SPATIAL DISTRIBUTION PATTERNS OF THE MAIN TREE POPULATIONS IN *ABIES* FORESTS IN SOUTHEASTERN XIZANG, CHINA

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Abstract. In recent years, the physiological decline of natural fir forests in southeastern Xizang, China, has threatened regional ecological sustainability. Tree populations from three fir forests in Nyingchi were surveyed. The pure *Abies georgei* var. *smithii* forest on Sygera Mountain in Bayi District had 408 trees ha^{-1}. The coniferous mixed forest in Zayu County, dominated by *Abies chayuensis*, *Pinus armandii*, and *Betula utilis*, had 745 trees ha^{-1}. The dark coniferous mixed forest in Motuo County, composed of *Abies delavayi* var. *motuoensis* and *Tsuga dumosa*, had 321 trees ha^{-1}. Among the three communities, only *B. utilis* spanned seven diameter classes, while the other five tree populations all exhibited a positive pyramidal structure with abundant seedlings but scarce medium and large-diameter trees. Point pattern analysis revealed clustered distributions for small trees and random distributions for large trees. Spatial correlations among populations were mostly negative or nonexistent. These findings elucidate local population strategies and support restoration efforts for fir forests in southeastern Xizang.

Keywords: *typical plot survey method, diameter structure, point pattern analysis, spatial correlation, fir forests*

Introduction

The spatial distribution patterns of populations have consistently been a core area of ecological research. These patterns not only reflect the spatial configuration of individual populations but also help to reveal population characteristics, interrelationships between populations, and survival strategies populations use to adapt to their environment (Liu et al., 2020). Studies have shown that the spatial distribution pattern of populations strongly depends on spatial scale, which may be influenced by factors such as intraspecies competition and diffusion limitations at relatively small scales. On a larger scale, it may be determined by habitat heterogeneity (Liu et al., 2024; Wang et al., 2024). Research conducted by Zhao et al. (2022) on the dark coniferous forest in the Miyaloa Mountains of western Sichuan has shown that populations of *Abies fargesii* var. *faxoniana* and *B.*

utilis at different developmental stages are influenced by various mechanisms within the 0–60 m spatial scale and that the spatial distribution patterns of the populations varied at different spatial scales. Therefore, in studying tree populations within a community on the basis of spatial distribution patterns, it is important to consider the influence of multiple factors. This information is beneficial not only for understanding differences in environmental adaptation mechanisms between populations at different developmental stages but also for revealing population maintenance mechanisms and predicting population developmental trends. It is also highly important for promoting population renewal, restoration, and for the protection of biodiversity in ecosystems (Lv et al., 2023; Wiegand et al., 2021).

The point pattern analysis is currently one of the most widely used methods in population spatial pattern research. It was first proposed by Ripley in 1977, with its core being the construction of a two-dimensional distribution point map based on the spatial coordinates of plant individuals (Ripley, 1977). This breaks the scaling limits of traditional sampling methods and enables continuous analysis of population spatial structure. In 1983, Diggle further enhanced the analytical depth of this method by introducing the Monte Carlo test (Diggle, 1983). Through simulations of random distribution models for significance testing, this method not only accurately determines the distribution pattern types of populations but also reveals ecological relationships within and between species. Since its introduction to China by Zhang (1998), this method has rapidly become an important tool in forestry and ecological research. For example, Zhang et al. (2019) applied point pattern analysis to study the spatial patterns of main tree species in a spruce-fir mixed forest in Changbai Mountain. Their research found that spruce seedlings tend to cluster around parent trees, while fir seedlings exhibit a random distribution. Based on these findings, they recommended supplementary planting around parent trees for spruce and uniform sowing for fir. These research results provide crucial evidence for formulating strategies to promote natural regeneration. Therefore, point pattern analysis can effectively connect population spatial characteristics with ecological processes, and has become a key tool for analyzing forest dynamics.

Abies is the second largest genus in the Pinaceae family, with approximately 50 species worldwide. China has the largest number of *Abies* plants, with approximately 28 species (Fu et al., 1999), which often form large-scale single-species and mixed forests in subalpine and valley areas and is becoming a typical representative community in southeastern Xizang. Trees of this genus are important for promoting ecological balance, maintaining forest biodiversity, and conserving water and soil resources. In recent years, owing to continuous changes in the global climate, biological limitations, frequent natural disasters, and other factors, the main forest layer of *Abies* forests in southeastern Xizang has declined. The structural characteristics of the forests, including tree composition, age, height, diameter, and spatial distribution, exhibit a state of imbalance, the deterioration of system functions and a continued decrease in the natural distribution area, which has had a strong impact on the integrity and stability of the ecological system in Xizang (Gao et al., 2021). Current research on fir forests in southeastern Xizang predominantly concentrates on endangered or rare plant species, with most studies confined to isolated geographical units, such as soil nutrient characteristics (Gao et al., 2021), tree life table analysis (Lu et al., 2010), and the impacts of freeze-thaw cycles on soil microbial community structure (Wei et al., 2024). While these investigations have provided crucial insights into the ecological traits and growth patterns of fir populations, systematic comparative studies across different regional forest types remain notably lacking, despite the extensive distribution of fir forests throughout southeastern Xizang. In addition, after an onsite ecological investigation, it was found that the number of large-diameter trees in fir forests is relatively small, and the crown width is generally narrow, indicating that there may be some issues with the sustainability and stability of these communities.

This study employed traditional plot survey methods to investigate the population structure of primary tree species within three natural fir communities in southeastern Xizang. The following questions were addressed: (1) What are the structural characteristics of each tree species in the fir forest in southeastern Xizang? (2) How the spatial distribution patterns of large trees, small trees, and different populations change with spatial scale? (3) How the spatial association between different populations changes with spatial scale? Ultimately, these strategies will contribute significantly to the entire region's sustainable development and ecological security. In summary, this study aims to systematically analyze the diameter class structure and multi-scale spatial patterns of major tree populations in the natural fir forests of southeastern Xizang, reveal the underlying ecological processes, and provide a scientific basis for the protection and sustainable management of the regional forest ecosystem.

