Unraveling the effects of species intra- and interspecific interactions and environmental factors on the spatial pattern of the tertiary relict plant *Tetracentron sinense* Oliver

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**Abstract**

* The spatial pattern is critical for understanding the plant population status. The distribution patterns of endangered plants are more vulnerable to intraspecific, interspecific, and environmental factors. *Tetracentron sinense* Oliver, a tertiary relict plant, the spatial pattern, and its influencing factors are poorly understood. We sought to figure out the spatial pattern of *T. sinense* and the factors responsible for this pattern.
* We utilized the point pattern, ordinary kriging, and canonical correlation analysis to identify distribution patterns, spatial interactions, and environmental factors.
* The results revealed that *T. sinense* individuals were highly aggregated, at a small scale. Similarly, there was a positive correlation between young and adult trees at smaller scales. In addition, the dominant species showed a positive correlation with *T. sinense*; the correlation gradually became non-significant or negative as the scale increased. Furthermore, the main environmental factors affecting the distribution of *T. sinense* were air humidity, altitude, litter depth, and potassium content.
* These results highlighted the importance of intra- and interspecific interaction and environmental factors for the spatial distribution of *T. sinense*. Our results provide new insights into endangered species' spatial patterns and main factors. Moreover, these findings have relevant implications for conserving and managing endangered trees in a constantly fragmented habitat.

**1 Introduction**

Biodiversity is fundamental to the functioning of the Earth providing many ecosystem services that are essential for biological and social development (Xue et al., 2021; Lykhovyd, 2021). Rare and endangered plants are an important component of biodiversity, and their increasingly narrow distribution areas, as well as their sensitivity to environmental changes, make it increasingly difficult for them to survive in nature (Yang et al., 2021). The spatial distribution pattern of plants, as an important characteristic of populations, is key to understanding the status of endangered plant populations (Zhang, 2017).

A spatial distribution pattern is the position and dispersion of individuals of a species in a spatial range (Perry et al.,2002). Spatial distribution patterns are usually categorized into three types: random, regular, and aggregated distributions (Dale, 1999). Different distribution patterns can directly reflect the ability and status of a population to use the environmental resources in a specific area in a certain period and can also intuitively reflect the position and viability of a population in a community (Dale, 1999). Since the 1920s, the spatial distribution pattern of plant populations has become a hot topic in ecological research (Greig-Smith, 1952; Luo et al., 2010; Liu et al., 2018; Guo et al., 2019). To overcome the influence of sampling area in the traditional spatial distribution pattern analysis method (Zhang, 1998) and provide comprehensive information for given spatial scales (Yang et al., 2006), point pattern analysis has become a common method for studying the spatial distribution patterns of species in recent years (Zhu, 1992; Ma, 65 2004; Xu et al., 2008; Luo et al., 2010; Liu et al., 2018; Guo et al., 2019). However, many studies have focused on the spatial distribution patterns of populations at large scales (Greig-Smith, 1952; Zhu, 1992; Zhang, 1998; Ma, 2004; Yang et al., 2006; Xu et al., 2008; Luo et al., 2010; Liu et al., 2018; Guo et al., 2019). The spatial distribution pattern of a population is closely related to the spatial scale (Condit et al., 2000). Studying the spatial distribution patterns of plants at small scales can further reveal the survival status of the population, like abundance, mortality, which is of great significance for the study of plant conservation, especially endangered plant conservation (Lin et al., 2008).

Many factors influence the spatial distribution patterns of plant populations, but at a small scale, the spatial interactions (intra-, and interspecific relationships) and environmental factors in a plant population are the main factors (Ofomata et al.,1999). Intra- and interspecific interactions can respond to environmental changes promptly, thus changing the habitat of the community in which they are located (Ofomata et al., 1999; Huang, 2008). Previous studies focused on the influence of intra- and interspecific relationships on community development, but little study has been conducted on the effects of these factors on the spatial distribution of plants (Liu et al., 2005; Han, 2014; Zhang, 2017; Liu et al., 2019; Xu et al., 2019). In addition, environmental factors (soil mineral elements, altitude, etc.) can also affect the distribution of various species (Dai et al., 2008). Therefore, by studying the spatial distribution patterns of endangered plants at different small spatial scales and the influence of intra- and interspecific relationships and environmental factors on their distribution patterns, we can gain a deeper understanding of the formation process and influence mechanisms of spatial distribution patterns of endangered plants, which is of significance for the proposed conservation measures of endangered plants (Lin et al., 2008).

