Spatial Distribution Patterns and Associations of Two Litsea Species in the Mulinzi Large Forest Plot (Postprint)

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Abstract

Taking congeneric species [Litsea pungens and L. elongate] in a 15 hm² large plot of Hubei Mulinzi National Nature Reserve as the research object, we analyzed the spatial distribution patterns, intra- and interspecific spatial associations of the two species using pair correlation functions and different null models (complete spatial randomness model, heterogeneous Poisson model, and antecedent condition model), and explored community assembly mechanisms from the perspective of spatial distribution patterns of congeneric species. The results showed that: (1) In the study of population spatial distribution patterns, the spatial distribution patterns of both species were generally aggregated. Based on the CSR null model, the aggregation scales for L. pungens and different diameter classes (saplings, small trees, medium trees, and adult trees) were 0-114 m, 0-103 m, 0-56 m, 0-34 m, and 0-16 m, respectively, while those for L. elongate and different diameter classes were 0-150 m, 0-150 m, 0-59 m, 0-56 m, and 0-14 m, respectively; based on the HP null model, the aggregation scale for L. pungens overall was 0-23 m, with saplings, small trees, and medium trees showing aggregated distribution at 0-22 m, and adult trees only showing aggregated distribution at the 0-3 m scale; for L. elongate overall, the aggregation scales were 0-36 m and 140-150 m, with aggregation scales of 0-35 m, 0-35 m, 0-12 m, and 0-6 m for each diameter class, respectively; (2) In the study of intraspecific associations, intraspecific associations among individuals of different diameter classes of both L. pungens and L. elongate showed positive associations at small scales, which became weakly negative or showed no association as the scale increased; (3) In the study of interspecific associations, the spatial relationships of L. pungens to L. elongate and L. elongate to L. pungens were generally similar. Overall, both species showed positive associations with the other species within the 30 m scale and negative associations within the 40-

68 m scale; associations among different diameter classes all showed no association, with occasional positive or negative associations. The study concluded that population spatial distribution patterns were basically aggregated, primarily influenced by habitat heterogeneity and dispersal limitation. The spatial distribution patterns of L. pungens and L. elongate in the Mulinzi large plot showed similarities, while different habitat preferences may be the reason for the coexistence of the two congeneric species.

Full Text

Preamble

Spatial Distribution Pattern and Association of Two *Litsea* Species in a Large Forest Plot in Mulinzi Nature Reserve

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Abstract

This study examined two congeneric species—*Litsea pungens* and *L. elongata*—within a 15 hm^2 forest plot in Hubei Mulinzi National Nature Reserve. Using pairwise correlation functions and three null models (Complete Spatial Randomness [CSR], Heterogeneous Poisson Process [HP], and Antecedent Condition [AC]), we analyzed the spatial distribution patterns, intraspecific associations, and interspecific spatial relationships to explore community assembly mechanisms from the perspective of congeneric species distribution. The results showed: (1) Both species exhibited aggregated distributions overall. Under the CSR null model, aggregation scales for *L. pungens* (and its different diameter classes: saplings, small trees, medium trees, and adult trees) were 0–114 m, 0–103 m, 0–56 m, 0–34 m, and 0–16 m, respectively. For *L. elongata*, corresponding scales were 0–150 m, 0–150 m, 0–59 m, 0–56 m, and 0–14 m. Under the HP null model, *L. pungens* showed aggregation at 0–23 m overall, with saplings, small trees, and medium trees aggregated at 0–22 m, while adult trees were only aggregated at 0–3 m. *L. elongata* exhibited aggregation at 0–36 m and 140–150 m overall, with diameter classes showing aggregation at 0–35 m, 0–35 m, 0–12 m, and 0–6 m. (2) Intraspecific associations were generally positive at small scales, shifting to weakly negative or no association as scale increased. (3) Interspecific relationships were similar in both directions: the two species showed positive association within 30 m and negative association at 40–68 m. Different diameter classes were generally not associated, with occasional positive or negative associations. We conclude that aggregated distribution patterns are primarily influenced by habitat heterogeneity and dispersal limitation. The spatial distribution patterns of the two *Litsea* species in the Mulinzi plot show similarities, while different habitat preferences may enable their coexistence.

Keywords: congeneric coexistence, point pattern, spatial distribution, spatial association

Introduction

Congeneric species share common ancestors and exhibit morphological and physiological similarities, often requiring similar resources. From a niche differentiation perspective, these similarities may lead to competitive exclusion rather than stable coexistence (Ackerly & Donoghue, 1998; Webb & Ackerly, 2002). However, congeneric species coexistence is commonly observed in tropical and temperate plant communities (Zhang, 2009), prompting intense ecological debate. Comparing congeneric species minimizes confounding effects of phylogenetic differences and allows examination of spatial structure and correlations (Swenson et al., 2006; Yao, 2016).

