Postprint: Spatial Structure Dynamics of the Mulun Karst Evergreen-Deciduous Broad-Leaved Forest

Authors: Yang Zhiqi, Du Hu, Song Tongqing, Zeng Fuping, Peng Wanxia, Zhang Lijin, Gan River, Yang Gairen

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Abstract

The spatial structure evolution patterns of forests in karst regions represent one of the key scientific issues in global forest research. To investigate the spatial structure dynamics of karst evergreen-deciduous broad-leaved forests, this study utilized a 2 hm^2 permanent monitoring plot of karst evergreen-deciduous broad-leaved forest within Mulun National Nature Reserve as the research object, and analyzed the dynamic changes in community spatial structure characteristics using spatial structure parameters including uniform angle index (Wi), mingling index (Mi), and dominance index (Ui) based on three survey datasets from 2007, 2012, and 2017. The results showed that: (1) The univariate distribution of spatial structure parameters indicated that from 2007 to 2017, the stand gradually evolved toward a slightly clumped distribution state as stand age increased; the mingling index remained at a high mingling level, showing a trend toward very high mingling; in terms of dominance index, the stand exhibited an intermediate state, transitioning toward a sub-dominant state with stand growth. (2) The results of spatial structure analysis for different diameter classes showed that for trees with diameter classes of 1-15 cm, the uniform angle index, dominance index, and mingling index gradually increased with stand growth; as diameter class increased, the dominance index values showed a gradually decreasing trend, while the mingling index showed a gradually increasing trend. (3) The results of spatial structure analysis for main dominant tree species indicated that during the decade from 2007 to 2017, all five dominant species groups exhibited slightly clumped distribution; the dominance index showed a distribution state biased toward sub-dominant and intermediate, with mingling level at a high mingling level, gradually evolving toward very high mingling. The study concluded that the current stand of Mulun karst evergreen-deciduous broad-leaved forest exhibits slightly clumped distribution, with relatively strong mingling degree, biased toward a sub-dominant distribution state, relatively stable community, good stand regeneration condition, and is gradually succeeding toward a climax community. The analysis of vegetation structure dynamic changes in karst evergreen-deciduous broad-leaved forests holds important reference significance for predicting future development trends of forests.

Full Text

Spatial Structure Dynamics of Karst Evergreen-Deciduous Broad-Leaved Forest in Mulun National Nature Reserve

YANG Zhiqi^{1,2,3}, **DU Hu**^{2,3}, **SONG Tongqing**^{2,3}, **ZENG Fuping**^{2,3}, **PENG Wanxia**^{2,3}, **ZHANG Lijin**^{2,3,4}, **GAN Jiang**^{2,3,4}, **YANG Gairen**^{1*}

1. Forestry College of Guangxi University, Nanning 530004, China
2. Key Laboratory of Agro-Ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, China
3. Huanjiang Observation and Research Station of Karst Ecosystem/Guangxi Key Laboratory of Karst Ecological Processes and Services, Chinese Academy of Sciences, Huanjiang 547100, Guangxi, China
4. Ecological Science Research Center, Jiangxi Agricultural University, Nanchang 330045, China

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Abstract

The evolution of spatial structure in karst forests represents a key scientific issue in global forest research. To investigate the dynamics of spatial structure in karst evergreen-deciduous broad-leaved forests, we analyzed a 2 hm^2 permanent monitoring plot in Mulun National Nature Reserve using survey data from 2007, 2012, and 2017. Spatial structure parameters—including the uniform angle index (Wi), mingling degree (Mi), and size inequality index (Ui)—were employed to characterize community spatial structure dynamics. Our results reveal: (1) Univariate distributions of spatial structure parameters showed that from 2007-2017, the stand gradually evolved toward a slightly clumped distribution pattern as stand age increased. The mingling degree remained at a strong mixing level, with a trend toward very strong mixing. The size inequality index indicated a moderate stand status that shifted toward subdominance as the stand matured. (2) Analysis of different diameter classes demonstrated that for trees with DBH of 1-15 cm, Wi, Ui, and Mi all increased with stand development. As diameter class increased, Ui values gradually decreased while

Mi values increased. (3) Analysis of dominant tree species revealed that all five dominant species groups exhibited slightly clumped distribution patterns during the ten-year period. The size inequality index showed a distribution state biased toward subdominance and moderate status, while the mingling level remained at strong mixing with a gradual evolution toward very strong mixing. We conclude that the karst evergreen-deciduous broad-leaved forest in Mulun currently exhibits slight clumping, strong mixing, and a tendency toward subdominant distribution. The community is relatively stable with good regeneration status, gradually succession toward a climax community. Analysis of vegetation structure dynamics in karst evergreen-deciduous broad-leaved forests provides important reference significance for predicting future forest development trends.