Materials and methods

Study site

The distribution area of *Abies* forests in southeastern Xizang, China, was determined through the Plan for the Protection and Construction of Ecological Security Barriers in Xizang approved by the State Council in 2009 and field surveys. Three typical forest stands were selected in Bayi District, Zayu County, and Motuo County in Nyingchi on the basis of the habitat characteristics of the fir forest communities: a natural single-species forest of *A. georgei* var. *smithii*, a natural mixed forest of *A. chayuensis–P. armandii–B. utilis*, and a natural mixed forest of *A. delavayi* var. *motuoensis–T. dumosa* with low levels of human intervention (*Fig. 1*). Precipitation in these three areas mostly occurs from June to September, and the area has long sunshine hours. The rainy and hot weather coincides with the plant growing season. The elevation is high in the north and low in the south, and the soil typically has a low pH value, exhibiting acidity, and its color tends to be brownish.

The Bayi District (93°27′-95°17′ E, 29°21′-30°15′ N) is in the Nyenchen Tanggula Mountain region. The total area is 1.02×10^4 km^2, with an average altitude of 3000 m. The area has a plateau temperate humid-semihumid monsoon climate, with an average annual precipitation of 654 mm and an average annual temperature of 8.5°C (Yu et al., 2023).

Zayu County (97°27′ E, 28°56′ N) is in the high mountain canyon area of southeastern Xizang in the western section of the Hengduan Mountains, with a total area of 3.17×10^4 km^2 and an average elevation of 2800 m. This area has a subtropical humid monsoon climate, with an average annual precipitation of 801.1 mm and an average annual temperature of 12°C (Yang et al., 2013).

Motuo County (93°45′-96°05′ E, 27°33′-29°55′ N) is located in the lower reaches of the Yarlung Zangbo River, with a total area of 3.4×10^4 km^2 and an average altitude of 1200 m; it has a subtropical humid climate zone, with an average annual temperature of 16°C and an annual precipitation of approximately 2358 mm (Si et al., 2024).

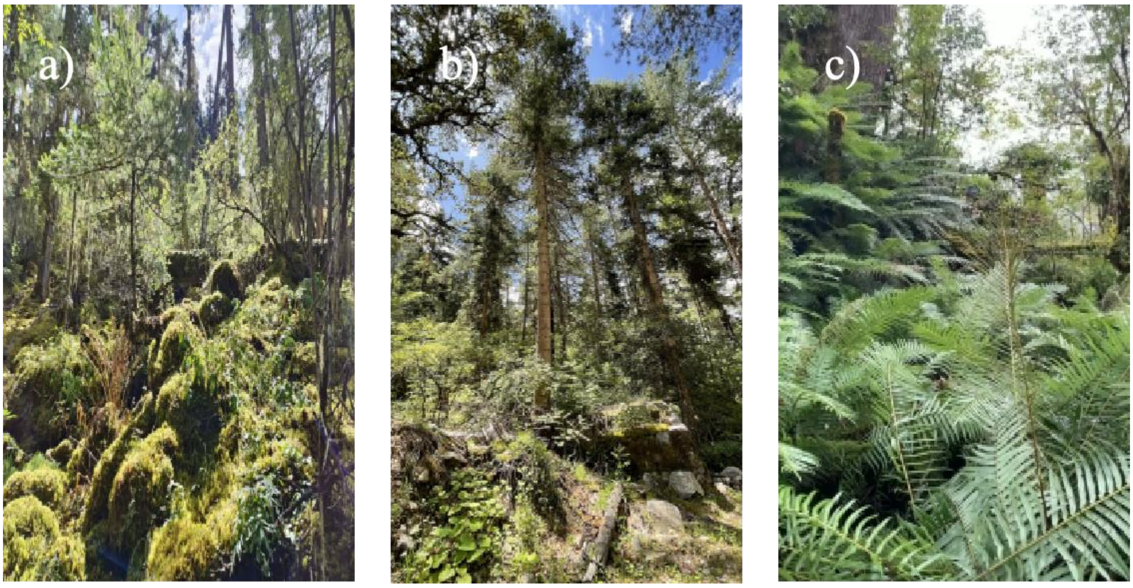

Figure 1. *Habitat of the Sample Plot. (a), (b), and (c) depict the sample plots in Bayi, Zayu, and Motuo, respectively*

Methods

Vegetation sampling

This study employed a differentiated plot design scheme that comprehensively considered the topographic characteristics and ecosystem heterogeneity of the research areas. In November 2018, a 100 m × 100 m fixed plot was established on the eastern slope of Sygera Mountain in Bayi District at an altitude of 3800 m. This decision was based on the relative ecological homogeneity of the fir forest ecosystem in this area, as larger plots are considered better suited to capturing the overall ecological characteristics of the region. Given the uniqueness of this sampling location, the plot was not assigned a specific numerical identifier. In contrast, within the natural fir forests of Cheyingou in Zayu County and near the 50K marker along the Zhamo Highway in Motuo County, where similar concerns about the overall condition of the fir forests exist, three 50 m × 50 m fixed plots (replicate plots) were established due to the complex terrain and other site-specific factors. These replicate plots were accordingly numbered (C_1-C_3 for Zayu County; M_1-M_3 for Motuo County) to distinguish sampling locations within each study area. The representativeness of the samples was enhanced by these replicate plots, enabling more accurate identification of common ecological features through repeated measurements of homogeneous ecosystem fragments (*Fig. 2*).

First, a coordinate system was established for each of the seven fixed plots, with due east as the X axis and due north as the Y axis. The fixed plot in Mount Sygera was divided into 25 20 m × 20 m cells, whereas each fixed plot in Zayu County and Motuo County was divided into 4 25 m × 25 m cells. Second, an adjacent grid method was adopted to conduct an individual tree measurement for all trees with base diameters ≥0.1 cm in each cell, tree species, base diameters, breast height diameters, tree heights, coordinates, and other indicators were measured and recorded. The basic information for the plots is shown in *Table 1*.