Plant population spatial distribution patterns—the horizontal arrangement of individuals—remain a central focus in ecology (Qu, 1984; Zhang, 1995; Wiegleb, 1989; Nathan, 2006). Ripley’ s point pattern analysis overcomes limitations of traditional methods (Condit, 2000; Zhang & Meng, 2004) and has been widely applied to single-species distributions (Fan et al., 2008; Huang et al., 2018), dominant tree species (Zhang et al., 2011; Zhang et al., 2016), interspecific relationships (Yao et al., 2018), and environment-pattern relationships (Liu et al., 2018; Yan, 2018). However, studies on congeneric or confamilial species remain limited (He et al., 2017; Chen et al., 2018).

The genus *Litsea* (Lauraceae) is widely distributed, with approximately 72 species in China (Chen, 2004). Mulinzi National Nature Reserve preserves one of the most intact subtropical evergreen-deciduous broadleaved mixed forests (Huang, 2016), containing only two *Litsea* species: *L. elongata* and *L. pungens*, which account for 4.8% of total individuals in the plot. While *L. pungens* has high medicinal value and *L. elongata* has commercial importance (Chen, 2004), ecological studies are scarce beyond research on leaf litter and nutrient characteristics (Shu, 2016). Although neither species is a dominant or pioneer species, studying their population spatial patterns as small trees is ecologically significant. This study uses the *g(r)* function to analyze spatial patterns and associations of these two congeneric species in the Mulinzi plot, exploring their formation mechanisms, similarities, and coexistence patterns to inform understanding of species coexistence in subtropical regions.

1. Study Area

The study area (109°59 30 -110°17 58 E, 29°55 59 -30°10 47 N) is located in Hefeng County, Hubei Province, covering 20,838 ha. This region represents the northeastern extension of the Yunnan-Guizhou Plateau, with elevations ranging from 1,100 m to 2,095.6 m. The climate is a humid continental monsoon type, characterized by mild winters, moderate summers, concurrent rainfall and heat, abundant sunshine, and distinct mountain climate features. Mean annual temperature is 15.5 °C, precipitation is 1,700–1,900 mm, relative humidity is 82%, and frost-free period is 270–279 days. Soils include yellow-brown earth, brown earth, and yellow earth.

The 15 hm^2 Mulinzi plot is located in the reserve core area at 1,588–1,780 m elevation with relatively gentle terrain. This subtropical montane evergreen-deciduous broadleaved mixed forest is dominated by *Eurya alata*, *Cyclobalanopsis multinervis*, *Carpinus fargesiana*, *C. myrsinifolia*, *Sorbus folgneri*, *Dendrobenthamia japonica* var. *chinensis*, *Castanea henryi*, *Quercus fabri*, *Symplocos sumuntia*, and *S. lancifolia* (Yao, 2016).

2. Methods

2.1 Plot Establishment and Field Survey

In 2013, a 15 hm^2 permanent monitoring plot was established following CTFS protocols, divided into 375 subplots of 20 m × 20 m. Stainless steel pipes marked the four corners of each subplot. Each subplot was further divided into four 10 m × 10 m quadrats, then into four 5 m × 5 m micro-quadrats. All woody plants with DBH 1.0 cm were tagged and marked with red paint at 1.3 m height. For each individual, species identity (family, genus, species) and coordinates (relative to the southwest corner of the plot) were recorded.

2.2 Population Size Classification

Using diameter classes as age surrogates and considering the size distribution characteristics of the two *Litsea* species, we defined four diameter classes: Class I (1 cm DBH $<$ 2.5 cm), Class II (2.5 cm DBH $<$ 5 cm), Class III (5 cm DBH $<$ 10 cm), and Class IV (DBH 10 cm), corresponding to saplings, small trees, medium trees, and adult trees.

2.3 Point Pattern Analysis

We used the pairwise correlation function $g(r)$, which analyzes patterns based on distances between all pairs of mapped individuals and eliminates the cumulative effects of Ripley’ s $K(r)$ function at large scales (Ripley, 1976; Wiegand et al., 2007). Analysis was conducted at scales up to half the shorter plot dimension (150 m) with a ring width of 1 m. We performed 199 Monte Carlo simulations to generate 99% confidence envelopes using maximum and minimum values from the simulations (Wiegand et al., 2006; Wiegand et al., 2009).