*Tetracentron sinense* Oliver, a tertiary relict species in the family Trochodendraceae is a deciduous tree mainly distributed in the temperate and subtropical regions of East Asia. It plays an important role in understanding the evolution of paleophyte flora and the systematics and origin of angiosperms (Fu and Jin, 1992). *T. sinense* also has very important ornamental, medicinal, and industrial values (Luo, 1998; Wu, 2004; Wang et al., 2006). Due to factors such as environmental changes and anthropogenic activities, its habitat has been fragmented, resulting in a small number of natural populations of *T. sinense*, which are now only sporadically distributed in mountainous areas and valleys; therefore, it is classified as a key protected wild plant in China. (Fu and Jin, 1992; Li, 2015).

To conserve the germplasm resources of *T. sinense*, much research has been carried out on its population dynamics, growth, development, and reproduction (Tang et al., 2013; Tian et al., 2018; Li et al., 2020; Zhang et al., 2020), seed production and dispersal (Ganet al*.*,2012; Gan et al.,2013; Han et al., 2015), seedling and young tree establishment (Luo et al., 2010; Cao et al., 2012; Li et al., 2015; Li et al., 2016; Lu et al., 2020; Fanet al., 2021), and genetic diversity (Sun et al., 2014; Han et al., 2017; Li et al., 2018; Li et al., 2020), and the mechanism of limiting regeneration has also been studied. To date, little is known about the spatial distribution pattern and influencing factors of the distribution of the natural *T. sinense* populations.

Xu, (2016) found that the effective dispersal distance of *T. sinense* seeds does not exceed 8 m and those younger individuals usually grow around parent trees, resulting in a patchy relic distribution pattern. Tian et al., (2018) held that there was a strong niche overlap between *T. sinense* and its dominant trees, indicating relatively strong intra- and interspecific competition. Does the spatial distribution of *T. sinense* present a pattern of aggregation at small scales similar to its seed distribution pattern? Do intra- and interspecific interactions and environmental factors have an impact on the spatial distribution and result in poor regeneration of *T. sinense*? Answering these questions can help reveal the factors limiting the natural regeneration of *T. sinense*, which is of great significance for the effective conservation and management of this species.

This paper studied the distribution pattern and main influence factors of *T. sinense* in Leigong Mountain at various small spatial scales. The aims of the study were (1) to reveal the distribution patterns of *T. sinense* at small spatial scales, and (2) to discuss the impacts of intra- and interspecific interactions and environmental factors on the distribution of *T. sinense*. We also discussed the effective strategies for the conservation and management of *T. sinense*.

**2 Materials and Methods:**

**2.1 Study Area**

# This study was conducted in Leigong Mountain, which belongs to the Miaoling Mountains in Guizhou Province, China. The region is characterized by a typical subtropical humid climate, with abundant rainfall and relatively little sunlight. The average annual temperature is 9.2 to 16.3 ℃, the average annual humidity is 85% to 91%, and the annual rainfall is 1,300 to 1,600 mm. The vertical distribution of vegetation is clear: evergreen broadleaved forest occurs at low altitudes (approximately 1350 m), evergreen and deciduous broadleaved mixed forest occurs in the middle (1350-2100 m), and shrubs are found in the high-attitudinal area above 2100 m. Here, *T. sinense* is mainly distributed in evergreen and deciduous broadleaved mixed forests and is with *Fagus longipetiolata* Seemen, *Cerasus szechuanica* (Batalin) T.T. Yu & C.L. Li, *Pterostyrax psilophyllus* [Diels ex Perkins](http://www.theplantlist.org/tpl1.1/record/tro-30800181), *Styrax japonicus* Siebold & Zucc. and *Acer sinense* Pax. In *T. sinense* communities, *Chimonobambusa angustifolia* C.D. Chu & C.S. Chao, which has narrow leaves, is the dominant shrub (Chen et al.,2012; Jiang et al., 2018; Luo et al., 2019; Zhang et al., 2020).

**2.2 Plot select**

The field survey was performed between early April and late June 2018. According to the field survey,*T. sinense* is mainly distributed in patches at altitudes of 1500 m to 2000 m. Four large plots were selected where the age structure of *T. sinense* populations in Leigong Mountain was relatively complete, which reflects the natural distribution of this species: Plot 1 (P1): 50 m ×140 m, Plot 2 (P2): 128 m ×150 m, Plot 3 (P3): 50 m ×148 m, and Plot 4 (P4): 60 m ×120 m (Figure 1 and Table 1). The four plots were further subdivided into 10 m × 10 m subplots. The large plots were used for spatial pattern analysis, and the subplots were for spatial correlation and soil analysis.

