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Distribution Patterns and Maintenance Mechanisms of Ancient Trees in Traditional Villages and Their Surroundings in Hebei Province, China

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ABSTRACT

Aim: To understand the drivers shaping biodiversity in long-inhabited anthropogenic landscapes, this study investigates how environmental filtering and cultural pressures jointly determine the species diversity and spatial distribution of ancient trees surrounding traditional villages.

Location: Focusing on 276 traditional villages in Hebei Province, North China, we aim to elucidate a dual maintenance mechanism that explains the persistence of this unique arboreal heritage.

Method: We employed a multi-scalar approach, integrating GIS-based spatial pattern analysis with a Bayesian structural equation model (SEM) to test hypothesised causal pathways influencing ancient-tree attributes (species diversity, density, age and diameter at breast height).

Results: A total of 2514 ancient trees were documented, representing 82 species, with *Styphnolobium japonicum*, *Platycladus orientalis* and *Pinus tabuliformis* comprising over 60% of individuals. The overall age structure is predominated by younger, tier-1 trees (100–299 years). Spatially, both villages and their ancient trees exhibit a significantly clustered distribution ($R < 1$), with hotspots concentrated along the eastern foothills of the Taihang Mountains. The Bayesian SEM revealed that both natural and anthropogenic gradients slightly reduced species diversity ($\beta = -0.05$). The model also identified the anthropogenic gradient as a strong, direct negative driver of tree density ($\beta = -0.33$), while species diversity, in turn, markedly enhanced density ($\beta = 0.50$).

Main Conclusions: We conclude that the diversity and distribution of ancient trees are governed by a critical dual mechanism: while broad anthropogenic pressures and environmental filters can limit species richness, cultural practices embedded within villages create conservation 'refuges' for relict populations. The positive effect of diversity on density underscores its functional importance. Therefore, conservation strategies must evolve from preserving individual trees to enhancing the species diversity of the entire cultural landscape to bolster long-term resilience.

1 | Introduction

Ancient trees, as invaluable ecological resources and cultural heritage, play a pivotal role in biodiversity conservation, the maintenance of ecosystem services, and the preservation of cultural memory (Blicharska and Mikusiński 2014; Lindenmayer 2017; Lindenmayer and Laurance 2017). In China's traditional villages and their surrounding areas,

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communities of ancient trees not only embody profound regional cultural connotations but also serve as critical ecological indicators for assessing long-term human–nature interactions. However, escalating global climate change and intensified anthropogenic activities are subjecting these communities to habitat fragmentation, isolation, and even disappearance (Lindenmayer et al. 2012; Locosselli et al. 2020). Consequently, accurately quantifying their spatial distribution patterns, elucidating the mechanisms underlying their formation, and identifying key driving factors are essential for both the conservation of ancient trees and the safeguarding of the cultural heritage embedded within China's traditional villages.

China's long history and rich biodiversity have fostered a vast assemblage of ancient trees (Huang, Jin, et al. 2020). These trees, together with remnant patches of natural forest, act not only as ecological buffers safeguarding human settlements but also as foundations for regional cultural identity and customs (Huang et al. 2021). At both global and regional scales, ancient-tree communities exhibit highly uneven spatial patterns (Huang, Jin, et al. 2020; Liu et al. 2022), reflecting the interplay of suitable habitats, conservation measures and village cultural traditions. Unlike ancient trees in purely natural settings, those within human-dominated landscapes are strongly modulated by anthropogenic activities (Liu, Lindenmayer, et al. 2019). Although destructive practices such as agricultural expansion and logging jeopardise tree survival (Lindenmayer and Laurance 2016), humans also actively protect certain species, enabling dense and taxonomically diverse ancient-tree assemblages to persist in settled areas despite long-term disturbance (Huang, Jin, et al. 2020). For instance, the plant community structure of modern Amazonian forests is deeply influenced by pre-Columbian human activities; the significant enrichment of domesticated tree species around ancient archaeological sites reveals the persistent shaping effect of plant domestication on forest composition (Levis et al. 2017). Similarly, in 11 key cities of the Yangtze River Basin, most ancient trees possess medicinal or timber value, underscoring a history of human selection (Jin et al. 2020). Beyond utilitarian value, many ancient trees in human settlements are deeply rooted in cultural beliefs (Huang, Tian, et al. 2020). For instance, in traditional villages of southern and southwestern China, numerous trees are preserved as 'fengshui trees' or 'fengshui forests' and subsequently attain great age (Huang, Tian, et al. 2020; Zhou et al. 2022). On the Indian subcontinent, *Ficus religiosa* is revered as sacred in Buddhism and thus receives special protection (Haberman 2013); similarly, *Ficus microcarpa*, *Azadirachta indica* and *Cedrus deodara* are conserved owing to local spiritual traditions (Anthwal et al. 2010). As integral components of natural ecosystems, the distribution of ancient trees near settlements is influenced not only by human disturbance but also by environmental factors such as climate and topography. Scattered ancient trees are positively associated with population density and mean annual precipitation, whereas clustered ancient trees are negatively associated with population density and the proportion of rural inhabitants (Liu, Lindenmayer, et al. 2019). In eastern China, *Ginkgo biloba* ancient trees occur predominantly in densely populated areas, with survival contingent on climate and soil conditions, and with tree density positively correlated with the intensity of human activity (Chi et al. 2020). At the regional scale, ancient trees in the ethnic minority settlements of China's southwestern mountains are mainly situated on slope landforms, and their distribution closely overlaps village locations (Huang, Tian, et al. 2020). Overall, species characterised by greater potential height, smaller leaves and diverse human uses have the highest likelihood of long-term persistence and of becoming ancient trees (Huang et al. 2023).

Located in the northern sector of the North China Plain, Hebei Province is one of the cradles of Chinese civilisation and a pivotal region in the formation of China's multi-ethnic cultural mosaic. Owing to its unique geographical setting and long settlement history, numerous well-preserved traditional villages have developed at the junction of the Taihang Mountain eastern foothills and the North China Plain, where extensive assemblages of ancient trees persist (Huang et al. 2023). These trees function simultaneously as 'living fossils' documenting natural and human history and as integral elements of the cultural landscape that embody traditional Chinese ecological wisdom. Nevertheless, systematic and quantitative investigations into the regional-scale spatial distribution patterns of ancient trees around traditional villages, and the mechanisms shaping those patterns, remain scarce. To address this gap, this study examines ancient trees within a 5 km buffer of 276 traditional villages across Hebei Province, integrating Geographic Information Systems with multivariate statistical analyses to elucidate their spatial configurations, formation mechanisms, and driving factors. Specifically, we aim to resolve three key questions: (1) What are the fundamental characteristics of ancient-tree resources in Hebei's traditional villages? (2) How are traditional villages and their associated ancient trees spatially distributed? (3) Which mechanisms and critical factors govern the observed spatial patterns of ancient trees? The findings will provide a robust scientific basis and decision support for the conservation and management of ancient trees in Hebei and the broader North China region.