2.4 Null Model Selection

Point pattern analysis requires testing for habitat heterogeneity effects. Generally, aggregation at scales >10 m suggests habitat heterogeneity influence.

The HP and AC models eliminate large-scale habitat heterogeneity effects. If small-scale aggregation persists after removing habitat heterogeneity, dispersal limitation is implicated. Therefore, selecting appropriate null models is critical (Liang et al., 2014). We used CSR and HP null models for univariate *g(r)* analysis, and the AC null model for bivariate *g(r)* analysis.

All analyses were performed using the "spatstat" package in R 3.4.1. Spatial distribution maps were created with Sigmaplot 13, and point pattern analysis figures with Origin 2018.

3. Results

3.1 Spatial Distribution Patterns of the Two Species

The plot contained 1,701 *L. pungens* individuals and 2,306 *L. elongata* individuals . The overall spatial distributions differed markedly [Figure 1: see original paper]: *L. pungens* primarily occupied low-elevation ridge areas, while *L. elongata* dominated high-elevation valley slopes with scattered individuals throughout the plot.

Overall spatial patterns [Figure 2: see original paper] showed that under CSR, *L. pungens* and *L. elongata* were aggregated at 0–114 m and 0–150 m, respectively. Under HP, *L. pungens* was aggregated at 0–23 m and randomly distributed at other scales, while *L. elongata* showed aggregation at 0–36 m and 140–150 m, with random distribution at 48–139 m.

Analysis by diameter class [FIGURE:3, FIGURE:4] revealed that under CSR, *L. pungens* saplings, small trees, and medium trees were aggregated at 0–103 m, 0–56 m, and 0–34 m, respectively, while adult trees were aggregated at 0–16 m. *L. elongata* saplings, small trees, medium trees, and adult trees were aggregated at 0–150 m, 0–59 m, 0–56 m, and 0–14 m, respectively. Under HP, *L. pungens* saplings, small trees, and medium trees were all aggregated at 0–22 m, with adult trees only aggregated at 0–3 m. For *L. elongata*, diameter classes showed aggregation at 0–35 m, 0–35 m, 0–12 m, and 0–6 m. Aggregation scale decreased with increasing diameter class for both species, with adult trees showing aggregation only at small scales and random distribution becoming more pronounced.

3.2 Intraspecific Associations by Diameter Class

Intraspecific associations for *L. pungens* [Figure 5: see original paper] showed that under AC, adult trees were not associated with saplings at any scale, while other diameter class pairs were positively associated at small scales (r 20 m): small trees with saplings (0–20 m), medium trees with saplings (0–18 m), medium trees with small trees (0–20 m), adult trees with small trees (0–14 m), and adult trees with medium trees (0–17 m).

For *L. elongata* [Figure 6: see original paper], adult trees were not associated with medium trees at any scale. Positive associations occurred between: small trees and saplings (0–36 m), medium trees and saplings (0–25 m), adult trees and saplings (8–15 m), medium trees and small trees (0–23 m), and adult trees and small trees (0–6 m).

3.3 Interspecific Associations

Using the AC null model to exclude habitat heterogeneity effects above 30 m, overall patterns [Figure 7: see original paper] showed *L. pungens* was positively associated with *L. elongata* at 0–30 m, while *L. elongata* was positively associated with *L. pungens* at 7–29 m. Among diameter classes [FIGURE:8, FIGURE:9], *L. pungens* saplings were positively associated with *L. elongata* saplings at 4–34 m; *L. pungens* small trees were positively associated with *L. elongata* saplings at 13–29 m but negatively associated at 42–67 m; *L. pungens* medium trees were negatively associated with *L. elongata* saplings at 40–50 m; *L. pungens* small trees were positively associated with *L. elongata* small trees at 0–25 m but negatively associated at 44–60 m; *L. pungens* medium trees were positively associated with *L. elongata* medium trees at 0–5 m but negatively associated at 47–54 m and 119–128 m. All other diameter class combinations showed no association.

Conversely, *L. elongata* saplings were positively associated with *L. pungens* saplings at 13–32 m and negatively associated at 42–76 m; *L. elongata* small trees were positively associated with *L. pungens* saplings at 0–13 m; *L. elongata* small trees were positively associated with *L. pungens* small trees at 0–15 m and negatively associated at 46–59 m. All other combinations showed no association.

Thus, interspecific relationships were similar in both directions, with only minor differences. Notably, adult trees of both species showed no significant ecological relationships with any diameter class of the other species.

