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Species diversity and spatial pattern of heritage trees in Taiyuan

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Heritage trees are key to maintaining biodiversity, supporting ecosystem services, and preserving cultural heritage. This study investigates the species composition, spatial distribution patterns, and conservation needs of heritage trees in ancient Taiyuan city in Northern China, focusing on their cultural-ecological significance and urbanization threats. Using redundancy analysis, we surveyed 4737 heritage trees across ten urban core, suburban and rural districts and nine habitat types and calculated their importance values, species diversity indices, and statistical associations with key socio-demographic and environmental factors. The prized stock comprised 57 species, dominated by *Ziziphus jujuba*, *Styphnolobium japonicum*, accompanied by four subdominants such as *Platycladus orientalis* and *Pinus tabuliformis*, and 39 uncommon to rare species, contributing considerably to species diversity. Spatial analysis and ecological assessments found distinct distribution patterns, with suburban and rural areas accommodating higher tree abundance and species richness than more urbanized districts. Factors such as altitude, cultivated area, economic activities, and particularly urban development, strongly influenced tree distribution. We analyzed their natural-cum-cultural value and threats from fast urban expansion, habitat fragmentation and loss, and insufficient conservation efforts. The findings underscored the urgent need for targeted and reinforced conservation strategies to safeguard these heritage trees, sustaining their precious legacy for future generations.

Keywords Conservation strategy, Distribution pattern, Environmental factor, Heritage tree, Species composition, Urbanization threat

Heritage trees, often exceeding a century in age and exceling in form, dimensions and species rarity, serve as living monuments and keystone components of urban ecosystems[1,2]. These prominent trees act as living witnesses to human and natural history, expressing the cultural narratives and environmental significance of their localities[3,4]. Their presence enriches urban landscapes, offering valuable natural and cultural ecosystem services[5,6]. Heritage trees occupy a unique and crucial position across multiple domains, including the city's ecological system, cultural context, historical association, collective memory, and aesthetic contribution[7,8].

Ecologically, the venerable trees are essential components of urban ecosystems. They provide heterogeneous microhabitats for diverse flora and fauna, stabilizing and enriching the soil, increasing water infiltration and retention, and conserving soil and water[9]. They also enhance air quality by cleansing air pollutants and absorbing carbon dioxide, which is increasingly important in the context of climate change[10]. Culturally, heritage trees embody the history and identity of a community, often linked to significant historical events or personalities[3,11]. They foster a sense of belonging and nurture cohesion among residents to enrich a city's cultural narrative[12]. Aesthetically, these beloved trees contribute to the beauty and character of the urban milieu. Their naturalistic grandeur contrasts and complement modern architecture, enhancing public spaces and promoting mental well-being[11–13]. Outstanding trees in streets and parks improve the overall ambiance, increase property values, and attract tourists[1].

In summary, heritage trees are invaluable inherited and inheritable assets that furnish important services that artifacts cannot supply. They support ecological health, enrich cultural heritage, and enhance aesthetic appeal in urban areas. Their preservation is justified for maintaining biodiversity, fostering community identity, and improving residents' quality of life[14,15]. Increasingly, a city's attractive green spaces have been enlisted for image enhancement and city branding[16,17], an attribute that can include outstanding trees. Recognizing the multifaceted roles of heritage trees can inform sustainable urban development strategies that honor both natural and human aspects[18,19].

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A complex interplay of ecological, environmental, and anthropogenic factors influences heritage tree distribution[3,20,21]. Key ecological determinants include species-specific traits that enable certain trees to attain a large size, such as growth rate, biological life span, stress tolerance, and resilience to disturbances. Environmental factors like soil quality, topography, and climate play crucial roles. For example, large trees are often found in areas with fertile soil and adequate moisture, which enhance growth and longevity[22,23]. Large tree density tends to be higher in flat, fertile sites compared to less fertile soil and rugged terrains, indicating that soil thickness and nutrients significantly influence their occurrence[24]. Additionally, climatic conditions, particularly mean annual rainfall, critically determine tree diversity and abundance[25,26]. Areas with ample rainfall typically support more heritage trees[27,28]. Furthermore, human activities associated with historical and current land use practices and local customs can affect the protection and management of old-growth forests and individual prized trees[29,30].

North China is an important historical and cultural region, boasting a rich endowment of heritage tree resources[31]. Recent studies have increasingly focused on the spatial distribution and species diversity of urban heritage trees in this region[25]. For instance, social factors dominated the distribution of large old tree in Beijing[32]. In Baoding (North China), rural residents accorded significant socio-cultural value to large old trees. Nevertheless, policymakers often overlooked them, highlighting the need for a multi-dimensional approach to their protection[18]. Moreover, the underlying factors of heritage trees' distribution pattern in most North China cities have received little attention.

Taiyuan, a key city in North China, features a distinctive natural and cultural landscape shaped by a unique geographical location and deep historical roots[33]. It has inherited a respectable endowment of outstanding trees. However, rapid urbanization has brought extensive construction, human activities, and environmental degradation, which have been compounded by climate change[34]. These acute impacts have imposed severe and mounting challenges on Taiyuan's heritage trees[35]. The city has undergone significant transformations over the past few decades, driven largely by its coal-based economy[36]. The massive industrial and urban growth, accompanied by pollution and habitat loss, has jeopardized efforts to preserve heritage trees. Despite these pressures, many remarkable specimens that have dwelt in the city for centuries manage to linger[34,35]. Additionally, previous research on heritage trees in Taiyuan has been limited[35,37,38], significantly hindering efforts to protect them.

This study aims to assess the species composition, distribution patterns, and conservation needs of heritage trees in Taiyuan. Our key research questions include: (a) What species of heritage trees are present in Taiyuan, and how do they vary in abundance and distribution? (b) What environmental factors influence the distribution patterns of these trees? (c) What are the current conservation challenges faced by them? (d) What can be recommended to improve their protection? By addressing these questions, this research hopes to understand the ecological dynamics and urbanization threats while highlighting the critical need for conservation intervention.

Materials and methods

Study area

Taiyuan (latitudes 37°27′ to 38°25′ N and longitudes 111°30′ to 113°09′ E) is a renowned historical and cultural metropolis of North China. The ancient city, with a lineage exceeding 2500 years, served as the capital of a succession of dynasties 33. Covering an area of 6988 km^2, it perches on the northern part of the Jinzhong Basin in central Shanxi Province.

Taiyuan's dustpan-shaped topography features diverse landforms comprising mountains, hills, plains, basins, and valleys[39]. Located in the interior of mainland China, it experiences a warm temperate continental monsoon climate. The annual average solar radiation is 4927.90 MJ/m^2, with annual sunshine of 2285–2587 h. The annual average precipitation is 390–423 mm, while the average temperature varies from 8.10 °C to 11 °C, and the accumulated temperature is 2375–3121 °C. The frost-free period lasts 153–178 days. Taiyuan's mid-latitude position in the northern hemisphere and the Shanxi Plateau's geographical features allow it to receive high solar radiation, resulting in abundant light and heat resources. Influenced by westerly circulation and intense insolation, the region experiences a dry climate with limited rainfall and significant diurnal temperature amplitude typical of a strong continental climate[40].

Taiyuan is divided into 10 administrative regions with a population of 5.435 million. The key information for its districts is listed in Table 1. Nine habitat types were classified based on the detailed records of heritage trees' growing sites[2]. They include villages and farmland (A), parks and gardens (B), roadside (C), other habitats that do not fit into any of the other eight groups (D), business and commercial premises (E), wooded areas and plant nurseries (F), government, institutional and community sites (G), residential areas (H), and religious sites and cemeteries (I).

Data sources

In July 2023–August 2024, we surveyed the heritage trees in Taiyuan. The multi-pronged data collection campaign was based on a literature review, news reports, original data from government forestry-related departments, our field investigations of trees and their habitats and environs, and communications with local residents. To confirm the scientific names of the ancient trees, we checked them against the latest Flora of China published at https://www.iplant.cn/.

