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Species diversity and spatial pattern of urban ancient trees in biodiverse Southwest China

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Introduction: Ancient trees are keystone ecological and cultural entities ancient that provide essential services to humans in settlements. The unique natural and cultural geography in the China-Vietnam border region provides relatively undisturbed habitats for ancient trees. Cross-border activities, policy disparities, and uneven conservation resources currently challenge their survival and diversity.

Methods: A study was conducted in Chongzuo city, a typical border city, to quantify the species diversity, abundance and distribution of ancient trees, and their relationship with varied habitats. Redundancy analysis (RDA) identified the primary factors influencing their spatial patterns.

Results: The results identified 15,722 ancient trees from 99 species, 73 genera and 35 families. Twenty-nine species were solitary with only one individual each, and 14 were listed as protected plants in China. The population was dominated by *Camellia drupifera*, *Ficus altissima*, *Dimocarpus longan*, and *Excentrodendron tonkinense*, collectively accounting for 84.05% of the recorded trees. Ancient trees decreased with tree age, height, DBH, and crown width, with the majority (95.33%) in the 100−299 years age group. More natural habitats, including mountains, villages, and farmlands, supported the highest trees abundance, while parks, nature reserves, and scenic spots accommodated the greatest species richness. Pingxiang township had the highest tree abundance (9,118), while Longzhou had the highest species richness (50). Ningming, however, had the largest Shannon-Wiener index (H = 2.42), making it the most important district for preserving tree diversity. Land area, built-up area, GDP, population density, forest coverage, farmland area, and altitude significantly influenced the distribution of ancient trees.

Discussion: The inherently high landform and habitat diversities in the study area support many ancient tree species. Due to the complex terrain, in-depth, long-term, and systematic research remains relatively scarce. Future studies could integrate natural and anthropogenic factors to explore the survival patterns and conservation needs, allowing the formulation of targeted strategies for their sustainable protection.

KEYWORDS

ancient trees, conservation strategy, distribution pattern, protected species, rare species, species composition

1 Introduction

Ancient trees are defined as trees over 100 years of age, often characterized by substantial girths, towering heights, extensive canopy cover, and unusual biomass structure (Blicharska and Mikusiński, 2014). They constitute precious natural resources nurtured by the fortuitous combination of geography, ecology, and human activities over time (Yan, 2023; Pan et al., 2025). Playing an important role in ecosystem functions, they altruistically offer a varied spectrum of microhabitats, shelters and foods to many companion plants and animals to enhance biodiversity conservation (Jim and Zhang, 2013; Nolan et al., 2020), including birds, mammals, insects, fungi and epiphytic plants (Lindenmayer, 2017).

Some trees serve as repositories of valuable genes from endangered species, making them critically important for species conservation and ecosystem continuity (Spooner and Shoard, 2016; Chi et al., 2020). Moreover, their root systems can enrich soil fertility and maintain soil structure and porosity to sustain infiltration, percolation, and plant-available water storage (Nolan et al., 2021). By enhancing soil stability, they improve soil and water conservation and suppress erosion. Their presence can create diverse abiotic and biotic microenvironments, which can increase habitat and species richness (Hubble et al., 2010; Li and Zhang, 2021). Their physiology and physiognomy can contribute effectively to carbon sequestration and microclimatic regulation (Jones et al., 2013).

The prominent doyens belong to a separate and special class of keystone plants, whose vicissitudes are intimately intertwined with adjoining human communities (Liu et al., 2022). Ancient trees offer serve as a living link to both historical and contemporary landscapes (Lindenmayer and Laurance, 2017). As persistent members of ecosystems, their life spans traverse multiple human generations, allowing for deep association with human and natural history, as well as related environmental changes (Andersson and Östlund, 2004; Lai et al., 2019). Some ancient trees embody or engender religious, spiritual, and cultural values for local communities, serving as a bridge between nature and culture, and essential connectors to collective memory and sense of place (Chen and Hua, 2015). For example, *Cupressus funebris* and *Ginkgo biloba* trees have been enlisted as the material expression and inheritance of time-honored customs and cultural beliefs (Liu et al., 2020; Hou et al., 2022).

Studying the species composition and spatial distribution patterns of ancient trees can be fruitfully accompanied by investigating the associated drivers and processes (Cannon et al., 2022). Ancient trees dwelling in different regions are influenced by different natural conditions and human interaction regimes (Pan et al., 2025). The existing population of ancient trees in a given locality is expected to express a unique collection of traits, including floristic profile, age structure, evolutionary progression, spatial patterns, and plant migration and adaptation to the environment (Jim, 2005; Lai et al., 2019).

However, over the past century, the distribution and abundance of ancient trees have been reduced by harmful biotic and abiotic changes (Stagoll et al., 2012; Le Roux et al., 2014). They include climate change, drought, excessive soil moisture, soil erosion, invasive exotic species, increased pest and disease attack, environmental destruction, wildfires, excessive deforestation, and economic development (Mahmouda et al., 2015; Gilhen-Baker et al., 2022). Such extensive degradation has progressively eliminated a significant proportion of ancient trees. The residual populations are confined to fragmented remnant patches, with collateral impacts on ecosystems and biodiversity (Piovesan et al., 2022). These deleterious changes have altered the species composition, abundance, and distribution patterns of ancient trees (Yao et al., 2024). For instance, the density of scattered ancient trees in China is positively correlated with human population density. In contrast, the density of clustered ancient trees is negatively influenced by human population density (Liu et al., 2019). Some ancient trees are less damaged in regions with more water availability and moderate temperatures (Venter et al., 2017).

Chongzuo, a Chinese city near the Vietnam border, features a karst-dominated and highly varied terrain with notable relative relief. Its complex geology and topography have created a fine mosaic of distinctive soil, moisture and microclimatic conditions to nurture and sustain rich plant resources (Zhang et al., 2013). The spatially differentiated natural conditions provide conditions for biotic diversification. Moreover, recent rapid urbanization has imposed intense human activities and environmental degradation, which has been compounded and exacerbated by climate change (Asanok et al., 2021). These impacts severely challenge the growth and survival of ancient trees in Chongzuo. However, the alarming loss of an irreversible and valuable resource base has not attracted in-depth research. The lack of scientific knowledge has hindered conservation efforts.

This study represents the first attempt to assess the condition and plight of ancient trees in Chongzuo. It assesses the species composition, distribution patterns, and conservation needs of ancient trees in Chongzuo. Our key research questions include: (1) What are the key traits (species composition, diversity, dimensions and age range) of ancient trees in the study area? (2) What are the distribution patterns of the trees? (3) What are the relationships amongst trees and environmental attributes, including altitudinal gradient? The findings could inform management decisions for ancient trees in tropical China and elsewhere facing similar remnant-tree conservation concerns.

2 Materials and methods

2.1 Study area

Chongzuo (21°36′–23°22′N, 106°33′–108°6′E) is located in the southwest of Guangxi Zhuang Autonomous Region (hereinafter referred to as "Guangxi"), China (Figure 1). The border city near Vietnam covers 17,377 km^2, comprising seven townships. Chongzuo is characterized by a complex terrain, comprising karst mountains, hills, terraces, and valleys. With an altitude ranging from 100 to 1358 m above sea level and situated just south of the Tropic of Cancer, the city has a subtropical humid monsoon climate, with an average temperature of 22.1°C. The annual sunshine is 1,600 h, and the average rainfall is 1,200 mm (Wang et al., 2022), with heavy rains occurring in summer. The year is divided into two distinct seasons: a dry season (October to March) and a rainy season (April to September). The frost-free period lasts 340 days. The dominant natural vegetation is subtropical karst seasonal rainforest.

Chongzuo accounts for 33% of Guangxi's sugar production, the largest in the province and approximately one-fifth of the national total, earning it the title of "Sugar Capital of China" (Zhu and Yang, 2023). In recent years, the continual expansion of sugarcane cultivation has led to the reduction of natural vegetation, leaving some ancient trees standing isolated amid the sugarcane fields. Additionally, road construction and cash crop cultivation, such as *Eucalyptus robusta* and *Macadamia ternifolia*, have accelerated the decline of vegetation. These land conversions pose a significant threat to the survival of ancient trees.

Chongzuo is divided into seven townships: Jiangzhou, Pingxiang, Fusui, Daxin, Tiandeng, Longzhou, and Ningming (Figure 1c; Table 1). Nine habitat types were classified based on detailed records of the ancient trees' growing sites. They include villages and farmlands (A), parks, nature reserves, and scenic spots (B), roadside (C), business and commercial (D), mountain (E), government and institutional (F), residential (G), religious and cemeteries (H), and others (I).

2.2 Data collection and treatment

In China, two national surveys of ancient and famous trees were conducted in 2001 and 2015. Moreover, the Chongzuo Forestry Department previously carried out a systematic survey of its ancient trees. On each tree, a plaque was installed to indicate its identification number, the names of the species, family, and genus, its protection level, and age. Building on these efforts, this study conducted a more comprehensive survey that covered the entire city, including undeveloped mountain, village, and urban areas.

