

Population Structure and Dynamics of the Chinese Endemic Plant *Torreya fargesii* Postprint

Authors: Jiang Bo, Zhou Xianrong, Shang Jin, Wang Jianhua, Song Hang, Qin Mingyi, Liu Xuening, Wang Qing

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Abstract

To investigate the population status and predict the dynamic trends of *Torreya fargesii*, an endemic gymnosperm in China, we examined 15 remnant populations distributed across Chongqing, Sichuan, Shaanxi, Hubei, Anhui, Henan, and Gansu provinces. We constructed diameter-class and height-class structure profiles, compiled static life tables, plotted survival curves, mortality and vanishing rate curves, and analyzed population dynamics using spectral analysis. The results showed that *T. fargesii* populations exhibited low density, averaging 5.33 individuals/100m². The Shennongjia population (SN) had the highest density at 9.58 individuals/100m², while the Chengkou population (CK) had the lowest density at 2.75 individuals/100m². The diameter-class structure was dominated by individuals in younger age classes, indicating a growing age structure. Diameter-class structures varied significantly among local populations; except for the Baoxing population (BX), all other populations showed incomplete diameter-class distributions. In the height-class structure, individuals below 6 m accounted for 88.74%, with the vast majority occupying the shrub layer of the community. Life expectancy fluctuated markedly among age classes, with lower values observed in age classes III and VII. The survival curve of *T. fargesii* populations tended toward Deevey-III type. The mortality and vanishing rate curves showed consistent trends, both peaking at age classes III and VII. In addition to being influenced by the fundamental wave, the population dynamics of *T. fargesii* also exhibited significant small periodic fluctuations at age classes III, V, and VII. *Torreya fargesii* is a long-lived relict plant with island-like patchy distribution, small population size, and poor natural regeneration capacity, facing extinction risk and requiring immediate conservation measures.

Full Text

Preamble

Population Structure and Dynamics of *Torreya fargesii* Franch., a Plant Endemic to China

Jiang Bo, Zhou Xianrong*, Shang Jin, Wang Jianhua, Song Hang, Qin Mingyi, Liu Xuening, Wang Qing

College of Life Science and Technology, Yangtze Normal University, Fuling 408100, China

Abstract

To assess the current status and predict population trends of *Torreya fargesii*, an endemic gymnosperm in China, we investigated remnant populations across Chongqing, Sichuan, Shaanxi, Hubei, Anhui, Henan, and Gansu provinces. Based on 18,000 m² of sample plots established at 15 sites, we constructed diameter-class and height-class structure diagrams, compiled a static life table, and analyzed population dynamics using spectral analysis.

Our findings reveal that *T. fargesii* populations exhibit low overall density, averaging 5.33 individuals per 100 m². The Shennongjia population showed the highest density (9.58/100 m²), while the Chengkou population was lowest (2.75/100 m²). The diameter-class structure demonstrated an expanding age structure with a higher proportion of younger age classes. However, significant variations existed among local populations, with most showing incomplete diameter-class distributions except for the Baoxing population. In the height-class structure, individuals shorter than 6 m accounted for 88.74% of all trees, indicating that most individuals occupy the shrub layer within their communities.

Life expectancy varied substantially across age classes, with relatively low values in the third and seventh age classes. The survivorship curve corresponded to a Deevey-III type, while mortality and disappearance rate curves exhibited peaks in the third and seventh age classes. Spectral analysis revealed that population dynamics followed one major trend with clear fluctuations in smaller growth and death cycles. *Torreya fargesii* is an ancient, long-lived relict species with patchy, isolated distribution, small population sizes, and poor natural regeneration, facing imminent extinction risk that requires urgent conservation action.

Keywords: *Torreya fargesii*; population density; diameter-class structure; height-class structure; static life table; survivorship curve; spectral analysis

Introduction

Population structure and dynamics are fundamental topics in population ecology. Population structure reflects not only the distribution and configuration of individuals of different sizes but also reveals population dynamics. Life tables and survivorship curves are core tools for studying quantitative changes in populations, while spectral analysis serves as a mathematical tool for exploring periodic fluctuations in population distribution, structural changes, and age replacement processes. The natural regeneration process of a population can be manifested through fluctuations in the number of individuals across different age classes.

Torreya fargesii (Taxaceae) is a rare Tertiary relict plant endemic to China, valued for timber, oil production, and afforestation. Its distribution has progressively contracted to scattered locations in subtropical mountainous regions, including the southern slopes of the Qinling Mountains, Daba Mountains, Qionglai Mountains, Dalou Mountains, Wushan, Wulingshan, and Dabie Mountains, at elevations of 800–2700 m. The species is currently vulnerable and under second-class state protection.

Previous research on *T. fargesii* has focused on resource distribution, genetic diversity, and seed characteristics, with limited studies on community features, species diversity, and population niches in specific regions. Inadequate understanding of community characteristics and population status has hindered effective conservation efforts, leading to severe population declines and community degradation. To comprehensively understand the population status of *T. fargesii* and predict its trends, this study analyzed 15 remnant populations across Chongqing, Sichuan, Shaanxi, Hubei, Henan, and Gansu. Using diameter class as a proxy for age class, we analyzed population structure, constructed survivorship, mortality, and disappearance curves, and applied spectral analysis to examine periodic fluctuations, providing a scientific basis for conservation of *T. fargesii* populations and natural forests.