**2.3 Species survey**

We identified and measured all trees as well as other woody and herbaceous species in each plot by measuring species names, numbers, coordinates (Wang et al., 2009, Wang et al., 2011, Zhao et al., 2018), tree height, crown width, coverage, phenology (growth period, flowering period, and fruit stage), and diameter at breast height (DBH) (Sakio et al., 2002; Tang et al., 2013; Liu et al., 2019). For individuals having more than one trunk, the maximum DBH was used as its DBH (Li, 2015).

**2.4 Sample collect**

Soil samples were collected in each subplot (Li, 2015). The upper layer of litter and gravel was removed, and the soil samples were collected at a depth of around 0-20 cm. Approximately 1 kg per subplot was sampled, and a total of 234 soil samples were collected. The soil samples were transported back to the laboratory and then dried naturally (Bao, 2000). After drying, the soil samples were ground and analyzed to determine their mineral elements. Referring to Bao (2000) and Lu (2000), the total contents of nitrogen (N), and phosphorus (P) were determined by UV spectrophotometer. Other mineral elements such as potassium (K), sodium (Na), magnesium (Mg), zinc (Zn), and calcium (Ca) were determined by flame photometer and atomic spectrophotometer.

**2.5 Data analysis**

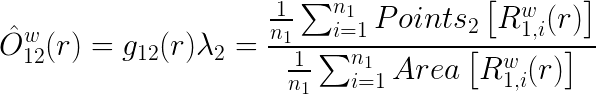
*2.5.1 Age- class of T. sinense populations in four plots*

The age of a tree can be determined by drilling the trunk and analyzing ring patterns. To prevent damage to the endangered species from this method, the DBH class was utilized to represent the age class of *T. sinense* (Zhang, 1998; Dale, 1999). According to previous studies (Zhang et al., 2020) and the age characteristics of *T. sinense* on Leigong Mountain were divided into 10 age classes: Ⅰ (seedling), H <0.33 m; Ⅱ (sapling), H >0.33 m, DBH <2.5 cm; Ⅲ, 2.5 ≤DBH <7.5 cm; Ⅳ, 7.5 ≤DBH <12.5 cm; Ⅴ, 12.5 ≤DBH <17.5 cm; Ⅵ, 17.5 ≤DBH <22.5 cm; Ⅶ, 22.5 ≤DBH <27.5 cm; Ⅷ, 27.5 ≤DBH <32.5 cm; Ⅸ, 32.5 ≤DBH <37.5 cm; and Ⅹ, DBH≥ 37.5 cm.

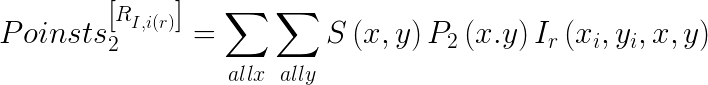
Due to the relative scarcity of seedlings and saplings in the four plots, the *T. sinense* individuals were divided into three classes to analyze the spatial correlation in the population. These groups were young trees (I~III), adult trees (IV~VI), and old trees (VII~X) (Luo et al., 2019).

*2.5.2 Analysis of spatial patterns and spatial interactions*

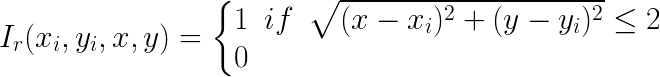
The spatial distribution and spatial interactions (intra-and interspecific interactions) of *T. sinense* were analyzed using the O-ring function for point pattern analysis which was performed with Programita 2010 (You et al., 2009). The approach was supplemented with Monte-Carlo random simulation. The univariate function (O (r)) was used to analyze the spatial distribution of *T. sinense* populations in the four plots, and the bivariate function (O12 (r)) was used to analyze the spatial interactions among different age classes of *T. sinense* and between *T. sinense* and dominant species in the same plot. The screening of the effective null hypothesis model was the key to accurately analyzing the distribution of populations and the relationship between them. In this study, a completely random distribution model (CSR) was chosen to perform the analysis. If the O(r) value is within the upper and lower wrap traces of the confidence intervals, the distribution is random or the two are directly independent of each other. If O(r) is above the upper and lower wrap traces of the confidence interval, the distribution is aggregated or there is a significant positive correlation between the two; on the contrary. If O(r) is below the upper and lower wrap traces of the confidence interval, the distribution is uniform or there is a significant negative correlation between the two species (Wang et al., 2006). The O-ring function for univariate statistics is a spatial correlation statistic by hypothesizing the pattern analysis of a single variable to a bivariate having two identical patterns. The bivariate O-ring statistic is calculated as follows (Wiegand et al., 2004; You et al., 2009):

(1)

where  is the number of individuals in pattern 1,  is the circle with  as the center,  is the radius, and  is the width in pattern 1.  is the number of points of pattern 2 in region X.  is the area size.