Data on ancient trees were collected from multiple sources, including the Guangxi Ancient and Notable Trees Management System, the China National Knowledge Infrastructure (https://www.cnki.net), government yearbooks, published papers, and internal files of forestry departments. When discrepancies exist in the records of the same ancient tree across different literature sources, we prioritize data from the more authoritative Guangxi Ancient and Notable Trees Management System, then carefully review to eliminate items that were duplicates or had ambiguous geographic coordinates. Field validation surveys were subsequently conducted from January to December 2024 following the Chinese national standard "Technical Regulation for Surveying of Old and Notable Trees" (China Society of Forestry, 2017).

During the fieldwork, data were collected on tree species, geographical location, elevation, habitat, ownership, age, diameter at breast height (DBH; measured at 1.3 m above ground), canopy

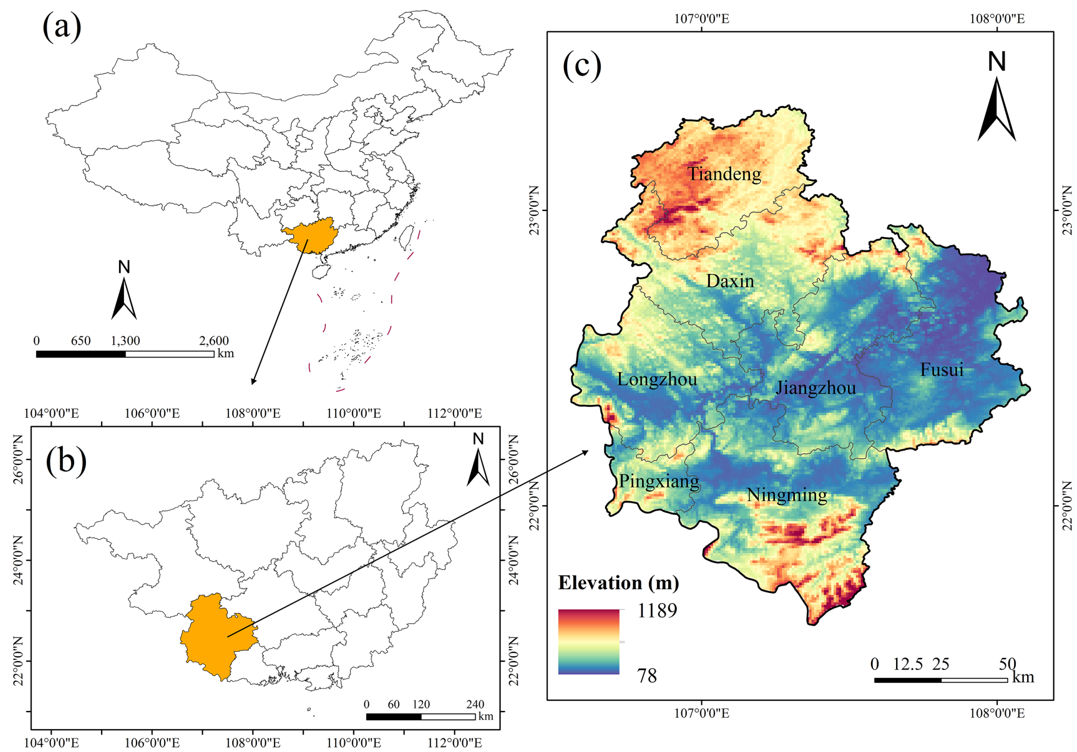

FIGURE 1
Maps of the study area: **(a)** location of Guangxi Zhuang Autonomous Region in Southwest China; **(b)** location of the study area, Chongzuo City, in the southwest part of Guangxi; and **(c)** the seven townships of Chongzuo and their elevation.

TABLE 1 Key land and population data of the seven townships of Chongzuo.

Township	Tree abundance	Species richness	Land area (km^2)	Farmland area (km^2)	Population density (persons/km^2)	Forest cover (%)	Built-up area	GDP
Daxin	1,558	36	2,747	332.11	139.53	55.08	7.70	3.97
Fusui	1,529	25	2,841	1,026.80	160.23	50.10	25.66	10.39
Jiangzhou	400	22	2,918	1,029.76	130.12	32.14	34.50	6.44
Longzhou	1,729	50	2,311	600.00	117.60	48.73	12.85	3.63
Ningming	1,006	47	3,705	833.33	86.20	52.57	11.17	4.76
Pingxiang	9,118	30	650	27.47	196.46	60.19	12.42	5.45
Tiandeng	382	28	2,165	424.60	207.86	51.35	9.05	4.02
Total	15722	238	17,337	4,274.07	1,038.00	350.16	113.35	38.66
Average	2246	34	2,477	610.58	148.29	50.02	16.19	5.52

size, growth potential, and site photographs (Figure 2). We employed the following tools: GPS units, compasses, laser altimeters, measuring tapes, diameter tapes, and cameras. Tree species identification was verified with reference to the Illustrated Handbook of Plants in Tropical Rainforest Area of China Plants of Guangxi (Luo et al., 2021) and Flora of China (Flora of China Editorial Committee, 2013).

According to local laws, the age of ancient trees cannot be assessed using any instruments that might harm the trees, even though some of these instruments can generate more accurate data (Yang et al., 2024). Hence, when an ancient tree is affixed with an official plaque issued by the forestry department, its age is ascertained in accordance with the information inscribed thereon. In the absence of such a plaque, the tree's age is evaluated based on the oral cultural history of local people, and village records (Pan et al., 2025). The species were grouped into four frequency classes: dominant (over 100 individuals per species), common (10<trees<100), rare (2<trees<9), and solitary (only one tree) (Xie et al., 2022). For protection purposes, they were further classified into three age tiers: tier 1 (≥500 years, "oldest trees"), tier 2 (300–499 years, "older trees"), and tier 3 (100–299 years, "old trees") (Yao et al., 2024). The class limits followed the national guidelines on the designation of old and valuable trees (China Society of Forestry, 2017).

2.3 Statistical analyses

The species importance value (IV) was calculated based on the relative abundance (RA) and relative dominance (RD) of each ancient tree species. The formula is: IV=(RA+RD) ×100/2. 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 (Jim and Zhang, 2013).

To facilitate tree sampling and spatial distribution analysis, the study area was divided into 10 km×10 km grids. This grid size was chosen based on a review of similar studies in landscape ecology and species diversity distribution patterns, aiming to capture the spatial patterns effectively and avoid excessive fragmentation (Brummitt et al., 2021; Chiarucci et al., 2011). Species diversity and evenness indices were calculated to quantify changes in ancient tree diversity between areas. The formula is: $H = -\sum_{i=1}^{S} P_i \ln P_i$, $E = H/\ln S$, where $P_i = N_i/N$, N_i is the number of individuals of i, N is the total number of individuals of all species, and S is the total number of species (Huang et al., 2025).

We adopted correlation analysis to assess the relationships between tree age and tree height, DBH, altitude, and crown width, and between altitude and tree abundance and species richness. We applied Redundancy Analysis (RDA) to assess the correlation between land area, built-up area, GDP, population density, forest coverage, farmland area, and the abundance and richness of ancient trees. We also selected altitude as a representative natural factor, and its relationship with the abundance and diversity of ancient trees was examined using scatter plots to generate regression curves. All analyses were conducted using R version 4.3.3 (R Development Core Team, 2024). All tests were two-tailed, with significance levels of 0.05.

3 Results

3.1 Species composition and importance value

We recorded 15,722 ancient trees, representing 99 species, 73 genera, and 35 families, indicating a high taxonomic diversity (Table 2). Based on frequency, 10 species were classified as dominant, 30 as common, 30 as rare, and 29 as solitary (Figures 3a-c). Only six dominant plant families contained more than five species each: Moraceae (11 species), Fabaceae (9 species), Euphorbiaceae (8 species), Theaceae (7 species), Anacardiaceae (5 species), and Lauraceae (5 species). Together, they contributed 45.45% of the total species. These ancient trees account for 3.22%,