2 | Materials and Methods

2.1 | Study Area

Hebei Province, situated in North China between 36°05′–42°40′ N and 113°27′–119°50′ E, spans more than 700 km from south to north and covers approximately 188,800 km^2 (Figure 1). Bordered by the Bohai Sea and Liaoning Province to the east, flanked by the imposing Taihang Mountains adjacent to Shanxi Province to the west, contiguous with Shandong and Henan provinces to the south, and abutting the Inner Mongolia Autonomous Region to the north, Hebei exhibits a topographic gradient that descends from the high northwest to the low southeast. Remarkably, it is the only Chinese province that simultaneously encompasses seven major landform types—plains, hills, mountains, grasslands, plateaus, lakes and coastlines—attesting to its geomorphological complexity (Zhang, Peng, and Shang 2024). Such environmental diversity has fostered a rich tapestry of regional cultures, while natural barriers created by mountains, plains and marine zones have reinforced their relative independence. Consequently, Hebei's cultural landscape integrates agrarian traditions on the plains,

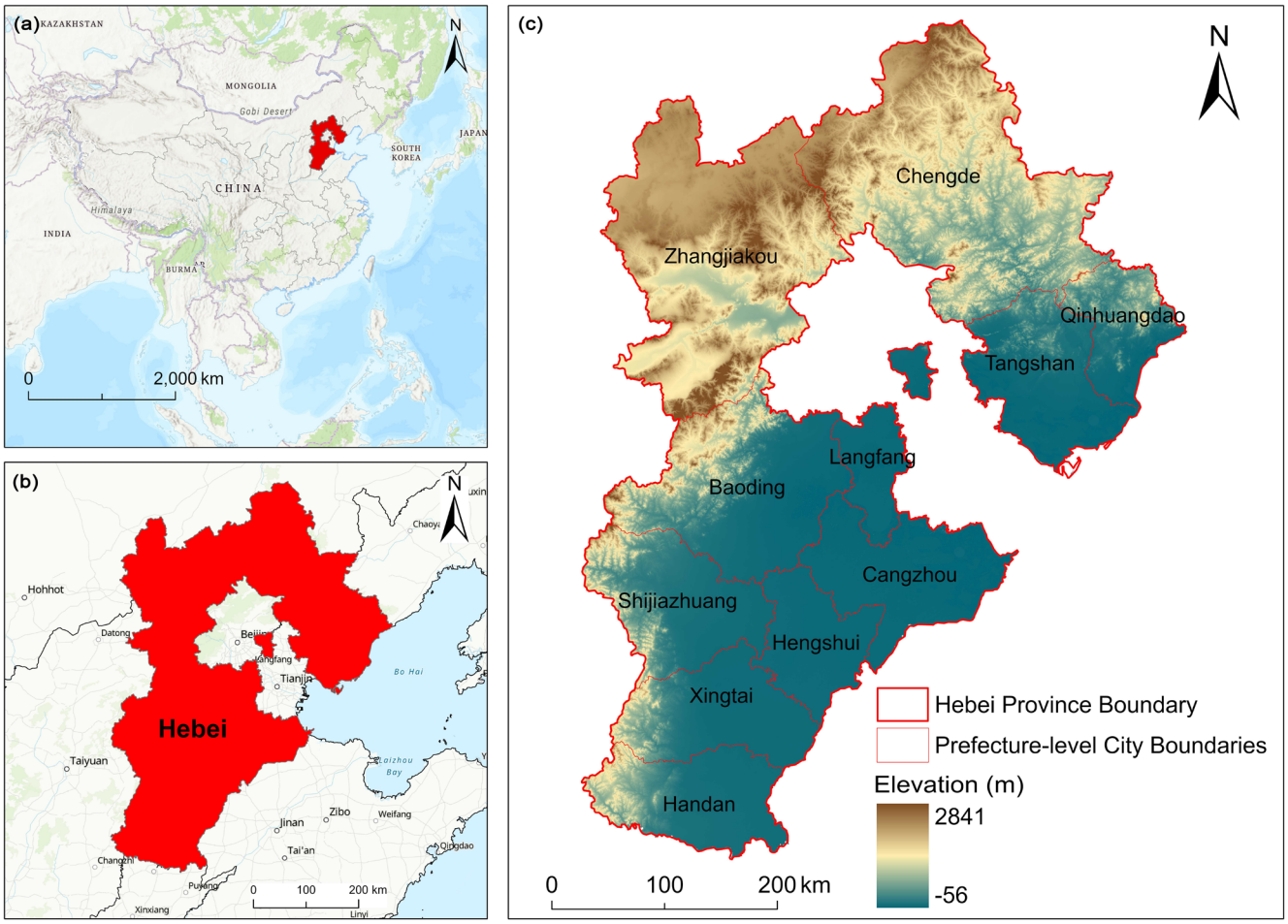


FIGURE 1 | Study area in Hebei Province, China. (a) Location of Hebei within East Asia; (b) Location of Hebei within northern China and (c) Topography of Hebei Province.

frontier culture in the northern basins, nomadic heritage across the highland grasslands and distinctive mountain culture in the Taihang range, collectively distinguishing the province from its counterparts (Yuan et al. 2014).

2.2 | Data Sources

Chinese traditional villages, the modern extension of the 'ancient village' concept, are generally defined as settlements established before the Republic of China era that have endured to the present day while retaining well-preserved historical layouts, architectural styles, folk customs and other traditional assets (Hu et al. 2014). As tangible legacies of the country's agrarian civilisation, these villages embody abundant historical information and distinctive cultural landscapes (Zhu et al. 2025). Since the launch of the National List of Chinese Traditional Villages in December 2012, a total of 276 villages in Hebei Province have been designated, ranking the province second in North China. In this study, we focused on all 276 villages, retrieving and validating their central coordinates via the Baidu Map API and determining their founding ages from archival records and local gazetteers. Given that rapid urbanisation, the New Countryside initiative, and rural–urban integration policies are continuously restructuring village spatial patterns (Zhang et al. 2022), we did not delineate administrative or cadastral boundaries. Instead, a 5-km radius buffer centred on each village was adopted to approximate the area influenced by the settlement's historical and environmental interactions (DeFries et al. 2022; Li 2022).

According to the *Technical Specifications for the Census of Ancient and Famous Trees*, an 'ancient tree' is defined as an individual that has persisted for more than 100 years; trees aged 100–299, 300–499, and ≥500 years are classified as Grade III, II and I, respectively. Since 2016, the forestry and landscaping authorities of Hebei Province have conducted a comprehensive inventory of such trees, systematically documenting their taxonomic identity, precise location, growth status, site conditions and estimated age. To ensure age accuracy, investigators employed a suite of complementary techniques—including historical literature tracing, ring-width/diameter regression, increment borer sampling, dendrochronological cross-dating, CT scanning and ^{14}C radiocarbon dating—resorting to interview-based estimates only when these methods proved infeasible. Consequently, the recorded ages can be regarded as robust. In October 2024, we downloaded the most recent census dataset from Hebei's Ancient and Famous Tree Information System (http://lycy.hebei.gov.cn/gsmm/search.html). After rigorous validation—removing entries with erroneous coordinates, dead individuals, incomplete information or logical inconsistencies—we retained 10,948 valid specimens. Latin binomials were subsequently verified and standardised against the online

Flora Reipublicae Popularis Sinicae (https://www.iplant.cn/frps). Finally, by applying a 5-km buffer around the centres of 276 traditional villages, we identified 2514 ancient trees that satisfied our research criteria and formed the basis for subsequent analyses.

2.3 | Traditional Villages and Their Surrounding Ancient Trees: Baseline Characteristics and Spatial Distribution Patterns

2.3.1 | Descriptive Statistics of Traditional Villages and Ancient-Tree Resources

At the species level, we first compiled baseline metrics for ancient trees surrounding traditional villages and then quantified the ecological prominence of each taxon using the importance value (IV). IV integrates relative abundance (RA) and relative dominance (RD) and is calculated as IV = (RA + RD)/2, where RA is the proportion of individuals of a given species relative to the total number of ancient trees in the study area, and RD is the proportion of the cumulative basal area at breast height contributed by that species to the total basal area of all ancient trees (Jim and Zhang 2013).