(2)

where are the coordinates of pattern 1,  is a variable,  is the number of points in pattern 2 per grid,  is the amount of change that occurs when changing the circle with the point  as the center, and  is the radius of the circle in pattern 1.

(3)

(4)

where  is the size of a grid. Similarly, the univariate O-ring statistic is computed by setting pattern 1 equal to pattern 2.

For all analyses, the Monte-Carlo simulation was repeated 199 times to yield a 99% confidence for each process with the corresponding null model. The spatial scales of P1, P2, P3, and P4, were 0-25 m, 0-64 m, 0-25 m, and 0-30 m, respectively, with a step size of 0.5 m. The correlation and point pattern analyses were performed in Programita2010. Origin2018 was used to create graphs (Wiegand et al., 2004; You et al., 2009).

*2.5.3 Analysis of dominant species*

The dominant species with *T. sinense* were determined by their importance value (W). The importance value was calculated as follows (Condit et al., 2000):

 (5)

 (6)

where RD (relative density) is the ratio of the number of species in a plot to the total number of all species in that plot. RF (relative frequency) is the ratio of the frequency of occurrence of a species in a sample to the sum of the frequency of occurrence of all species in that plot. RP (frequency of prominence) is the ratio of the sum of the area at the breast height of one species in the plot to the sum of the area at the breast height of all species in that plot. and RC (relative coverage) is the ratio of the cover of species to the sum of the covers of all species in the plot.

*2.5.4 Canonical correspondence analysis (CCA)*

The soil mineral elements were analyzed by ordinary kriging (Cui, 2015). CCA was used to analyze the effects of environmental factors on the spatial distribution of *T. sinense*. Canonical correspondence analysis (CCA) is a nonlinear multivariate direct gradient analytical method. CCA combines correspondence analysis with multiple regressions and can provide a detailed analysis of the relationships between species and the environment (Braak et al., 1995). Using only unimodal analyses (such as CCA) can be avoided obtaining inaccurate valuations by linear analysis (Ter Braak, 1987; Leksungnoen et al., 2022). In addition, it can represent the relationship between species in the distribution and environmental factors in the low-dimensional space simultaneously (Ter Braak, 1987). The axes of CCA were constrained to be linear combinations of environmental factors, where the axes indicate the variables that resulted in the greatest separation or variation in samples. The mean of the environmental factors was used to perform CCA (Hill, 1991). The relative importance of each CCA axis was indicated by its eigenvalue, a statistical measure that shows the extent to which a linear combination of environmental factors can explain the factors in the distribution of *T. sinense* (Leksungnoen et al., 2022). Coordinated data related to *T. sinense*, dominant species and environmental factors in each plot were sorted. A plant data matrix was obtained for *T. sinense* and dominant speciesin plots according to the method by Wang et al., (2004). Environmental factors such as soil mineral elements and altitude were integrated into the environmental factor matrix. The forward selection was used to filter out the most important environmental factors. Significance was tested using 999 Monte Carlo replications. Finally, the plant data matrix and the selected environmental factors were described on CCA biplots by Canoco 5 (Wang et al., 2004).

**3 Results**

**3.1 Spatial patterns**

The numbers of individuals of *T. sinense* were 155 in the four plots, including 33 for P1, 51 for P2, 34 for P3, and 37 for P4 (Table 2; Figure 2).

The overall spatial distributions of *T. sinense* were similar in the four plots. In P1, the individuals showed a significant aggregation on a small scale (0-14 m) and then a random distribution. In P2, the individuals were clustered in the range of 0-34 m, were randomly distributed between 35 m and 38 m, and then were evenly distributed at larger scales. In P3, the individuals were clustered at scales up to 8 m and then randomly distributed with increasing spatial scale. On the whole, the individuals in P4 were aggregated in the range of 0 to 8 m and then randomly distributed at scales greater than 9 m (Figure 3).