4. Discussion

4.1 Causes of Spatial Distribution Patterns

Plant spatial distribution patterns result from both biological characteristics and environmental factors, with different developmental stages showing distinct patterns (Frost & Rydin, 2000). Our results demonstrate aggregated distributions under both CSR and HP null models, transitioning to random or uniform distributions at larger scales—consistent with most studies (Zhu et al., 2011; Guo et al., 2013). Habitat heterogeneity is considered a primary driver of vegetation patterns, with aggregation at scales >10 m typically interpreted as habitat-driven (Takyu et al., 2002; Getzin et al., 2008). Under CSR, *L. pungens* and *L. elongata* were aggregated at 0–114 m and 0–150 m, respectively. Using HP to exclude habitat heterogeneity above 30 m reduced aggregation scales to random distribution, indicating strong habitat heterogeneity effects. The temporal sequence from saplings to adult trees showed a clear trend from aggregated to random distribution, following general ecological principles (Vargas et al., 2010;

Zhang et al., 2011). For both species, aggregation scale decreased with diameter class: saplings > small trees > medium trees > adult trees. Habitat heterogeneity most strongly affected saplings, likely because small, vulnerable individuals require aggregated distributions for mutual protection and population stability (Zhang, 1998; Wang et al., 2014). Adult trees were minimally affected by habitat heterogeneity, with negative density dependence outweighing heterogeneity effects. As diameter increased, resource and space demands intensified intraspecific competition, causing self-thinning and mortality that produced random or uniform distributions (Shu et al., 2019).

At small scales, dispersal limitation may cause aggregation. HP model analysis revealed small-scale aggregation for both species, indicating dispersal limitation effects. Seeds fall near maternal trees due to gravity and wind, creating density gradients that generate small-scale aggregation. Both species have globular fruits dispersed primarily by gravity, limiting dispersal distance. *L. elongata* showed larger aggregation scales than *L. pungens*, possibly because *L. elongata* is a medium-sized tree (up to 12 m) versus *L. pungens* as a small tree (3–10 m), resulting in greater seed dispersal range.

Intraspecific and interspecific competition also influence aggregation. Intraspecific association reflects spatial relationships among different developmental stages of the same species (Wang et al., 2010). We found weak intraspecific and interspecific competition. The only notable negative intraspecific association occurred between *L. elongata* small trees and saplings, suggesting that during early succession, these stages have similar resource requirements, creating unstable, mutually exclusive interactions where sapling growth is suppressed by small trees. Interspecific competition was weak, with most diameter class combinations showing no association and only occasional weak positive or negative associations at small scales. This likely reflects different habitat preferences: *L. pungens* favored high-elevation ridge areas, while *L. elongata* preferred low-elevation valley slopes.

4.2 Similarity and Coexistence Mechanisms of Congeneric Species

Congeneric species in the same habitat should exhibit similar spatial distribution patterns. Our results show similarities between *L. pungens* and *L. elongata* in overall and diameter-class-specific distribution patterns, intraspecific associations, and reciprocal interspecific relationships. Both species showed aggregated distributions overall and across diameter classes. Intraspecific associations were similar except for *L. pungens* adult-sapling and *L. elongata* adult-medium tree relationships. Interspecific associations showed strong ecological relationships only between saplings and between small trees, with other diameter class combinations showing no significant relationships. The spatial distribution differences between species likely reflect distinct habitat requirements.

Species coexistence requires interspecific relationships within a region (Zong et al., 2018). Overall, *L. pungens* and *L. elongata* showed negative association only at 40-68 m, with positive or no association at other scales. Different diameter class combinations were mostly unassociated, with negative associations only at very small scales. This pattern likely reflects habitat preference differentiation that reduces resource competition. Research on *Quercus* species in Baotianman found weak interspecific competition facilitates coexistence of less abundant species (Wei, 2015). Similarly, our study shows weak competition between the two *Litsea* species, with mutual facilitation promoting coexistence and collective resistance to other species.

In conclusion, the two congeneric *Litsea* species show similar spatial distribution patterns shaped by habitat heterogeneity, dispersal limitation, and intra-/interspecific competition. Habitat heterogeneity most strongly affected saplings. Dispersal limitation resulted in larger aggregation scales for *L. elongata* than *L. pungens* after removing habitat effects. Both species showed positive intraspecific associations at small scales and weak interspecific competition. Different habitat preferences appear fundamental to their coexistence, potentially allowing them to form mutualistic protection against other species —though this requires further investigation.

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Note: Figure translations are in progress. See original paper for figures.