2.3.2 | Kernel Density Estimation

At the spatial scale, we performed kernel density (KD) analysis on both traditional-village locations and ancient-tree points, using a bandwidth of 10 km to evaluate their overall clustering intensity and hotspot distribution. Kernel density estimation is an approach that interpolates discrete point features into a continuous surface by applying a smoothing function to each point, thereby quantifying the probability density of occurrences per unit area and revealing spatial aggregation patterns and gradient changes across the study region (Silverman 1986):

$$D = \frac{1}{nh} \sum_{i=1}^{n} k \frac{(x - x_i)}{h}$$

where D is the kernel density, k is the Gaussian kernel function, $(x - x_i)$ is the distance from the estimated point x to the event point x_i, h is the bandwidth and n is the number of traditional villages or ancient trees.

2.3.3 | Nearest Neighbour Index

The nearest neighbour index (NNI) quantifies the spatial arrangement of point-based geographic features by comparing the observed mean nearest-neighbour distance with the theoretical expectation under complete spatial randomness within the same area. It is calculated as follows:

$$R = \frac{1}{N} \sum_{i=1}^{N} d_i \times 2\sqrt{\lambda}$$

In the equation, N denotes the total number of point features within the study area, d_i is the distance from feature i to its nearest neighbour, and λ represents feature density, calculated as the number of points per unit area. When $R = 1$, the distribution approximates randomness; $R > 1$ indicates a uniform (dispersed or regular) pattern, whereas $R < 1$ signifies a clustered distribution.

2.3.4 | Centre of Gravity Model

To further characterise the overall shift and dispersion of traditional villages and ancient trees, all point features were projected onto a 10 km × 10 km regular grid, after which a Standard Deviational Ellipse analysis was performed. We then applied a Centre of Gravity (CG) model to quantify the spatial centroid and its trajectory. The CG is typically expressed in geographic coordinates (Zhang et al. 2012), and in this study it is defined as follows:

where $\bar{x}$ and $\bar{y}$ are the longitude and latitude corresponding to

$$\bar{x} = \frac{\sum_{i=1}^{n} x_i \times m_i}{\sum_{i=1}^{n} m_i}, \bar{y} = \frac{\sum_{i=1}^{n} y_i \times m_i}{\sum_{i=1}^{n} m_i}$$

the centre of gravity; m_i is the attribute value of the grid number i; n is the total number of grids in the study area; x_i and y_i correspond to the longitude and latitude of the geometric centre of the ith grid, respectively.

2.4 | Explanatory Variables

To capture both biophysical and socio-economic influences, the explanatory variables were drawn from two domains. (i) Natural-environment factors comprised: geographic-topographic attributes—longitude, latitude, elevation and slope; soil physicochemical properties—cation-exchange capacity (CEC), pH and bulk density; and 12 climate descriptors—cloud cover (cld), diurnal temperature range (dtr), frost-day frequency (frs), potential evapotranspiration (pet), precipitation (pre), daily minimum temperature (tmn), mean temperature (tmp), maximum temperature (tmx), vapour pressure (vap), wetness index (wet), global aridity index (AI) and reference evapotranspiration (ET_0) calculated via the penman–monteith equation. These datasets were obtained from the Harmonised World Soil Database (FAO IIASA 2023), the Climatic Research Unit Time-Series v4.06 (Harris and Jones 2017) and the Global Aridity Index & Potential Evapotranspiration database v2 (Zomer et al. 2022). (ii) In the anthropogenic domain, nine variables were used to characterise human influence. Five indicators capture development intensity: regional GDP (Kummu et al. 2025), population density (Lebakula et al. 2024), road density (Zhang, Yin, et al. 2024), the human footprint Index (Mu et al. 2022) and distance to the nearest city centre (Tianditu, www.tianditu.gov.cn). Four indicators represent cultural heritage: village founding age, number of protected cultural-relic units (Ye et al. 2024), number of religious establishments and number of intangible cultural-heritage items (China Intangible Cultural Heritage Digital Museum, www.ihchina.cn).

2.5 | Response Variables

To characterise the structural and functional attributes of ancient-tree communities within each 5-km village buffer, we calculated the mean tree age, stand density and diameter at breast height (DBH) for every village. Species-diversity metrics were subsequently derived with the *vegan* package (v2.6–2) in R v4.5.0 (Oksanen et al. 2022), focusing on the Margalef richness index, $D = (S-1)/\ln N$, where S is the number of species and N is the total number of ancient trees in the buffer. These variables served as the response set for subsequent modelling, enabling us to elucidate spatial variation in community structure, function and diversity.

2.6 | Structural Equation Model

To elucidate the combined influence of natural and anthropogenic factors on ancient-tree communities surrounding traditional villages, we developed a Bayesian structural equation model (SEM) in R v4.5.0 using the *brms* package (Bürkner et al. 2024). The conceptual framework targets the 5-km buffers where coupled human–environment processes prevail. Ritual or aesthetic preferences within villages selectively safeguard a limited set of species, thereby reducing species diversity (Bhagwat and Rutte 2006; Ma et al. 2024). Conversely, long-term husbandry and institutional protection markedly increase tree DBH and age (Tian et al. 2024), yet the resulting isolated plantings lower overall density (Liu, Lindenmayer, et al. 2019). Suitable natural settings exert positive environmental-filtering effects on diversity, age and DBH (Laughlin et al. 2012). Higher diversity enhances community stability, facilitating DBH enlargement and density gains (Tatsumi and Loreau 2023; Tilman 1999). As trees age, DBH expands; large-DBH individuals, occupying disproportionate space, suppress stand density (Chisholm and Gray 2025; Lutz et al. 2018). Human activities frequently occur in environmentally favourable areas, producing a significant spatial coupling with natural conditions and exerting additive impacts on ancient trees (Ellis and Ramankutty 2008). Guided by these insights, we specified an a priori SEM (Figure 2) wherein natural environment and anthropogenic pressure are exogenous latent variables, while species diversity, mean age, DBH and density serve as endogenous observed variables; a covariance term between the two latent variables captures their spatial co-variation.

To mitigate collinearity and curb model complexity, we first reduced the dimensionality of geographic, climatic, edaphic and anthropogenic variables via principal component analysis (PCA). Each response variable was $\log_{1+}$-transformed to alleviate skewness, and standardised coefficients (β) derived from linear models were used to construct composite predictors; coefficient robustness and significance were assessed with 10,000 bootstrap resamples. Given the prevalence of zeros and heavy tails in the dataset, a Bayesian multivariate SEM with a hurdle–Gamma specification was fitted to accommodate zero inflation and long-tail distributions. Model convergence and reliability were rigorously evaluated using posterior predictive checks,

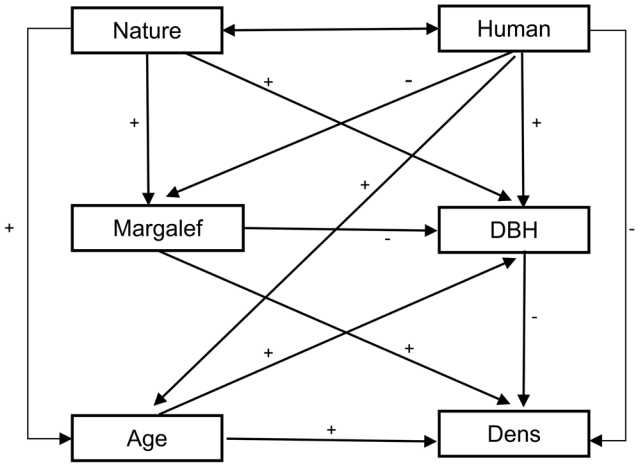


FIGURE 2 | Initial conceptual structural equation model (SEM). Nature: Composite of Clim_PC1 (climate PC1 axis), Soil_PC1 (soil PC1 axis), GETO_PC1 (geo-topographic PC1 axis), GETO_PC2 (geo-topographic PC2 axis). Human: Composite of Cul_PC1 (village culture PC1 axis), Cul_PC2 (village culture PC2 axis) and deve_PC1 (village development PC1 axis). The '+' symbol indicates a promoting effect, while the '–' symbol denotes a weakening effect.

leave-one-out cross-validation (LOOCV), Pareto-k diagnostics and posterior residual analyses, ensuring the robustness and scientific validity of the findings.