The assessment and measurement of the heritage trees followed the *Technical Specifications for the Survey of Ancient and Famous Trees* (LY/T 2738-2016), as specified in the *Forestry Industry Standards of the People's Republic of China*. A handheld GPS instrument obtained the precise locations of the trees. A Brunel altimeter and measuring tape measured key dimensions, including diameter at breast height (DBH), crown width, tree height, and height to the first major branch (Fig. S1). We also recorded the habitat conditions and the general health of the trees and took tree and site photographs (Fig. 1). Age determination of heritage trees presented challenges. To protect the precious trees, we refrained from the invasive technique of taking wood cores to

District	Abbreviation	Development gradient	Area (km^2)	Urbanization rate (%)	Population density[b] (persons/km^2)	Vegetation cover (%)	Altitude (m)	Main topography
Gujiao	GJ	Rural	1512	76.14	140	42.40	1000–3000	Hills
Jiancaoping	JCP	Suburban	286	94.51	1881	27.01	780–1865	Plains, hills, mountains
Jinyuan	JY	Suburban	289	85.09	1135	28.54	760–1866	Plains, mountains
Loufan	LF	Rural	1289	51.18	69	23.00	1030–2789	Mountains
Qingxu	QX	Rural	609	43.30	572	16.20	800–1841	Mountains, plains
Wanbailin	WBL	Core-Suburban	305	100.00	3205	38.19	776–1553	Plains, hills, mountains
Xiaodian	XD	Core	295	93.60	4842	7.19	763–780	Plains, hills
Xinghualing	XHL	Core	170	93.88	4655	37.97	800–1670	Hills
Yangqu	YQ	Rural	2071	54.02	62	34.51	800–2102	Hills, mountains
Yingze	YZ	Core	117	98.13	5089	28.67	800–591	Plains, hills, mountains
Average			694	78.99	2165	28.37		

Table 1. Basic urban and tree information of the ten districts in Taiyuan[a]. [a]The information was mainly acquired from the official website of Taiyuan (https://stats.taiyuan.gov.cn/) and Red & Black Population Database (https://www.hongheiku.com/). [b]The population density was based on 2022 data.

measure tree rings. Instead, tree age was based on official government assessments and documentation. For a small number of trees without age records, we interviewed local residents and referred to relevant historical sources to estimate the age.

Statistical analyses

The species importance value (IV) was calculated by considering the relative abundance (RA) and relative dominance (RD) of each heritage tree species. The IV formula is: $IV=(RA+RD)\times 100/2$, where RA is the number of trees of a species divided by the total number of trees in the study area. RD is the basal area at the breast height of a species divided by the total basal area in the study area[41].

The true species diversity index was calculated using R-4.4.2 for Windows by Community Data_R package version 1.2[42,43]. The evenness index was determined using the formula: $E=H'/\ln s$, where H' is the Shannon–Wiener diversity index and s is the total number of species[44]. Both indices were calculated using PAST 12b software[45].

We selected seven environmental factors for analysis: district area, urbanization rate, GDP (Gross Domestic Product), GDP per capita, population, population density, forest cover, and cultivated area. These factors were then integrated with the tree abundance and species richness of heritage trees for Redundancy Analysis (RDA) using Canoco 4.5 software[46]. We also selected altitude as a representative natural factor. Scatter plots were used to generate regression curves to examine their impact on the abundance and diversity of heritage trees. Additionally, QGIS Desktop 3.34.0 visualized the abundance and diversity of heritage trees across different habitats, presented in pie charts[47].

Results

Species composition and importance value

The study area is home to a diverse array of heritage trees composed of 57 species (25 families) and 4737 trees across three age classes (Tier 1: >500 years, Tier 2: 300–499 years, and Tier 3: 100–299 years) (Table 2, Fig. S2). These species were subsumed under 26 families and 44 genera, reflecting a rich taxonomic diversity. The two dominant species with individual tree counts exceeding 1000 take up 3453 trees or 72.94% of the heritage tree stock. The top six species with individual tree counts exceeding 100 contribute 4345 trees (91.78%). Thus, the species composition is heavily skewed towards the small cohort of dominant and subdominant species. As many as 39 uncommon to rare species have individual tree counts under 10, indicating their heavy contribution to species diversity. Despite supplying merely 131 trees (2.77%), they considerably enrich the floristic diversity of the heritage tree population by furnishing 68.42% of the species makeup.

The importance value (IV) and tree count are presented in Table 2. The two dominant species contribute 73.20% of the aggregate IV and 73.56% of the cumulative DBH of the heritage tree stock. Thus, their biomass contributions are equivalent to their tree count proportion of 72.94%. *Ziziphus jujuba* from the Rhamnaceae leads the list with an impressive IV of 40.9, with a strong representation across all age classes. This species' 2186 trees also contribute significantly to the cumulative diameter at breast height (DBH), underscoring its dominant ecological role in the area. Following closely in IV is *Styphnolobium japonicum* of the Leguminosae. Despite a lower tree count (1267 trees), it achieves an IV of 32.3. This species is more represented in the older age classes, with substantial contributions from Tiers 1 and 2 trees, indicating its longevity and ecological importance. The third most important species, *Platycladus orientalis* (Cupressaceae), also exhibits considerable longevity, with a majority of trees in the 100–299 years range (Tier 3). Although its tree count is smaller (348 trees), the IV of 6.6 reflects its ecological significance.

The two dominant species are important for maintaining the ecological balance in urban environments. These trees provide shelter and food for wildlife, including birds, insects, and small mammals. *Ziziphus jujuba*, for example, produces fruits that attract birds and mammals, contributing to local biodiversity. The dense foliage of *Styphnolobium japonicum* offers habitats for various insects, including pollinators like bees and butterflies.

