

Population structure and dynamic characteristics of *Cercidiphyllum japonicum* in Houhe National Nature Reserve, Hubei Province

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Abstract

Cercidiphyllum japonicum is a tertiary relict species that was once widespread across the Northern Hemisphere but is now a rare and endangered plant in China, valued for its ornamental, medicinal, and scientific importance. Understanding the structure and dynamics of its wild populations is essential for forecasting their future and informing conservation strategies. This study, conducted in the Houhe National Nature Reserve, Hubei Province, analyzed a population of 62 individuals across 23 sampling plots. Based on detailed field measurements of diameter at breast height (DBH), a static life table was compiled and population dynamics were projected using age class dynamics indices and time series analysis. Results showed the population inhabits sandy, organic-rich, weakly acidic yellow-brown soils. The age structure approximated an irregular, spindle-shaped pyramid, characterized by a complete absence of germinated seedlings and a reliance on sprouting for regeneration. The population dynamic indices ($V_{pi} > V'_{pi} > 0$) indicated a marginally growing but stable population that is highly sensitive to environmental and anthropogenic disturbances. The survival curve conformed to the Deevey-III type, indicating high mortality in early life stages. Time-series forecasting suggested that the current abundance of middle-aged individuals could maintain the population in the short term. We conclude that recruitment failure, intense environmental filtering, and historical logging are the primary drivers of its endangered status. Conservation efforts must therefore prioritize artificial regeneration to supplement seedlings, active management of existing sprouts, and the establishment of a long-term monitoring program for this vulnerable population.

Keywords: *Cercidiphyllum japonicum*; conservation management; dynamic index; population structure; static life table

Introduction

A population, defined as a group of interbreeding individuals of the same species within a specific spatiotemporal context, has a structure that is a central focus in ecological research (Condit *et al.*, 2000). Population structure and its dynamic changes reflect the current status of a population, its response to

Received: 18 Feb 2025. Received in revised form: 01 Dec 2025. Accepted: 07 Dec 2025. Published online: 21 Dec 2025.

From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

disturbances, and can be used to predict its developmental trajectory (Suzán-Azpiri *et al.*, 2002; Kang *et al.*, 2014). This aids in elucidating the ecological characteristics of populations, their renewal strategies, and the formation and succession patterns of communities (Taylor and Halpern, 1991). Understanding the survival status and developmental dynamics of plants, and revealing their survival characteristics, potential, and mechanisms of endangerment, holds great significance for the conservation and management of rare and endangered plant species (Hedrick, 2005; Aguilar *et al.*, 2006).

In recent years, research and conservation of endangered species have garnered widespread global attention (Qiu *et al.*, 2004; Aboukhalid *et al.*, 2017). *Cercidiphyllum japonicum*, a Tertiary relict plant, was once distributed across the entire Northern Hemisphere but is now found only in certain parts of Japan and China (Sakio and Kubo, 2022). In 1989, it was listed as a rare and endangered plant in China, sporadically distributed in provinces such as Anhui, Zhejiang, Jiangxi, Hubei, Sichuan, Shaanxi, Shanxi, and Gansu (Yan *et al.*, 2007; Li *et al.*, 2020). Despite its significant ornamental, medicinal, and scientific value (Zou *et al.*, 2022), wild *C. japonicum* populations are limited in number and scale, often occurring as scattered individuals (Jiang *et al.*, 2002). Some studies indicate that the species is in a state of decline (Li *et al.*, 2009). In terms of reproductive biology, its dioecious nature leads to inefficient pollination, coupled with seed dispersal limitations and difficulties in seedling establishment, resulting in significantly weakened natural regeneration capacity (Li *et al.*, 2009; Wei *et al.*, 2025). At the ecological genetics level, extant populations exhibit a fragmented distribution and ongoing loss of genetic diversity, posing a risk of regional extinction (Ma *et al.*, 2019). While stump sprouting can occur (Yang *et al.*, 2012), this does not mitigate the primary threat: human-induced logging and habitat destruction remain the dominant drivers of population decline (Xu, 2018). Therefore, strengthening the protection of wild *C. japonicum* is extremely urgent.

Current research on *C. japonicum* primarily focuses on genetic characteristics (Qi *et al.*, 2012), spatial genetic structure of canopy trees (Sato *et al.*, 2006), the relationship between life-history traits and environmental factors (Kubo *et al.*, 2004), ecological niche modeling (Zeng *et al.*, 2020), the relationship between seedling regeneration and environmental conditions (Kubo *et al.*, 2005), and its coexistence mechanisms with other species (Sakio *et al.*, 2002; Masaki *et al.*, 2007). Although the mechanisms sustaining its populations in Japan have been preliminarily clarified, the species in China faces unique distribution patterns and survival challenges, often growing sporadically in vulnerable mountainous valleys and even demonstrating a patchy or insular, disjunct distribution pattern (Wang and Liu, 2002; He *et al.*, 2009). This situation underscores the urgency of conducting targeted conservation research on Chinese populations. However, systematic studies on the population structure and dynamics of *C. japonicum* remain scarce.

Previous studies have shown that by adopting a "space-for-time substitution" approach, constructing static life tables, plotting survival curves, applying four survival analysis functions, quantitative indices for population dynamics, and time-series projection, it is possible to effectively reveal the structural characteristics and dynamic patterns of wild *C. japonicum* populations (Yang *et al.*, 2012; Zhang and Bi, 2018; Ding *et al.*, 2022). In this study, we focus on the wild *C. japonicum* population in the Houhe National Nature Reserve of Hubei Province. Following this research paradigm, we systematically analyze the current status and development trends of the population, aiming to provide theoretical support for its sustainable conservation and management, and to lay a scientific foundation for elucidating the endangered mechanisms of *C. japonicum*. The specific objectives of this study were: (1) to characterize the current age structure and identify the dominant regeneration strategy of the population; (2) to quantify population dynamics and project future trends through survival analysis and time-series forecasting; and (3) to assess the key factors contributing to its endangerment. The aim is to predict the future succession trends of the population, provide a theoretical basis for the sustainable development of wild *C. japonicum* populations, and lay a foundation for elucidating the mechanisms behind its endangerment, thereby informing effective conservation strategies.