**3.2 Spatial interactions**

The intraspecific interactions between individuals of *T. sinense* were studied in the three life-history stages (Figure 4). The intraspecific interactions were different among the three classes in four plots. In P1, young trees and adult trees showed significant positive interactions in the ranges of 0-1 m and 12-13 m, respectively, while there was no correlation at other scales. There was no obvious correlation between young trees and old trees within the study. The adult and old trees were positively correlated at scales of 0.5-1.125 m and 12.2-13.2 m, and no correlation was observed at the remaining scales. The distribution among different types of *T. sinense* was different in P2. The young trees and adult trees were significantly positively correlated at 0-11 m, and little correlation was observed at other scales. The young trees and old trees showed a certain positive correlation in the small-scale range of 2.5 to 7.5 m. The adult trees and old trees showed a negative correlation and a negative or no correlation with the increase in the study scales. There was no significant correlation among the other types of trees in P3 except between young and adult trees in the range of 1-2 m. Similarly, in P4, young trees, and adult trees had a significant positive correlation at very small scales, and no correlation appeared among the other types of trees.

The interspecific interactions between *T. sinense* and its dominant species were further tested in four plots on Leigong Mountain (Figure 5). In the four plots, the numbers ofindividuals of the five tree species (*Acer sinense* Pax, *Prunus* *tomentosa* (Thunb.) Wall., *Styrax japonicus* Sieb. et Zucc., *Pterostyrax psilophyllus* Diels ex Perk., and *T. sinense*) were all higher than those of the other species. The importance values of *A. sinense*, *P. tomentosa*, *S. japonicus*, and *P. psilophyllus* were above 55%, indicating that they were the dominant species with *T. sinense*. In the shrub layer, the number of *C. angustifolia* individuals accounted for 95% of the plants, and the importance value of this species reached 189.96. Because *C. angustifolia* was so widely distributed and its cover was so large, its roots were highly developed, causing there to be few herbs in the herbaceous sample plots and even a few small shrubs or seedlings and saplings of *T. sinense*. Therefore, four tree species were selected as the dominant species of *T. sinense*, and their influence on the distribution pattern of *T. sinense* was further studied (Table 3).

In P1, there was no correlation between *T. sinense* and *S. japonicus* or *P. psilophyllus* at any of the study scales, a negative correlation between *T. sinense* and *P. tomentosa* in the range of 16-22 m, and a negative correlation between *A. sinense* and *T. sinense* in the ranges of 2.5-5 m and 9-12 m (Figure 5, A-D). In P2, the relationship between *T. sinense* and its dominant species changed greatly. *S. japonicus* and *T. sinense* showed a strong positive correlation in the range of 12-25 m, a positive correlation in ranges of 33-36 m and 41-45 m, and no correlation at the other scales. *P. tomentosa* and *T. sinense* showed a positive correlation at scales of 11-14 m and 40-44 m and no correlation at the remaining scales. *A. sinense* and *P. psilophyllus* showed a negative correlation with *T. sinense* at a smaller scale of 0-13 cmand a positive correlation with *T. sinense* at larger scales (26-27 cm and 32-57 cm) (Figure 5, E-H). In P3, there was no correlation between *T. sinense* andany of the four dominant species (Figure 5, I-L). In P4, *T. sinense* had no correlation with its dominant species in the range of 0-27 m and a negative correlation with *P. psilophyllus.* No correlation was observed between *T. sinense* and *S. japonicus* or *A. sinense* at any of the study scales*.* The correlation between *T. sinense* and *P. tomentosa* was negative at smaller scales. As the scale gradually increased, there was no correlation and a positive correlation (Figure 5, M-P).

**3.3 Contribution of environmental factors of *T. sinense***

In four plots of Leigong Mountain, the soil mineral elements (N, P, K, Na, Ca, Mg, Zn) were analyzed by ordinary kriging. The results indicated that the mineral elements had a spatial auto-correlation and were aggregated. The results also showed that mineral elements were mainly distributed in bands and their content changes were significantly correlated with altitude. The mineral elements were mostly concentrated in mid-and low-altitude areas (Table 4 and Figure 6).

The main environmental factors that affect the distribution of *T. sinense* in each plot were selected based on forward selection and the Monte Carlo permutation test. In P1, the most important environmental factors were litter depth, humidity, shade density, Altitude, K, and Zn. In P2, the most important environmental factors were altitude, humidity, litter depth, P, Ca, and K. In P3, the most important environmental factors were shade density, altitude, P, Ca, K, and Zn. In P4, the most important environmental factors were humidity, altitude, litter depth, N, P, and K (Table 5).