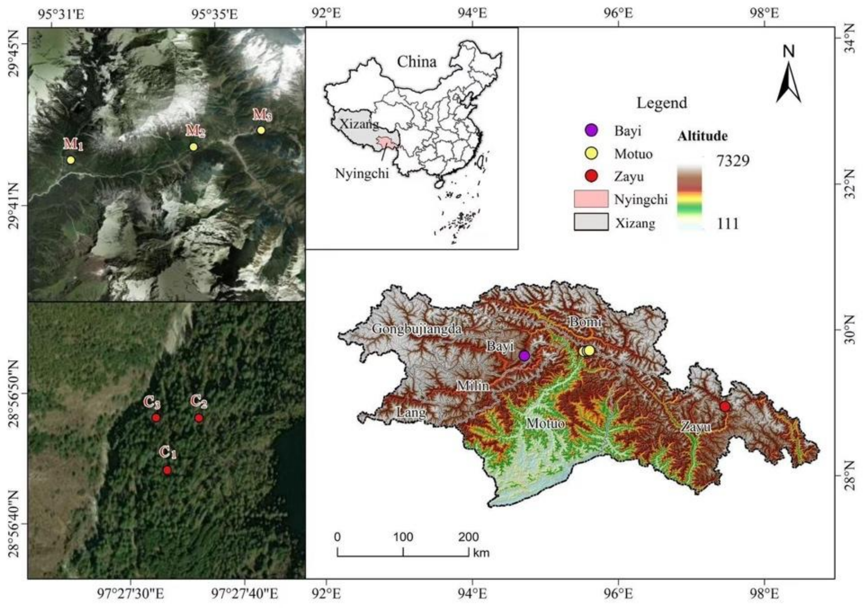

Figure 2. *Distribution map of sampling points*

Table 1. *Sample plot information*

Sampling point	Sample plot number	Latitude and longitude	Altitude/ m	Slope/°	Slope direction	Canopy density	Living land coverage/%	Proportion of tree species
Bayi		94°42′38.24″E 29°38′34.62″N	3800	16	E	0.70	90	1
Zayu	C_1	97°27′33.19″E 28°56′44.12″N	3061	4	NW	0.75	55	5:5.3:1
	C_2	97°27′35.98″E 28°56′48.12″N	3045	21	NW	0.64	45	1.6:1:1.3
	C_3	97°27′32.22″E 28°56′48.14″N	3071	7	NW	0.66	35	2.4:2.3:1
Motuo	M_1	95°31′28.24″E 29°42″7.77″N	2647	7	SE	0.17	89	1:4.4
	M_2	95°34′28.77″E 29°42′27.28″N	2768	6	SE	0.30	83	1:6.3
	M_3	95°36′8.18″E 29°42′51.35″N	2883	15	SW	0.68	86	1.5:1

The aspect codes in this table represent slope orientations. "E" is East slope (facing east), "NW" is Northwest slope (facing northwest), "SE" is Southeast slope (facing southeast), and "SW" is Southwest slope (facing southwest). The proportions of tree species in each sample plot are as follows: Bayi: *A. georgei* var. *smithii*; Zayu: *A. chayuensis*, *P. armandii*, *B. utilis*; Motuo: *A. delavayi* var. *motuoensis*, *T. Dumosa*

Diameter classification

Based on the growth and development characteristics of trees and the specific conditions of the study area, and referring to previous methods for classifying diameter classes in fir forests (Ren et al., 2021), this study selected basal diameter and diameter at breast height (DBH) as indicators for classifying the diameter classes of tree species in the forest. Specifically, the basal diameter of trees was measured at the base of the trunk using a vernier caliper, while DBH was measured at 1.3 m above the ground using a diameter tape. Crown width and coordinates were measured with a tape measure. For diameter class classification, trees with a DBH < 10 cm were uniformly classified into three levels based on basal diameter: Grade 1: 0.1 cm ≤ D < 3.0 cm, Grade 2: 3.0 cm ≤ D < 6.0 cm, and Grade 3: 6.0 cm ≤ D < 10.0 cm. For trees with a DBH ≥ 10 cm, DBH was used as the standard, and classification was performed in 10 cm increments. Based on the above method, *A. georgei*var. *smithii* was divided into 13 diameter classes, covering a range of 0.1 cm ≤ D < 110.0 cm; *A. chayuensis* was divided into 24 diameter classes, covering 0.1 cm ≤ D < 220.0 cm; *P. armandii* was divided into 18 diameter classes, covering 0.1 cm ≤ D < 160.0 cm; *B. utilis* was divided into 7 diameter classes, covering 0.1 cm ≤ D < 50.0 cm; *A. delavayi* var. *motuoensis* was divided into 20 diameter classes, covering 0.1 cm ≤ D < 180.0 cm; and *T. dumosa* was divided into 25 diameter classes, covering a range of 0.1 cm ≤ D < 230.0 cm.

According to the survey, the tree populations were then divided into two categories: small trees (diameter < 10 cm at breast height) and large trees (diameter ≥10 cm at breast height). This met the technical requirements for point pattern analysis, and the importance of natural regeneration was considered in maintaining the stability of forest ecosystems.

Spatial distribution pattern

Ripley's point pattern method (Ripley, 1977) was used in this study to analyze the spatial pattern of plant populations (*Eq. 1*), where the *K* function was used to calculate the number of plant individuals within a circular area with any point as the center and a spatial scale (r) as the radius. The formula for calculating the *K*-function is as follows:

$$K(r) = \frac{A}{n^2}\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{I_r(u_{ij})}{W_{ij}}(i \neq j) \qquad \text{(Eq.1)}$$

where A is the area of the plot; n is the number of individuals within the plot; u_{ij} is the distance between two plants, i and j; r is the spatial scale; and when $u_{ij} \leq r$, $I_r(u_{ij}) = 1$. When $u_{ij} > r$, $I_r(u_{ij}) = 0$. W_{ij} represents the proportion of the circumference of a circle centered at i with radius u_{ij} that lies within area A. Here, it serves as a weight for edge correction.

The ecologist Diggle (8) applied edge correction and linearization to the *K* function and proposed the *L* function (*Eq. 2*), which has the following formula:

$$L(r) = \sqrt{K(r)/\pi} - r \qquad \text{(Eq.2)}$$

The association analysis of populations builds upon the previously calculated spatial distribution characteristics of a single population and extends this approach to the relationships between two different populations (*Eq. 3*). The formula for calculating the $K_{12}(r)$-function is as follows:

$$K_{12}(r) = \frac{A}{n_1 \times n_2}\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{I_r(u_{ij})}{W_{ij}}(i \neq j) \qquad \text{(Eq.3)}$$

In the formula, n_1 and n_2 represent the number of individuals of different grades in two populations or the same population, respectively, and the other indicators have the same meaning as $K(r)$ *Equation 4*. The specific formula for the bivariate L function is as follows:

$$L_{12}(r) = \sqrt{K_{12}(r)/\pi}\text{-}r \tag{Eq.4}$$

Software selection and parameter settings

In the C_3 plot, there were 8 ***B.** utilis* trees and 6 small ***A.** chayuensis* trees. In the M_1 plot, there was 1 large ***A.** delavayi* var. *motuoensis* tree and were 4 large ***T.** dumosa* trees. In the M_2 plot, there were only 2 large trees of ***A.** delavayi* var. *motuoensis*, indicating a small sample size and limited significance for conducting pattern analysis.