Materials and Methods

Study area

Houhe National Nature Reserve is located in Wufeng Tujia Autonomous County, Hubei Province (30°2'45" - 30°8'40"N; 110°29'25"–110°40'45"E), in the eastern section of the Wuling Mountains, and constitutes a vital component of the biodiversity hotspot in the Sichuan-East Hubei region of China (Figure 1). The reserve covers a total area of 40,964.9 hm², characterized by mountainous terrain with significant topographical complexity and an elevational gradient ranging from 398.5 to 2,252.2 m. The region experiences a transitional climate between the central and northern subtropical zones, featuring distinct seasons, synchronous rainfall and heat periods, and pronounced vertical climatic zonation (Zhang *et al.*, 2013). The mean annual temperature is 11.5 °C, with an average annual precipitation of 1814 mm, an average annual evaporation of 1,185.7 mm, and a frost-free period of 211 days. The geological substrate is predominantly limestone, and the corresponding soil type is typical yellow-brown earth (Li *et al.*, 2002). The zonal vegetation consists of evergreen broad-leaved forests and mixed evergreen-deciduous broad-leaved forests. The area is rich in vascular plant resources and hosts 29 rare and endangered protected plant species, earning it the reputation as the "Three Gorges Emerald" (Zha *et al.*, 2006; Zhang *et al.*, 2013; Zha *et al.*, 2016).

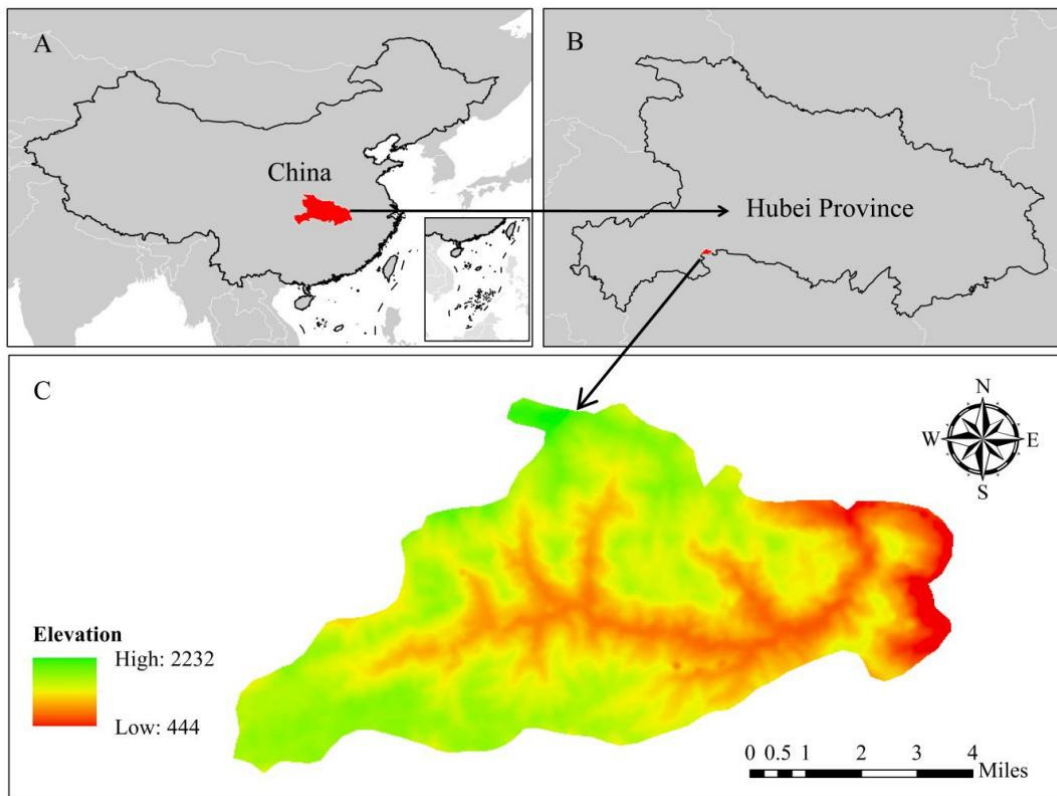


Figure 1. Location of the study area: (A) The geographical position of Hubei Province in East Asia (red area); (B) The geographical position of Houhe National Nature Reserve in China (red area) and (C) Basic situation of the Houhe National Nature Reserve

*Note: The shapefile of the reserve boundary was acquired from <https://zenodo.org/records/14875797>

Cercidiphyllum japonicum is a light-demanding, tall deciduous tree that thrives in cool, moist environments with deep, well-drained, slightly acidic soils (Zeng *et al.*, 2020). Within the reserve, its

populations are mainly distributed in valley bottoms at elevations between 1,200 and 1,350 m, often associated with tree species such as *Tetracentron sinense*, *Davidia involucreata*, and *Tapiscia sinensis*, and exhibit a strong capacity for sprouting regeneration. Furthermore, field surveys and local interviews revealed that the area experienced logging from 1960 until the reserve's creation in 1988, a period of which the 1970s were the most severe (Ding *et al.*, 2022).