According to the CCA, the first two axes explained the relationships between the species and environment in P1, P2, P3, and P4 were 64.62%, 53.77%, 71.63%, and 49.27%, respectively (Figure 7, Table 6). In P1, humidity, altitude, and K explained 86.3% of the variance, whereas altitude alone explained 30.8%. Humidity and altitude were the most important factors overall, followed by K. In P2, humidity alone explained 22.6%, altitude alone explained 13.1%, and litter depth alone explained 11.1%. humidity, altitude, and litter depth were the most important factors. In P3, Ca alone explained 32.4%, shade density alone explained 23.9%, and altitude alone explained 22.7%, they were the most important factors. In P4, humidity, altitude, and K were the most important factors, with the explained 47.4% (Figure 7, Table 5). The response of *T. sinense* and its dominant species to six environmental factors in four plots was studied. In P1, *T. sinense*, *A. sinense*, *P. tomentosa*, *S. japonicus*, *P. psilophyllus*, and environmental factors were mainly aligned in the first axis, and the distribution of *T. sinense* was significantly positively correlated with Zn and negatively correlated with humidity, altitude, litter depth, and K. In P2, the distribution of *T. sinense*, *A. sinense*, *P. tomentosa*, *S. japonicus*, *P. psilophyllus*, and environmental factors was mainly aligned in the second axis, and the distribution of *T. sinense* was significantly positively correlated with humidity, altitude, and litter depth, and negatively correlated with K. In P3, *T. sinense*, *A. sinense*, *P. tomentosa*, *S. japonicus*, *P. psilophyllus*, and environmental factors were aligned in the first axis, and the distribution of *T. sinense* was negatively correlated with altitude, P, K, and shade density, and positively correlated with Ca. In P4, *T. sinense*, *A. sinense*, *P. tomentosa*, *S. japonicus*, *P. psilophyllus*, and environmental factors were aligned on the first axis, and the distribution of *T. sinense* was significantly positively correlated with K and negatively correlated with altitude, humidity, and litter depth (Figure 7). The results revealed that humidity, altitude, litter depth, and K were the most important factors affecting the distribution of *T. sinense* in four plots*.*

**4 Discussion**

In this study, the age structure of *T. sinense* in four plots was generally similar, with missing seedlings, more adult trees, and fewer old trees, which were poorly updated and showed a decline-type age structure, which is consistent with the results of Zhang et al., (2020). The spatial distribution pattern of *T. sinense* in Leigong Mountain differed with scale and showed a highly aggregated distribution in small scales. A regular distribution and random distribution were alternately observed with increasing scale. The highly aggregated distribution on a small scale might be attributed to the close effective dispersal distance of *T. sinense* seeds, which was consistent with the results reported by Nathan et al., (2000); Xu, (2016); Wang, (2017); and Kong et al., (2021). As the scale increased, the distribution pattern of *T. sinense* became regular or random, whichmight be the result of gradually decreasing intraspecific competition. Instead, the effect of environmental factors on the spatial distribution of the tree became more significant (Hanet al., 2021).

The distribution relationship between different age classes of *T. sinense* showed that adult trees and old trees were relatively independent on a small scale and then tended to have a negative correlation at increasing scales, while young trees and adult trees had a strong positive correlation on a certain spatial scale. These results were the same as those of *Pinus koraiensis* [Siebold & Zucc.](http://www.theplantlist.org/tpl1.1/record/kew-2561659) and *Tilia amurensis* [Rupr.](http://www.theplantlist.org/tpl1.1/record/kew-2518211) (Zhang et al., 2007). The significant positive correlation between young trees and adult trees in the *T. sinense* indicated that individuals with a larger DBH supported the survival of individuals with a smaller DBH by changing the niche within the plot. Two individuals with adjacent diameter sizes showing interdependence could act synergistically when utilizing habitat resources and competing with other species within the community. As the study scales increased, the relationship between adult trees and old trees tended to be negative, which might be attributed to the number of adult trees being far greater than that of old trees (Zhang et al., 2020), resulting in fierce competition for space, essential nutrients and other external conditions, which was consistent with the results reported by Yang et al., (2021). The spatial correlation between the adjacent diameter sizes of *T. sinense* changed from a positive to a negative correlation, predicting stronger competition between individuals, which was not conducive to habitat adaptation. Moreover, this changing trend reflected the limited survival and development abilities of *T. sinense*, indicating that thenatural population of this species on Leigong Mountain is in decline, which was consistent with the results reported by Zhang et al., (2020).