Keywords: uniform angle index (Wi), mingling degree (Mi), size inequality index (Ui), structural characteristics, dynamic change

Introduction

Karst topography forms through the action of rainfall and groundwater on carbonate bedrock such as limestone. Southwest China contains the world' s largest karst forest region, characterized by weak ecosystem stability, strong habitat heterogeneity, and exposed bedrock [?, ?]. Evergreen-deciduous broad-leaved forests represent a unique feature of karst landscapes in southwest China, with complex community structure, rich biodiversity, and high habitat heterogeneity, making them ideal communities for studying forest productivity. Compared with non-karst subtropical forests in China, karst forests exhibit higher species diversity under different species compositions. During vegetation succession in Guangxi karst regions, species richness, Shannon-Wiener index, Simpson index, and evenness index all gradually increase with forward succession [?, ?]. Karst forest ecosystems are typical fragile ecosystems. On one hand, unreasonable utilization and management of forest resources have led to missing stand structure, weakened ecosystem functions, and reduced stability of forest ecosystems [?, ?]. On the other hand, during rocky desertification control, planted forests suffer from problems such as single species composition, simple structure, and unreasonable layout, resulting in gradually highlighted phenomena of low ecological protection functions, low biodiversity, and poor system stability [?, ?]. Therefore, studying the spatial structure of karst forests can provide theoretical basis for the healthy development of forest ecosystems in karst regions.

The relationship between neighboring trees largely determines the most fundamental characteristics of forest structure [?, ?]. Research has shown that spatial structure parameters characterizing neighbor relationships—including uniform angle index, size inequality index, and mingling degree [?, ?]—can be applied to spatial structure analysis of living trees in forests. Univariate, bivariate, and multivariate distributions of these parameters can be used to analyze stand spatial structure characteristics, tree competition, population size trends, species dominance, and species diversity, as well as to reconstruct and optimize forest structure [?, ?].

Studies have found that the mingling degree of forest communities at different succession stages changes gradually [?, ?], with both mingling degree and DBH-based size inequality index increasing as succession proceeds, and trees gradually trending toward random distribution patterns [?, ?, ?], which facilitates stable succession toward climax communities [?, ?, ?]. Forest biodiversity continues to increase, and stand spatial structure gradually develops toward a stable direction [?, ?].

During forest succession, spatial structure characteristics exhibit a series of changes. At the horizontal structure level, the proportion of random distribution in karst forests is almost unaffected by tree size but significantly influenced by habitat heterogeneity and life forms [?, ?], maintaining an ideal normal distribution in univariate distributions based on uniform angle index. With increasing stand age, stand aggregation gradually decreases, and the distribution patterns of various species regeneration also change dynamically [?, ?]. Higher mingling degree corresponds to higher community species diversity [?, ?]. Regarding size inequality index, Wang and Guo [?, ?] found in natural forest vegetation surveys that large-diameter individuals affect the spatial distribution of neighboring trees, with the aggregation range of neighboring trees continuously decreasing as DBH increases. Forest species diversity also changes continuously during succession [?, ?]. To fully utilize space, structurally diverse stands can store more trees within their stands [?, ?], and increased diversity significantly promotes forest biomass [?, ?]. Trees in dense forests face intense competition, and their carrying capacity decreases, making control of stand density extremely important. Application of spatial structure parameters provides an effective approach for improving forest quality [?, ?]. Stand spatial structure research often uses parameter means and univariate distributions to study overall stand characteristics. This study incorporates bivariate distributions [?, ?] to analyze stand spatial structure, enabling simultaneous analysis of stand spatial characteristics from different horizontal levels.