Survey design

In October 2016, a 1 km² sampling area was established within the core distribution zone of the *C. japonicum* community in Houhe National Nature Reserve. A total of 23 random quadrats (20 m × 20 m each), each containing at least one living individual, were surveyed. Within each quadrat, all living individuals of *C. japonicum* were censused. A distinct individual (genet) was defined as a standalone seedling or a cluster of physically connected ramets (sprouts) sharing a common root system. For each individual, the diameter at breast height (DBH) of all above-ground stems was measured at 1.3 m above ground level using a diameter tape, with the thickest or most dominant stem defined as the main trunk. Any stem with a DBH of less than 1 cm was recorded as a seedling, applying this criterion uniformly to both germinated seedlings and sprouted ramets. As soil conditions are a critical factor limiting plant growth, distribution, and population regeneration, and since *C. japonicum* exhibits specific requirements for its habitat soil (Zeng *et al.*, 2020), a five-point sampling method was employed to determine soil moisture content and electrical conductivity. Composite soil samples from a depth of 0–20 cm were collected from each quadrat and transported to the laboratory for analysis of soil type and properties.

Soil analysis

Soil type and properties were determined following standard methods (Bao, 2004). The soil texture composition was calculated as follows:

$$W_{\text{Sand}} (\%) = M_{\text{sand}} / M_1 \times 100$$

$$W_{\text{Silt}} (\%) = M_{\text{silt}} / M_1 \times 100$$

$$W_{\text{Clay}} (\%) = 1 - (W_{\text{Sand}} + W_{\text{Silt}})$$

where W_{sand} , W_{silt} , and W_{clay} represent the mass fractions of sand, silt, and clay, respectively; M_{sand} is the mass of sand before sieving; M_{silt} is the dry mass of silt after removing sand; and M_1 is the initial dry mass of the unsieved sample.

Moisture content was determined by the gravimetric method: fresh soil samples were dried at 105 °C to constant weight, and moisture content was calculated from the mass difference. Electrical conductivity (EC) was measured in a 1:5 soil-water suspension using a conductivity meter after 30 minutes of equilibrium. Soil pH was determined potentiometrically in a 1:2.5 soil-water suspension using a calibrated pH meter. Alkali-hydrolyzable nitrogen was measured by the alkali diffusion method using 1.0 M NaOH hydrolysis and boric acid absorption. Available phosphorus was extracted with 0.5 M NaHCO₃ (pH 8.5) and determined by the molybdenum-blue method using spectrophotometry. Available potassium was extracted with 1 M NH₄OAc (pH 7.0) and quantified by flame photometry. Organic matter content was determined by the potassium dichromate oxidation method (external heating version) and titrated with ferrous sulfate (Bao, 2004).

Population structure

Within a species, diameter and age classes respond to a given environment in a similar manner (Frost and Rydin, 2000). To avoid destructive sampling, diameter class structure is widely used as a proxy for age structure in analyzing population structure and dynamics (Wu *et al.*, 2010; Boulanger-Lapointe *et al.*, 2014). In this study, the diameter at breast height (DBH) of the main trunk were categorized into 8 age classes (Henry and Walters, 2023): Age class I (0 cm ≤ DBH < 10 cm), II (10-20 cm), III (20-30 cm), IV (30-40 cm), V (40-50 cm), VI (50-60 cm), VII (60-70 cm), and VIII (70-80 cm). Based on the number of wild *C. japonicum*

individuals in each age class, the percentage of individuals was calculated. The age class was used as the abscissa, and the percentage of individuals was used as the ordinate to plot the age structure.

Static life table preparation and survival curve

The static life table and the survival curve can intuitively show the actual survival number, the number of deaths, and the survival trend of the population at different age classes (Díaz *et al.*, 2000). To avoid negative mortality rates during compilation, a “smoothing technique” was applied to adjust the actual number of individuals in each age class. The smoothed individual counts (a_x) were used to construct static life tables (Zhao *et al.*, 2017; Shen *et al.*, 2018). A static life table includes the following parameters: A_x : existing individual number within age class x ; a_x : existing individual number within age class x after the application of the “smoothing technique”; l_x : standardized survival number at the beginning of age class x (generally converted to 1000); $\ln l_x$: logarithmic standardized survival number; d_x : standardized death number within the interval from age class x to $x+1$; q_x : mortality rate; L_x : average survival number within the interval from age class x to $x+1$; T_x : total survival number from age class x and beyond; e_x : life expectancy of individuals entering age class x ; K_x : disappearance rate of the population. the formula is as follows:

$$\begin{aligned}
 l_x &= (a_x/a_0) \times 1000 \\
 d_x &= l_x - l_{x+1} \\
 q_x &= (d_x/l_x) \\
 L_x &= (l_x + l_{x+1})/2 \\
 T_x &= L_x + L_{x+1} + L_{x+2} + \dots + L_{x+n} \\
 e_x &= T_x/l_x \\
 K_x &= \ln l_x - \ln l_{x+1}
 \end{aligned}$$

The survival curve is drawn with the age class as the horizontal coordinate and the natural pair value of the survival number $\ln l_x$ as the vertical coordinate. Using the exponential function ($N_x=N_0e^{-bx}$) and the power function ($N_x=N_0x^{-b}$) to describe the Deevey- II type and Deevey-III type survival curves (Hett and Loucks, 1976).