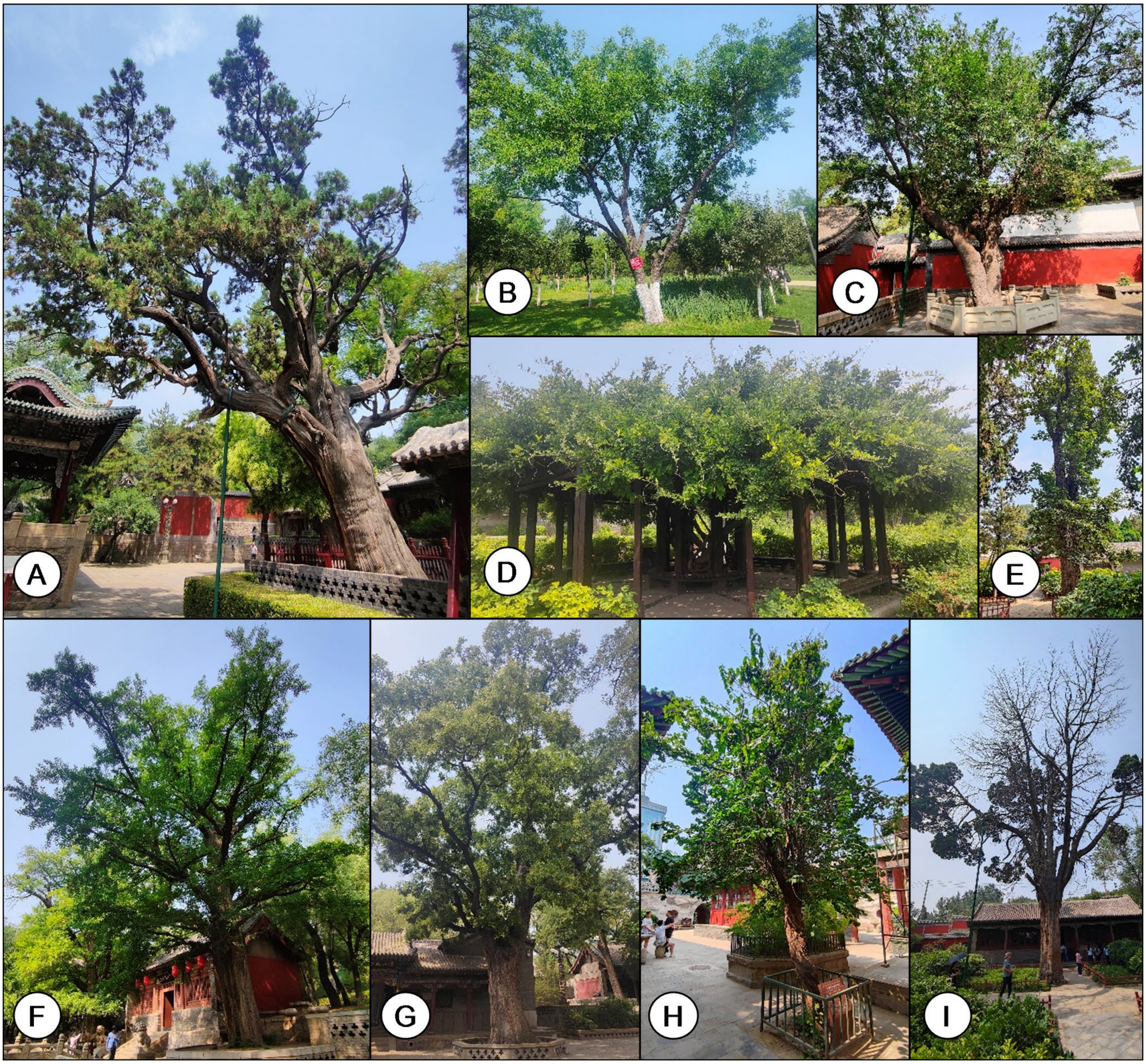


Fig. 1. Images of some typical specimens of heritage trees in Taiyuan. (**A**) denotes *Platycladus orientalis*; (**B**) *Ziziphus jujuba*; (**C**) *Gleditsia sinensis*; (**D**) *Wisteria sinensis*; (**E**) *Catalpa ovata*; (**F**) *Ginkgo biloba*; (**G**) *Styphnolobium japonicum*; (**H**) *Syringa reticulata* subsp. *amurensis*; (**I**) *Juniperus chinensis*.

Additionally, both species are known for their resilience to urban pollution, providing a green cover that helps improve air quality and reduces the urban heat island effect.

Species such as *Pinus tabuliformis* (Pinaceae) and *Ulmus pumila* (Ulmaceae) contribute moderate importance values (IV = 5.0 and 4.5, respectively), with tree counts of 251 and 190. These species dominate the mid-age classes (Tiers 2 and 3) and help maintain the overstory tree community. The remaining species in the dataset, such as *Prunus vulgaris* (Rosaceae), *Syringa oblata* (Oleaceae), and *Salix matsudana* (Salicaceae), bring less ecological contributions, as evidenced by their much lower IVs of 0.1–0.9. While *Ginkgo biloba* (Ginkgoaceae) is more prevalent in North China, its IV in Taiyuan is only 0.3 with tree counts of 10.

Species diversity and spatial differentiation

The biological characteristics of heritage trees across Taiyuan's districts show notable variations in tree count, mean height, DBH, and canopy size (Table 3). JY and YQ have the highest tree counts (845 and 1125 trees, respectively) (Table 3; Fig. 2a), with JY also exhibiting a relatively large average height (13.1 m) and canopy size (12.1 m). Conversely, WBL and LF have fewer trees (1011 and 60, respectively), with WBL showing smaller average heights (9.3 m) and canopies (7.8 m). In terms of DBH, YZ has the largest average at 14.6 cm, while QX and WBL have the smallest average DBH (9.1 cm and 9.3 cm, respectively), suggesting that districts like YZ accommodate older, more mature trees, while QX and WBL have younger or smaller trees.

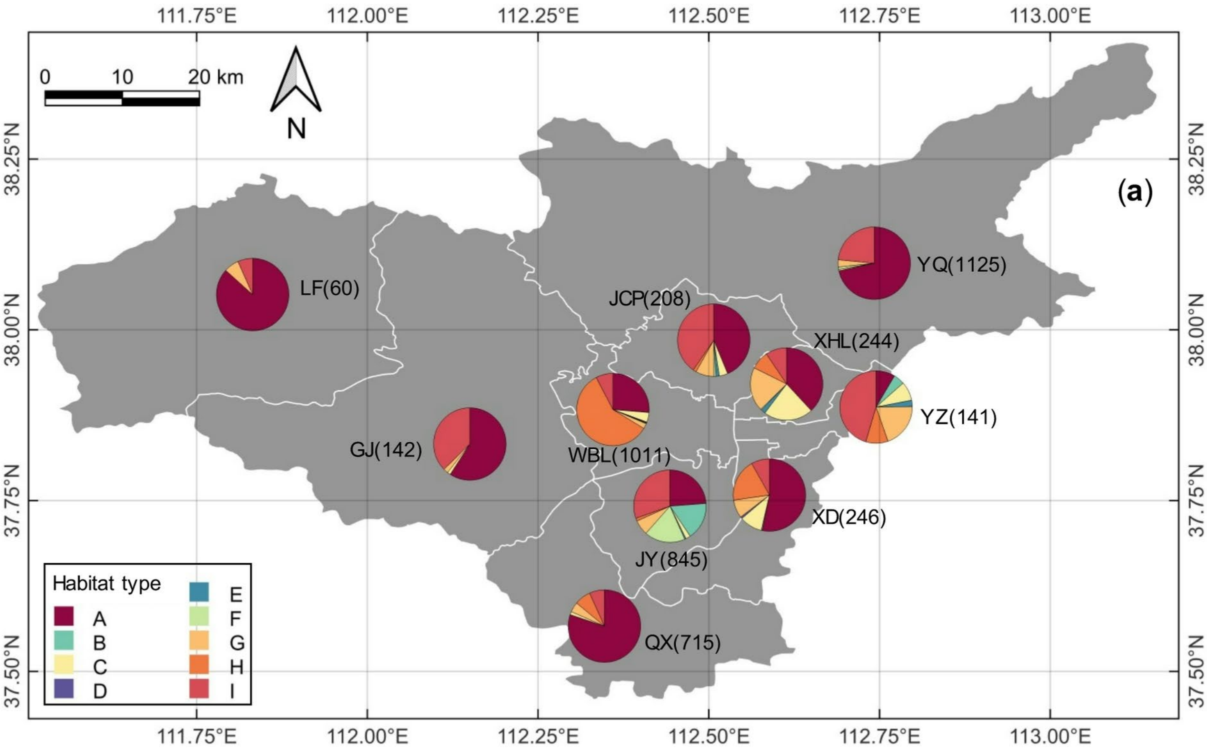
Species	Family	Tier 1	Tier 2	Tier 3	Tree count	Cumulative DBH	IV
Ziziphus jujuba Mill.	Rhamnaceae	12	134	2040	2186	101,062.6	40.9
Styphnolobium japonicum (L.) Schott	Leguminosae	293	350	624	1267	107,244.3	32.3
Platycladus orientalis (L.) Franco	Cupressaceae	82	92	174	348	16,750.0	6.6
Pinus tabuliformis Carrière	Pinaceae	26	58	167	251	13,112.5	5.0
Ulmus pumila L.	Ulmaceae	11	32	147	190	14,255.7	4.5
Catalpa bungei C. A. Mey.	Bignoniaceae	7	8	88	103	5369.7	2.0
Juglans regia L.	Juglandaceae	2	5	46	53	3844.3	1.2
Salix matsudana Koidz.	Salicaceae		2	28	30	3339.5	0.9
Robinia pseudoacacia L.	Leguminosae			32	32	2400.3	0.8
Ziziphus jujuba var. *spinosa* (Bunge) Hu ex H.F.Chow	Rhamnaceae	5	5	21	31	1233.1	0.5
Celtis bungeana Blume	Cannabaceae	1	10	16	27	1387.3	0.5
Toona sinensis (Juss.) Roem.	Meliaceae			18	18	1034.4	0.4
Gleditsia sinensis Lam.	Leguminosae	2	7	7	16	989.5	0.3
Salix babylonica L.	Salicaceae		3	10	13	964.6	0.3
Juniperus chinensis Roxb.	Cupressaceae	10			10	1015.0	0.3
Ginkgo biloba L.	Ginkgoaceae	2	6	2	10	845.9	0.3
Morus alba L.	Moraceae	1		9	10	739.2	0.2
Malus pumila Mill.	Rosaceae			11	11	466.6	0.2
Ailanthus altissima (Mill.) Swingle	Simaroubaceae		5	3	8	506.4	0.2
Populus simonii Carrière	Salicaceae		3	2	5	681.5	0.2
Syringa oblata Lindl.	Oleaceae		6	3	9	350.6	0.2
Syringa reticulata subsp. *amurensis* (Rupr.) P. S. Green & M. C. Chang	Oleaceae			8	8	330.9	0.1
Euonymus maackii Rupr.	Celastraceae		1	6	7	374.2	0.1
Populus tomentosa Carrière	Salicaceae			6	6	374.8	0.1
Xanthoceras sorbifolium Bunge	Sapindaceae	2	2	2	6	372.3	0.1
Prunus armeniaca L.	Rosaceae	1		5	6	360.5	0.1
Paeonia × suffruticosa Andrews	Paeoniaceae	1	2	2	5	257.0	0.1
Others		2	18	51	71	3509.2	1.4
Total		460	749	3528	4737	283,171.9	100.0