Karst peak-cluster depressions occupy 10%–15% of land area [?, ?] and play extremely important roles in global ecosystems. Research on forest types in karst regions can provide effective restoration and reconstruction of karst rocky desertification. Currently, research on evergreen broad-leaved forests in China' s karst regions mainly focuses on forest appearance changes, with studies on succession patterns, ecological functions and protection, and spatial dynamics still very limited. Using a 2 hm^2 permanent monitoring plot of karst evergreen-deciduous broad-leaved forest in Mulun National Nature Reserve and based on survey data from 2007, 2012, and 2017, this study addresses the following questions: (1) How do community structure and population dynamics change in karst evergreen-deciduous broad-leaved forests? (2) What are the changes and differences in spatial characteristics of trees across different diameter classes? (3) What are the spatial change characteristics of dominant species over the ten-year period?

1.1 Study Area Description

The study site is located in Mulun National Nature Reserve in Huanjiang County, Guangxi Zhuang Autonomous Region (25°06 09 N–25°12 25 N, 107°53 29 E–108°05 42 E). The topography consists primarily of karst peak-cluster depressions. The reserve contains extremely rich evergreen-deciduous broad-leaved mixed forests, with a total forest area of 10,829.7 hm^2 and forest coverage of 95.4%. This vegetation type represents one of the important forest types in subtropical mountainous regions and serves as a crucial barrier for maintaining regional ecological security and protecting biodiversity [?, ?]. Elevation ranges from 250–1,028 m, with mean annual temperature of 15.0–18.7 ℃ and mean annual precipitation of 1,530–1,820 mm. Rainfall is concentrated from April to August, maintaining relatively humid forest conditions with humidity of 80%–90%. Soils are primarily limestone soils. Mulun Nature Reserve possesses unique natural resources and advantages, belonging to a mid-subtropical limestone evergreen-deciduous mixed forest ecosystem. Connected with Guizhou Maolan National Nature Reserve, it forms the largest contiguous and best-preserved karst forest ecosystem at the same latitude globally, representing an important region for karst and forest research with significant scientific and conservation value.

In 2007, a typical slope was selected within the reserve to establish a sample plot with a projected area of 200 m × 100 m. The entire plot was divided into 50 subplots of 20 m × 20 m. Following CTFS (The Centre for Tropical Forest Science) standards, vegetation surveys were conducted for every tree. Individual plants with DBH $\geq$ 1 cm were tagged, with species name, DBH, tree height, crown width, and coordinate location recorded [?, ?]. The study forest is primary forest. In terms of biomass, woody plants with DBH $\geq$ 1 cm constitute the absolute main body; therefore, individuals with DBH $<$ 1 cm and herbaceous plants were not considered in this study [?, ?]. The selection of woody plants with DBH $\geq$ 1 cm follows the survey method adopted by American scientist S.P. Hubbell when establishing the 50 hm^2 plot in Panama in 1980. The plot is resurveyed every five years, with three surveys conducted in 2007, 2012, and 2017. The forest type studied is karst evergreen-deciduous broad-leaved forest.

[Figure 1: see original paper] Schematic diagram of sample plot in Huanjiang County

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1.3 Data Processing Methods

Dominant tree species: Importance value IV = (RF relative frequency + RA relative abundance + RD relative dominance)/3 [?, ?]. Species importance value represents species dominance, with larger values indicating greater importance in community structure and can be used to characterize structural changes in plant community species.

Biomass calculation:

$$BIO = a \times DBH^b$$

where BIO represents woody plant biomass, DBH is tree diameter at breast height (cm), and a and b are regression coefficients [?, ?]. Species biomass was estimated using regression equations for karst forest tree biomass from our research group' s previous studies. Biomass models using DBH as a variable can effectively estimate organ and total biomass of major tree species in Guangxi. Based on previous group research, a = 0.35 and b = 1.989 [?, ?].