In this study, the ADE–4 spatial point pattern analysis software was used to analyze the spatial distribution pattern of tree species. The complete spatial randomness (CSR) model was selected, and the significance threshold was set at $\alpha = 0.01$. The spatial scale of *A. georgei* var. *smithii* was 0-50 m, whereas the spatial scale of the remaining populations was 0–25 m. Through 100 Monte-Carlo random simulations, we obtain the upper and lower envelope lines for a 99% confidence interval. If the $L(r)$ value is above the confidence interval, the population exhibits aggregated distribution; if the $L(r)$ value falls within the confidence interval, the population exhibits random distribution; if the $L(r)$ value is below the confidence interval, the population exhibits uniform distribution. If the $L_{12}(r)$ value is above the confidence interval, the population exhibits positive association; if the $L_{12}(r)$ value falls within the confidence interval, the population exhibits no correlation; if the $L_{12}(r)$ value is below the confidence interval, the population exhibits negative association. A coordinate graph was drawn via Microsoft Excel 2016 software with spatial scale r on the horizontal axis and the L value on the vertical axis.

Results

Diameter structure of tree species

To determine the survival status of tree populations in the studied plots, we first aimed to determine the diameter structure of tree species via the plot survey method. The statistical results of diameter grades (*Fig. 3*) revealed 408 *A. georgei* var. *smithii* per hectare in the single-species forest of Mount Sygera (*Fig. 3a*). The diameter grades had an overall inverted "*J*" structure, including 13 diameter grades with no missing grades. Among the grades, the number of individuals in the first diameter class was the highest, accounting for 21.08% of the total population. With increasing diameter, the number of individuals at the 1-3 diameter level decreased significantly, whereas there was slight fluctuation at the 3-9 diameter level. Above a 9- diameter, the number of individuals sharply decreased. The number of individuals with DBH < 10 cm accounted for 45.34% of the total population.

In contrast with the single-species forest of Mount Sygera, three types of trees existed in the coniferous mixed forest in Zayu County, with a total density of 745 trees per hectare. The percentage of each tree population to the total density was as follows: *A. chayuensis* (43%) > *P. armandii* (40%) > *B. utilis* (17%). The number of individuals in the first diameter class of *A. chayuensis* was the maximum (*Fig. 3b*), 2.76 times greater than that in the second diameter class. As the diameter class increased, the number of individuals decreased continuously and showed fluctuations in the eighth diameter class. The number of trees with DBHs ≥ 10 cm in this population accounted for only 32.92%,

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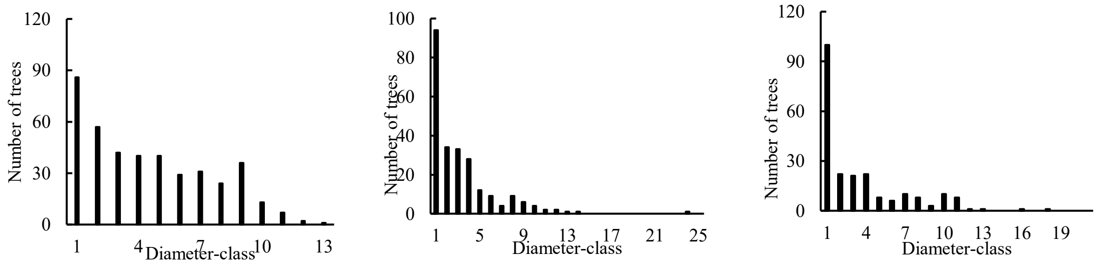
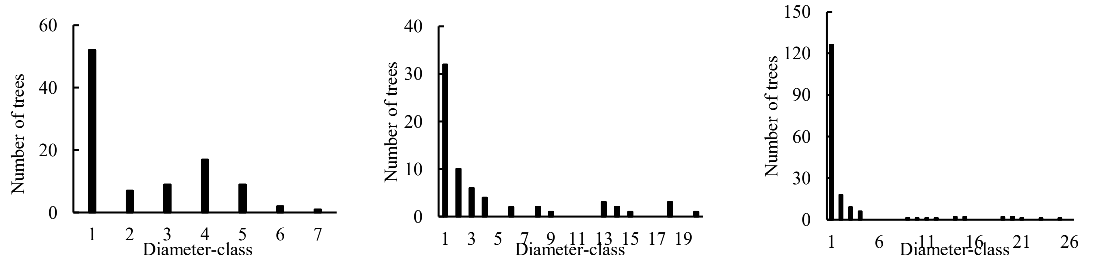
and the 15-23 diameter class was missing. The number of individuals in the 1-4 diameter class of *P. armandii* accounted for 74.32% of the overall population (*Fig. 3c*), whereas the 5-11 diameter class showed a wavy distribution, and the 14-, 15-, 17-, and 19-24 diameter classes were missing. Similar to the trends in *A. chayuensis*, the overall size distribution of the two species showed an inverted "*J*" structure, and the number of individuals decreased sharply after the fourth diameter class. *B. utilis* only had 7 diameter classes (*Fig. 3d*), with a breast height diameter of less than 50 cm. The number of individuals with DBHs ≥ 10 cm accounted for only 29.90% of the population.

The dark coniferous, mixed forest in Motuo County had only 89 *A. delavayi* var. *motuoensis* trees per hectare and 232 *T. dumosa* trees per hectare. Individuals belonging to *A. delavayi* var. *motuoensis* were mainly found in the 1-3 diameter class (*Fig. 3e*), accounting for 71.64% of the total population. Starting from the fourth diameter class, the population sizes of the diameter classes showed irregular fluctuations with increasing diameter class, with the 5-, 7-, 10-12, 16-, 17-, and 19 diameter classes being missing. *T. dumosa* had the highest number of individuals in the first diameter class (*Fig. 3f*), accounting for 72.41% of the overall population. As the diameter class increased, three phenomena were observed: a rapid decrease in the number of individuals in the 1-2 diameter class, a slow decline in the 2-4 diameter class, and a random distribution in the 4-25 diameter class. The diameter classes 5-8, 13, 16-18, 22, and 24 were missing.

In summary, except for that of *B. utilis*, the diameter structure of the populations included a high proportion of seedlings and young trees representing the growing population. However, the proportion of medium- and large-diameter individuals was relatively small. There were also multiple discontinuities in diameter classes, and the diameter structure fluctuated significantly.