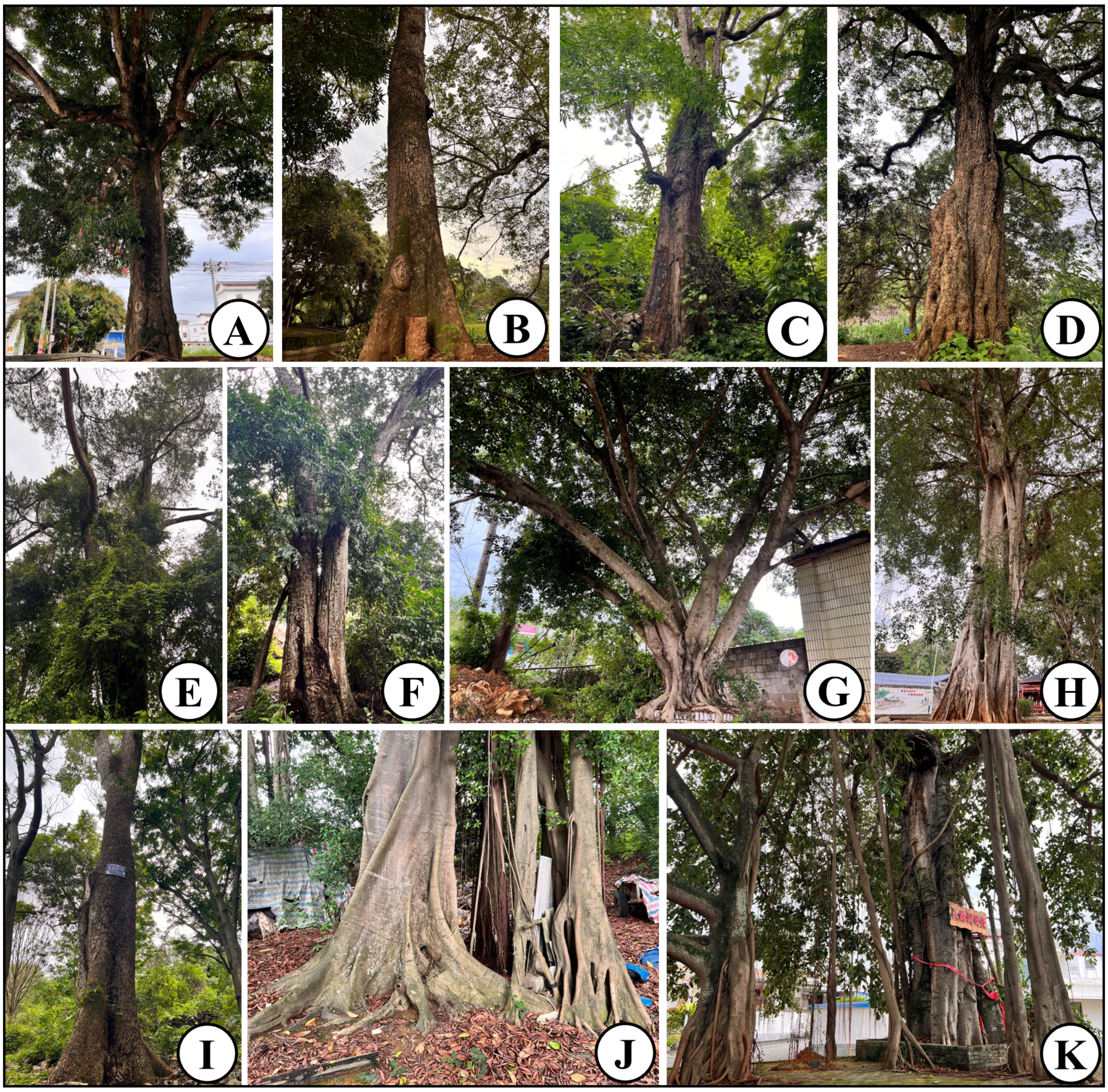

FIGURE 2
Photographs of notable ancient trees and their habitats in the Chongzuo: **(A, B)** *Mangifera persiciforma*; **(C)** *Pistacia chinensis*; **(D)** *Dimocarpus longan*; **(E)** *Pinus massoniana*; **(F)** *Syzygium cumini*; **(G, H)** *Ficus macrocarpa*; **(I)** *Bombax ceiba*; **(J, K)** *Ficus altissima*.

6.50%, and 14.98% of the total plant species (3,071), genera (1,123), and families (234) in Chongzuo, respectively.

The top three species by importance value (IV) were *C. drupifera*, *F. altissima*, and *D. longan*, at 41.99, 15.03, and 12.57, respectively (Table 2). The results showed that these species were abundant in tree count and endowed with a large DBH, resulting in significantly higher ecological value and physical presence than other species.

The tree population was heavily represented by the four most abundant species, each with over 1,000 individuals (Table 2). They were *Camellia drupifera* (Theaceae), *Dimocarpus longan* (Sapindaceae), *Excentrodendron tonkinense* (Tiliaceae), and *Ficus altissima* (Moraceae), jointly accounting for 13,215 (84.05%) of the tree count. Only two species came under the dominant families. Thus, the species composition is heavily skewed towards a tiny cohort of dominant and subdominant species. In contrast, the 29 solitary species, each maintaining only one individual (Table 3), collectively constitute 29.29% of the total species composition, thereby significantly enhancing the ancient tree diversity in Chongzuo.

The dominant species with 1337 trees, *E. tonkinense*, is included as a Class II protected species under the List of National Key Protected Wild Plants (2021) in China (https://www.gov.cn/zhengce/zhengceku/2021-09/09/content_5636409.htm). Other Class II ancient tree species in the study area include: *Camellia chrysanthoides, C. micrantha, C. petelotii, Cycas pectinata, Deutzianthus tonkinensis, D. longan, Diplodiscus trichosperma, Garcinia paucinervis, Horsfieldia hainanensis, Ilex kaushue, Litchi chinensis, Pistacia chinensis*, and *Podocarpus macrophyllus*.

TABLE 2 Tree count by age groups, cumulative DBH and importance value (IV) of ancient tree species with frequency >1 in Chongzuo.

Species	Family	Tree count				Cumulative DBH (cm)	IV
		Tier-1	Tier-2	Tier-3	Total		
Camellia drupifera	Theaceae			8,937	8,937	230,623.00	41.99
Dimocarpus longan	Sapindaceae	29	195	1,526	1,750	119,041.35	12.57
Excentrodendron tonkinense	Tiliaceae	51	81	1,205	1,337	73,328.82	8.57
Ficus altissima	Moraceae	53	179	959	1,191	190,904.98	15.03
Ficus microcarpa	Moraceae		11	306	317	40,220.60	3.38
Camellia fangchengensis	Theaceae			287	287	7,465.60	1.35
Mangifera persiciforma	Anacardiaceae		11	273	284	32,417.60	2.81
Bombax ceiba	Bombacaceae	1	14	204	219	24,432.99	2.13
Liquidambar formosana	Hamamelidaceae		1	166	167	13,163.09	1.31
Ficus virens	Moraceae	14	19	80	113	20,104.92	1.54
Syzygium cumini	Myrtaceae			94	94	8,443.08	0.80
Cinnamomum camphora	Lauraceae		4	76	80	6,997.14	0.67
Bischofia javanica	Euphorbiaceae	1	2	62	65	7,148.91	0.63
Deutzianthus tonkinensis	Euphorbiaceae			62	62	3,779.50	0.42
Drypetes perreticulata	Euphorbiaceae			59	59	3,474.80	0.39
Canarium pimela	Burseraceae			55	55	4,653.37	0.45
Litchi chinensis	Sapindaceae	2	5	42	49	4,962.34	0.45
Garcinia paucinervis	Guttiferae	2	3	43	48	2,919.92	0.32
Alphonsea monogyna	Annonaceae			47	47	3,170.14	0.34
Amesiodendron chinense	Sapindaceae			41	41	2,398.50	0.27
Ficus racemosa	Moraceae	1	1	34	36	4,705.60	0.39
Dracontomelon duperreanum	Anacardiaceae	7	7	21	35	6,736.24	0.51
Choerospondias axillaris	Anacardiaceae			28	28	2,221.30	0.22
Saraca dives	Fabaceae			28	28	2,014.10	0.21
Averrhoa carambola	Oxalidaceae	1	2	23	26	1,844.04	0.19
Alstonia scholaris	Apocynaceae	1	4	20	25	3,182.80	0.27
Pistacia chinensis	Anacardiaceae			24	24	2,279.87	0.21
Diplodiscus trichospermus	Tiliaceae			23	23	1,356.14	0.15
Lysidice rhodostegia	Fabaceae			19	19	1,647.10	0.16
Bischofia polycarpa	Euphorbiaceae		5	13	18	2,066.40	0.18
Canarium album	Burseraceae			15	15	1,288.19	0.12
Celtis sinensis	Ulmaceae		2	13	15	1,131.80	0.11
Cycas pectinata	Cycadaceae	2	3	10	15	595.20	0.08
Horsfieldia kingii	Myristicaceae			14	14	886.59	0.10
Schima wallichii	Theaceae			13	13	1,024.60	0.10
Mangifera indica	Anacardiaceae			12	12	1,261.50	0.11
Adenanthera microsperma	Fabaceae	1		11	12	1,145.95	0.11

(Continued)

