et al. Severe decline in large farmland trees in India over the past decade. *Nat. Sustain.* **2024**, *7*, 860–868. [\[CrossRef\]](#)

68. Bauhus, J.; Puettmann, K.; Messier, C. Silviculture for old-growth attributes. *For. Ecol. Manag.* **2009**, *258*, 525–537. [[CrossRef](#)]
69. Franklin, J.F.; Spies, T.A.; Van Pelt, R.; Carey, A.B.; Thornburgh, D.A.; Berg, D.R.; Chen, J. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.* **2002**, *155*, 399–423. [[CrossRef](#)]
70. Caetano-Andrade, V.L.; Clement, C.R.; Weigel, D.; Trumbore, S.; Boivin, N.; Schöngart, J.; Roberts, P. Tropical trees as time capsules of anthropogenic activity. *Trends Plant Sci.* **2020**, *25*, 369–380. [[CrossRef](#)] [[PubMed](#)]
71. Locosselli, G.M.; Brien, R.J.W.; Leite, M.d.S.; Gloor, M.; Krottenthaler, S.; Oliveira, A.A.d.; Barichivich, J.; Anhu, D.; Ceccantini, G.; Schöngart, J.; et al. Global tree-ring analysis reveals rapid decrease in tropical tree longevity with temperature. *Proc. Natl. Acad. Sci. USA* **2020**, *117*, 33358–33364. [[CrossRef](#)]
72. Gao, J.; Fang, K.; Chen, J.M.; Li, J.; Rossi, S.; Chen, D.; Linderholm, H.W.; Camarero, J.J.; Esper, J.; Davi, N.K.; et al. Climate-driven patterns of global tree longevity. *Commun. Earth Environ.* **2025**, *6*, 610. [[CrossRef](#)]
73. Searcy, C.A.; Howell, H.J.; David, A.S.; Rumelt, R.B.; Clements, S.L. Patterns of non-native species introduction, spread, and ecological impact in South Florida, the world’s most invaded continental ecoregion. *Annu. Rev. Ecol. Evol. Syst.* **2023**, *54*, 195–218. [[CrossRef](#)]
74. Marini, L.; Battisti, A.; Bona, E.; Federici, G.; Martini, F.; Pautasso, M.; Hulme, P.E. Alien and native plant life-forms respond differently to human and climate pressures. *Glob. Ecol. Biogeogr.* **2012**, *21*, 534–544. [[CrossRef](#)]
75. Daru, B.H.; Davies, T.J.; Willis, C.G.; Meineke, E.K.; Ronk, A.; Zobel, M.; Pärtel, M.; Antonelli, A.; Davis, C.C. Widespread homogenization of plant communities in the Anthropocene. *Nat. Commun.* **2021**, *12*, 6983. [[CrossRef](#)]
76. Chen, Y.; Myers, J.A.; Ordonez, A.; Yu, J.; Ye, J.; Lin, F.; Fang, S.; Mao, Z.; Wang, X. Multiple processes jointly determine ecological uniqueness across forest plant life-forms in Northeast China. *J. Biogeogr.* **2024**, *51*, 1133–1147. [[CrossRef](#)]
77. Qian, H.; Qian, S.; Kessler, M. Spatial and climatic drivers of β -diversity in assemblages of angiosperm genera across the world. *J. Ecol.* **2024**, *112*, 2876–2886. [[CrossRef](#)]
78. Asefa, M.; Wen, H.-D.; Cao, M.; Hu, Y.-H. Key Community Assembly Processes Switch between Scales in Shaping Beta Diversity in Two Primary Forests, Southwest China. *Forests* **2020**, *11*, 1106. [[CrossRef](#)]
79. Sandor, M.E.; Chazdon, R.L. Remnant Trees Affect Species Composition but Not Structure of Tropical Second-Growth Forest. *PLoS ONE* **2014**, *9*, e83284. [[CrossRef](#)] [[PubMed](#)]
80. Meyer, C.; Weigelt, P.; Kreft, H. Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecol. Lett.* **2016**, *19*, 992–1006. [[CrossRef](#)] [[PubMed](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.