Quantitative of population dynamics

The population dynamic index quantitative analysis method (Liu *et al.*, 2023) was used to analyze the population age structure dynamics of wild *C. japonicum* by introducing the population dynamics between two adjacent age classes (V_n), ignoring the population dynamics of external interference (V_{pi}), the population dynamics of external disturbances caused (V'_{pi}) by the number of individuals (S_n) and the number of age classes (k). The formula is as follows:

$$\begin{aligned}
 V_n &= \frac{S_n - S_{n+1}}{\max(S_n, S_{n+1})} \times 100\% \\
 V_{pi} &= \frac{\sum_{n=1}^{k-1} (S_n \times V_n)}{\sum_{n=1}^{k-1} S_n} \\
 V'_{pi} &= \frac{\sum_{n=1}^{k-1} (S_n \times V_n)}{k \times \min(S_1, S_2, S_3, \dots, S_k) \sum_{n=1}^{k-1} S_n}
 \end{aligned}$$

$$P_{\max} = \frac{1}{k \times \min(S_1, S_2, S_3, \dots, S_k)}$$

Survival analysis functions

Applied to the survival function $S_{(i)}$ in the survival analysis, the cumulative mortality rate function $F_{(i)}$, the mortality density function $f_{(i)}$, and the hazard rate function $\lambda_{(i)}$ Population dynamics (Ma, 2021) of wild *C. japonicum* trees in each region. Where P_i is the survival rate, h_i is for age width. The formula is as follows:

$$S_{(i)} = P_1 \times P_2 \times P_3 \dots P_i$$

$$F_{(i)} = 1 - S_i$$

$$f_{(i)} = \frac{S_{i-1} - S_i}{h_i}$$

$$\lambda_{(i)} = \frac{2(1 - S_i)}{[h_i(1 + S_i)]}$$

Time sequence prediction model

The average passage method in time series model analysis was used to predict the dynamic trend of the wild *C. japonicum* population after 2, 4, and 6 years (Díaz *et al.*, 2000). The formula is as follows:

$$M_t^{(1)} = \frac{1}{n} \sum_{k=t-n+1}^t X_k$$

where n is the future period to be predicted; $M_t^{(1)}$ is the size of the population at diameter class t in the future n years; X_k is the current size of the population at diameter class k .

Description of statistical analysis

All the obtained data were treated using Excel (version 2020), and all the figures in this work were created using Origin (version 2021).

Results

Living status and age structure of C. japonicum population

A total of 62 individuals of *C. japonicum* were recorded in the survey. The population distribution area is characterized by sandy yellow-brown soil (Table 1), with the trees predominantly growing in slightly acidic habitats rich in organic matter (Table 2), reflecting the species' preference for fertile and moist environments.

Table 1. Soil texture composition in the sampling plots of the *Cercidiphyllum japonicum* population (n=23)

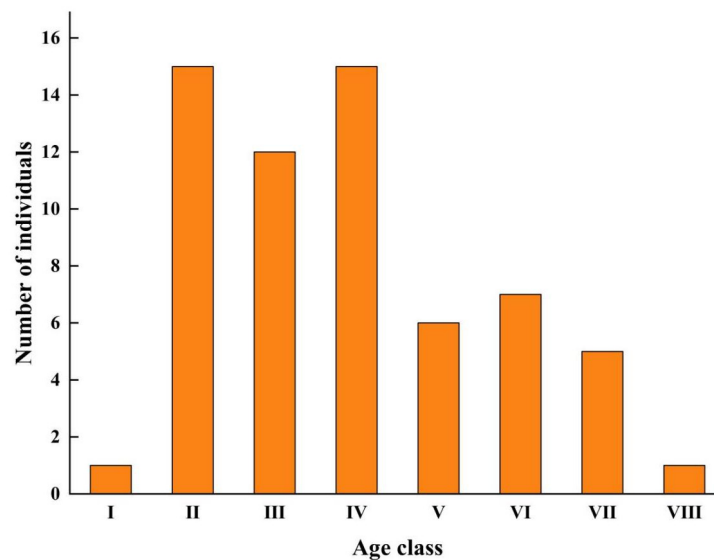
Soil fraction	Percentage (%)	Standard deviation (%)
Sand	17.64	1.25
Silt	76.77	11.11
clay	5.61	2.03

Table 2. Soil properties in the sampling plots of the *Cercidiphyllum japonicum* population (n=23)

Soil properties	Mean \pm SD
Moisture content (%)	20.57 \pm 9.24
Conductivity (mv)	529 \pm 181.39
pH	5.72 \pm 0.50
Alkali-hydrolyzable nitrogen (mg kg ⁻¹)	569.47 \pm 82.46
Rapidly available phosphorus (mg kg ⁻¹)	31.43 \pm 8.92
Rapidly available potassium (mg kg ⁻¹)	243.55 \pm 51.61
Organic matter (mg kg ⁻¹)	431.82 \pm 99.15

*Note: Values represent mean \pm standard deviation (SD)

The population structure of *C. japonicum* was continuous, with individuals distributed across all eight age classes (Figure 2). Notably, no germinated seedlings (from seed) were found in the plots. The individuals in age class I emerged as sprouts from stumps, comprising 1.59% of the population. Individuals were primarily concentrated in age classes II-IV (68.25% of the total), while age classes V-VIII accounted for 30.65%. The peak occurred in age class II and IV, indicating a structure with sufficient middle-aged individuals but a severe deficiency of young-aged individuals, along with relatively few old-aged individuals. Beginning from age class IV, the number of individuals showed a general declining trend, with the exception of a minor fluctuation in age class VI. Overall, the age structure approximated a spindle-shaped, irregular pyramid.