TABLE 2 Continued

Species	Family	Tree count				Cumulative DBH (cm)	IV
		Tier-1	Tier-2	Tier-3	Total		
Antiaris toxicaria	Moraceae	2	3	5	10	1,912.31	0.14
Pinus massoniana	Pinaceae			10	10	992.90	0.09
Cephalomappa sinensis	Euphorbiaceae			10	10	705.12	0.07
Sarcosperma laurinum	Sapotaceae		1	6	7	677.40	0.06
Quercus acutissima	Fagaceae			7	7	427.40	0.05
Aphanamixis polystachya	Meliaceae		1	5	6	637.00	0.06
Cleistanthus sumatranus	Euphorbiaceae			6	6	248.70	0.03
Ficus benjamina	Moraceae			5	5	591.50	0.05
Cratoxylum cochinchinense	Guttiferae			5	5	345.77	0.04
Zenia insignis	Fabaceae	1	1	2	4	573.00	0.05
Sterculia monosperma	Sterculiaceae			4	4	324.53	0.03
Tapiscia sinensis	Staphyleaceae			4	4	292.00	0.03
Clausena lansium	Rutaceae			4	4	230.50	0.03
Pterospermum heterophyllum	Sterculiaceae			4	4	219.60	0.03
Aphanamixis grandifolia	Meliaceae			4	4	131.80	0.02
Camellia chrysanthoides	Theaceae			4	4	104.10	0.02
Castanopsis hystrix	Fagaceae	1		2	3	309.80	0.03
Artocarpus heterophyllus	Moraceae			3	3	285.10	0.03
Syzygium nervosum	Myrtaceae			3	3	280.00	0.03
Dalbergia balansae	Fabaceae			3	3	260.10	0.02
Pterospermum truncatolobatum	Sterculiaceae			3	3	177.20	0.02
Ficus religiosa	Moraceae			2	2	257.70	0.02
Cylindrokelupha eberhardtii	Fabaceae			2	2	212.90	0.02
Castanea mollissima	Fagaceae		1	1	2	208.60	0.02
Alphonsea mollis	Annonaceae		1	1	2	208.60	0.02
Litsea dilleniifolia	Lauraceae			2	2	182.70	0.02
Mytilaria laosensis	Hamamelidaceae			2	2	162.40	0.02
Acacia confusa	Fabaceae			2	2	152.40	0.02
Michelia × alba	Magnoliaceae			2	2	136.89	0.01
Ligustrum lucidum	Oleaceae			2	2	122.50	0.01
Cinnamomum cassia	Lauraceae			2	2	121.00	0.01
Citrus maxima	Rutaceae			2	2	105.20	0.01
Podocarpus macrophyllus	Podocarpaceae			2	2	85.50	0.01
Other		2	4	23	29	2,593.84	0.24
Total		172	561	14,989	15,722	849,314.12	100.00

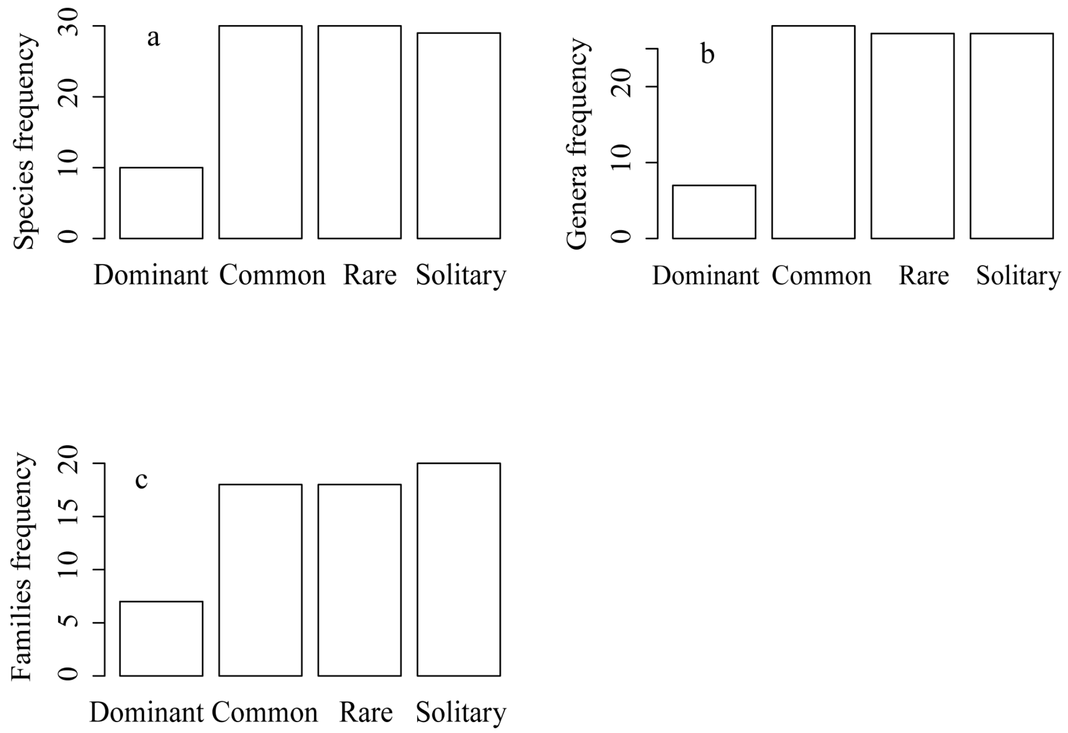

FIGURE 3
Frequency distribution of **(a)** species, **(b)** genera, and **(c)** families of ancient trees in Chongzuo.

3.2 Age and dimensional traits

The ancient trees had an average age of 166.49 ± 80.96 years (Figure 4a). The minimum age was 100 years, with 348 individuals qualifying as ancient trees under current national legislation. Thirty-one trees were 1,000 years or older, with *E. tonkinense* contributing 21 trees. *E. tonkinense* was the species with the highest mean age of 1216 years, including the oldest tree of 2,300 years in the Nonggang National Nature Reserve (Figure 4a; Table 4). For the age distribution, most trees (95.33%) were in the tier-3 age group, with only 561 in tier-2 and merely 172 in tier-1 (Table 2). The age distribution was notably skewed toward younger classes, declining sharply with age and indicating a reverse J-shaped pattern (Figure 4a).

The average DBH of ancient trees was 54.13 ± 48.79 cm (Figure 4b). *F. altissima* (471.1 cm) had the largest DBH, and the smallest was a *C. drupifera* (20 cm). The 20–40, 40–60, and 60–80 cm DBH groups had the largest tree counts, at 9395, 1706, and 1444, respectively, accounting for 79.79% of the total. The average height of ancient trees was 12.73 ± 7.51 m (Figure 4c). The maximum height was *Dracontomelon duperreanum* (58.6 *m*), and the minimum was *C. drupifera* (2.3 m). The 5–10, 10–15, and 15–20 m height groups had the largest tree counts at 8574, 1880, and 2065, respectively, or 79.63% of the total. The average crown width of ancient trees was 9.95 ± 7.79 m (Figure 4d). An *F. altissima* had the largest crown width of 64.0 m, while a *C. drupifera* had the smallest of 1.5 m. The 0–5 m, 5–10 m, and 10–15 m crown width groups had the largest tree counts, at 3,216, 7,674, and 2,154, respectively, accounting for 82.97% of the total tree count.

Correlation analysis revealed that age had a significant positive correlation with crown width (r=0.384, P<0.001), height (r=0.326, P<0.001), and DBH (r=0.571, P<0.001) (Figures 5a, b, d). This result a trend of increasing tree dimensions with age, implying that a notable proportion of ancient trees was able to maintain their biomass structure largely intact, with limited branch losses. In contrast, a significant negative correlation was observed with altitude (r=-0.086, P<0.001) (Figure 5c), suggesting that higher elevations were unfavorable for the growth and survival of ancient trees.

3.3 Tree dimensions, species diversity and spatial differentiation

There were significant differences in ancient tree species richness, abundance, average height, DBH, and crown width among the seven townships of Chongzuo. Among them, Pingxiang ranked first with 9,118 ancient trees (58.00% of the total), considerably more than other townships, which had 382 to 1,729 trees (Table 5). For species, Longzhou ranked first with 50 species (50.51%), followed by Ningming with 47 species (47.47%) (Table 5). Conversely, Tiandeng had the fewest trees (382 trees, 2.43%), but it was endowed with the tallest mean tree height at 23.32 m and the second widest mean crown width and the second

TABLE 3 The age, DBH and importance value (IV) of solitary tree species with only one individual each in Chongzuo, arranged in descending order of DBH.