(a) *A. georgei* var. *smithii* (b) *A. chayuensis* (c) *P. armandii*



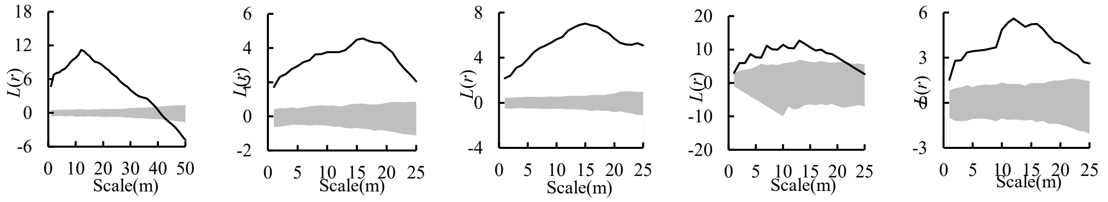
(d) *B. utilis* (e) *A. delavayi* var. *motuoensis* (f) *T. dumosa*

Figure 3. *Diameter structure. The diameter class classification was as follows: for individuals with DBH < 10 cm, three basal diameter classes were used (Grade 1: 0.1 cm ≤ D < 3.0 cm, Grade 2: 3.0 cm ≤ D < 6.0 cm, and Grade 3: 6.0 cm ≤ D < 10.0 cm). For those with DBH ≥ 10 cm, 10-cm interval DBH classes*

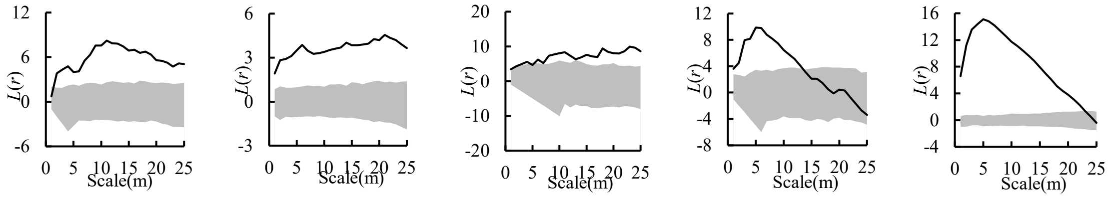
Spatial distribution pattern

To identify the ecological processes underlying the spatial distribution patterns of tree populations within the study area, we employed the point pattern analysis method to infer the interactions within the population and their relationships with environmental factors. (1) The results of the analysis of six populations of small trees revealed that the observed values *L*(*r*) of the small trees in the *A. georgei* var. *smithii* population were above the confidence interval at a spatial scale of 0-40 m (*Fig. 4a*), indicating a clustered distribution. As the spatial scale increased, the observed values *L*(*r*) gradually entered and eventually fell below the confidence interval, suggesting a transition from clustered to random and then possibly uniform distributions for this population. For the three species with small tree populations (*Fig. 4b-h*), namely, *A. chayuensis*, *P. armandii*, and *B. utilis*, their observed values *L*(*r*) were generally located above the confidence interval at a spatial scale of 0-25 m, with only a few trees within the confidence interval, this indicated that the overall distribution pattern of small trees in the three populations was characterized by clustering, with only a few spatial scales achieving random distribution. The observed values *L*(*r*) of two populations of small trees (*Fig. 4i-m*), *A. delavayi* var. *motuoensis* and *T. dumosa*, were above the confidence interval at a small spatial scale, indicating clustered distributions, which gradually transitioned to a random distribution at larger spatial scales. (2) A study on the spatial distribution patterns of large trees in six populations (*Fig. 4n-y*) revealed that the observed values *L*(*r*) of different tree populations were mainly within the confidence interval at the scale studied in each plot, indicating that the large trees were mainly distributed randomly. Only a few populations show clustered distributions at small and medium spatial scales in a few plots. In addition, the observed values *L*(*r*) of *B. utilis* large trees in plot C_1 (*Fig. 4q*) were above the confidence interval at spatial scales of 0-25 m, indicating an aggregated distribution.

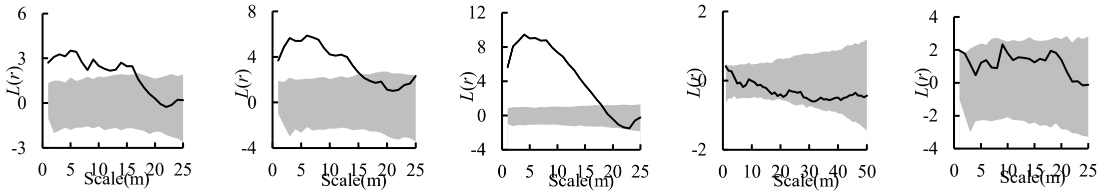
Analysis of the spatial correlation between different developmental stages of trees and different tree populations revealed the following patterns. (1) In the research area (*Fig. 5a-g*), Except for plots C_3 (*Fig. 5d*) and M_2 (*Fig. 5f*), where large trees and small trees showed no correlation across all spatial scales, the observed values $L_{12}(r)$ for both groups in other plots gradually shifted from below the confidence interval to within it as spatial scales increased, indicating that the populations gradually shifted from a negative correlation to no correlation, with positive correlations were rarely observed. (2) There was mainly a negative correlation and no correlation between (*Fig. 5h, k, n*) *A. chayuensis* and *P. armandii*. The observed values $L_{12}(r)$ fell below the confidence interval within the spatial scales of 0-20 m in the C_1 plot (*Fig. 5h*) and 4-7 m in the C_2 plot (*Fig. 5k*), indicating a negative correlation. At other spatial scales, there was no correlation between the two species. (3) The observed values $L_{12}(r)$ (*Fig. 5i, l, o*) between *A. chayuensis* and *B. utilis* were within the confidence interval, indicating a predominantly uncorrelated relationship. Negative correlations were only observed at small scales of 0-2 m in the C_1 plot (*Fig. 5i*) and 0-11 m in the C_2 plot (*Fig. 5l*), where the values fell below the confidence interval. (4) The observed values $L_{12}(r)$ (*Fig. 5j, m, p*) between *P. armandii* and *B. utilis* were mainly within the confidence interval across the studied scale, indicating a predominantly uncorrelated relationship. A negative correlation was only observed at the small scale of 2-12 m in the C_2 plot (*Fig. 5m*), where the values fell below the confidence interval. (5) There was mostly no correlation between *A. delavayi* var. *motuoensis* and *T. Dumosa* (*Fig. 5q, r, s*). The observed values closely followed the lower edge of the confidence interval at the 0-5 m scale in the M_3 plot (*Fig. 5s*) and showed little or no correlation.