Table 2. Indices denoting the quantity and importance value (IV) of the main heritage tree species in Taiyuan, arranged in descending order of IV. The tree counts of species distributed in three age tiers (1 for > 500 years, 2 for 300–499 years and 3 for 100–299 years) are included.

District [a]	Species count	Tree count	Density (tree/10 km^2)	Mean height (m)	Mean DBH (cm)	Mean canopy (m)	True diversity index (T)	Evenness index (E)
GJ	13	142	0.9	10.6	68.1	9.3	1.79	0.48
JCP	19	208	7.3	13.0	72.7	10.4	2.02	0.41
JY	38	845	29.2	13.1	69.4	12.1	1.99	0.20
LF	12	60	0.5	9.9	59.1	8.2	1.58	0.44
QX	20	715	11.7	9.1	59.1	8.5	1.22	0.17
WBL	12	1011	33.2	9.3	47.4	7.8	0.74	0.18
XD	8	246	8.3	10.8	67.5	9.1	1.06	0.36
XHL	9	244	14.3	14.2	76.9	12.1	0.93	0.29
YQ	28	1125	5.4	10.7	58.3	8.9	1.98	0.26
YZ	14	141	12.1	14.6	36.2	11.3	1.28	0.27
Overall	57	4737	12.3	11.5	61.47	9.8	1.46	

Table 3. The frequency, dimensions and diversity of heritage trees in the study area composed of ten administrative districts in Taiyuan. [a]Refer to Table 1 for the meaning of district abbreviations.

The diversity of tree species across the districts displays considerable spatial differentiations (Table 3; Fig. 2b). JCP has the highest species richness with 19 species and the highest true diversity index (T = 2.02), indicating a more balanced species distribution. JY also shows high species richness (38 species) and a relatively high diversity index (T = 1.99). In contrast, WBL (12 species) and QX (20 species) exhibit lower diversity, with WBL showing the lowest diversity index (T = 0.74). The evenness index results echo the diversity patterns, with GJ and LF exhibiting higher evenness (E = 0.48 and 0.44), suggesting a more even species distribution. On the other



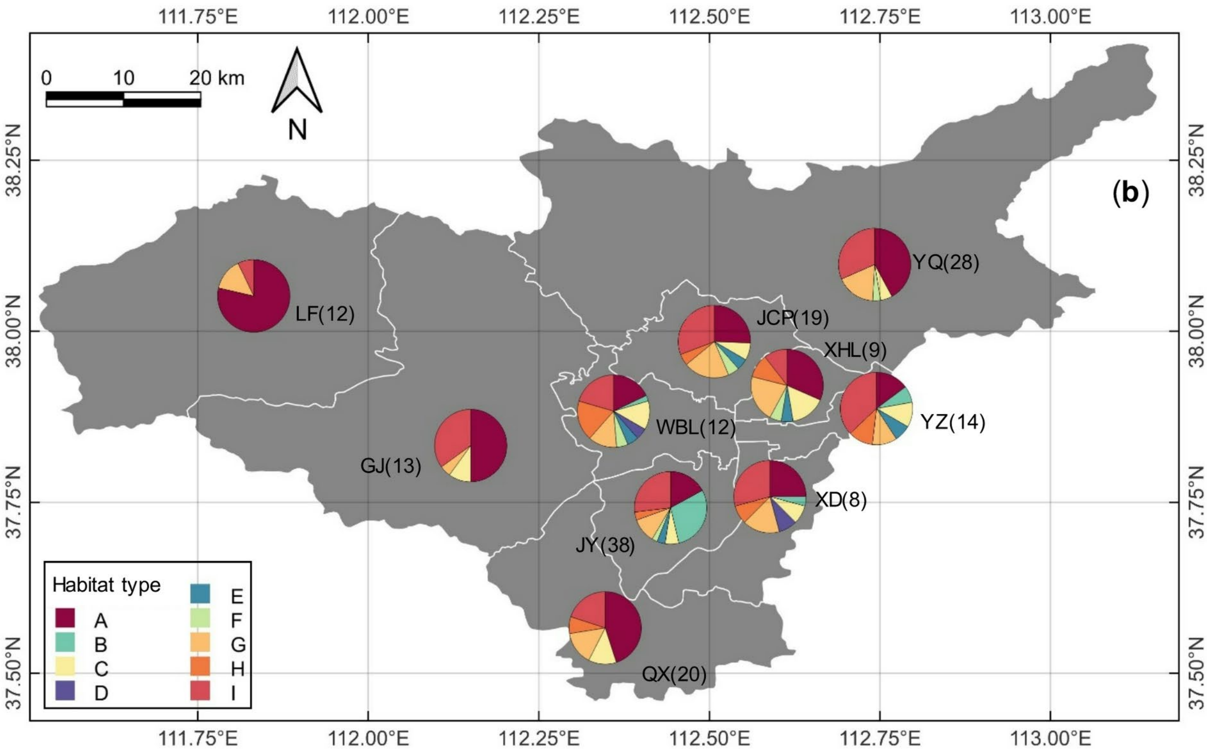


Fig. 2. The heritage tree distribution in nine habitat types in Taiyuan's districts: (**a**) tree abundance (numbers in brackets); (**b**) species richness (numbers in brackets). The colors in the pie charts represent tree abundance or species richness in different habitats: A denotes villages and farmland, B parks and gardens, C roadside, D others (not adequately explained or do not fit into any of the other eight groups), E business and commercial premises, F wooded areas and plant nurseries, G government, institutional and community sites, H residential areas, and I religious sites and cemeteries.

hand, districts like JY and WBL have lower evenness ($E = 0.20$ and 0.18), indicating that a few species dominate their tree populations.

The abundance of heritage trees also varies notably across habitats in Taiyuan, reflecting urbanization and habitat effects (Fig. 2a). Villages and farmland (A), with a total of 2308 trees, and religious sites and cemeteries (I), with 894 trees, have the highest abundances (Table 4). Residential areas (H) also support many heritage trees (740), especially in suburban districts like QX. In contrast, more urbanized habitats such as businesses and commercial premises (E) (19 trees) and roadside areas (C) (180 trees) show significantly lower abundances. Moderate abundances are observed in wooded areas and plant nurseries (F) (172 trees) and government sites (G) (268 trees).