Species	Family	Age	DBH (cm)	IV	Habitat	Conservation status	Origin
Garuga forrestii	Burseraceae	380	180.2	0.0138	B	good	wild
Ficus tinctoria	Moraceae	200	153.0	0.0122	H	good	wild
Tarennoidea wallichii	Rubiaceae	500	143.2	0.0116	C	good	wild
Acrocarpus fraxinifolius	Fabaceae	100	125.7	0.0106	B	good	wild
Falcataria moluccana	Fabaceae	150	124.1	0.0105	G	good	wild
Syzygium levinei	Myrtaceae	650	119.7	0.0102	H	good	wild
Ficus carica	Moraceae	125	108.6	0.0096	C	good	wild
Hubera cerasoides	Annonaceae	400	108.2	0.0096	A	good	wild
Canarium bengalense	Burseraceae	190	105.1	0.0094	A	good	wild
Sinosideroxylon pedunculatum	Sapotaceae	180	105.1	0.0094	E	good	wild
Keteleeria fortunei	Pinaceae	250	101.9	0.0092	E	good	wild
Michelia champaca	Magnoliaceae	200	101.9	0.0092	F	good	wild
Apodytes dimidiata	Icacinaceae	120	92.0	0.0086	A	good	wild
Cordia dichotoma	Boraginaceae	300	91.0	0.0085	H	good	wild
Castanopsis fissa	Fagaceae	260	89.1	0.0084	C	good	wild
Cinnamomum burmannii	Lauraceae	250	87.5	0.0083	E	good	wild
Ilex kaushue	Aquifoliaceae	315	80.2	0.0079	A	good	wild
Litsea glutinosa	Lauraceae	130	73.2	0.0075	F	good	wild
Broussonetia papyrifera	Moraceae	130	71.6	0.0074	E	good	wild
Toona sinensis	Meliaceae	129	68.7	0.0072	E	good	wild
Melia azedarach	Meliaceae	110	66.9	0.0071	H	good	wild
Aleurites moluccanus	Euphorbiaceae	120	66.8	0.0071	B	good	wild
Araucaria cunninghamii	Araucariaceae	100	63.0	0.0069	B	good	wild
Baccaurea motleyana	Euphorbiaceae	133	57.6	0.0066	B	good	wild
Schima superba	Theaceae	130	56.3	0.0065	A	good	wild
Radermachera glandulosa	Bignoniaceae	107	56.3	0.0065	B	good	wild
Osmanthus fragrans	Oleaceae	110	54.1	0.0064	F	good	wild
Camellia micrantha	Theaceae	102	25.3	0.0047	B	good	wild
Toona sinensis	Theaceae	113	17.5	0.0042	E	good	wild
Total		5984	2593.8	0.2451			
Average		206	89.4	0.0085			

widest DBH. For DBH and crown width, Jiangzhou had the largest average DBH and crown width (140.97 cm and 23.40 m, respectively). In comparison, Pingxiang had the smallest average DBH and crown width (27.53 cm and 6.20 m, respectively). Thus, Jiangzhou tended to accommodate older or larger, whereas Pingxiang had younger or smaller trees.

The species diversity index (*H*) of the seven townships ranged from 0.15 to 2.42, with an average of 1.75 (Table 5). Ningming had the highest diversity index (*H* = 2.42), indicating a more balanced species distribution. Tiandeng had a higher evenness index (E = 0.69), indicating a more equitable species representation. In comparison, Pingxiang had a lower diversity index (*H* = 0.15) and evenness (*E* = 0.04), indicating a tree population dominated by a small number of that a few species.

Ancient trees were unevenly distributed across habitat types in terms of tree abundance and species richness (Table 6). Mountains (E) accommodated the highest abundance (9,365 trees), followed by villages and farmlands (A) (3,029 trees). In contrast, more urbanized habitats such as residential (G) (17 trees) and business and commercial (D) (88 trees), had notably fewer trees. In terms of

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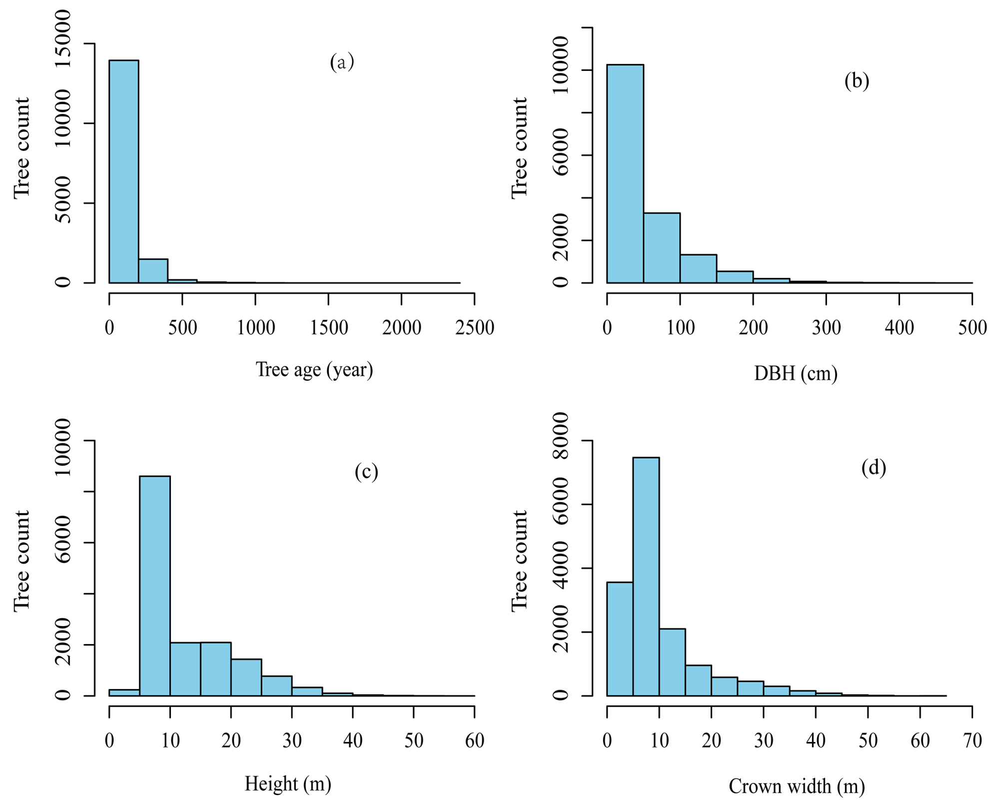

FIGURE 4
Distribution of ancient trees by: **(a)** tree age, **(b)** DBH, **(c)** height, and **(d)** crown width in Chongzuo.

species richness, parks, nature reserves, and scenic spots (B) exhibited the highest richness (47 species), followed by villages and farmlands (A) (45 species), underscoring the importance of more natural or less disturbed environments for biodiversity. In comparison, more urbanized habitats such as residential (C) (6 species) and business and commercial (D) (9 species) showed low species richness, constrained by space limitations and urban pressures. Overall, mountainous, rural, and green spaces offered more suitable habitats for the survival and conservation of more ancient trees with higher diversity in Chongzuo (Table 6).

Considering all age tiers, the highest concentrations of ancient trees were located in the southwestern (Pingxiang) and western (Longzhou) parts (Figure 6a). Trees are present in almost all cells, mainly with 1–73 trees each. This pattern was considerably dictated by and therefore similar to the distribution of the dominating tier-3 trees (Figure 6d). In comparison, tier-1 showed a notable concentration in the northwestern (Daxin), followed by western (Longzhou) and northwestern (Tiandeng), with 64, 31 and 30 individuals (deep red cells; Figure 6b). Only about half of the cells harbored tier-1 trees. Tier-2 trees showed a notable abundance also in the northwestern (Daxin) with 242 individuals, followed by eastern (Fusui) and western (Longzhou), with 67 and 66 individuals (deep red and orange cells; Figure 6c). For tier-3 trees, the highest concentration was found in the southwestern (Pingxiang) with 9,102 trees, followed by eastern (Fusui) and northwestern (Daxin), with 1,451 and 1,252 ancient trees (Figure 6d).

3.4 Distribution patterns by main factors

Redundancy analysis (RDA) identified the key socio-demographic and environmental factors influencing the distribution of ancient trees in Chongzuo (Figure 7). The results revealed that land area, built-up area, GDP, population density, and farmland area were positively correlated with species richness. In contrast, forest cover was negatively correlated with species richness; however, nature reserves, which are characterized by high forest coverage, exhibit high species richness. This pattern suggests that nature reserves differ from extensive natural forests in their capacity to sustain ancient tree diversity. Furthermore, the abundance of ancient trees was positively correlated with forest cover, and negatively correlated with the other factors (Figure 7).

As altitude increases, both tree abundance and species richness decline. Tree abundance decreased linearly, as described by the regression equation y=-3.36x+3600.43, with an R^2 value of 0.13, indicating a very strong correlation (Figure 8a). Similarly, species richness of ancient trees decreased with increasing altitude, following the regression equation y=-0.05x+55.68, with an R^2 value of 0.27, suggesting a strong correlation (Figure 8b).

TABLE 4 Indices denoting the frequency, age, dimensions and importance value (IV) of 31 ancient trees aged ≥1000 years in Chongzuo.