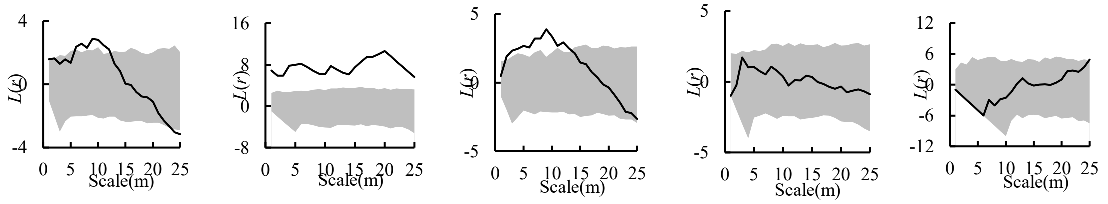
(a) Small *A. georgei* var. *smithii*
(b) C_1 small *A. chayuensis*
(c) C_1 small *P. armandii*
(d) C_1 small *B. utilis*
(e) C_2 small *A. chayuensis*



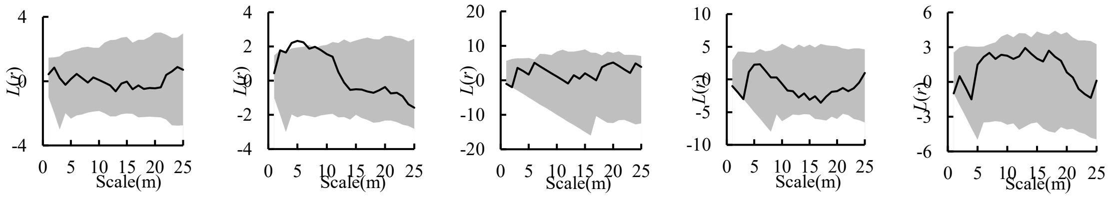
(f) C_2 small *P. armandii*
(g) C_2 small *B. utilis*
(h) C_3 small *P. armandii*
(i) M_1 small *A. delavayi* var. *motuoensis*
(j) M_1 small *T. dumosa*



(k) M_2 small *T. dumosa*
(l) M_3 small *A. delavayi* var. *motuoensis*
(m) M_3 small *T. dumosa*
(n) Large *A. georgei* var. *smithii*
(o) C_1 large *A. chayuensis*



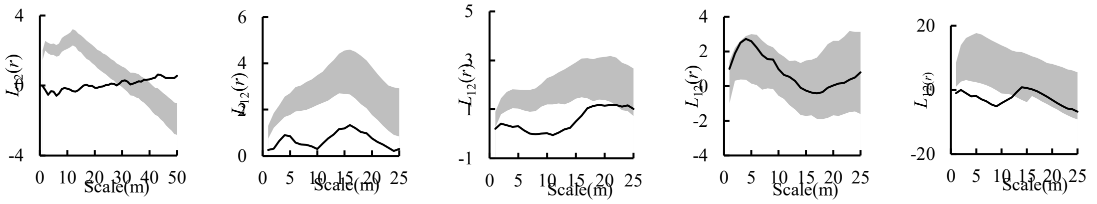
(p) C_1 large *P. armandii*
(q) C_1 large *B. utilis*
(r) C_2 large *A. chayuensis*
(s) C_2 large *P. armandii*
(t) C_2 large *B. utilis*



(u) C_3 large *A. chayuensis*
(v) C_3 large *P. armandii*
(w) M_2 large *T. dumosa*
(x) M_3 large *T. dumosa*
(y) M_3 large *A. delavayi* var. *motuoensis*

Figure 4. *Spatial distribution pattern of different populations under complete random model. The solid line represents the observed values of the L(r) function, while the gray area represents the bounds of the 99% confidence interval formed by 100 Monte Carlo simulations*

Overall, from the perspective of the spatial distribution patterns of the six populations at different developmental stages, the patterns of various populations shifted from a clustered distribution to a random distribution with increasing diameter, and a uniform distribution was rarely observed. The spatial relationships between and within these populations at various developmental stages shift from negative correlation to no correlation as the spatial scale expands, with only a negligible number of spatial scales exhibiting positive correlation. This underscores the intense competition at small to medium spatial scales.



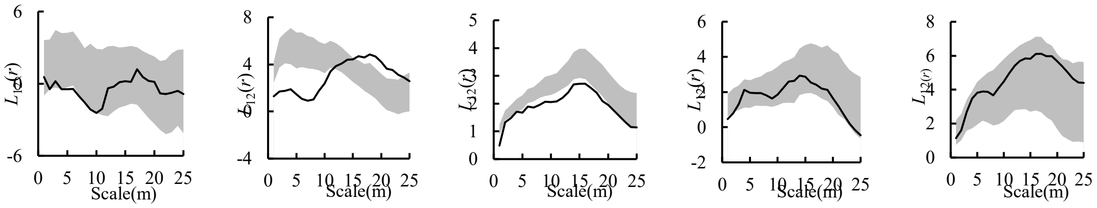
(a) *A. georgei* var. *smithii* large-small