Villages and farmland (A) exhibit the highest species richness, with 35 species, especially in the YQ district, followed by religious sites and cemeteries (I), which host 34 species, highlighting the importance of less disturbed environments for biodiversity (Fig. 2b). Parks and gardens (B) also support a moderate number of species (25 species), primarily in the JY district, while government sites (G) contribute 24 species, particularly in YQ. In contrast, more urbanized habitats like roadside areas (C) (12 species) and businesses and commercial premises (E) (6 species) show low species richness, likely due to space constraints and urban pressures. Habitats such as wooded areas and plant nurseries (F) (6 species) and residential areas (H) (8 species) support fewer species. Overall, the data indicate that suburban and rural areas, such as villages and farmland, provide more amenable habitats for the survival and protection of heritage trees in Taiyuan (Table 1).

Distribution patterns by main factors

Redundancy analysis (RDA) explains the key socio-demographic and environmental factors influencing Taiyuan's distribution of heritage trees (Fig. 3). District area, cultivated area, and forest coverage positively correlate with species diversity distribution. However, GDP, GDP per capita, population, and population density are negatively correlated. The abundance of heritage trees is also positively correlated with forest coverage, cultivated area, and district area, while most other factors show negative correlations (Fig. 2).

Figure 4 shows the relationship between altitude and two heritage-tree characteristics: species richness (blue line) and abundance (orange line). As altitude increases, both the richness and abundance of species decline. The abundance decreases linearly, as described by the regression equation $y = -119.33x + 1130$, with an R^2 value of 0.93, indicating a very strong correlation. Similarly, the richness of heritage trees also decreases with increasing altitude, following the regression equation $y = -3.33x + 37.8$, with an R^2 value of 0.85, suggesting a strong correlation.

Discussion

City history and heritage trees

As an ancient city with a history surpassing 2500 years, Taiyuan's rich legacy has created enabling conditions for the growth, protection and bequest of heritage trees[34,35]. Heritage tree development in Taiyuan is shaped by the geographic environment and the city's rich historical and cultural context. In 497 BCE, Zhao Yang, a noble of the Jin State, founded Jinyang City along the Fen River[33]. As the capital of many dynasties, it served as China's political, military, economic and cultural hub for over a millennium. The protracted urban history offered opportunities to nurture heritage trees through ongoing cultural exchanges and resource accumulation[36]. Historically, the city as the high-level administrative center embodied many government, institutional and religious structures and associated gardens. The palaces and residences of high-ranking officials also include spacious grounds and gardens[48]. Such land uses tended to have a generous provision of landscaping spaces. In the modern era, the assiduous efforts to protect cultural relic sites offer collateral protection of their constituent monumental trees. In particular, the heritage trees in the Jin Temple site (Fig. 1) deliver rich historical narratives and cultural significance. An interpretation of this site signifies the tree cultivation and preservation history in the grounds of important religious and other institutional establishments.

Jin Temple is one of the primary concentrations of heritage trees in Taiyuan. As one of China's earliest royal gardens, it is the largest, the most steeped in historical roots, and the best preserved Tang-Song-style classical temple garden still in existence[49]. Besides preserving a treasured collection of ancient buildings, painted

Habitat types	Tree abundance	Species richness
Villages and farmland (A)	2308	35
Parks and gardens (B)	151	25
Roadside (C)	180	12
Business and commercial premises (E)	19	6
Wooded areas and plant nurseries (F)	172	4
Government, institutional and community sites (G)	268	24
Residential areas (H)	740	8
Religious sites and cemeteries (I)	894	34
Others (D)[a]	5	2
Total	4737	57

Table 4. Tree abundance and species richness of heritage trees in the study area composed of nine habitats in Taiyuan. [a]Not adequately explained or do not fit into any of the other eight groups.

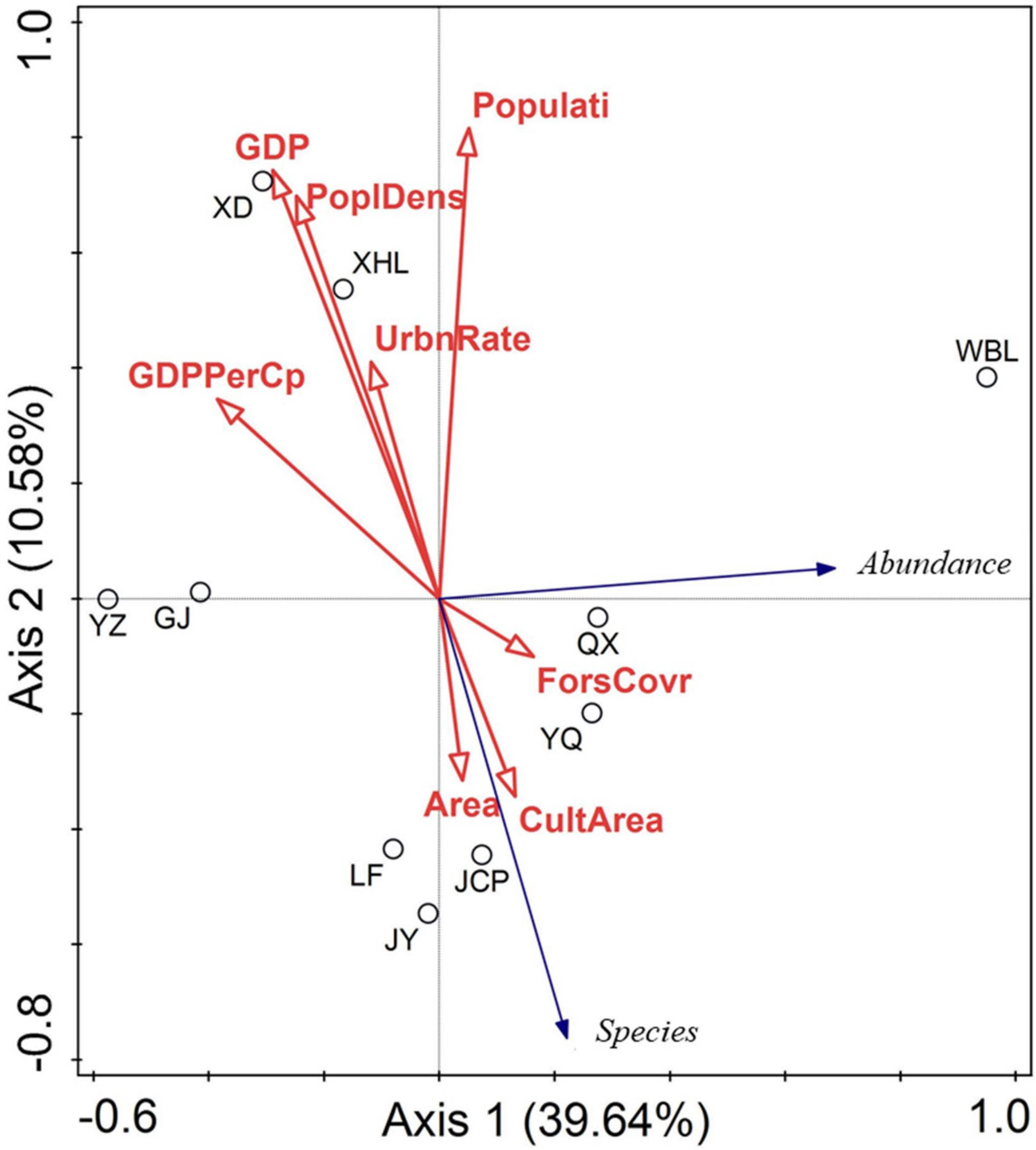


Fig. 3. Redundancy analysis (RDA) ordination illustrating the relationship between the species diversity and tree abundance of heritage trees and environmental factors in Taiyuan. Solid arrowheads represent the dependent variables (species diversity and tree abundance), while hollow arrowheads denote the independent variables (environmental factors). The angle between the arrows indicates the nature of the correlation: an acute angle denotes positive correlation, an obtuse angle negative correlation, and a right angle no correlation. The hollow dots represent various districts within Taiyuan and refer to Table 1 for the meaning of district abbreviations.