3 | Results and Analysis

3.1 | Distribution and Age Structure of Traditional Villages

A total of 276 villages in Hebei Province are listed in the National Register of Chinese Traditional Villages. These settlements are highly clustered along the eastern foothills of the Taihang Mountains—spanning Handan, Xingtai and Shijiazhuang—with sparser occurrences in Zhangjiakou and Baoding; village density declines progressively toward the northeast (Figure 3). The majority of villages are of considerable antiquity: roughly 80% were founded more than 500 years ago and nearly 25% exceed a millennium in age, most of which also lie along the Taihang foothills. The temporal gradient shows marked spatial heterogeneity. Shijiazhuang, Xingtai and Handan host the densest concentrations, accounting for about 75% of all millennium-old villages. Although Baoding contains fewer traditional villages overall, nearly 90% are older than 500 years and about 40% surpass 1000 years. In Zhangjiakou, village ages largely range from 300 to 1000 years, whereas Tangshan, Qinhuangdao, Hengshui and Chengde contain only scattered examples, generally less than 500 years old. Collectively, Hebei's traditional villages exhibit a dual spatial–temporal pattern characterised by dense and ancient settlements in the southwest, intermediate densities in the north, and sparse, relatively young settlements along the coastal and low-lying zones.

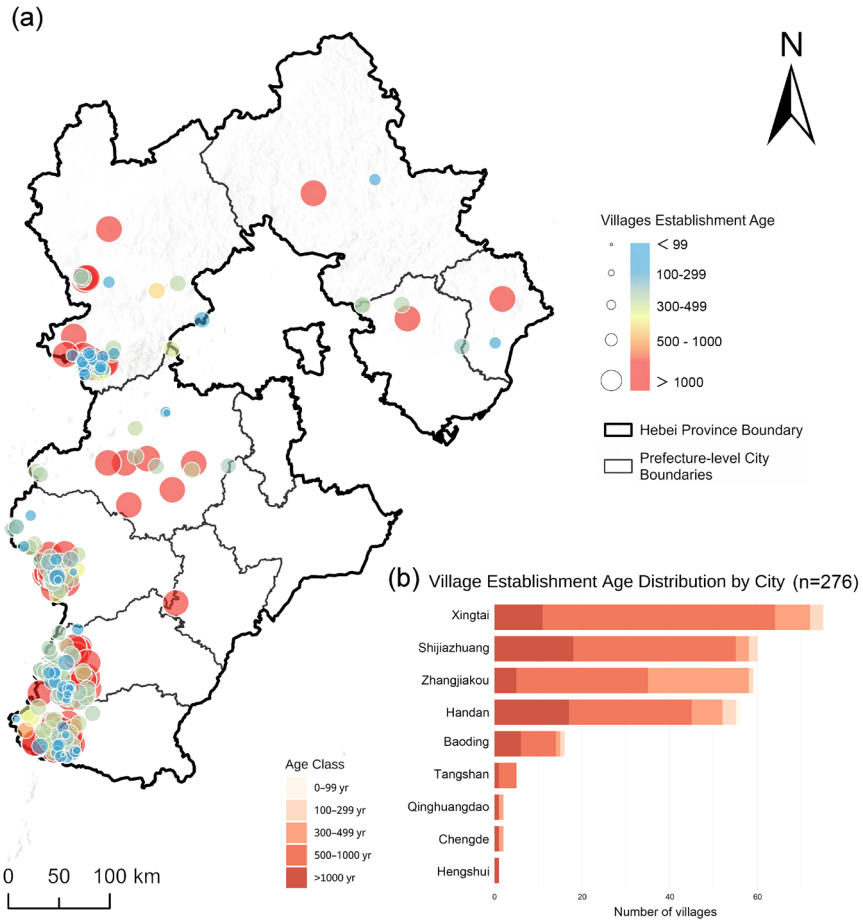


FIGURE 3 | Spatial pattern and prefecture-level frequency of establishment ages for nationally listed traditional villages in Hebei Province ($n = 276$). (a) Point map of individual villages. Each circle marks one village; fill colour denotes its establishment-age class—grey (< 99 years), blue (100–299 years), yellow (300–499 years), green (500–1000 years) and red (> 1000 years). Symbol diameter increases stepwise with age class to aid visual separation. (b) Horizontal stacked bars summarising the same five age classes for each prefecture-level city (bars ordered by total village number). Colours correspond exactly to panel (a), allowing direct comparison between the provincial map and city-level counts.

3.2 | Composition and Structure of the Ancient Tree Assemblage

Within the 5-km buffers of the 276 traditional villages, we documented 2514 ancient trees representing 82 species, 55 genera and 28 families. Fabaceae, Cupressaceae, Pinaceae, Fagaceae and Rosaceae dominate the assemblage, while *Styphnolobium*, *Platycladus* and *Pinus* together account for more than 60% of all individuals. At the species level, *Styphnolobium japonicum*, *Platycladus orientalis* and *Pinus tabuliformis* are the three most abundant taxa, numbering 804 (31.9%), 420 (16.7%) and 360 (14.3%) trees, respectively (Figure 4). Age-class analysis of the 10 leading species shows a predominance of tier-1 individuals (100–299 years), followed by tier-2 (300–499 years); tier-3 trees (≥ 500 years) constitute notable proportions only in *S. japonicum* (256) and *P. orientalis* (108), and never exceed 19 individuals in other species. Relative abundance (RA), relative dominance (RD), and importance value (IV) decline in concert with decreasing abundance. *S. japonicum* exhibits markedly higher RD, RA and IV—31.9%, 38.7% and 35.3%, respectively—than any other species. *P. orientalis* and *P. tabuliformis* have mid-range values (10%–20%), whereas all remaining taxa fall below 10%. Although *S. japonicum* and *Pistacia chinensis* possess large mean diameters and ages, the latter is represented by only 62 individuals, with RD, RA and IV of merely 2.46%, 2.76% and 2.61%, respectively.

3.3 | Spatial Distribution Patterns of Traditional Villages and Ancient Trees in Hebei

3.3.1 | Kernel Density and Standard Deviational Ellipse Analysis

Kernel density maps reveal a pronounced belt of traditional villages along the south-eastern foothills of the Taihang Mountains, with two major hotspots at the Handan–Xingtai junction (south) and near Shijiazhuang (central), plus a secondary high-value zone in south-western Zhangjiakou; densities elsewhere are low (Figure 5a). The kernel density surface for ancient trees is broadly similar, peaking along the same Taihang segment while displaying two additional hotspots in north-eastern Baoding and Qinhuangdao; these hotspots outnumber those of villages and extend farther northeastward (Figure 5b). The southern hotspots coincide closely, indicating strong co-location of tree preservation and village agglomeration, whereas in the central-northern sector ancient-tree hotspots are offset and village density weakens.