Species	Frequency	Mean tree age (year)	Mean tree height (m)	Mean DBH (cm)	Mean crown width (m)	IV
Excentrodendron tonkinense	21	1216	31.93	196.72	20.56	0.092
Ficus altissima	4	1201	30.40	269.65	41.53	0.022
Garcinia paucinervis	2	1000	35.60	105.50	19.70	0.009
Antiaris toxicaria	1	1000	33.00	245.00	32.00	0.005
Ficus racemosa	1	1000	16.00	365.00	15.50	0.004
Ficus virens	1	1000	22.00	324.80	22.00	0.004
Litchi chinensis	1	1000	18.00	239.00	29.00	0.005
Average	4	1060	26.70	249.38	25.76	0.020

4 Discussion

Ancient trees are keystone components of landscapes, and studying their diversity is critical for achieving long-term conservation (Hartel et al., 2018; Miklín et al., 2018; Xie et al., 2024). Our results showed that Chongzuo has abundant ancient tree resources distributed across the region (Table 2; Figures 2, 3). These resources are closely linked to the high plant diversity of Southwest China (López-Pujol et al., 2011). The diverse flora and associated ecosystem functions supported by this regional richness are key to ensuring the long-term survival and natural regeneration of ancient trees (Lindenmayer et al., 2012).

In addition to these biotic underpinnings, the complex terrain and suitable climate in Chongzuo are key factors sustaining the abundant ancient tree resources. The diverse landforms of the region, including karst landscapes, hills, and plains, create a distinct mosaic of varied habitats for ancient tree species with varying needs. The heterogeneous terrains, rich in microhabitats

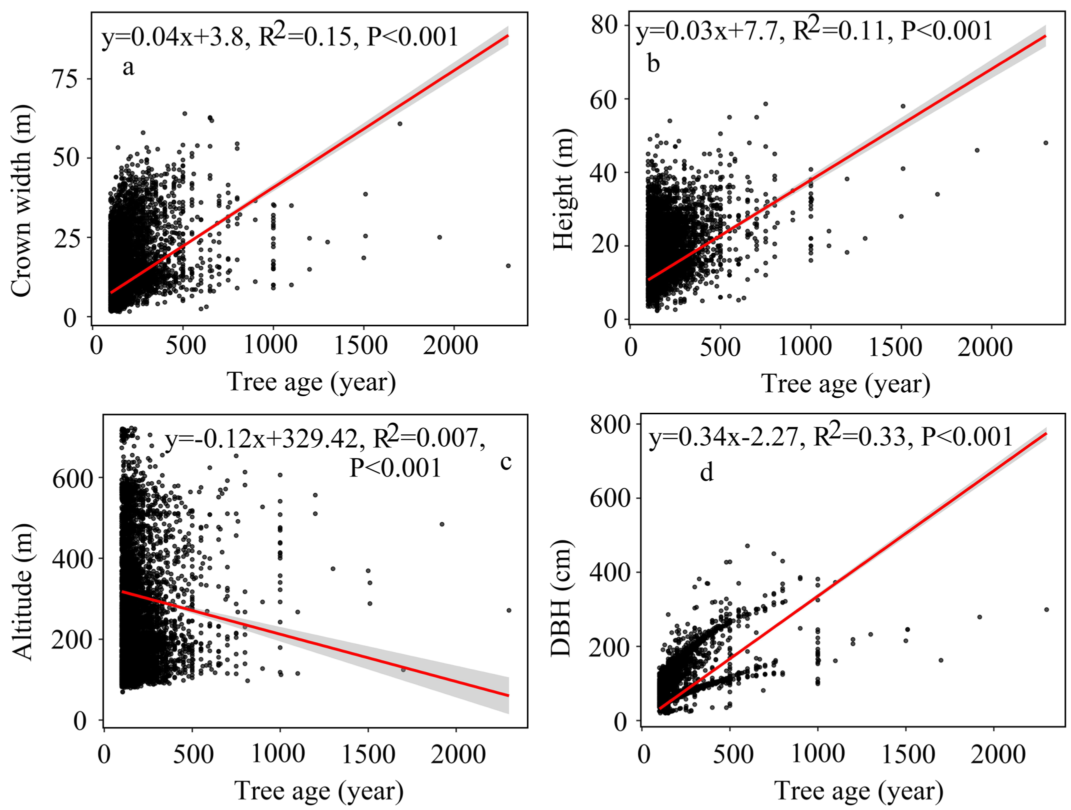

FIGURE 5
The correlations between age and **(a)** crown width, **(b)** height, **(c)** altitude, and **(d)** DBH. The black dots in the figure represent the original observed data, recording tree ages and their corresponding growth indicators.

TABLE 5 The frequency, dimensions and diversity of ancient trees in the seven townships in Chongzuo, arranged in descending order of tree abundance.

Township	Species richness	Tree abundance	Mean tree height (m)	Mean DBH (cm)	Mean crown width (m)	Shannon diversity index (H)	Evenness index (E)
Pingxiang	30	9,118	7.96	27.53	6.20	0.15	0.04
Longzhou	50	1,729	21.23	72.90	11.31	2.01	0.51
Daxin	36	1,558	18.65	92.34	15.36	1.50	0.42
Fuisui	25	1,529	15.21	81.15	14.57	1.81	0.56
Ningming	47	1,006	21.42	99.88	17.56	2.42	0.63
Jiangzhou	22	400	20.23	140.97	23.40	2.08	0.67
Tiandeng	28	382	23.32	124.72	18.73	2.31	0.69
Total	238	15,722	128.02	639.49	107.13	12.28	3.52
Average	34	2,246	18.29	91.36	15.30	1.75	0.50

with varying elevation, slope gradient, soil thickness and quality, plant-available water, and microclimate allow diverse plant species to selectively utilize the assorted sites (Guo et al., 2013). The natural setting provides a complex collection of relatively small and isolated habitat silos, allowing for independent evolutionary development and the accumulation of species endowment. The inherently high beta landscape diversity offers the precursor for high floristic beta diversity. This spatial multiplicity of habitats underpins evolutionary processes among vegetation species, which in turn supports diverse forest community structures and rich ancient tree species compositions (Du et al., 2017).

Moreover, the rugged karst topography, notoriously difficult to navigate, serves as a natural physical barrier to reduce the anthropogenic pressures of agricultural and urban expansion, thereby fostering *in situ* conservation of ancient tree populations (Guo et al., 2017). Having adapted to these harsh karst conditions over time, a proportion of Chongzuo's ancient trees reveals not only the uniqueness of their habitat but also the profound interplay between natural selection and ecological adaptation. Furthermore, the subtropical humid monsoon climate in the region provides ample sunshine and rainfall throughout the year, fostering a favorable environment that enhances the vitality and resilience of ancient trees in conjunction with the broader biotic community (Woodruff, 2010; Wang et al., 2020).

Beyond nature's inheritance, folk cultures and religious beliefs play a crucial role in maintaining ancient trees in pristine condition (Huang et al., 2020; Yan, 2023). The mountainous border region is predominantly inhabited by ethnic minorities, including the Zhuang, Yao, and Miao peoples, who have preserved traditions of nature worship and spiritual reverence toward ancient trees. For instance, species such as *F. altissima*, *Liquidambar formosana*, and *Pistacia chinensis* are venerated as sacred trees. Residents conduct ritual observances on specific dates, praying to these trees for divine protection and blessing. Through cultural preservation and intergenerational transmission, these traditions have been institutionalized as binding village regulations and customary agreements (Huang et al., 2025), ensuring effective conservation of ancient trees.

There are significant differences in the number of ancient trees among different families and genera, with 54 plant species belonging to single families and genera, exhibiting relatively small populations (Table 2; Figure 3). In contrast, a small number of species is strongly represented. This pattern indicates that Chongzuo maintains high species richness in ancient tree resources. However, the population is dominated by a small cohort of common species, accompanied by a large number of uncommon to rare and solitary species. Other studies confirm that when plant communities contain many taxa from a single genus, this composition generates distinctive diversity patterns within regional vegetation (Huang et al., 2025).

Several biotic and anthropogenic factors may explain these observed disparities in tree abundance. Species that occur in greater numbers are generally well-adapted to the local climate and have been culturally valued, which has facilitated their preferential as ancient trees. Moreover, most of these abundant

TABLE 6 Tree abundance and species richness of ancient trees in nine habitats in Chongzuo.