**Figure 2.** Age class structure of *Cercidiphyllum japonicum* population

*Note: The individuals represent genetically distinct individuals

The dynamics of the population age class structure and sensitivity index indicate fluctuations within the *C. japonicum* population (Table 3). Values of V_I , V_{III} , and V_V were negative, indicating a decline in transitions from age class I to II, III to IV, and V to VI. The values of V_{II} , V_{IV} , V_{VI} , and V_{VII} were positive, indicating population growth during the transitions from age class II to III, IV to V, and VI to VIII. The overall quantitative dynamic index of the population, V'_{pi} (which incorporates external disturbances), was lower than V_{pi} (under random disturbances alone), though both were greater than zero. The fact that V'_{pi} approaches zero suggests that the population exhibits limited growth and is tending toward stability. Furthermore, the *C. japonicum* population showed high sensitivity to environmental or anthropogenic disturbances. The maximum

stochastic disturbance risk value (P_{max}) was positive but very small, indicating that the population remains relatively vulnerable.

Table 3. Age class dynamic index of *Cercidiphyllum japonicum* population

Dynamic index	Dynamic index value (%)
V_I	-93.33
V_{II}	20.00
V_{III}	-20.00
V_{IV}	60.00
V_V	-14.29
V_{VI}	28.57
V_{VII}	80.00
V_{pi}	22.27
V'_{pi}	2.78
P_{max}	12.5

Static life table and survival curve of C. japonicum population

With plant development, all key survival parameters of the *C. japonicum* population - including the standardized survival number (l_x), standardized mortality (d_x), mean survival number (L_x), and total survival number (T_x) - consistently decreased (Table 4). Individual life expectancy (e_x) demonstrated a pattern of initial increase followed by subsequent decline with advancing age class. The maximum life expectancy occurred in age class III, reflecting more vigorous growth among middle-aged individuals. Beyond age class IV, a gradual reduction in life expectancy was observed, indicating progressively evident senescence.

Table 4. Static life table of *Cercidiphyllum japonicum* population

Age class	Diameter at breast height (cm)	Mid-value of class	A_x	a_x	l_x	$\ln l_x$	d_x	q_x	L_x	T_x	e_x	K_x
I	0-10	5	1	66	1000	6.91	652	0.65	674	1371	1.37	1.05
II	10-20	15	15	23	348	5.85	167	0.48	265	697	2.00	0.65
III	20-30	25	12	12	182	5.20	61	0.33	152	432	2.38	0.41
IV	30-40	35	15	8	121	4.80	30	0.25	106	280	2.31	0.29
V	40-50	45	6	6	91	4.51	30	0.33	76	174	1.92	0.41
VI	50-60	55	7	4	61	4.10	15	0.25	53	98	1.63	0.29
VII	60-70	65	5	3	45	3.82	0	0.00	45	45	1.00	0.00
VIII	70-80	75	1	3	45	3.82	-	-	-	0	0	-

The survival curve of the *C. japonicum* population showed a declining trend overall (Figure 3). A sharp decrease was observed from age class I to II, followed by a more gradual decline from age classes II to V. The rate of decline intensified again between age classes V and VI, after which the population stabilized from age classes VI to VIII. Model fitting of the survival curve demonstrated that both the power function and exponential function models reached a highly significant level ($p < 0.001$). The exponential function model yielded a lower R^2 value but a higher F-value compared to the power function model (Table 5), suggesting that the survival curve of *C. japonicum* approximates the Deevey-III type, characterized by high mortality in early life stages (Deevey, 1947). These modeling results are generally consistent with the observed trends in the survival curve. Both the mortality rate (q_x) and the disappearance rate (K_x) curves displayed an overall decreasing trend, with mortality rate showing relatively minor fluctuations (Figure 4). Notably, both curves

reached a trough at age class IV and peaked at age class V. The two survival curves Deevey- II and Deevey-III approach the exponential function and the power function respectively.

Table 5. Test models of survival curves of *Cercidiphyllum japonicum* population

Survival curve	Fitting model	Fitting result	R ²	F	P
Deevey- II	$N_x = N_0 e^{-bx}$	$N_x = 6.975e^{-0.084x}$	0.944	119.442	0.000
Deevey-III	$N_x = N_0 x^b$	$N_x = 7.092x^{-0.298}$	0.985	447.899	0.000

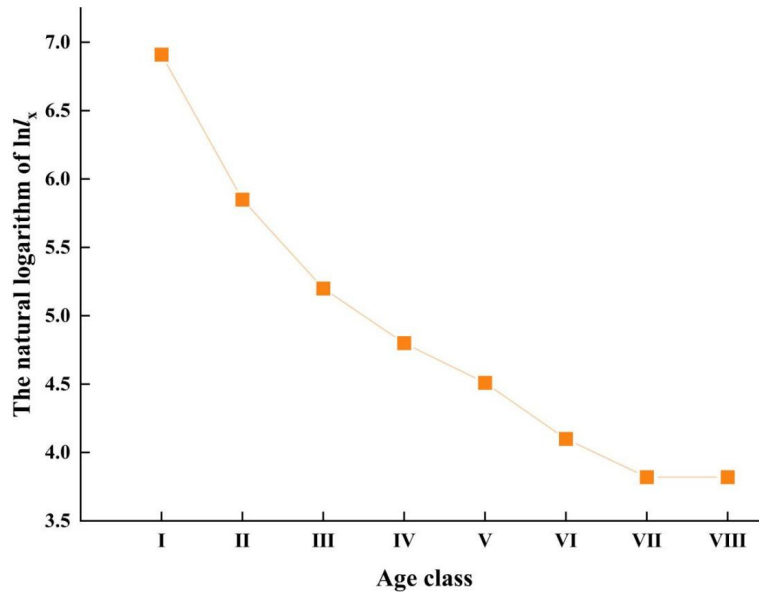


Figure 3. Survival curve of *Cercidiphyllum japonicum* population
 $\ln l_x$: logarithmic standardized survival number