Spatial structure characteristic indices: Forest spatial structure analysis can utilize either single indices or combinations of two indices (bivariate distributions) to better describe forest spatial structure. Three structural parameters –uniform angle index (Wi) [?, ?], mingling degree (Mi) [?, ?], and size inequality index (Ui) [?, ?]–were used to characterize forest spatial features. Any tree in a stand and its n nearest neighboring trees constitute a spatial structure unit, with n = 4 adopted in this study. Each parameter has five possible values: 0.00, 0.25, 0.50, 0.75, and 1.00. For uniform angle index, forest communities consist of five distribution states: very uniform, uniform, random, clumped, and very clumped. Wi > 0.517 indicates clumped distribution, 0.475 < Wi < 0.517 indicates random distribution, and Wi < 0.475 indicates uniform distribution [?, ?]. Mingling degree represents zero, weak, moderate, strong, and very strong mixing states [?, ?]. Size inequality index represents dominant, subdominant, moderate, suppressed, and absolutely suppressed status [?, ?]. The superiority of stand spatial structure reflects forest community stability. Random distribution represents the optimal pattern; higher stand mingling degree indicates superior structure; and higher proportions of dominant or subdominant trees are preferable. Bivariate distributions combine three superior microstructures: randomly distributed trees in high mixing state, moderate-to-dominant trees with random distribution, and moderate-to-dominant trees in high mixing state [?, ?].

Uniform angle index (Wi) describes the uniformity of neighboring trees around a reference tree i [?, ?, ?]. The formula is:

$$Wi = \frac{1}{n} \sum_{j=1}^{n} Z_{ij}$$

where Wi is the uniform angle index, Zij is a discrete variable (Zij = 1 when the jth α angle is smaller than the standard angle \$ \$0 = 72°, otherwise Zij = 0).

Mingling degree (Mi) describes the species relationship between a reference tree and its neighbors [?, ?]. The formula is:

$$Mi = \frac{1}{n}\sum_{j=1}^{n} V_{ij}$$

where Mi is the mingling degree, Vij is a discrete variable (Vij = 1 when the neighbor tree is a different species from the reference tree, otherwise Vij = 0).

Size inequality index (Ui) describes the degree of size differentiation among individual trees [**?**, **?**]. The expression is:

$$Ui = \frac{1}{n}\sum_{j=1}^{n} K_{ij}$$

where Ui is the size inequality index, Kij is a discrete variable (Kij = 1 when the neighbor tree' s DBH is larger than the reference tree, otherwise Kij = 0). Lower Ui values indicate fewer neighboring trees with larger DBH than the reference tree.

Winkelmass software was used to calculate stand uniform angle index (Wi), size inequality index (Ui), and mingling degree (Mi). R 4.1.3 was used to calculate importance values of dominant species. Data processing results used the average values calculated for each individual, with Origin 2022 used for mapping.

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2. Results

2.1 Community Structure Change Characteristics

As shown in Table 1 , stand density decreased from 2,627 to 1,889 plants • hm^{-2} (a 28.1% reduction) between 2007 and 2017. Species richness decreased by 7 species over the ten-year period. Mean DBH increased from 5.07 cm to 6.73 cm, while aboveground biomass increased from 52.51 Mg • hm^{-2} to 67.81 Mg • hm^{-2} (a 29.2% increase). Stand uniform angle index ranged from 0.524–0.539, with all values exceeding 0.517, indicating an overall clumped spatial pattern. Mingling degree showed an increasing trend over years, ranging from 0.842–0.864. Size inequality index shifted from moderate status toward subdominance over time.

Basic characteristics of stand in different years

2.2 Spatial Structure Parameter Distributions

2.2.1 Univariate Distribution Characteristics As shown in Figure 2 [Figure 2: see original paper], for uniform angle index, random distribution dominated the community from 2007–2017, followed by clumped distribution, with uniform distribution being the least common. The proportions of random and uniform distributions showed gradual decreasing trends, while clumped distribution showed an increasing trend. Overall, the stand gradually exhibited slight clumping over time. For size inequality index, trees in dominant status accounted for the lowest proportion (19.72%) in 2007, while trees in absolutely suppressed status accounted for the highest proportion (20.7%). When trees were in absolutely suppressed status, their relative frequency gradually decreased over years (20.68%, 20.11%, and 20.0%, respectively). Proportions of trees at different dominance levels were similar, all around 20.0%. For mingling degree, most trees were in very strong and strong mixing states. From 2007–2017, very strong mixing accounted for 59.9%, 59.1%, and 61.4%, respectively, while strong mixing accounted for 24.47%, 26.25%, and 26.3%, respectively, both showing increasing trends. Moderate, weak, and zero mixing states all showed decreasing trends over years.