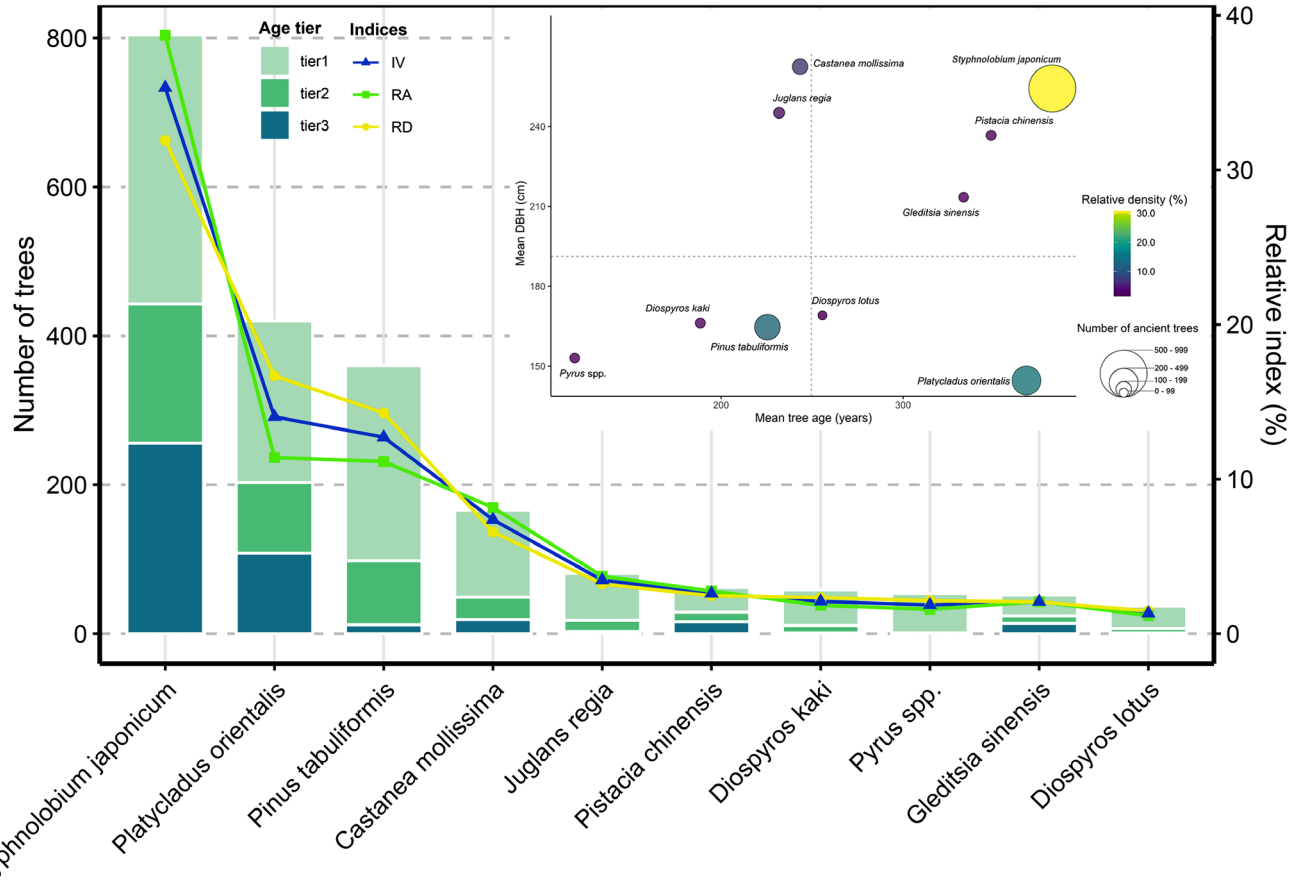


FIGURE 4 | Age-tier composition and dominance metrics of the 10 most abundant ancient-tree species in Hebei. Stacked bars depict the number of individuals in each age tier (tier-1 ≤ 299 years, tier-2 300–499 years and tier-3 ≥ 500 years); overlaid lines show relative abundance (RA), relative dominance (RD) and importance value (IV). Inset bubble plot relates mean tree age to mean DBH; bubble area scales to total individual count and fill colour to RD.

Grid statistics show that both village counts (blue) and tree counts (magenta) reach their maxima on the southern Taihang piedmont. Moving north or east, tree-bearing grid cells decline more slowly than village-bearing cells, enlarging their disparity. Standard deviational ellipses further demonstrate that the ancient-tree ellipse (magenta) is narrower and slightly north-shifted, while the village ellipse (blue) is elongated and fans southward; the centroids are less than 50 km apart. Collectively, ancient trees are more tightly concentrated along the northern piedmont, whereas villages exhibit greater southerly extent—reflecting the dual constraints of topography and traditional arboriculture on tree persistence, in contrast to village distribution, which is additionally shaped by modern development and urbanisation.

3.3.2 | Nearest-Neighbour Analysis

Nearest-neighbour index (NNI) values indicate that traditional villages in Hebei Province are significantly clustered overall ($R < 1$; Table 1). At the municipal level, village distributions in Shijiazhuang, Handan, Xingtai and Zhangjiakou exhibit clustering, whereas those in Tangshan, Qinhuangdao, Baoding and Chengde approximate randomness. In contrast, ancient trees surrounding villages show uniformly clustered patterns across all regions (NNI < 1), suggesting pronounced spatial self-organisation within village spheres of influence and a stronger tendency toward aggregation for ancient trees than for villages themselves.

3.4 | PCA Analysis

Principal component analysis yielded the following insights (Table 2):

1. Soil factors: PC1, accounting for 96.73% of the variance, is dominated by bulk density (−0.584), CEC (−0.580), and pH (−0.568), capturing a composite gradient from light, acidic, and low-fertility soils to heavier, alkaline and high-fertility soils; PC2 (2.59%) discriminates high-CEC acidic soils from alkaline soils.
2. Geo-topographic factors: PC1 explains 49.62% of the variance and is driven mainly by latitude (−0.752) and longitude (−0.427), reflecting latitudinal–longitudinal position; PC2 (34.18%) is governed by elevation (0.784) and slope (0.479), indicating vertical relief.
3. Climatic factors: PC1 explains 74.26% of the variance, correlates positively with temperature, potential