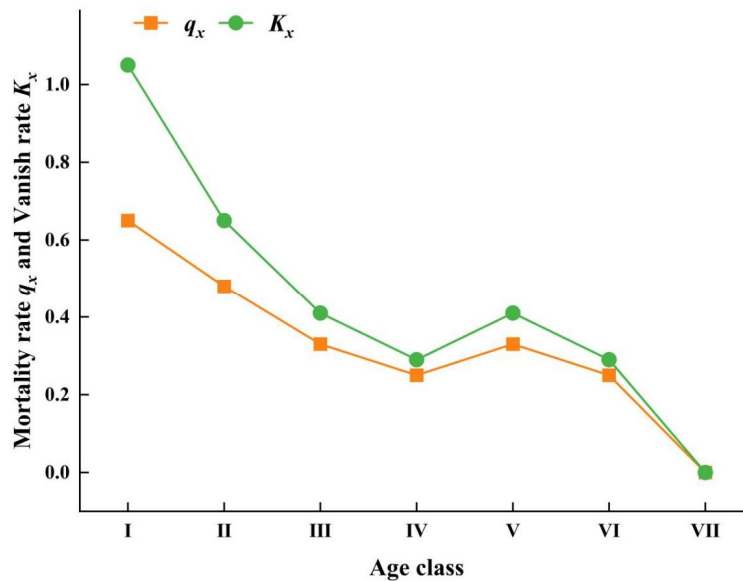


Figure 4. Mortality rate and vanish rate of *Cercidiphyllum japonicum* population
 q_x Indicates the mortality rate, K_x indicates the vanish rate

Survival analysis of C. japonicum population

As the plants developed, the survival rate $S_{(i)}$ of the *C. japonicum* population decreased, while the cumulative mortality rate $F_{(i)}$ increased, with the former remaining considerably lower than the latter throughout the observed period (Figure 5). The mortality density function $f_{(i)}$ and the hazard rate function $\lambda_{(i)}$ exhibited similar trends, both peaking in age class I and decreasing sharply from age class I to II (Figure 6). After age class II, the changes in both curves stabilized, though the hazard rate consistently remained above 0.25. By age class VI, the survival rate had declined to 0.05, and the cumulative mortality rate had risen to 0.95, while the mortality density reached its minimum value (0). Collectively, the four survival function curves reflect a population dynamic marked by early-stage decline, mid-term stability, and late-stage senescence.

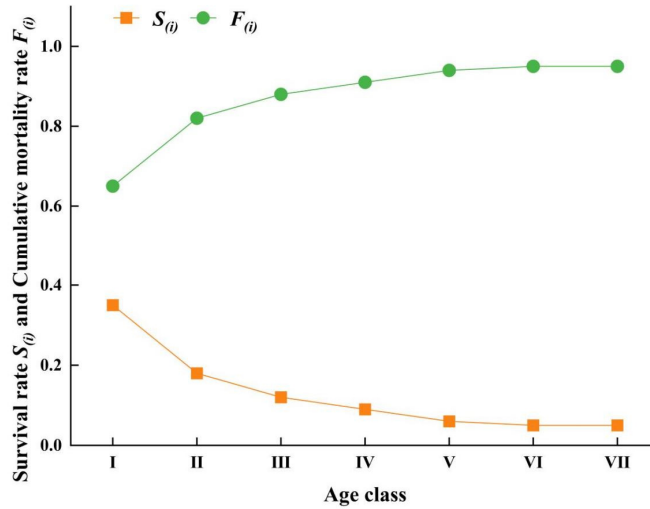


Figure 5. Survival rate and cumulative mortality rate functional curves of *Cercidiphyllum japonicum* population
 $S_{(i)}$ indicates the survival rate, $F_{(i)}$ indicates the cumulative mortality rate

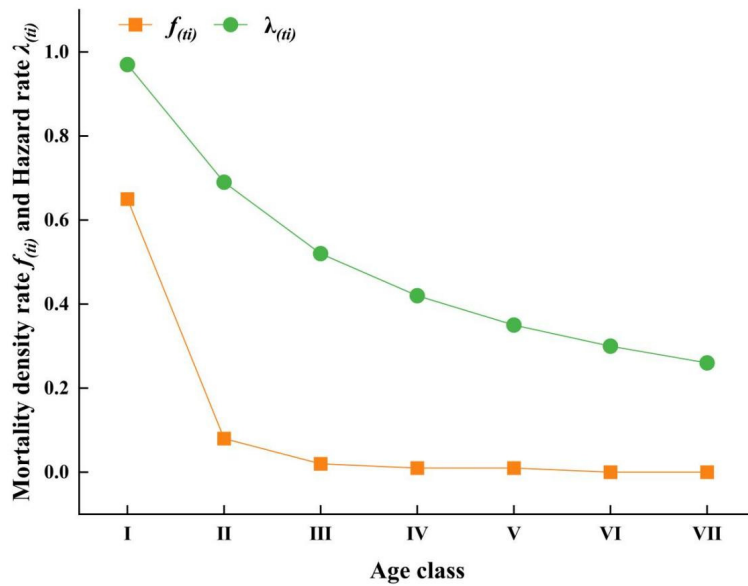


Figure 6. Mortality density and hazard rate functional curves of *Cercidiphyllum japonicum* population
 $f_{(i)}$ indicates the mortality density rate, $\lambda_{(i)}$ indicates the hazard rate

Time sequence prediction of C. japonicum population

Using the current number of individuals in each age class as the baseline, time-series forecasting was performed based on the single moving average method to project population sizes after 2, 4, and 6 age classes (Figure 7). After 2 age classes, the number of individuals in age classes II and IV decreased, while that in age class VI remained stable; all other age classes showed an increase in predicted individual numbers. After 4 or 6 age classes, only age classes IV and VI experienced a decline in individual numbers, whereas all other classes continued to increase. The overall fluctuation in population numbers across future age-class intervals can be attributed to the scarcity of young trees in the current population structure.