1. Study Area Overview

The study area encompassed 15 sites across subtropical China, including: Jinpo Mountain National Nature Reserve in Nanchuan District, Chongqing; Wulipo National Nature Reserve in Wushan County, Chongqing; Daba Mountain National Nature Reserve in Chengkou County, Chongqing; Huae Mountain National Nature Reserve in Wanyuan City, Sichuan; Baoxing County, Sichuan; Lueyang County, Shaanxi; Zhenping County, Shaanxi; Shennongjia National Nature Reserve, Hubei; Shibalichangxia National Nature Reserve in Zhuxi County, Hubei; Yingshan County, Hubei; Changyang Tujia Autonomous County, Hubei; Wufeng County, Hubei; Foziling Nature Reserve in Huoshan County, Anhui; Huangbaishan National Forest Park in Shangcheng County,

Henan; and Wudu District, Gansu. The region features a subtropical humid monsoon climate.

2. Methods

2.1 Plot Survey

Based on comprehensive reconnaissance, we established plots in locations with relatively concentrated *T. fargesii* distribution and intact community preservation. Plot areas varied from 800–2400 m² depending on habitat conditions and population size, totaling 18,000 m² across all sites. Each plot was divided into 20 m × 20 m quadrats, which were further subdivided into 5 m × 5 m subplots for census of all *T. fargesii* individuals.

2.2 Population Structure Analysis

We used diameter class as a proxy for age class to analyze population age structure. Based on growth patterns and life history characteristics of *T. fargesii*, and referencing classification standards for species such as *Davidia involucrata* and *Pinus dabeshanensis*, we divided diameter at breast height (DBH) into 11 classes (I–XI): Class I, <0.33 m; Class II, DBH < 2.5 cm; and subsequent 5 cm intervals up to Class XI, DBH 42.5 cm. Height classes were defined with 2 m intervals below 10 m and 5 m intervals above 10 m. We counted individuals in each diameter and height class and constructed structure diagrams with percentage of individuals on the horizontal axis and class levels on the vertical axis.

2.3 Static Life Table Compilation

Following established principles for static life table construction and using smoothing techniques to adjust actual individual counts within age classes to avoid negative mortality rates, we compiled a static life table for *T. fargesii* using standing tree diameter classes to represent age classes. Parameters were calculated following methods described in previous studies.

2.4 Survivorship, Mortality, and Disappearance Curves

Based on the static life table, we plotted survivorship, mortality, and disappearance curves with age class (corresponding to diameter class) on the horizontal axis and standardized survival numbers, mortality, and disappearance rates on the vertical axis.

2.5 Spectral Analysis

Spectral analysis, based on Fourier series expansion, is widely used to study natural regeneration processes by revealing periodic fluctuations in population size.

The natural regeneration process of *T. fargesii* can be expressed through fluctuations in individual numbers across age classes. Complex periodic phenomena can be decomposed into sine waves:

$$N_t = A_0 + \sum_{k=1}^{n/2} A_k \sin(\omega_k t + \theta_k)$$

where N_t is population size at time t , A_0 is the mean of periodic variation, A_k is the amplitude of each harmonic (reflecting the importance of each cycle), ω_k and θ_k are harmonic frequency and phase angle, t is the time series, and n is the total length of the time series (i.e., number of age classes). Parameters were estimated using standard formulas.

3. Results

3.1 Population Density

Across the 18,000 m² survey area, we recorded 959 *T. fargesii* individuals, with an average density of 5.33 individuals per 100 m². Significant variation existed among local populations, with Shennongjia (SN) showing the highest density (9.58/100 m²) and Chengkou (CK) the lowest (2.75/100 m²). [Figure 1: see original paper]

3.2 Diameter-Class Structure

Local populations exhibited distinct diameter-class structures, reflecting both habitat influences and population dynamics. Based on structural completeness, populations were classified as either normal or abnormal types. Baoxing (BX), Lueyang (LY), Shennongjia (SN), and Zhuxi (ZX) were normal-type populations with complete or nearly complete, continuous diameter distributions and adequate seedlings, indicating healthy regeneration.

Abnormal-type populations, including Nanchuan (NC), Wushan (WS), Chengkou (CK), Wufeng (WF), and Shangcheng (SC), showed severe diameter-class deficiencies, predominantly in small size classes. Seedlings and saplings accounted for 68.00%, 76.92%, and 86.00% of individuals in these populations, respectively. The overall population showed a pyramidal age structure, but with extremely low proportions of seedlings and middle-aged individuals, suggesting weak potential for natural regeneration and instability during transition from young to middle age classes. Continued decline in young individuals may lead to population recession. [Figure 2: see original paper]