(b) C_1 large-small

(c) C_2 large-small

(d) C_3 large-small

(e) M_1 large-small



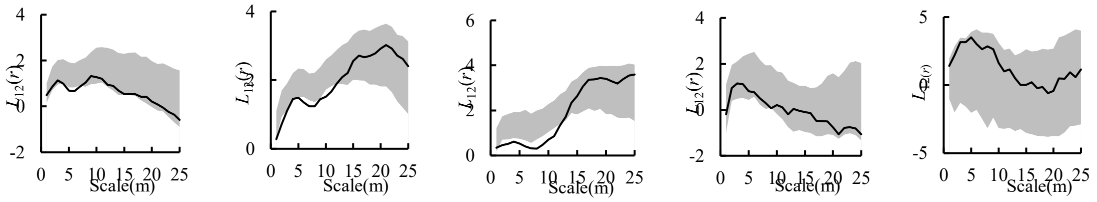
(f) M_2 large-small

(g) M_3 large-small

(h) C_1 *A. chayuensis-P. armandii*

(i) C_1 *A. chayuensis-B. utilis*

(j) C_1 *P. armandii-B. utilis*



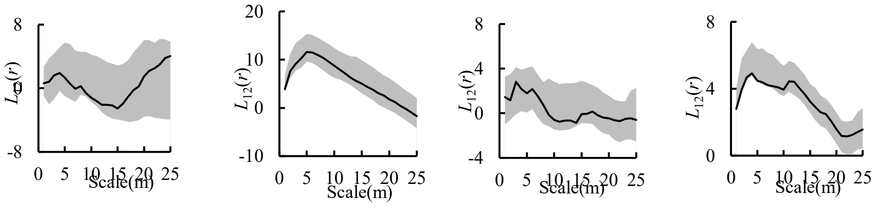
(k) C_2 *A. chayuensis-P. armandii*

(l) C_2 *A. chayuensis-B. utilis*

(m) C_2 *P. armandii-B. utilis*

(n) C_3 *A. chayuensis-P. armandii*

(o) C_3 *A. chayuensis-B. utilis*



(p) C_3 *P. armandii-B. utilis*

(q) M_1 *A. delavayi* var. *motuoensis-T. dumosa*

(r) M_2 *A. delavayi* var. *motuoensis -T. dumosa*

(s) M_3 *A. delavayi* var. *motuoensis-T. dumosa*

Figure 5. *Spatial correlation of different populations under complete random model. The solid line represents the observed values of the L12(r) function, while the gray area represents the bounds of the 99% confidence interval formed by 100 Monte Carlo simulations*

Discussion

Structural characteristics of trees

This study focuses on the survival status of the natural fir forests in southeastern Xizang under global climate change, analyzing the diameter class structure through the typical plot method. The results show significant changes in the fir forests' quantity and diameter class, particularly the lack of medium- and large-diameter trees. Except for *B. utilis*, the diameter structure of the populations of the other species had a pyramid-shaped structure, with more

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individuals of smaller diameter classes than larger diameter classes, indicating population growth. As tree diameter increased, the number of individuals in various groups significantly fluctuated. Although many populations had high seed germination rates, with many seedlings and young plants and sufficient reserves, their ability to sustain population development was poor, and the number of medium- and large-diameter trees was relatively small. This phenomenon is similar to the research findings of Zhang and Li (2025) on the population structure of the *Acer mono*, On the one hand, this is related to the understory vegetation layer. The average coverage of the moss layer in the *A. georgei* var. *smithii* forest is as high as 90% (Ren et al., 2021). Although the moss layer in the *A. chayuensis* and *A. delavayi* var. *motuoensis* plots is underdeveloped, understory herbaceous plants are well developed. Studies have shown that herbaceous and mossy plants have dual effects on understory seedlings. Although they may promote the improvement of microhabitats to some extent and provide favorable conditions for the regeneration and growth of tree seedlings, in most cases, they significantly reduce the retention rate of understory seedlings (Yin and Fan, 2020; Wang et al., 2016), which results in the death of many young individuals. On the other hand, as seedlings and young trees continue to develop, individuals' demand for environmental resources gradually increases. Competition within and between species strengthens "self-thinning and other thinning" effects, which also eliminates many individual seedlings, making the gradual supplement of medium- and large-diameter trees difficult. In addition, there were varying degrees of fluctuations in the number of medium- and large-diameter trees in the five populations within the three communities, especially in the areas of Zayu and Motuo, where a lack of medium- and large-diameter trees was relatively common. This suggests that there may have been frequent disturbances in the forest in the past, possibly stemming from natural disasters such as extreme climatic conditions and pests and diseases that caused forest instability. However, the actual causes must be determined on the basis of long-term, systematic monitoring data. The proportion of small-diameter individuals in the *B. utilis* population was high, while the proportion of medium-diameter trees was low, and there was a lack of large-diameter trees. This may have occurred because this population is a broad-leaved deciduous tree species with large crown width and high demand for light resources. Field surveys revealed that *B. utilis* is the secondary forest layer in these forests, being below the main canopies of *A. chayuensis* and *P. armandii*. It is greatly shaded by *A. chayuensis* and *P. armandii* individuals and can only survive in the gaps of these species. With succession in the community, *B. utilis* may be eliminated. Through the analysis of three types of fir forests in southeastern Xizang, multiple factors influencing the development of seedling and sapling populations, which has led to the scarcity of medium- and large-diameter trees, were explored. Although further research is required to pinpoint the exact causes, this discovery still emphasizes the importance of strengthening forest management and ecological conservation efforts to ensure the sustainable utilization of resources.

Spatial distribution patterns of tree populations

Spatial distribution patterns reflect the ecological response of populations to environmental changes and competitive pressures and strongly depend on spatial scales (He and Duncan, 2000). During spatial pattern analysis, the observed distribution patterns significantly deviated from the 99% confidence intervals generated by Monte-Carlo simulations based on complete spatial randomness, revealing that strong non-random ecological processes dominate community assembly. The main driving mechanisms include: habitat heterogeneity promoting population aggregation in resource patches;

seed dispersal limitation leading to intense clustering of recruits near parent trees; and stochastic disturbances such as windthrow and landslides shaping random mortality patterns at larger tree scales. The combined effects of these processes fundamentally account for the divergence between simulated and observed results. The spatial distribution results show that the six populations of small trees were clustered, whereas the patterns of large trees were random. This spatial distribution pattern of forest communities conforms to the universal law of natural renewal (Lara-Romero et al., 2016), Some studies have noted that seed dispersal restrictions influence the spatial patterns of individuals at the small-diameter trees. Even though distance regulation may increase the mortality rate of individuals around a mother plant due to the limited dispersal ability of seeds, most individuals still grow around the mother plant, forming a clustered distribution pattern in the early stages of their life history (Li et al., 2015). Habitat heterogeneity is another important factor affecting population distribution patterns, determining (Gu et al., 2021), for example, the random distribution of small trees in populations of *A. georgei* var. *smithii*, *A. delavayi* var. *motuoensis*, and *T. dumosa* on a large spatial scale. This may occur due to the uneven distribution of environmental factors such as light, temperature, and humidity caused by extreme climatic conditions and the complex mountainous environments. This further exacerbates the heterogeneity of the forest environment, leading to the random distribution of small trees in the population on a large spatial scale. Large trees might be randomly distributed due to the harsh environments prevailing in high-altitude mountainous areas, which are characterized by low temperatures, short growing seasons, and poor soil quality. In addition, fierce competition occurs within and between species, leading to a slower growth rate in trees (Lu et al., 2009). During the growing period, various natural disasters may also occur, and most disturbances have random effects on individual trees, which leads to a random distribution in large trees. However, in this study, the large *B. utilis* trees in the C_1 plot of this study presented a clustered distribution at all the studied scales, possibly due to a combination of growth characteristics and habitat heterogeneity. In this plot, the *A. chayuensis*, *P. armandii*, and *B. utilis* ratios were 5:5.3:1. The *B. utilis* was a deciduous sun-loving tree species and could only survive in the forest windows of *A. chayuensis* and *P. armandii*, so a clustered distribution was dominant.