[Figure 2: see original paper] Unitary distribution characteristics in different years

2.2.2 Bivariate Distribution Characteristics Bivariate distributions were obtained by combining any two of the three parameters (uniform angle index, mingling degree, and size inequality index). As shown in Figure 3 [Figure 3: see original paper], within the same year, as uniform angle index increased from 0 to 1.00, the number of trees at the same mingling degree first increased and then gradually decreased, reaching maximum values at Wi = 0.50. Under the same uniform angle index, as mingling degree classes increased, the number of trees also increased, reaching maximum values at Mi = 1.00. Comparing 2007, 2012, and 2017, with mingling degree unchanged, relative frequencies of trees at Wi = 0.00, 0.25, and 0.50 showed gradual decreasing trends, while tree numbers at Wi = 0.75 and 1.00 showed gradual increasing trends. In 2017, when Wi = 0.50 and Mi = 1.00, relative frequency reached the maximum (34.14% in 2007 and 34.6% in 2017), indicating gradual evolution toward slight clumping. With uniform angle index unchanged, tree numbers showed continuous decreasing trends over years when Mi = 0.00–0.5. At Mi = 1.00, tree distribution frequency was highest in 2017. Very strong mixing combined with clumped distribution was the most common stand structural unit, with this trend becoming increasingly evident as community succession progressed.

As shown in Figure 4 [Figure 4: see original paper], the frequency of the same size inequality index first increased and then decreased as uniform angle index classes increased, reaching maximum relative frequency at Wi = 0.5. Under the same uniform angle index class, differences in stand tree numbers among different size inequality indices were relatively small, indicating no significant difference in superiority levels among species with the same distribution pattern. Similar patterns were observed during the 2007–2017 period. With size inequality index unchanged, relative frequencies of suppressed and absolutely suppressed trees showed gradual increasing trends as uniform angle index increased over years, while dominant, subdominant, and moderate trees showed gradual decreasing trends.

[Figure 4: see original paper] Bivariate distribution of angular scale (Wi) and size ratio (Ui) in different years

As shown in Figure 5 [Figure 5: see original paper], relative frequencies of trees at the same size inequality index gradually increased as mingling degree classes increased, reaching maximum relative frequency at Mi = 1, with similar patterns from 2007-2017. In the Wi-Ui bivariate distribution, when mingling degree was zero or weak (Mi = 0.00, 0.25), relative frequencies at all size inequality index classes decreased by about half from 2007-2017. Under very strong mixing conditions, frequencies of trees at all size inequality index classes showed gradual increasing trends over years, reaching maximum values in 2017. The three surveys showed maximum relative frequencies at absolutely suppressed, suppressed, and subdominant levels (Ui = 1.00, 0.75, 0.25), accounting for 12.4%, 11.9%, and 12.5%, respectively.

[Figure 5: see original paper] The bivariate distribution changes of mixing degree (Mi) and size ratio (Ui) in different years

2.3 Spatial Characteristic Changes of Trees in Different Diameter Classes

As shown in Table 2 , except for individuals with DBH $\geq$ 15 cm, uniform angle index, size inequality index, and mingling degree of trees in other diameter classes all increased gradually with community development. Within the same period, as diameter class increased, size inequality index gradually decreased, while mingling degree generally increased, reaching maximum values in the DBH $\geq$ 15 cm class. Overall, no significant changes in uniform angle index were observed among the four diameter classes across the three surveys. Size inequality index for DBH $\geq$ 15 cm was significantly smaller than other classes, while mingling degree was significantly larger. Except for the 10-15 cm class in 2007 and DBH $\geq$ 15 cm class in 2012, which showed random distribution with uniform angle index between 0.475-0.517, all other mean values exceeded 0.517, indicating clumped distribution.