Habitat type	Tree abundance	Species richness
Villages and farmlands (A)	3,029	45
Parks, nature reserves, and scenic spots (B)	1,743	47
C Roadsides (C)	799	32
Business and commercial (D)	88	9
E Mountains (E)	9,365	32
Government and institutional (F)	170	24
G Residential (G)	17	6
Religious and cemeteries (H)	504	35
Others (I)	7	3
Total	15,722	99
Average	1,747	11

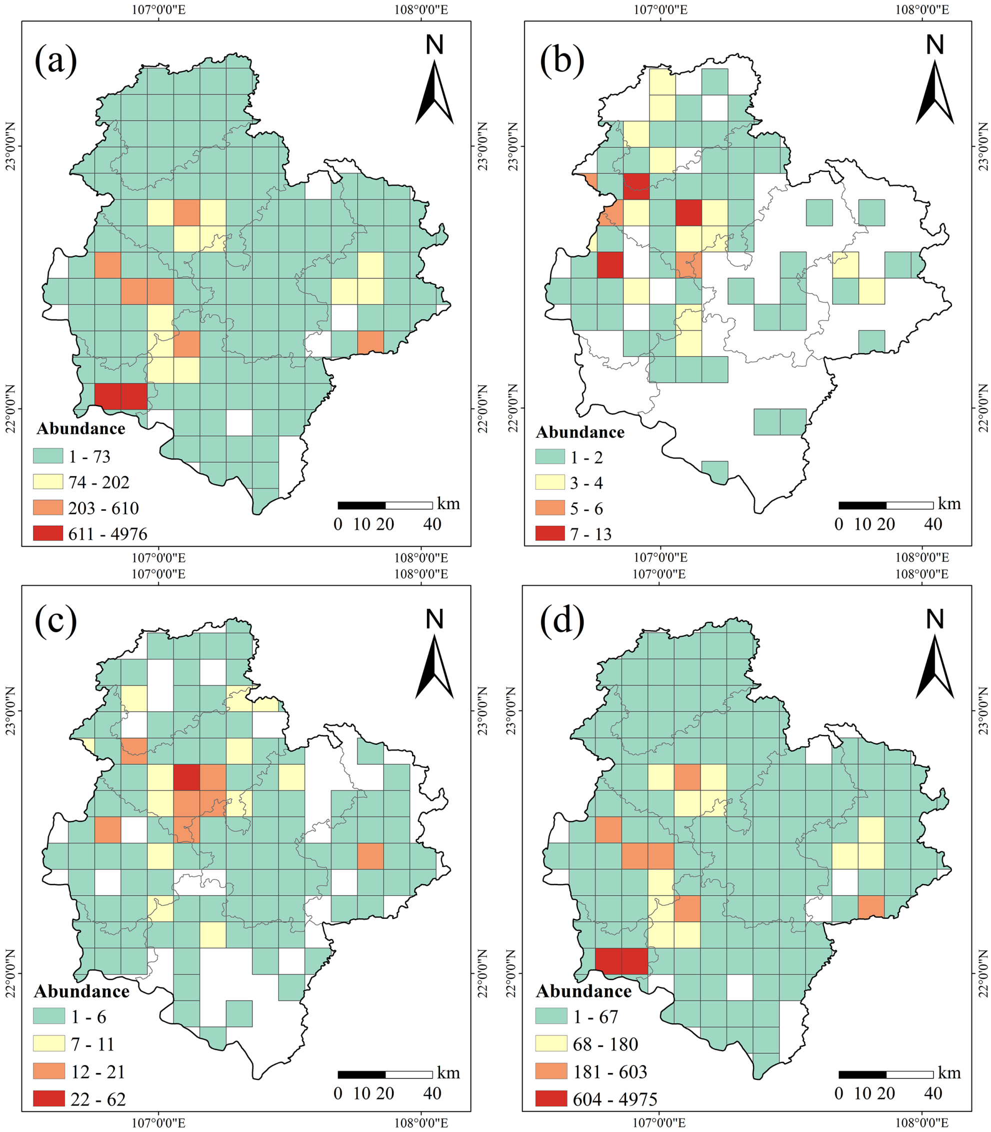

FIGURE 6
Ancient tree abundance in Chongzuo mapped in 10 km×10 km grid cells: **(a)** all trees, **(b)** tier-1 trees, **(c)** tier-2 trees, and **(d)** tier-3 trees. Blank cells indicate the absence of ancient trees.

species are long-lived trees. In contrast, shrubs and other short-lived woody plants are less likely to reach ancient status due to biological constraints, resulting in fewer preserved individuals (Yang et al., 2024).

Ancient trees embrace natural and cultural qualities, making them a unique biological group (Nolan et al., 2021; Fröhlich et al., 2024). The number of ancient trees decreased considerably with increasing tree age, height, DBH, and crown width (Figures 4, 5); this pattern is reflected by the fact that 95.33% of individuals belong to the tier-3 age group (Figure 4) and is likely driven by a combination of environmental and physiological factors. The terrain of Chongzuo is predominantly characterized by karst landforms, which give rise to a distinctive habitat marked by fragmented terrain, sparsely and unevenly distributed soils, a weak water retention capacity, and a low threshold for resisting external disturbance (Liu et al., 2021; Hu et al., 2023). Such chronic stresses inherently limit the growth and sustainability of ancient species. Concurrently, tree aging leads to physiological senescence, reducing stress resistance and increasing susceptibility to pathogens and natural disasters, thereby shortening their lifespans (Wang et al., 2020; Clark et al., 2019).

Furthermore, climate change-induced high frequency of extreme climate events, such as prolonged droughts, heavy rainfall, and sudden temperature fluctuations, which in turn alters the spatial distribution and size of ancient tree populations (Lindenmayer et al., 2012). These changes pose a severe threat to fragmented karst habitats, as their lack of adequate ecological buffers to mitigate the impacts of extreme events, the adaptive capacity and migratory potential of ancient trees in response to climate change.

The composition of ancient trees is not only constrained by natural environmental factors, but also influenced by complex

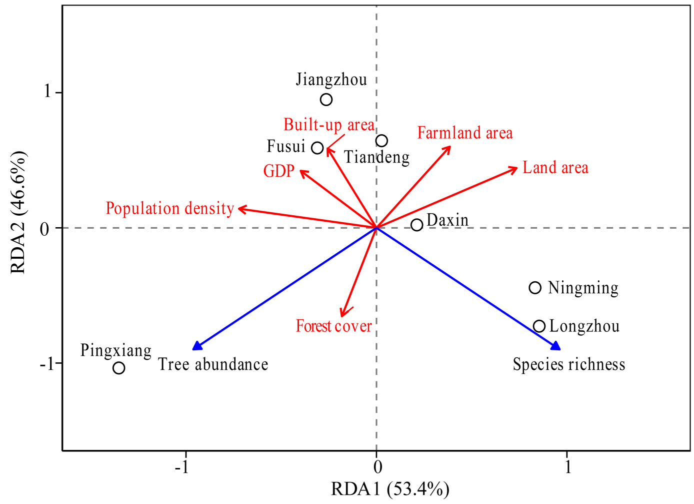

FIGURE 7
Redundancy analysis (RDA) ordination illustrating the relationship between the species richness and tree abundance of ancient trees and environmental factors in Chongzuo. Blue arrowheads represent the dependent variables (species richness and tree abundance), while red arrowheads denote the independent variables (environmental factors). The angle between the arrows indicates the nature of the correlation: an acute angle denotes positive correlation, an obtuse angle denotes a negative correlation, and a right angle denotes no correlation. The small circles represent the townships of Chongzuo.

human activities and ethnic customs (Orłowski and Nowak, 2007). Our results indicate that the ancient trees in Chongzuo are dominated by *C. drupifera, D. longan, E. tonkinense*, and *F. altissima*, with trees counts exceeding 1000 each (Table 2; Table 4). *C. drupifera* dominates Chongzuo ancient tree populations due to its environmental adaptability and economic value. This species is primarily distributed in clusters and exhibits high ecological resilience. With a have high fat concentration, the seeds are extracted for use in cooking oil, chemical, food processing, and livestock feed industries (Zhang, 2008). This widespread use has led to extensive cultivation by local villagers. Furthermore, this nutrient-rich fruit will also be transported and stored by rodents after maturity, which will to some extent increase its distribution area (Xiao et al., 2015).

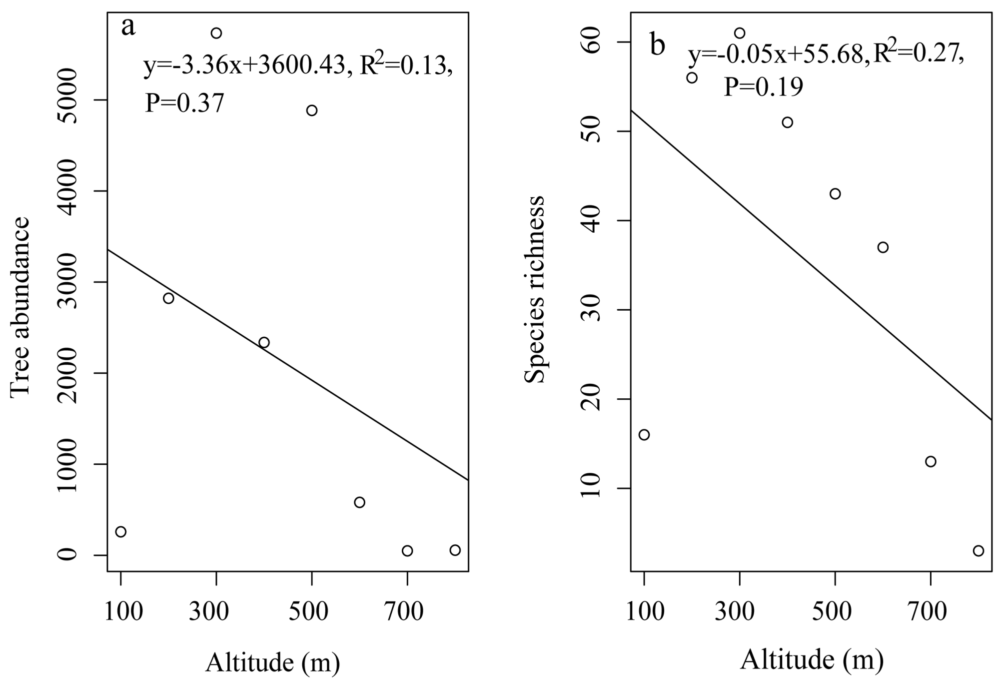

FIGURE 8
Vertical distribution patterns of the ancient trees in Chongzuo in relation to: **(a)** tree abundance, and **(b)** species richness.