sculptures, inscriptions, couplets, and plaques, Jin Temple is home to many precious heritage trees. It provides a genial abode to 93 trees representing 14 species, including *Platycladus orientalis*, *Juniperus chinensis*, *Catalpa bungei*, *Pinus tabuliformis*, *Ginkgo biloba*, and *S. japonicum*[38]. Some exceptional heritage trees preserved within Jin Temple, such as the Wolong Zhou Cypress and the ancient ginkgo trees, bear witness to Taiyuan's history[35]. The Wolong Zhou Cypress is recognized as one of the "Three Wonders of Jin Temple" in tandem with its thousands of years of history, offering a faithful testament to the city's extended historical legacy[50]. The old ginkgo trees are associated with the eminent personality of Wang Qiong, a prominent official from the Ming Dynasty, highlighting the significance of old trees as carriers of culture[38]. These trees are not merely natural heritage but also symbolize the city's celebrated historical and cultural identity, embodying rich regional characteristics and nostalgic memories. In addition to the Jin Temple, heritage trees in historical gardens and institutional grounds offer compelling narratives of cultural and historical significance. These examples underscore the multifaceted value of heritage trees as living monuments that bridge natural and cultural heritage[51,52].

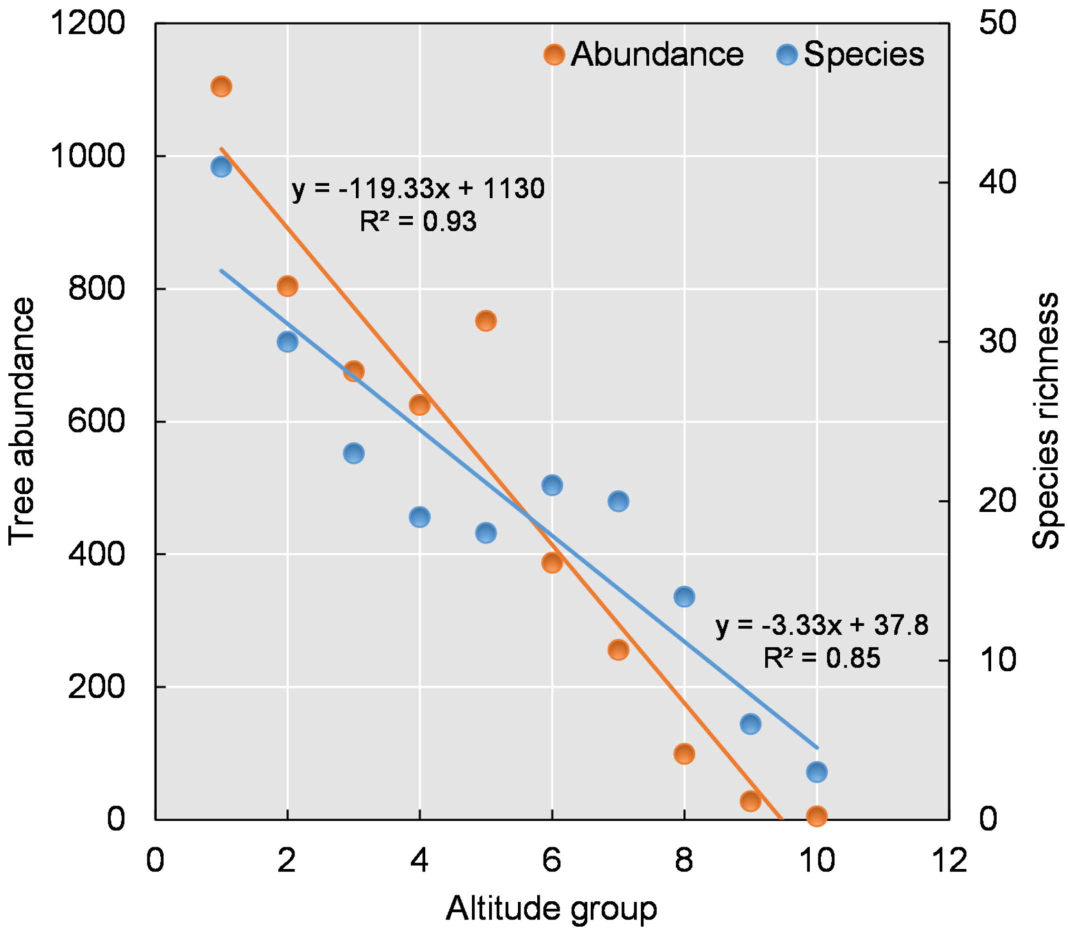


Fig. 4. Vertical distribution patterns of the heritage trees in Taiyuan in relation to species richness (blue color) and species abundance (orange color). There are ten gradient levels with altitudes ranging from 750 to 1750 m, and each group is separated by 100 m.

Species diversity and dominance

Heritage trees embrace natural and cultural qualities, making them a unique biological group. Therefore, the vicissitudes of heritage trees incorporated in human habitats are not only constrained by natural environmental factors[26,53] but also influenced by complex human activities and ethnic customs[4,11]. The heritage trees in the Taiyuan are dominated by *Z. jujuba* and *S. japonica*, with tree counts exceeding 1000 each. *Z. jujuba* has 7000 years of cultivation history in China since the Neolithic age. The species is one of the oldest cultivated fruits in the world. The origin of domestication can be traced to the middle and lower reaches of the Yellow River. It has been widely planted since ancient times in the arid and semi-arid marginal lands of Northern China[54]. The nutrient-rich and delicious fruit (Chinese date or Chinese jujube), with high economic value, has made the tree a staple in traditional agriculture[55].

The common occurrence of *Z. jujuba* in Taiyuan is attributed to its remarkable adaptability to dry and nutrient-poor soils[56]. Located in the eastern part of the Loess Plateau, the city experiences a temperate semi-humid climate with hot summers with concentrated rainfall and cold-dry winters[57]. *Z. jujuba* can thrive in these harsh conditions, particularly in arid environments, where it can survive and flourish despite limited water availability. *Z. jujuba* also have minimal soil requirements, allowing them to grow in the region's hilly, mountainous, and arid landscapes[58]. Over time, *Z. jujuba* has become an essential part of local agrarian culture, frequently planted in family courtyards or near villages as a reliable food source.

Heritage trees of *S. japonicum* in Taiyuan are widely distributed due to their ecological adaptability, cultural significance, and historical cultivation practices[59]. This species is highly resistant to coldness and drought, thriving in the cold winters typical of temperate regions[60]. In areas like Taiyuan, where winters are harsh and dry, *S. japonicum* can adapt to challenging environmental conditions. The attractive ornamental tree is popular for urban greening, roadside planting, and courtyard decoration[61]. The timber of *S. japonicum* with an attractive grain is known for its hardness, strength, durability and workability, making it an essential material since historical times for construction, flooring, furniture, and other high-order wooden products[62]. Many old *S. japonicum* trees have been preserved as heritage trees in cities and villages in Taiyuan[63]. Moreover, *S. japonicum* harbors significant cultural connotations in China, epitomizing auspiciousness and longevity[64]. Known vernacularly as the scholar tree, the cherished species connotes the virtues of honor, nobility and sacrifice. Traditionally, it has been planted in courtyards and villages, often imbued with religious and cultural symbolism.

In addition, *Platycladus orientalis*, *Pinus tabuliformis*, *Ulmus pumila*, and *Catalpa bungei* surpass 100 trees each (Table 2). For example, *P. orientalis* with notable ornamental traits has been widely planted in China for centuries, including Taiyuan, in temple gardens, roadsides, and historical sites[53]. Over time, many of these trees have matured into heritage trees. The species is often valued for its ecological benefits and symbolic significance in Chinese culture, denoting strength and endurance[65]. Thus, natural attraction, cultural attachment, ecological resilience, historical cultivation, and human protection have jointly nurtured and treasured them to attain heritage tree status in Taiyuan.