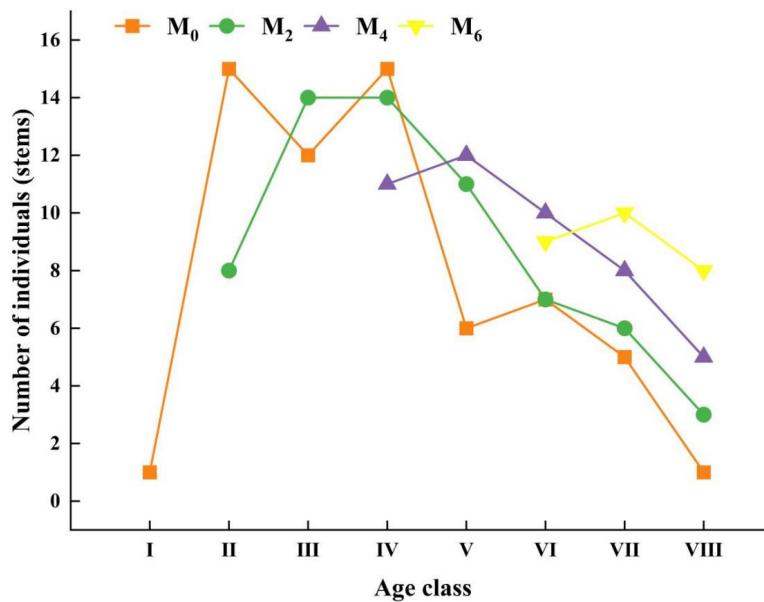


Figure 7. Time sequence prediction of number dynamics of *Cercidiphyllum japonicum* population. M₀ is the current number distribution curve of *C. japonicum* in various age classes; M₂ is the predicted 2-age classes curve; M₄ is the predicted 4-age classes curve; M₆ is the predicted 6-age classes curve

Discussion

Population structure characteristics

Population age structure is influenced by both biotic and abiotic factors (Velázquez *et al.*, 2016). This study found that wild *C. japonicum* in the Houhe National Nature Reserve predominantly grows in weakly acidic, organic-rich sandy yellow-brown soils (Table 1, Table 2). This soil type aligns with the species' known habitat preferences and is considered favorable for its growth (Yang *et al.*, 2012). The population exhibits an irregular spindle-shaped pyramid structure, a pattern consistent with many rare and endangered woody plants such as *Acer yangbiense* (Tao *et al.*, 2020), *Parakmeria omeiensis* (Yu *et al.*, 2020), and *Cinnamomum chago* (Zhang *et al.*, 2020). A defining feature of this structure is the severe scarcity of young individuals, particularly germinated seedlings, coupled with the dominance of middle-aged trees (Figure 2).

The current seedling population of *C. japonicum* primarily consists of sprouts, facing a shortage of seedlings originating from seeds. This is likely due to the wide spacing between individuals or scattered distribution, which limits pollination and fertilization. The dioecious nature of *C. japonicum* further intensifies the difficulty of seedling establishment through sexual reproduction (Yang *et al.*, 2012). Numerous studies have also identified sprouting as a prominent regeneration strategy in this species, particularly when seedling

establishment is constrained (Sakio *et al.*, 2002; Kubo *et al.*, 2005). While sprouting helps compensate for the lack of seedlings and contributes to short-term population maintenance (Bond and Midgley, 2001), the complete absence of germinated seedlings in age class I in this study strongly supports the prevalence of this vegetative strategy. However, although sprouting can prolong the lifespan of genetic individuals in the short term, it may lead to reduced genetic diversity and diminish the population's capacity to adapt to environmental changes in the long run. This reliance on vegetative regeneration is also observed in other rare woody species in montane riparian zones, such as *C. japonicum* and *Euptelea pleiosperma* (Wei *et al.*, 2015; Meng *et al.*, 2020).

The number of individuals decreases from the middle age classes toward both younger and older classes (Table 4; Figure 3). The scarcity of young individuals undermines the long-term stability of middle-aged and older cohorts (Swamy *et al.*, 2011). When subjected to external disturbances, the population becomes highly vulnerable to decline. The high maximum stochastic disturbance risk (P_{max}) further indicates the population's sensitivity to habitat conditions, aligning with the established principle that populations lacking renewable young individuals are prone to regression (Table 3; Sirkiä *et al.*, 2010). In summary, the current relative stability of this *C. japonicum* population - characterized by its spindle-shaped structure, absence of seedlings, and dominance of sprouting - heavily depends on existing middle-aged individuals, indicating a high risk of future population decline.

Population dynamics and development trends

Population dynamics reflect the interaction between individual viability and environmental conditions (Fuchs *et al.*, 2000; Bierzychudek, 2014). Within this process, seedling growth and survival directly determine the success of natural regeneration (Ellsworth *et al.*, 2004; Wright *et al.*, 2015) and govern population renewal (Comita *et al.*, 2009). In this study, the survival curve of the *C. japonicum* population conformed to the Deevey-III type (Table 5). Four survival functions - mortality rate, disappearance rate, and the population dynamic index (V'_{pi} approaching 0) - collectively indicated high juvenile mortality (Table 3; Figure 4). Similar patterns have been reported in populations from the Rhodope Mountains in Greece (Milios *et al.*, 2008) and Parque Nacional Puyehue in Chile (Lusk *et al.*, 2011), underscoring the role of species-specific biological traits and environmental filtering. Although *C. japonicum* produces abundant small, winged seeds to enhance dispersal and evade predation (Li *et al.*, 2008; Wu and Du, 2008), the resulting seedlings are fragile (Tíscar, 2019) and experience intense environmental filtering. Combined with the limited nutrient reserves in the seeds (Qi *et al.*, 2012), these factors contribute to low seedling survival rates (Zhang *et al.*, 2015). Furthermore, naturally sprouted ramets often cluster under the canopy, leading to high juvenile mortality due to strong self-thinning (Comita *et al.*, 2009). Furthermore, the forest floor litter hinders newly germinated seedlings from establishing contact with the soil in a timely manner, thereby contributing to the low survival rate of young individuals (Kubo *et al.*, 2004). Successful seedling establishment typically requires more drastic disturbances, such as valley floor flooding that clears away the litter and exposes bare soil, to create the habitat conditions necessary for the germination and survival of this species (He *et al.*, 2009).