D. longan, as an edible fruit and traditional Chinese medicine, has a planting history of over 2000 years in China (Zhang et al., 2020). Longan pulp is rich in nutritional phytochemicals, including protein, carbohydrates, vitamin C, and polysaccharides, as well as polyphenols, which exhibit multiple biological activities such as antioxidant, immunomodulatory, and antitumor effects (Yang et al., 2011), making it a widely planted fruit tree in Chongzuo City.

E. tonkinense ranks third in abundance among ancient tree species in Chongzuo, a position attributable to its distinctive ecological traits. As a key constructive species in karst seasonal rainforests, it is recognized alongside *Erythrophleum fordii* and *Garcinia paucinervis* as the three important hardwood timber trees of Guangxi. The timber demonstrates significant economic value, particularly in crafting durable butcher blocks and furniture, driving its widespread cultivation (Xiang et al., 2013). Additionally, its small seeds possess membranous wings adapted for wind dispersal, enabling them to colonize germination-suitable microhabitats. This dispersal strategy helps to reduce mortality from high-density constraints around parent trees while expanding the species' spatial distribution and population size.

There are significant spatial variations in the species richness and abundance of ancient tree resources across Chongzuo City, with Pingxiang possessing the highest species richness and abundance (Table 5; Figure 6). This is attributed to the presence of 8,937 ancient *C. drupifera* specimens within its territory gives Pingxiang an absolute quantitative advantage in ancient tree abundance, and this can be explained by the extensive cultivation history of this economic crop. Longzhou hosts the second-highest species richness and abundance of ancient trees in Chongzuo City (Table 5; Figure 6). This is partly attributable to the Guangxi Nonggang National Nature Reserve within its territory, which contains one of the world's rarest, most structurally intact, and most representative northern tropical karst seasonal rainforests, and ranks as one of China's 14 key biodiversity hotspots areas (Hu et al., 2023), which collectively explain the township's exceptionally high biodiversity.

Jiangzhou and Tiandeng exhibit the lowest abundance of ancient trees in Chongzuo City (Table 5; Figure 6), a pattern attributable to interconnected factors including geomorphology, ecological conditions, land utilization patterns, and socioeconomic development. In Jiangzhou, karst features dominate the western sector, western sector while hills and small plains characterize the eastern and central regions. However, farmland has converted a significant portion of the natural vegetation, with sugarcane cultivation dominating the landscape (Wang et al., 2025). Moreover, as Chongzuo's sole urban core, the township experiences accelerated urbanization. These combined pressures leave limited space or opportunity for preserving ancient trees. Tiandeng's landscape is characterized by typical karst topography, with rocky surfaces covering 71% of its total area. The region is also facing severe rocky desertification, a process in which vegetation cover and fertile soil are lost, leaving behind barren, rocky surfaces (Guo et al., 2022). This landscape degradation severely damages the growth ability of trees and limits the population of ancient trees.

Among the nine tree habitats in Chongzuo, mountain (E), villages and farmlands (A), and parks, nature reserves, and scenic spots (B) had the highest numbers and species of ancient trees (Table 6). Especially the number of ancient trees in mountain (E) accounts for 59.57% of the total, indicating the crucial role of natural forest ecosystems in nurturing and protecting ancient trees. Mountains provide trees with more open, large, and natural conditions, which can allow ancient trees to flourish with enough room and a less stressful environment (Du et al., 2017). In addition, compared with the other seven habitats, ancient trees in business and commercial (D) and residential (G) habitats had a lower proportion of numbers and species (Table 6). This constraint may be related to their surfaces extensively sealed by buildings, roads and other paved areas, limited plantable space, confined greenery sites, and strong human disturbance.

Our analysis revealed distinct correlations between socio-environmental factors and ancient tree species richness (Figure 7). A positive correlation was observed with land area, built-up area, GDP, population density, and farmland area. This relationship can be attributed to the selective preservation of diverse species driven by cultural and economic development activities (Mahmouda et al., 2015). They include the preservation of natural habitats or the creation of artificial habitats that provide suitable ecological niches (Beninde et al., 2015), as well as moderate disturbance that suppresses competitive dominance (Cannon et al., 2022), all of which can collectively promote species richness.

In contrast, forest coverage was negatively correlated with species richness. This pattern arises primarily in areas with high forest coverage, where habitats are predominantly composed of a few dominant species (Mori et al., 2017). Additionally, minimal human disturbance in these regions does not furnish the conditions or generate the need for introducing diverse ancient tree species (Hou et al., 2022). Meanwhile, natural ecological succession tends to allow a limited number of dominant species to progressively monopolize resources (Jucker et al., 2014), thereby suppressing and even displacing other ancient tree species and ultimately reducing overall species richness.

The abundance of ancient trees shows a positive correlation with forest coverage (Figure 7), which is attributable to the stable and undisturbed habitats provided by densely forested areas that support the completion of their full life cycle (Lindenmayer et al., 2012). Conversely, the negative correlation with land area, built-up area, GDP, population density, and farmland area (Figure 7) is due to the associated intensive human activities. Through direct clearing, land development, habitat destruction, and environmental pollution, these human actions systematically threaten the survival and persistence of ancient trees (Grimm et al., 2008).

Altitude can bring considerable climatic changes that affect plant growth, development, and metabolism, thereby shaping the growth of ancient trees (Pinto-Junior et al., 2020; Vetaas and Grytnes, 2002). Our results showed that elevation negatively correlated with the species richness and abundance of ancient trees (Figures 8a, b), indicating that high altitude significantly limits their distribution.

In Chongzuo, habitat heterogeneity intensifies with altitude, characterized by stronger sunlight, reduced soil moisture, thinner soil layers, stronger wind, and increased rock exposure, thereby constraining the adaptability of ancient trees (Chen et al., 2015). The shifts in distribution, structure and species diversity of ancient trees from low to high elevations reflect their adaptation to progressively drier and harsher conditions, highlighting their capacity to exploit karst microhabitats and optimize survival strategies under environmental stress (Wang et al., 2025).

Our results reveal that ancient trees in Chongzuo are characterized by high species richness yet uneven population distribution, featuring the coexistence of numerous rare and solitary species alongside a small cohort of dominant species. Furthermore, their survival and regeneration are closely intertwined with regional environmental factors (e.g., karst terrain, climate conditions) and socioeconomic activities (e.g., human disturbance, cultural preservation practices), which jointly shape their current distribution patterns and population dynamics. Consequently, targeted spatial planning and the integration of habitat and socioeconomic considerations are imperative for formulating effective conservation strategies to ensure their long-term survival (Lindenmayer and Laurance, 2017).

To more effectively conserve ancient tree resources, we propose the following targeted and differentiated protection measures: implement special conservation initiatives for national key protected species and solitary tree species, including formulating exclusive conservation plans and establishing germplasm banks to enhance their long-term survival capacity; strengthen systematic maintenance and rejuvenation of middle-aged ancient trees while maintaining the ecological balance of dominant tree populations (Pan et al., 2025); adopt differentiated regional conservation strategies, designate key areas as core reserves, and construct ecological corridors to connect fragmented habitats; meanwhile, optimize urban and agricultural planning to mitigate the disturbances of human activities and environmental pressures on ancient tree habitats (Gilhen-Baker et al., 2022). In addition, a comprehensive dynamic monitoring system should be established to track the real-time growth status of ancient trees, providing scientific support for adaptive conservation management and thus facilitating the harmonious coexistence of human development and natural heritage.

5 Conclusion

Our results showed that Chongzuo City support an abundance of ancient tree resources, yet exhibits significant spatial variations in species composition and tree abundance. This spatial heterogeneity stems from the combined effects of natural and anthropogenic factors. Future investigations could integrate habitat, soil, climate, land use, and local cultures to explore the spatial distribution patterns of ancient trees across macro- and micro-scales. Such a multiscale analysis will enable identification of conservation hotspots and inform targeted protection strategies based on comprehensive assessments of tree health status and local geomorphological characteristics.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

LW: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. GW: Formal analysis, Investigation, Methodology, Writing – original draft. XL: Formal analysis, Investigation, Methodology, Writing – original draft. HZ: Formal analysis, Investigation, Methodology, Writing – original draft. JY: Formal analysis, Investigation, Methodology, Writing – original draft. LP: Supervision, Writing – review & editing. CJ: Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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