For the small crop of rare and threatened species, Taiyuan should prioritize their conservation by designating them as focal points in conservation planning. This could involve targeted protection measures such as establishing tree protection zones around them and conducting more frequent and elaborate health assessments. Other specific actions can include removing invasive species and natural enemies that threaten them, implementing habitat restoration measures, and introducing seed banking programs to preserve genetic diversity. Public education campaigns about the importance of these rare species could heighten awareness and garner community support for their protection.

Spatial distribution patterns

Based on the distribution pattern of heritage trees across Taiyuan, the top three areas by abundance are YQ, WBL, and JY. They are outside the city's most developed central urban zone. This pattern suggests that the urban spatial plan limits the presence of heritage trees in the urban core 19. Historically, the city center adopted the high-density development mode with an extensive impermeable cover of buildings, roads and hard paving. Recent urban development brought densification and infilling of original non-built-up areas, squeezing existing trees from the urban fabric and further depriving the plantable spaces. Such compact spatial layouts significantly limit heritage trees due to a combination of environmental stressors, spatial constraints, species failing to adapt to site degradations, and inadequate management[1,28,31]. Also, urbanized environments present harsh conditions, including high pollution levels and compacted and confined soils, to suppress tree growth and vitality[66]. Urban planning commonly prioritizes gray over green infrastructures, resulting in limited soil and aerial spaces to accommodate large trees[67]. Thus, existing trees are trapped and cloistered, and new trees have no room to expand.

Additionally, prevailing impervious surfaces in built-up areas exacerbate water availability and soil health, further restricting tree growth[23,68]. The site requirements of old trees, exceeding those of ordinary urban trees, may not be met or can be degraded due to space limitations and competing land uses, jeopardizing their health and survival[3]. Furthermore, heritage trees often lack adequate protection under urban planning regulations, making them vulnerable to removal or damage from development activities[68].

The diversity and abundance of heritage trees across various habitats and the RDA results in Taiyuan confirm the contrast in the capacity to preserve heritage trees. Suburban environments are more conducive to heritage tree growth than the urban core. Rural areas (village and farmland) harbor more heritage trees due to the synergy of factors favorable for their growth and preservation[29,30]. Firstly, rural environments are relatively free from acute human-driven disturbances, such as construction and pollution, than urban areas[7]. Secondly, traditional land-use practices in rural areas often include planting and protecting large and old trees for practical and cultural reasons. They include providing shade, creating living landmarks, marking boundaries, or observing local customs[69]. The meritorious or important trees are less likely to be removed or damaged due to lower population density and less development pressure[12]. Thirdly, rural landscapes typically offer larger and more stable habitats, providing and sustaining the necessary space and resources for trees to grow to the old age[18,70]. Better soil quality and favorable water conditions support long-term tree survival[71]. Lastly, many rural communities value and protect heritage trees for their time-honored cultural significance[4,5,11,65], leading to their unremitting preservation over generations.

The heterogeneous topography creates diverse habitats to support the heritage trees. However, the high altitude significantly limits their distribution. Changes in altitude result in spatial variations in water and heat conditions in tandem with environmental gradients such as temperature, precipitation, wind speed, light, and soil composition[72]. The altitudinal variations of these factors influence the distribution and structure of plant communities and species diversity[53]. These gradients can mold species diversity distribution in different ways, including negative correlation, positive correlation, a combination of both associations or no discernible trend[73,74].

Our Taiyuan study indicates that heritage trees are negatively correlated with altitude in relation to species richness and tree abundance. Geographically, Taiyuan is wrapped by mountains on the east, north and west sides, while the central and south areas are part of the Fen River Valley Plain[57]. The city's general terrain is higher in the north and lower in the south. Historically, heritage trees are closely associated with human activities[26,75], such as the widely distributed *Z. jujuba* and *S. japonicum*[63]. Thus, many trees are found around villages or cultivated land, mainly in the plains[30]. More people dwelling in the plains with site conditions more amenable to tree performance can bestow more outstanding trees. Moreover, the urban land uses conducive to nurturing heritage trees, including government, institutional, religious, and home of important personalities, are usually concentrated in the low-altitude plains. The gardens in these compounds are breeding grounds for heritage trees.

On the other hand, Taiyuan is part of the Loess Plateau, where soils in the high-altitude areas are typically thin, infertile, and have poor water retention capacity[76], all of which hinder the growth and diversity of heritage trees. Moreover, Taiyuan's warm temperate continental monsoon climate brings notable decreasing temperatures and precipitation with altitude, creating more challenging growth conditions at higher elevations[77]. Overall, less people living at high elevations means less tree planting. For the small number of trees planted in high-elevation mountain areas, they are less likely to grow well and attain the heritage caliber.

Challenges to heritage trees in Taiyuan

Protecting heritage trees in Taiyuan presents some significant environmental and socio-political challenges. The decline in habitat conditions of the trees may threaten their continued growth and long-term survival[1,78]. Since 2015, Taiyuan has renovated 174 urban villages (found in some cities where villages have been occluded into expanding urban areas but retain their rural administrative status and land-use practices. They are former rural settlements embedded incongruously in the urban fabric, a remnant byproduct of rapid urbanization in China[79], with 487 heritage trees affected by consequential environmental degradations[37]. Local industries and farming practices can directly influence the distribution of heritage trees through land-use changes[2,31]. Expanding industrial areas or agricultural lands can lead to habitat loss and fragmentation, which may displace tree populations. For example, expanding cultivated land can result in tree removal, and agricultural pesticide use near trees can harm their health. The study found that areas with high agricultural activity or industrial development had fewer heritage trees, suggesting that such activities contribute to the decline in tree abundance and diversity.

Some trees occluded into the urban fabric have since grown for many years and developed stable, symbiotic-like relationships with the adjacent old buildings[80]. It refers to the unique and often mutually reinforcing interactions between heritage trees and adjoining historical structures. Over time, these trees have become integrated into the building fabrics, benefiting from the more genial micro-environment provided by their adjacency. The buildings may shelter the trees from harsh weather conditions, while the tree roots may contribute to stabilizing the soil around the building foundation. These long-established abiotic-biotic alliances have created a stable environment for trees and buildings. However, urban redevelopments and construction activities often disrupt this reciprocal accommodating association to stress the trees. Removing or altering companion buildings can damage tree roots and expose the trees to harsher environmental conditions to jeopardize their health and survival. In particular, the originally sheltered niches may become open to wind and strong insolation. The exposed trees may not adapt to sudden and drastic environmental changes. For instance, strong winds, especially gusts, have severely damaged some trees. Taiyuan has experienced several major incidents where extremely precious heritage trees have died due to these site changes[35,37].

The other pertinent issue is urbanization, often leading to habitat fragmentation and loss. As cities expand, heritage trees are frequently threatened by construction activities, which can damage their root systems, the soil envelope, and surrounding ecosystems[81]. This urban encroachment reduces the available space for trees to thrive and isolates them from other green spaces, limiting their ecological connections, interactions and resilience[82]. Moreover, the socio-cultural values associated with heritage trees are often overlooked in urban planning and development. While these trees hold historical or cultural significance for local communities, their value is frequently underrated compared to economic development goals[83]. This disconnect can lead to insufficient public support for conservation initiatives and inadequate funding for preservation efforts[35]. Lastly, the policy and governance dimensions present additional hurdles. In many urban areas, the lack of comprehensive policies pinpointing heritage tree protection brings inconsistent and ineffective management practices[63,84]. Without clear regulations or guidelines, these trees may be left vulnerable to neglect or harm during urban development projects.

Protecting tree diversity presents challenges in every city, particularly in Taiyuan, China, where tree preservation often conflicts with the overwhelming and pressing urban development[85]. A multifaceted approach to protecting heritage trees is recommended in more urbanized parts of the city, especially from the impacts of fast urbanization. Identifying and mapping heritage trees within these areas is the crucial initial step, allowing for targeted protection efforts. GIS offers a powerful tool for mapping and managing heritage trees[53]. It can create detailed maps of tree locations, track changes in tree health over time, and monitor the effectiveness of conservation strategies[86]. GIS can also help identify areas most vulnerable to urban development or climate change, enabling planners to make informed and timely decisions about where and when to introduce conservation efforts. In Taiyuan, GIS could create an interactive heritage tree database, allowing for real-time updates and citizen engagement in monitoring tree health.