There were differences in the correlation between *T. sinense* and its dominant species in different study scales. On a small scale, the dominant species were negatively correlated with *T. sinense*, showing intense competition between them. In other words, the distribution of *T. sinense* was inhibited by its dominant species, which might be a major reason for its aggregated distribution on a small scale. As the study scale increased, the correlation gradually changed into unrelated or positive, showing that the competitive relationship between species had improved. This might be because young trees of *T. sinense* are not competitive enough and are gradually being eliminated, and then adult trees constantly adapted to the environment in the community. As the number of old trees greatly decreased, the competition with the dominant species was reduced and the interference in the distribution of *T. sinense* decreased. Generally, if community succession is at an early stage and the niches between species are similar, there will often be negative interactions between species, and there is a competitive relationship between species at this time (Wang, 2017). As succession continues, the relationship becomes positive (Xing, 2001), and the niches between species differentiate as coexistence is achieved. When coexistence occurs, the community is at the stage of late succession (Zhao et al., 2022).

The mineral elements of the soil on Leigong Mountain showed an obvious spatial autocorrelation and tended to be aggregated. Ordinary kriging suggested that mineral elements were mostly concentrated in mid-and low-altitude areas. In other words, altitude might be one of the main environmental factors affecting the distribution of the mineral elements. This finding was consistent with those of previous studies (Huang et al., 2004; Liu et al., 2011). The results showed that altitude is the most critical factor in determining the spatial distribution pattern of *T. sinense*, which was confirmed by Zhang et al., (2009). According to the CCA, other major environmental factors affecting the distribution of *T. sinense* were humidity, litter depth, and K, which was consistent with the results reported by Liu et al., (2009) and Zhang et al., (2010). Therefore, the mid-and low-altitude areas with relatively little K, large humidity, and low litter depth were suitable for *T. sinense*; similar findings were observed for other relict plants, such as *Taxus mairei* (Zhu, 2016).

*T. sinense*, is a second-class nationally protected plant in China (Fu and Jin, 1992; Li, 2015; Zhang et al., 2020; Fan et al., 2021). In this study, the survival status and factors limiting the natural regeneration of *T. sinense* have been studied. On a small scale, individuals of *T. sinense* were highly clustered, and there were interactions between different diameter classes, which might reduce genetic diversity; intense competition within populations led to declines in the populations. Therefore, proper thinning of seedlings and transplanting of *T. sinense* will help reduce population declines caused by competition. Moreover, artificial breeding technology can be used to breed well-growing *T. sinense* seedlings and expand their population. On the other hand, *T. sinense* and its dominant species had a strong competitive relationship on a small scale, with *T. sinense* being in adisadvantaged position. To change this situation without changing the stability of the community, appropriately cutting down the dominant species would help the growth and survival of *T. sinense*. Our studies showed that *T. sinense* was suitable for distribution in mid-altitude areas with high humidity, low litter depth, and little K. Given these findings when returning artificial seedlings to the wild, the location should be selected based on quantitative analyses.

**5 Conclusions**

Overall, our results highlighted the importance of intra- and interspecific correlation and environmental factors for the spatial distribution of *T. sinense*. This study disentangles the spatial pattern of *T. sinense* and its influencing factors. Furthermore, it has relevant implications for conserving and managing endangered trees in a constantly fragmented habitat. However, soil microorganisms can also influence the distribution pattern of plants; this paper does not consider soil microorganisms as an influencing factor for the time being. Future studies should further investigate the influence of soil microorganisms on the distribution pattern of the endangered plant, *T. sinense*.

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**Author Contributions**

Xiaohong Gan conceived the project, designed the experiments, and performed the experiment partly; Huan Zhang wrote the manuscript and performed the experiment; HongPing Deng performed the experiment and statistical analysis.

**Data availability statement**

The original contributions presented in the study are included in the article. Further inquiries can be directed to the corresponding author.

**Conflict of interest statement**

The authors declare no conflict of interest.

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Figures:

Figure 1 The study sites and geographical distribution of the four plots in Leigong Mountain, Guizhou province, China. Triangles represent the four plots; they are in evergreen and deciduous broadleaved mixed forest.

Figure 2 Individual distribution in three stages of *T. sinense* (P1, P2, P3 and P4) in the four plots. Young tree, DBH <7.5 cm; adult tree, DBH < 22.5 cm; old tree, DBH ≥22.5 cm.