The spatial correlations of small and large trees within the three communities were mainly uncorrelated, but some negative correlations were also observed. A negative correlation was observed at small spatial scales, which is consistent with the Janzen–Connell hypothesis. This hypothesis suggests that seed survival rate is inversely proportional to spatial distance from the mother plant due to density and distance constraints (Janzen, 1970; Connell, 1971). This indicates asymmetric competition between larger individuals and young individuals in the survey area, resulting in delayed growth and development or death of young individuals and leading to difficulties in population renewal. As spatial scale increases, seeds that are slightly farther from the mother tree can grow normally due to weaker inhibition by the mother tree. Their spatial distribution pattern may be more influenced by terrain and population preference attributes, showing no correlation at large spatial scales. This study revealed a positive correlation between large and small trees in the *A. georgei* var. *smithii* and M_3 plots at a large spatial scale. This may have occurred because, when small trees are seedlings, large trees still have some reproductive capacity, which increases the distribution of small trees in the surrounding areas. Therefore, there is a certain positive correlation between large and small trees at a large spatial scale (Pan et al., 2023).

The results of interspecific association studies indicate that spatial association between different populations varies depending on sample site, with mainly uncorrelated and negatively correlated patterns and unstable community structures observed. This phenomenon is similar to the research findings of *P. armandii* forests in Bomi Gang Township (Yao et al., 2021). The analysis shows that it may be caused by the combination of species' own biological characteristics, interspecific competition and habitat heterogeneity. For example, *A. chayuensis* is a shade-tolerant plant that tends to grow in environments with weak light, *P. armandii* is a mesophytic plant that prefers mild and cool temperatures, and *B. utilis* is a sun-loving plant that is more suited for conditions with strong light. Both *A. chayuensis* and *B. utilis* rely on wind for seed dispersal, yet factors like wind speed and direction can lead to uncertainties in the spread direction and distance. As for *P. armandii*, its seeds are animal - dispersed, with the spread direction and distance restricted by the animal's activity range (Qu, 2019). Field surveys revealed that plots C_1 and C_3 have relatively gentle slopes and uniform resource distribution, leading to spatially isolated seedling establishment due to differential dispersal capacities among species and weakened competitive interactions. Furthermore, in these plots, the number of *A. chayuensis* and *P. armandii* individuals in both plots was approximately 5 times greater than that of *B. utilis* individuals, and they occupied the canopy layer as the dominant species. On the other hand, *B. utilis* lived in the subcanopy layer and occupied different ecological niches; therefore, *A. chayuensis* and *P. armandii* competed less with *B. utilis*. The negative correlation in the C_2 plot at the small scale may have occurred due to the uneven distribution of water and light resources caused by the steep slope of the plot. The tall trees and large crown widths of *A. chayuensis* and *P. armandii* inhibit the regenerative growth of understory *B. utilis*. In C_1 and C_2 plots, the number of small trees of *A. chayuensis* and *P. armandii* accounted for 80.9% and 59.35% of the total number of samples, respectively. The niche of small trees was easy to overlap, and the interspecific competition was more intense, so the two populations showed a negative correlation on small and medium spatial scales. As the spatial scale increases, however, habitat heterogeneity also increases. Due to differences in dispersal abilities, the spatial distribution of the two species gradually diverges, reducing their mutual influence and enabling them to grow more independently. This indicates that the spatial correlation between species is an adaptation to environmental and spatial resource utilization.

In comparison to the interspecific spatial associations observed among diverse populations within the fixed plots of Zayu County, no correlation was found between *A. delavayi* var. *motuoensis* and *T. dumosa* in the Motuo County plots. indicating weak competition between species, which differs from the obvious strong spatial correlations observed between dominant tree species in other forests (Lan et al., 2019; Wang et al., 2023). From the perspective of population density, *A. delavayi* var. *motuoensis* and *T. dumosa* exhibit relatively low distribution densities, which may reduce the frequency of resource competition between them and consequently weaken the intensity of their interactions. Field surveys indicate that small-diameter individuals of both species constitute over 70% of their respective populations. The herbaceous layer in this region reaches 80% coverage, and its robust development likely makes it the primary competitor for arbor populations, thereby diminishing direct competitive interactions between tree species. This suggests that resource partitioning with the herbaceous layer, rather than interspecific tree competition, dominates the ecological dynamics in this system. Therefore, competition between these two populations plays a weak role in community dynamics.

Limitation and development

While this study has made certain progress in revealing the survival status and spatial distribution of fir forests in southeastern Xizang, there are still deficiencies, mainly manifested in limited sample size, incomplete time scales, incomplete consideration of environmental factors, and inadequate assessment of ecosystem service functions. Therefore, future studies need to expand the sample size further to cover more regions and ecological types and enhance the representativeness of the conclusions. At the same time, long-term monitoring should be implemented to deepen investigations into the quantitative relationships among soil physicochemical properties, climatic factors, and fir forest distribution patterns, and higher-precision remote sensing data sources should be selected for verification in combination with field investigations to provide more scientific and accurate theoretical data for the conservation and sustainable development of fir forests in southeastern Xizang.

Conclusions

This study investigates the dynamics of tree population structure and spatial patterns in fir forests of southeastern Xizang across spatial scales to inform ecological restoration and management. Key findings include:

(1) All populations in the three fir communities are growing, with a high proportion of small-diameter trees. Despite adequate seedling reserves for current community development, few trees have reached medium or large diameters.

(2) The spatial distribution of main tree populations in the three fir communities is influenced by ecological factors like biological traits, developmental stages, habitat diversity, and asymmetric competition. Small trees cluster, while large trees are randomly scattered. Large trees exhibit a significant inhibitory effect on small trees at small and medium scales, and intense inter-population competition at these scales directly impacts population renewal and stability.

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