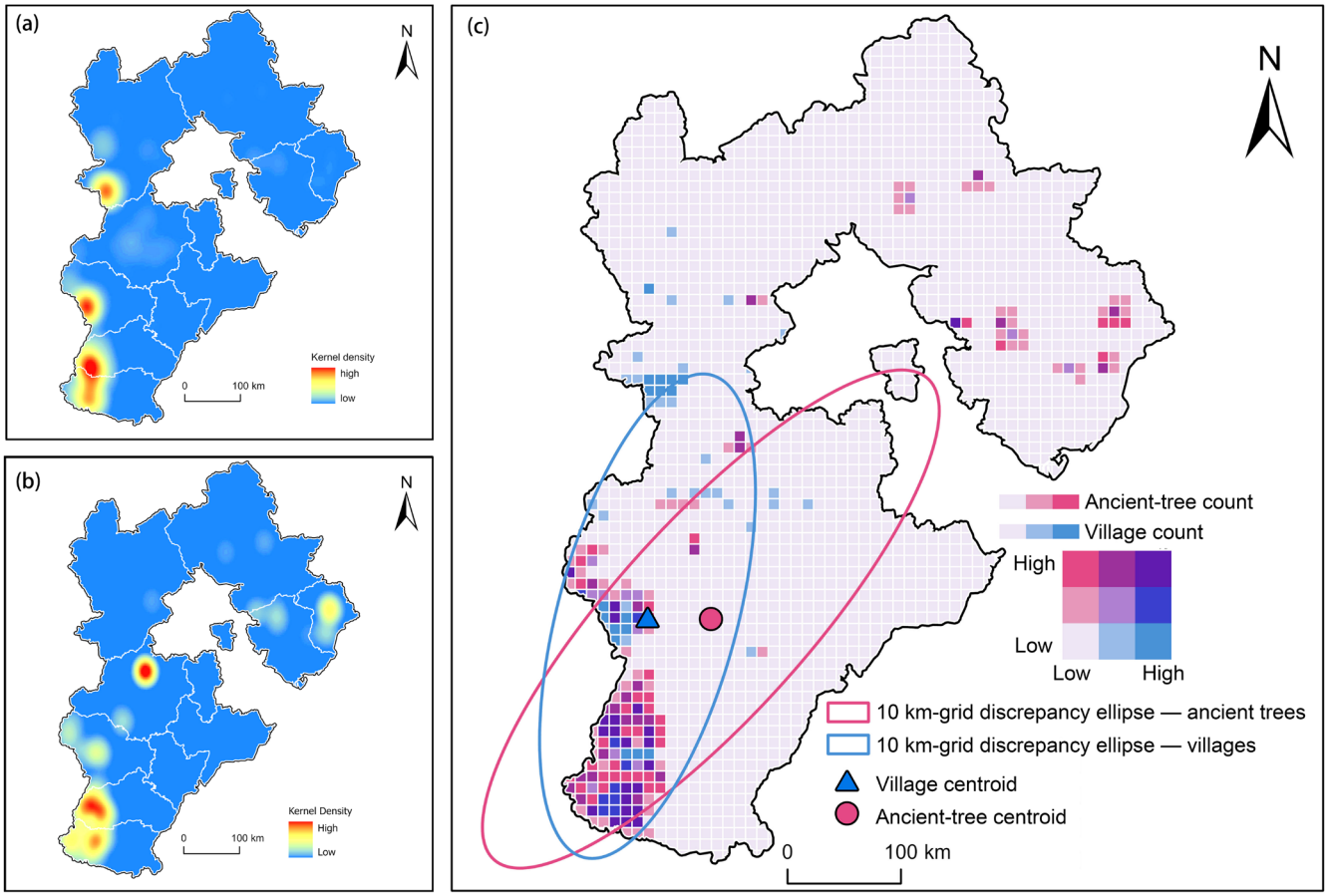


FIGURE 5 | Spatial correspondence between traditional villages and ancient trees in Hebei Province, China. (a, b) Kernel-density surfaces derived with a Gaussian kernel (bandwidth = 10 km): (a) traditional villages and (b) ancient trees. (c) Bivariate 10 × 10 km grid: Cell colours represent village count (blue ramp) and ancient-tree count (magenta ramp). Filled symbols indicate distribution centroids (▲villages, ● trees); 1-SD standard-deviation ellipses outline the directional spread of each dataset.

TABLE 1 | Nearest Neighbour Index (NNI) for traditional villages and their surrounding ancient trees in Hebei Province.

Region	Number of traditional villages	NNI	Spatial pattern	*Z*	*p*	Number of ancient trees	NNI	Spatial pattern	*Z*	*p*
Hebei Province (overall)	276	0.40	Clustered	−19.22	< 0.01	2514	0.10	Clustered	−86.39	< 0.01
Shijiazhuang	60	0.50	Clustered	−7.39	< 0.01	311	0.17	Clustered	−27.99	< 0.01
Tangshan	5	0.70	Random	−1.28	0.20	118	0.11	Clustered	−18.50	< 0.01
Qinhuangdao	2	1.40	Random	1.09	0.27	247	0.12	Clustered	−26.53	< 0.01
Handan	56	0.55	Clustered	−6.34	< 0.01	732	0.26	Clustered	−38.41	< 0.01
Xingtai	75	0.41	Clustered	−9.75	< 0.01	675	0.17	Clustered	−41.29	< 0.01
Baoding	16	0.84	Random	−1.15	0.25	373	0.03	Clustered	−35.75	< 0.01
Zhangjiakou	59	0.39	Clustered	−8.98	< 0.01	17	0.03	Clustered	−7.65	< 0.01
Chengde	2	0.88	Random	−0.32	0.75	38	0.04	Clustered	−11.27	< 0.01
Cangzhou	0	—	—	—	—	0	—	—	—	—
Langfang	0	—	—	—	—	0	—	—	—	—
Hengshui	1	—	—	—	—	3	0.02	Clustered	−3.25	< 0.01

TABLE 2 | Principal component analysis of topographic, climatic, edaphic and socio-cultural variables.

Variable	Eigenvector scores (PCA)	
	PC1	PC2
Soil PCA (96.73%) (2.59%)		
Cation exchange capacity (CEC)	−0.58	0.749
pH	−0.568	−0.653
Bulk density	−0.584	−0.109
Geographical-topography PCA (49.62%) (34.18%)		
Longitude (lon)	−0.427	−0.166
Latitude (lat)	−0.752	0.358
Altitude (alt)	−0.052	0.784
Slope	0.5	0.479
Climate PCA (74.26%) (16.46%)		
Cloud cover (cld)	0.259	0.29
Diurnal temperature range (dtr)	−0.299	−0.191
Frost days (frs)	−0.333	0.107
Potential evapo-transpiration (pet)	0.326	−0.109
Precipitation rate (pre)	0.22	0.439
Minimum temperature (tmn)	0.336	−0.027
Mean temperature (tmp)	0.334	−0.092
Maximum temperature (tmx)	0.333	−0.098
Vapour pressure (vap)	0.334	−0.076
Wet days (wet)	−0.194	0.467
Reference evapotranspiration (ET_0)	0.18	−0.459
Global aridity index (AI)	0.249	0.459
Village development PCA (82.07%) (8.31%)		
GDP	−0.473	0.022
Population density	−0.488	−0.097
Road density	−0.402	0.742
Human footprint	−0.468	0.006
City distance	0.398	0.663
Village culture PCA (46.43%) (24.28%)		
Village establishment age	0.088	0.709
Number of cultural relic units	−0.666	−0.132
Number of religious sites	−0.31	0.687
Number of intangible cultural heritage items	−0.673	−0.092

evapotranspiration, and vapour pressure, and negatively with frost days and diurnal temperature range, thus depicting a gradient from cold–dry to warm–humid conditions; PC2 (16.46%) links precipitation, wet days, and evapotranspiration, representing moisture availability.

4. Village development intensity: PC1 explains 82.07% of the variance, with high negative loadings for population density, GDP, human footprint, and road density and a positive loading for distance to cities, describing an urban–rural gradient from high to low development intensity; PC2 (8.31%) highlights disparities in road networks and urban accessibility.
5. Village historical-cultural factors: PC1 explains 46.43% of the variance and is marked by intangible cultural-heritage items and protected relics, indicating cultural richness, while PC2 (24.28%) loads on village age and religious sites, capturing historical depth and religious landscape.