3.3 Height-Class Structure

In the overall population height-class structure, individuals below 6 m accounted for 88.74% of all trees, with proportions decreasing at higher levels (45.78%, 21.79%, and 14.39% for successive classes). Most individuals occupied the shrub layer within their communities. Baoxing (BX), Lueyang (LY), Zhenping (ZP), Shennongjia (SN), and Wanyuan (WY) showed relatively complete height-class distributions, while other populations exhibited significant gaps. Mean tree height was lowest in Huoshan (HS) at 1.31 m and highest in Baoxing (BX) at 4.40 m. The height-class structure mirrored the diameter-class structure, forming an approximate pyramid shape closely related to diameter composition. [Figure 3: see original paper]

3.4 Static Life Table

Due to incomplete diameter-class structures in most populations (especially abnormal types), we compiled a single static life table for the entire species rather than separate tables for each population. Using smoothing techniques to adjust age classes with irregular survival numbers, we processed the data in segments. Life expectancy varied considerably across age classes, peaking in the second age class and declining thereafter. High mortality in the third age class caused a life expectancy fluctuation, with mortality and disappearance rates showing peaks in both the third and seventh age classes.

3.5 Survivorship, Mortality, and Disappearance Curves

The survivorship curve tended toward Deevey-III type, reflecting a concave pattern characteristic of growing populations with high early mortality followed by relatively low, stable mortality later. This aligns with the diameter-class structure analysis. Mortality and disappearance curves showed identical trends with two distinct peaks at the third and seventh age classes. The first peak likely results from intense environmental filtering during early life stages due to weak competitive ability, while the second peak reflects increased resource competition as trees age. [FIGURE:4, FIGURE:5]

3.6 Spectral Analysis of Population Dynamics

Due to large differences in individual numbers across age classes, we log-transformed the data before analysis. The total number of age classes was 11, yielding six harmonics. The fundamental wave (first harmonic) showed the largest amplitude, indicating it plays the dominant role in population dynamics and represents the inherent periodic fluctuation. Small-cycle fluctuations were evident in various populations: Chengkou (CK) and Shangcheng (SC) showed fluctuations at the third harmonic; Wanyuan (WY) and Zhenping (ZP) at the second harmonic; and Zhuxi (ZX) and Wudu (WD) at the fourth harmonic. These small cycles relate to growth phases during young and middle age stages,

where increased demands for light and nutrients trigger intense self-thinning and competition, resulting in high mortality and low life expectancy.

4. Discussion

Torreya fargesii is sporadically distributed in localized mountainous regions of China's subtropical zone, scattered within evergreen broad-leaved forests, mixed conifer-broadleaf forests, evergreen-deciduous broadleaf mixed forests, or shrub communities. The species exhibits low population density, small population sizes, and island-like discontinuous distribution, confirming its relict status.

The extremely scarce seedlings in *T. fargesii* populations indicate weak potential regeneration capacity. Our previous research found low fruiting rates, seed dormancy, and heavy predation by squirrels, particularly flying squirrels, resulting in extremely low seed production and germination rates. These factors create a major bottleneck for natural regeneration. While seedlings prefer shade, insufficient light for saplings and adults may hinder physiological activities, flower bud differentiation, and seed development.

Normal-type populations (Shennongjia and Zhuxi) showed pyramidal diameter-class structures with relatively abundant young individuals and continuous distributions. In contrast, abnormal-type populations exhibited severe diameter-class deficiencies, predominantly small size classes, with scarce or absent seedlings and middle-aged trees. Human disturbances such as logging, fuelwood collection, and grazing have severely impacted primary habitats, causing vegetation degradation into patchy secondary shrub communities. Poor site conditions, soil erosion, and reduced soil moisture in karst landscapes have further impaired seed germination and seedling growth.

The Deevey-III survivorship curve, high early mortality, and peaks in mortality/disappearance rates at the third and seventh age classes all indicate population decline characteristics consistent with other rare plants such as *Taxus yunnanensis* and *Cinnamomum micranthum*. The asynchronous dynamics among local populations reflect basic periodic fluctuations within fundamental cycles, related to both biological characteristics and varying degrees of competition and human disturbance.

Metapopulation theory suggests that local populations may experience stochastic extinction due to fragmented habitats or establish new populations through inter-patch migration. Habitat fragmentation limits population size, making small populations susceptible to genetic drift and inbreeding depression. Altitude appears to be the primary ecological factor affecting distribution, and global warming may shift optimal elevations upward, further intensifying habitat fragmentation and threatening species survival.

Conservation Implications

Given the endangered status of *T. fargesii*, we recommend: (1) strengthening in-situ conservation of local populations and their habitats to prevent ecosystem destruction, particularly establishing protected areas for populations in unprotected regions such as Baoxing, Lueyang, and Wufeng; (2) prioritizing protection of normal-type populations with relatively complete structures; (3) implementing ex-situ conservation measures for abnormal-type populations with few individuals, severe class deficits, and heavily disturbed habitats by transplanting them to suitable areas; (4) conducting in-depth research on reproductive biology, including factors affecting seed production, dormancy mechanisms, and vegetative propagation techniques such as cutting and tissue culture to improve germination and seedling survival rates; and (5) studying photosynthetic physiology and gap characteristics to regulate canopy closure and enhance natural regeneration.

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