Urban planning can include limiting construction near valuable trees, improving tree care and maintenance, and expanding tree planting programs in urban spaces. For example, planting more native species well-adapted to urban environments could enhance the tree canopy in these areas. Balancing urban growth with tree conservation requires a strategic approach to urban planning[87]. Integrating heritage tree conservation into zoning and building plans can help preserve these valuable natural resources. One practical approach would be establishing green corridors or heritage tree protection zones, especially in areas where urbanization is expanding by sprawling, infilling and densification. Urban redevelopment can be planned around these zones. New developments can include urban forests or tree-lined streets to ensure that infrastructure growth and heritage conservation go hand in hand. Urban planning can support the preservation of heritage trees by incorporating green infrastructure into city design to counteract the usual domination of gray infrastructure[88]. This could include creating buffer zones around heritage trees, setting up tree conservation areas, and requiring developers to plant trees or preserve existing ones in their projects. Enacting tree preservation ordinances or incentives for developers to preserve mature trees could also be introduced. Establishing a comprehensive legal framework to address heritage tree conservation can provide assured protection against urban development and illegal felling.

In addition, implementing continuous monitoring programs will ensure tree health and growth are regularly assessed, allowing for timely interventions. The successful experiences of heritage tree conservation in other Chinese cities, such as Beijing[32], Luoyang[31], and Chengdu[28,65], can serve as valuable references. Other cities have successfully implemented various strategies to reduce habitat loss for heritage trees[1]. For instance, some cities have introduced policies that protect heritage trees by designating them as cultural landmarks or natural monuments. In addition, creating green spaces like parks or tree-lined streets to envelop the old trees can mitigate habitat loss. Taiyuan could implement similar strategies, such as developing heritage tree conservation areas and incorporating more green spaces into urban designs. Examples from other cities, like Singapore's urban greening initiatives or Paris's protection of historic trees, can offer useful models for Taiyuan's conservation efforts.

Climate change could alter the growth patterns of heritage trees in Taiyuan. Changes in temperature, precipitation, and extreme weather events such as droughts or floods could shift the suitable habitats for certain tree species. For example, more frequent heat waves or longer dry spells may stress less drought-resistant trees[89]. Additionally, shifts in the timing of the growing season could affect the trees' phenology, such as flowering and fruiting cycles[90]. Monitoring temperature and rainfall patterns can identify trends and predict how future climate conditions might impact these trees. In particular, temperature and water availability are key factors that influence species growth and distribution.

The community can play a vital role in protecting heritage trees. To pump prime their participation, citizen science may be proactively mobilized as a novel way to raise public awareness and engage people in tree monitoring, reporting damage, assessment, management, and conservation activities such as tree planting or organizing awareness campaigns. Engaging with schools, local organizations, and environmental groups could also help foster a sense of community stewardship for these trees. Establishing educational programs that teach residents about the ecological and cultural value of heritage trees can encourage them to participate actively in conservation endeavors. Citizen science has emerged as a powerful tool for conserving and studying heritage trees, engaging local communities pragmatically to protect these vital natural resources[91]. By involving citizens in data collection, monitoring, and awareness campaigns, citizen science initiatives empower individuals to contribute to understanding and preserving heritage trees, which are crucial for biodiversity, climate resilience, and cultural heritage[92].

A notable example of a citizen science approach is the Ancient Tree Hunt (ATH), where volunteers are trained to identify, measure, and document old trees in their local areas[93]. This grassroots effort helps create comprehensive databases that track the health and distribution of heritage trees and raises public awareness about their ecological importance. Participants gain valuable tree biology and ecology knowledge, fostering a deeper connection to their environment[94]. Furthermore, citizen science projects often promote stewardship by encouraging community members to advocate tree protection against threats such as urban development and climate change[95]. By harnessing the collective efforts of individuals passionate about nature, these initiatives enhance conservation outcomes while fostering a sense of community pride and responsibility toward preserving the heritage tree legacy for future generations. Therefore, citizen science represents a promising approach to safeguarding heritage trees in Taiyuan.

Heritage trees are an excellent resource for environmental education, as they represent both ecological and cultural heritage. Schools and local organizations can use their sites as living classrooms, where people can learn about biodiversity in urban areas, climate change impacts, and the multiple roles of trees in urban environments. Interpretive signage and guided tours for heritage tree sites can be provided to engage the public. The local government could sponsor events like tree-protection campaigns or educational workshops on conserving heritage trees. These efforts would help increase public awareness and promote sustainable city practices.

Taiyuan has capitalized on its exceptional endowment of ancient trees to promote tourism. The natural-cum-cultural resource base has been organized into a three-level hierarchy, ranging from ancient-tree villages to towns, parks, and streets. This municipal initiative has triggered the development of a *Special Plan for the Protection of Ancient and Famous Trees in Taiyuan City (2021–2035)* driven by the Municipal Planning and Natural Resources Bureau[96]. A tree-themed ecotourism program can be designed to connect tree appreciation with the proximal cultural relics to form hybrid cultural greenways. The enthusiasm of some ecotourists can be tapped to become citizen tree stewards in conjunction with the citizen science initiative. The city can use its outstanding living landmarks to enhance its image and branding[16,17]. A portion of the tourism revenue can be fed back to the tree conservation program to create a win-win arrangement. This new enterprise can provide an alternative and effective incentive to strengthen the protection of precious trees.

Conclusion

The study found that Taiyuan's heritage trees, comprising 57 species and 4737 individual trees, demonstrate significant taxonomic diversity and ecological importance. Dominant species, such as *Z. jujuba*, *S. japonica*, and *P. orientalis*, account for large proportions of the tree population, reflecting their historical bequest and ecological significance. The long list of species with few individuals furnishes remarkable diversity. The species distribution varies across districts, with suburban and rural areas, especially villages and farmland, showing higher tree abundance and species richness than the urban core. Urbanized habitats like commercial and roadside areas display significantly lower diversity, highlighting the adverse effects of urban development on ancient tree preservation. Environmental factors, such as altitude, have a marked influence on the distribution of these trees, with tree abundance and species richness decreasing with altitude.

A complex interplay of ecological and socio-cultural factors influences the spatial distribution patterns and diversity of heritage trees in Taiyuan. The historical and cultural significance of trees, such as those in the Jin Temple, contributed to their preservation, but rapid urbanization with limited protection measures poses substantial challenges to their survival. Urban sprawl, construction activities, and habitat fragmentation threaten the welfare and longevity of these precious trees, while inadequate protection and socio-cultural undervaluation further exacerbate these threats.

To address the chronic challenges, the study suggests adopting comprehensive protection strategies similar to successful global initiatives, such as creating a "citizen science", augmenting public education and implementing legal protection and habitat restoration efforts. An innovative hybrid ecotourism program can be developed by combining the appreciation of heritage trees and heritage sites. These proactive actions can ensure the preservation of ancient Taiyuan's equally ancient heritage trees as sustainable ecological and cultural gems.

The past has provided the necessary conditions for many heritage trees to be nurtured in the ancient city. This highly valuable living endowment must not be left to routine treatments, degradation by default, or neglect. It is incumbent upon the present generation to adopt dedicated and tailor-made efforts to ensure that this precious inheritance can be conserved, sustained and cherished.

Data availability
This study's heritage tree information is available on Science Data Bank: https://doi.org/10.57760/sciencedb.19426.

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PY, XC and CYJ conceived and designed the research; XC, PY and WS performed research; WS, XC, and PY curated the data; XC Wrote the original draft; CYJ reviewed and edited. All authors had read and agreed to the published version of the manuscript.

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Declarations

Competing interests
The authors declare no competing interests.

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