The static life table reflects fundamental population attributes and adaptive conditions under intraspecific and interspecific interactions (Wang *et al.*, 2004; Omelko *et al.*, 2018). Life expectancy (e_x) in the *C. japonicum* population increased initially, peaking in age class III, indicating highest environmental adaptability at this stage (Table 4). As plants grew, limited resources and space intensified competition, which led to a decline in life expectancy. This pattern is consistent with findings from Rhododendron populations (Zhang *et al.*, 2024), where strong competition was associated with high hazard rates and low survival throughout the life cycle. It is hypothesized that the observed increase in mortality and vanish rates at Age Class V is a consequence of historical excessive logging (Figure 4), rather than a result of physiological senescence (which typically begins at a DBH of 115-125 cm; Ding *et al.*, 2022) or size-related constraints. Anthropogenic disturbance is a major driver of population decline (Vacek *et al.*, 2015). Field surveys and local accounts confirm

that *C. japonicum*, valued for its high-quality timber (Zou *et al.*, 2022), has been subjected to overharvesting, drastically reducing population size and exacerbating its endangered status (Guan *et al.*, 2016). The inferred impact of historical logging aligns with survival analysis, which revealed a pattern of early decline, mid-term stability, and late senescence (Figure 5; Figure 6). Although the population is classified as growing (V'_{pi} approaches 0), its growth is minimal - consistent with observations in *Populus wulianensis* (Wu *et al.*, 2021). This marginal growth is likely sustained by the current abundance of middle-aged individuals, which may support short-term regeneration in the absence of disturbance. Furthermore, time-series projections also suggest a limited potential for population recovery (Figure 7).

Conservation and restoration of the populations

The extant *Cercidiphyllum japonicum* population is small, exhibits almost no natural seedling regeneration, and has low resistance to disturbance and limited regenerative capacity. Protecting the ecological environment for young individuals, ensuring sufficient seedling supply, and enhancing the population's natural reproductive and dispersal capabilities are crucial to halting its decline and promoting recovery. Based on these findings, we recommend the following conservation measures: First, implement precision habitat management to promote natural regeneration. Given that *C. japonicum* is concentrated in valley bottoms at elevations of 1,200-1,350 m and depends on slightly acidic, organic-rich soils, such areas should be designated as core protection zones. To address the severe shortage of seedlings in the understory, moderate thinning should be applied to create forest gaps and improve light conditions. This should be complemented by artificial seeding and seedling protection measures to directly enhance seedling establishment and survival rates, thereby facilitating natural regeneration of the population (Perrino and Wagensommer, 2021). Second, enhance the maintenance of existing individuals and reinforce population structure. In light of the reliance on sprouting for regeneration, middle-aged and older individuals should receive regular care, including appropriate pruning to stimulate vigorous sprouting and maintain the vitality of genetic individuals. Concurrently, artificial propagation and ex-situ conservation should be actively implemented to expand population size (Tian *et al.*, 2024) and mitigate the high hazard rates and low survival resulting from resource competition. Finally, establish a long-term conservation and collaborative management framework. Building on the permanent plots established in this study, a long-term monitoring network should be established to regularly assess population dynamics. At the same time, given the historical felling of *C. japonicum* by local residents, community cooperation should be strengthened through awareness campaigns and protective education to eliminate illegal logging (Kroon *et al.*, 2000), integrating scientific management with community-based stewardship.

Conclusions

This study elucidates the current status and future trajectory of the *Cercidiphyllum japonicum* population in Houhe National Nature Reserve, Hubei Province. Key findings reveal a spindle-shaped age structure characterized by a complete absence of germinated seedlings and reliance on sprouting for regeneration. Although population dynamic indices classify it as growing and approaching stability ($V_{pi} > V'_{pi} > 0$), this stability is precarious and largely dependent on existing middle-aged individuals. Survival analysis indicates a Deevey-III type survival curve, reflecting high early-age mortality. Time-series projections further confirm an uncertain future trajectory due to insufficient recruitment of young individuals. Based on these findings, conservation efforts should prioritize overcoming the bottleneck in seedling regeneration. Specifically, targeted measures - including precision habitat management, maintenance of healthy sprouting individuals, and establishment of long-term monitoring - are essential for the sustainable persistence of this endangered population. This study provides critical data support and clear guidance for the scientific conservation of *C. japonicum*.

Authors' Contributions

Conceptualization: YLY; Data curation: DB and PQ; Formal analysis: DB; Funding acquisition: YLY; Investigation: DB, HQK, YLY, and PQ; Methodology: YLY and DB; Software: DB; Visualization: DB and LCY; Writing - original draft: DB; Writing - review and editing: YLY.

All authors read and approved the final manuscript.

Acknowledgements

This work was supported by the Jingzhou City Jingzhou District Lingjiao Lake National Wetland Park management office project (grant number HBCM-2023N-016).

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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