Figure 3 Univariate point pattern analysis of *T. sinense* in the four plots. A: the distribution of *T. sinense* in P1; B: the distribution of *T. sinense* in P2; C: the distribution of *T. sinense* in P3; D: the distribution of *T. sinense* in P4. Red fold lines indicate the g11(r) function; dotted lines indicate the upper and lower limits of the 99% confidence interval. Points above the upper limits indicate an aggregated distribution, those within the intervals indicate a random distribution, and those below the lower limits indicate a regular distribution. The 99% confidence intervals were calculated using the 5 highest and 5 lowest values of g11(r) derived from 199 Monte-Carlo simulations of the heterogeneous Poisson null model.

Figure 4 Bivariate point pattern analysis examples for intraspecific association of *T. sinense* among different age classes in each plot. Red fold lines indicate observations. Dotted lines indicate the upper and lower limits of the 99% confidence interval. Points above the upper envelope indicate a positive correlation between different age- class trees, points between the envelopes indicate no association between the different age- class trees, and points below the lower envelope indicate a negative association between the different age- class trees. The 99% confidence intervals were calculated using the five highest and five lowest values of g12(r) derived from 199 Monte-Carlo simulations of the heterogeneous Poisson null model. A-C: the intraspecific association of *T. sinense* among different age classes in P1, A, young and adult trees; B, young and old trees; C, adult and old trees; D-F: the intraspecific association of *T. sinense* among different age classes in P2, D, young and adult trees; E, young and old trees; F, adult and old trees; G-I: the intraspecific association of *T. sinense* among different age classes in P3, G, young and adult trees; H, young and old trees; I, adult and old trees; J-L: the intraspecific association of *T. sinense* among different age classes in P4, J, young and adult trees; K, young and old trees; L, adult and old trees.

Figure 5 Bivariate point pattern analysis examples for interspecific associations among *T. sinense* and its dominant species in four plots. Red fold lines indicate the g12(r) function; dotted lines indicate the upper and lower limits of the 99% confidence interval. Points above the upper limits indicate positive associations, points within the intervals show non-significant associations, and points below the lower limits show negative associations. The 99% confidence intervals were calculated using the five highest and five lowest values of g12(r) derived from 199 Monte-Carlo simulations of the heterogeneous Poisson null model; A-D: the interspecific associations among *T. sinense* and its dominant species in P1 ,*A, T. sinense*+ *P. psilophyllus*; B, *T. sinense*+ *S. japonicus*; C, *T. sinense*+ *P. tomentosa*; D, *T. sinense*+ *A. sinense;* E-H: the interspecific associations among *T. sinense* and its dominant species in P2, E, *T. sinense*+ *P. psilophyllus*; F, *T. sinense*+ *S. japonicus*; G, *T. sinense*+ *P. tomentosa*; H, *T. sinense*+ *A. sinense;* I-L: the interspecific associations among *T. sinense* and its dominant species in P3, I, *T. sinense*+ *P. psilophyllus*; J, *T. sinense*+ *S. japonicus*; K, *T. sinense*+ *P. tomentosa*; L, *T. sinense*+ *A. sinense;* M-P: the interspecific associations among *T. sinense* and its dominant species in P4, M*, T. sinense*+ *P. psilophyllus*; N, *T. sinense*+ *S. japonicus*; O, *T. sinense*+ *P. tomentosa*; P, *T. sinense*+ *A. sinense.*

Figure 6 Spatial distribution of *T. sinense* in relation to mineral elements (N (g/kg), P (g/kg), K (g/kg), Zn (mg/kg), Mg (g/kg), Na (mg/kg), Ca (g/kg)) in four plots. A: Spatial distribution of *T. sinense* in relation to mineral elements in P1; B: Spatial distribution of *T. sinense* in relation to mineral elements in P2; C: Spatial distribution of *T. sinense* in relation to mineral elements in P3; D: Spatial distribution of *T. sinense* in relation to mineral elements in P4.

Figure 7 Canonical correlation analysis of the environmental factors and species. TS, *T. sinense*; SJ, *S. japonicus*; PP, *P. psilophyllus*; AS, *A sinense*; PT, *P. tomentosa*. A: the environmental factors in P1, included altitude, humidity, litter depth, shade density, K (potassium) and Zn (zinc); B: the environmental factors in P2, included altitude, humidity, litter depth, P (phosphorus), Ca (calcium) and K; C: the environmental factors in P3, included shade density, altitude, P, Ca, K and Zn; D: the environmental factors in P4, included humidity, altitude, litter depth, N (nitrogen), P and K.