3.5 | Structural Equation Model

Using a Bayesian multivariate hurdle–Gamma SEM ($n = 276$), we quantified the joint effects of anthropogenic disturbance and natural conditions on ancient-tree community attributes in traditional villages. All MCMC chains converged satisfactorily ($\hat{R} = 1.00$; Bulk_ESS > 9000; no divergences), indicating stable model fits. Posterior checks yielded Bayes-R^2 values ranging from 0.28 to 0.99, with all leave-one-out cross-validation Pareto-k values below 0.7; posterior predictive curves enveloped the observed distributions, confirming that the zero-inflated Gamma specification accurately captured data structure and produced reliable inferences. Overall, the model accounted for 47% of the variance in species diversity (Margalef index), 64% in mean tree age, 99.5% in diameter at breast height (DBH) and 28% in stand density, demonstrating that ancient-tree attributes are strongly shaped by the interplay of human and natural gradients, with DBH and age being the most tightly explained (Figure 6).

Based on the PCA results, the natural latent variable was constructed from climate (Clim_PC1), soil (Soil_PC1) and topography (GETO_PC1, GETO_PC2); higher scores denote warmer, moister conditions and gentler relief. The anthropogenic latent variable combined cultural factors (Cul_PC1, Cul_PC2) with development intensity (deve_PC1), whereby higher scores indicate stronger socio-economic activity. Within the natural dimension, climate contributed most strongly (0.618) whereas soil showed a slight negative loading (−0.065); in the anthropogenic dimension, cultural indicators dominated (0.523 and 0.362). The SEM revealed parallel direct effects of the two gradients: both slightly reduced species diversity ($\beta = -0.05$), marginally increased mean age ($\beta = 0.01$) and depressed tree density (natural $\beta = -0.05$; anthropogenic $\beta = -0.33$). Internally, diversity exerted a negligible negative influence on mean DBH ($\beta = -0.01$) but markedly enhanced density ($\beta = 0.50$); mean age strongly promoted DBH growth ($\beta = 0.04$) while minimally reducing density ($\beta \approx -0.06$). Consequently, the natural gradient's indirect pathway—'lower diversity → altered DBH/density'—imparts an almost nil positive effect on DBH (~+0.0005) and a modest negative effect on density (~−0.025). The anthropogenic gradient yields the

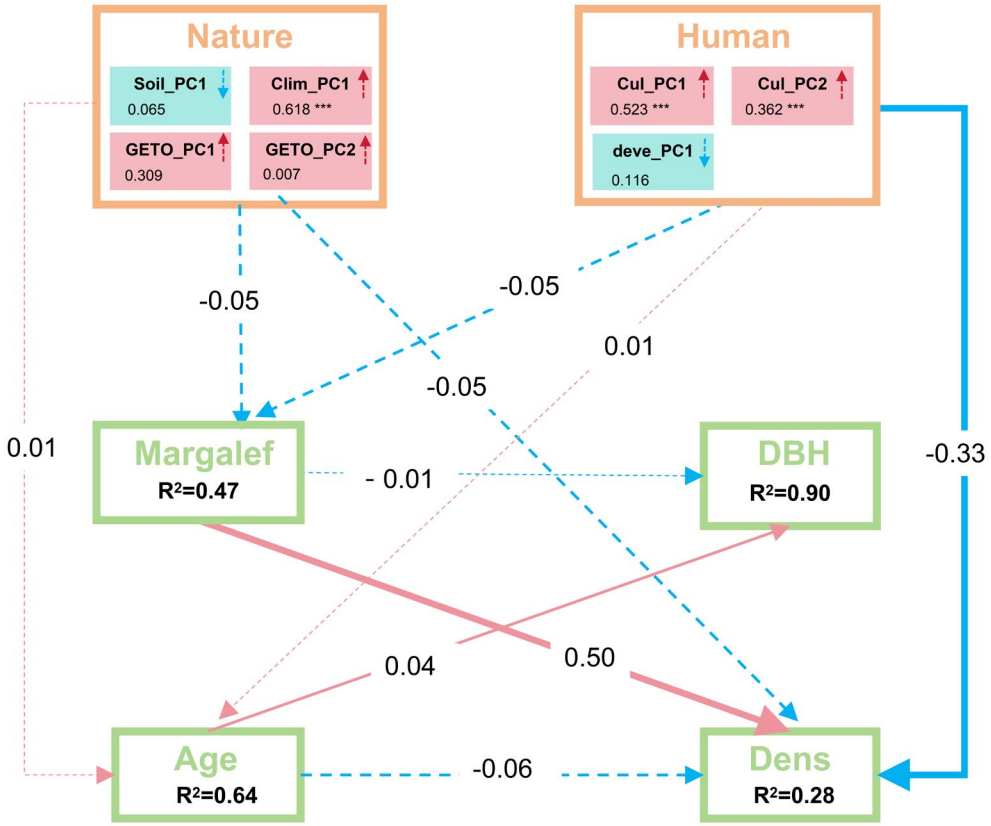


FIGURE 6 | Structural equation model of human and natural controls on ancient-tree community attributes in traditional villages ($n = 276$). Path coefficients are posterior medians from Bayesian multivariate SEM (hurdle–Gamma), with 95% credible intervals indicated by solid (CI not spanning zero) or dashed (CI spanning zero) arrows. Arrow colour denotes effect direction (red = positive and blue = negative); line width is proportional to absolute coefficient magnitude. Node R^2 values are Bayesian R^2 for each μ-equation; all chains converged ($\hat{R} \approx 1.00$, Bulk_ESS > 9000). Inset panels: Human and Nature composite indices were constructed by weighted sums of principal components (PC1/PC2) with bootstrap-derived weights (***p(directional) > 97.5%).

same indirect direction, yet its larger direct negative effect on density (−0.33) remains the predominant driver of stand density variation.

4 | Discussion

4.1 | Characteristics of Ancient-Tree Resources in Hebei's Traditional Villages

Ancient-tree communities within 5 km of Hebei's traditional villages exhibit marked species dominance and a 'youthful' age profile, shaped by the interplay of long-term human selection and environmental filtering. Of the 2514 individuals recorded, *Styphnolobium japonicum*, *Platycladus orientalis* and *Pinus tabuliformis* together account for more than 60%. Such dominance patterns arise when species are both ecologically adapted and culturally valued: *S. japonicum* is prized for nitrogen fixation, shade and deep cultural symbolism noted as early as the pre-Qin *Classic of Mountains and Seas* (Anonymous et al. 2021; Hou et al. 2022), whereas *P. orientalis* and *P. tabuliformis* are long-lived, drought- and cold-tolerant gymnosperms with religious associations (Huang, Jin, et al. 2020; Jin et al. 2020). *S. japonicum* also far exceeds other taxa in RD, RA and IV, underscoring the synergy of cultural preference and ecological suitability; similar patterns have been reported in the Yangtze River Basin (Jin et al. 2020; Liu, Lindenmayer, et al. 2019).

Age-class analysis shows that tier-1 trees (100–299 years) dominate, whereas tier-3 individuals (≥ 500 years) are rare and concentrated in *S. japonicum* and *P. orientalis*. Hebei's extensive plains (43.4% of the province) and intensive land use mean that high-value farmland and commercial forests seldom harbour large ancient trees (Lindenmayer and Laurance 2016). Climate warming may speed growth yet shorten lifespan (Liu et al. 2025; Locosselli et al. 2020), while urban expansion and infrastructure development further constrain habitat for old trees (Crowther et al. 2015; Lindenmayer and Laurance 2016). By contrast, temples and ancestral halls provide 'cultural refuges' that safeguard venerable individuals (Huang et al. 2025; Zhou et al. 2022). Species dominance correlates positively with mean DBH and age: although *S. japonicum* and *Pistacia chinensis* share large sizes and ages, only 62 individuals of the latter were found, yielding low RD, RA and IV, illustrating how ecological fitness, cultural preference and life-history strategy jointly determine persistence (Huang et al. 2023). In sum, Hebei's ancient-tree assemblages are governed by a dual mechanism of natural filtering and cultural selection, producing conspicuous species dominance and a youthful age distribution. The strong

dominance of a few long-lived, large-crowned species also implies that a relatively small subset of ancient trees is likely to supply a disproportionate share of habitat resources (e.g., tree hollows, floral rewards and microclimatic buffering) for wildlife in village landscapes, as documented for large old trees in other rural and urban systems (Lindenmayer and Laurance 2017; Manning et al. 2013). In Hebei's traditional villages, these veterans therefore act as keystone structures that support pollinators, cavity-nesting birds, and other fauna while simultaneously delivering shade, local cooling and other regulating services that directly enhance human well-being (Lindenmayer 2017). Conservation efforts should therefore preserve genetic diversity within dominant taxa, enhance protection of rare species, incorporate both the intangible (cultural) and tangible (provisioning) values of large old trees into ecosystem service assessments, and integrate functional diversity and structural stability into village planning to bolster ecosystem resilience and long-term sustainability (Blicharska and Mikusiński 2014; Lutz et al. 2018).

4.2 | Spatial Pattern of Ancient Trees in Hebei's Traditional Villages

Ancient trees around Hebei's traditional villages display marked clustering and pronounced spatial heterogeneity. Kernel density, standard deviational ellipse and gravity-centre analyses show substantial overlap between ancient-tree hotspots and village clusters along the eastern foothills of the Taihang Mountains, yet the two distributions are not perfectly congruent. The densest village corridor—Handan–Xingtai–Shijiazhuang—lies in a low-elevation transition zone between mountains and plains and aligns with the historic Taihang transport artery, the 'Eight Passes', reflecting settlement preferences that balance farming, housing, and accessibility (Liu et al. 2023). This co-location underscores the geo-ecological integration typical of Chinese traditional settlements (Liang et al. 2025; Han 2001). Ancient-tree hotspots extend beyond this corridor northeastward into Baoding and Qinhuangdao, indicating that suitable habitats and culturally significant sites jointly shape their distribution (Huang, Jin, et al. 2020). Qinhuangdao, on the well-forested eastern Yanshan range, offers favourable rainfall, temperature and soil fertility—conditions conducive to ancient-tree persistence (Jones 1997; Slik et al. 2013). Coastal villages also preserve 'fengshui forests', providing anthropogenic refuge for old trees (Zhou et al. 2022). North-eastern Baoding, adjoining Beijing and rich in protected monuments—including the Western Qing Tombs—likewise harbours hotspots where vegetation conservation and cultural taboos coincide (Zhang 2011). In sum, Hebei's ancient-tree spatial pattern reflects a dual mechanism: selective cultural protection fosters local aggregation, whereas complex topography and intact ecosystems furnish enduring environmental shelter (Huang, Jin, et al. 2020; Jin et al. 2020; Liu, Lindenmayer, et al. 2019).

4.3 | Maintenance Mechanisms of Ancient Trees in Hebei's Traditional Villages

PCA combined with a Bayesian SEM demonstrates that the spatial pattern of ancient trees in Hebei is jointly shaped by natural conditions and human activities, though via distinct mechanisms. Within the natural domain, climate—chiefly temperature and moisture—exerts the strongest influence: warmer, more humid sites favour community development, and tree lifespan declines as climate-related habitat severity increases (Kobayashi and Akasaka 2025). At macro-scales, rainfall and temperature are likewise decisive (Slik et al. 2013). For ancient ginkgo, temperature is a primary limiting factor, and the likelihood of occurrence rises markedly with increasing warmth and precipitation (Chi et al. 2020). Topographically, gentle slopes and low-elevation hills promote long-term persistence, contrasting with the common assumption that the oldest trees occur mainly in remote, high mountains (Liu, Yang, and Lindenmayer 2019); this is consistent with studies in the North China Plain, where traditional villages occupy relatively flat terrain (Liu et al. 2023). On the anthropogenic side, cultural factors dominate: regions with long histories and abundant heritage resources preferentially retain certain species to sustain cultural and religious landscapes, leading to concentrations of ancient trees at temples, tombs and other sacred sites (Chen 2010; Huang et al. 2025; Zhang et al. 2017). The SEM further shows that, relative to natural factors, anthropogenic drivers exert a significant, direct negative effect on ancient tree density. Synthesising these findings with empirical research on sacred groves and domesticated forest assemblages, we identify a 'cultural filter' mechanism that is critical yet functionally bounded: once local communities decide to preserve specific taxa, these culturally protected trees can maintain high dominance and diversity at the local scale (Bhagwat and Rutte 2006; Levis et al. 2017); however, intensifying land use and habitat fragmentation progressively diminish the availability of patches capable of supporting large-diameter veterans, thereby imposing an upper limit on the efficacy of this cultural filter with respect to species richness and population density (Lindenmayer and Laurance 2016). Nevertheless, human activities do not significantly depress diversity per se, implying that protective management partly offsets anthropogenic stress. Species diversity itself markedly elevates density, supporting the 'lottery winner' hypothesis whereby optimal habitats sustain both high richness and density (Cannon et al. 2022; Liu, Lindenmayer, et al. 2019). Finally, mean age strongly increases DBH, aligning with evidence that ancient trees, though slow-growing, continue to accumulate diameter over time (Stephenson et al. 2014).

5 | Conclusion

Ancient tree communities surrounding traditional villages in Hebei represent distinctive biocultural legacies shaped by centuries of human-mediated selection and environmental filtering. Our findings suggest that these assemblages are not simply remnants of native forest; instead, they are characterised by disturbance-tolerant species and a predominance of early-to-mid age classes, consistent with a long history of active management. Spatially, their concentration along the piedmont ecotone of the Taihang Mountains highlights this zone as a potential refugium where suitable habitat coincides with sustained cultural valuation. SEM helps disentangle the pathways underlying these patterns: environmental gradients appear to constrain potential tree size and longevity, whereas human factors are more strongly associated with abundance and survival. Together, these results portray ancient trees as emergent outcomes of long-term coupled dynamics between

landscapes, governance, and local stewardship. Accordingly, conservation policy should move beyond protecting isolated individuals toward managing these landscapes as dynamic biocultural systems. Priority should be given to safeguarding high-density corridors along the Taihang piedmont, reducing fragmentation and promoting the regeneration of diverse taxa. Effective management will require integrating these ecological and governance considerations into provincial planning to sustain the resilience of this living heritage.

Author Contributions

Conceptualisation: Yifu Liu and Pingping Tian; methodology: Yifu Liu and Pingping Tian; formal analysis: Pingping Tian and Yihao Dan; data collection: Pingping Tian and Yihao Dan; project administration: Pingping Tian; software: Yifu Liu and Pingping Tian; writing – original draft: Yifu Liu; writing – review and editing: Yifu Liu and Pingping Tian.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Ancient-tree records used in this research are publicly available from the Hebei Ancient and Famous Tree Information System: http://lycy.hebei.gov.cn/gsmm/search.html. Datasets for Chinese traditional villages, religious establishments, protected cultural-relic units, and intangible cultural-heritage items are included with this article as Data S1–S4.

Peer Review

For transparency, the peer review documents associated with this article are available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi70164.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ddi70164-sup-0001-AppenidixS1.csv.