Spatial characteristics of trees with different diameter classes

2.4 Spatial Characteristic Changes of Dominant Species

Analysis of the top five dominant species based on importance values across three surveys (Table 3) revealed that *Sinosideroxylon pedunculatum* showed a decreasing then increasing trend in uniform angle index, while *Boniodendron minus* and *Handeliodendron bodinieri* showed increasing trends that strengthened over time. *Ligustrum quihoui* and *Radermachera sinica* showed decreasing trends, with *R. sinica* exhibiting random distribution (Wi = 0.512) in 2017. Size inequality index values for *S. pedunculatum*, *L. quihoui*, *H. bodinieri*, and *R. sinica* increased gradually over time, with mean values between 0.25-0.50, indicating certain dominant status. *B. minus* showed a gradually decreasing trend in size inequality index but remained between 0.25-0.50, indicating subdominant status in its structural unit. Overall, all five dominant species were between subdominant and moderate status, with a trend toward moderate status. Mingling degree values for all five dominant species were Mi ≥ 0.75 across the ten-year period, with few conspecific aggregations. Mingling degree values for *S. pedunculatum*, *B. minus*, and *R. sinica* decreased gradually over time, while values for *B. minus* and *H. bodinieri* increased, reaching 0.908 and 0.906 in 2017, representing increases of 4.2% and 1.5% compared with 2007, respectively.

Spatial characteristics of dominant species of trees

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3. Discussion and Conclusion

Analysis of spatial structure dynamics in the evergreen-deciduous broad-leaved forest community in Mulun Nature Reserve from 2007–2017 revealed that the overall community showed clumped distribution with strengthening trends. Tree species mingling evolved toward strong and very strong mixing states. The stand was mostly in moderate distribution status, with a trend toward subdominance, consistent with succession patterns in natural forests [**?**, **?**]. From the perspective of diameter class structure, small-diameter trees were numerous with relatively continuous diameter distribution and no obvious gaps, showing an overall inverted "J" distribution, consistent with previous research results [**?**, **?**].

The formation reasons for population spatial patterns are relatively complex, with plant reproductive characteristics, competition intensity, and habitat differences all influencing the spatial distribution patterns of certain species. In univariate distributions of forest community structural parameters, relative frequency first increased and then decreased as uniform angle index increased, showing normal distribution [**?**, **?**], with the highest relative frequency proportion at Wi = 0.5. Over the ten-year period, community uniform angle index ranged from 0.524–0.539. Hui et al. [**?**, **?**] proposed that forest communities show clumped distribution when Wi > 0.517. This study showed clumped distribution throughout the ten-year period, while the ideal distribution pattern for forests is random distribution [**?**, **?**], indicating that this community has not yet reached ideal conditions. Forest spatial distribution patterns are closely related to habitat heterogeneity effects [**?**, **?**]. As stand age increases, the sharp increase in environmental resource requirements by young trees leads to intensified intraspecific competition, causing self-thinning or other-thinning mortality [**?**, **?**]. The number of large-diameter trees gradually increases, spacing between living trees gradually expands, and mortality of dominant species in evergreen-deciduous broad-leaved forests is considered a possible adaptation mechanism [**?**, **?**]. No significant differences existed in relative frequencies across size inequality index classes, all accounting for about 20.0%. Over time, mean size inequality index ranged from 0.497–0.504, indicating no significant DBH differences and moderate stand status, consistent with results from Zhang et al. [**?**, **?**]. Strong mixing frequency accounted for 36.6%-37.8% and very strong mixing accounted for 39.4%-47.3% during the ten-year period, indicating high mixing status. Previous studies have shown that as communities gradually succeed toward climax communities, frequencies of strong and very strong mixing gradually increase [?, ?]. The studied forest community has relatively complex structure and is developing toward a stable direction [?, ?]. Higher stand mingling degree indicates superior stand spatial structure, greater forest stability, and stronger disaster resistance, which benefits sustainable forest development. As trees continuously recruit and die, mean DBH shows an overall increasing trend, and forest community distribution patterns continuously change. However, mingling degree showed small variation ranges (0.757-0.811). Under natural conditions, changes in evergreen-deciduous broad-leaved mixing degree constitute a long-term process [?, ?], and community succession to climax still requires considerable time. At small scales, karst mountain habitats show almost no continuous, relatively consistent species composition and environmental factors, presenting large-area heterogeneity. Additionally, influenced by different microtopographies and soil types within the region, ecological niche distributions of biological populations in habitats are highly uneven. Therefore, karst mountain habitats often exhibit highly dispersed and heterogeneous spatial structure characteristics at small scales.

In bivariate distributions of forest community structural parameters, for combinations of uniform angle index and mingling degree, tree numbers peaked at Wi = 0.50 when mingling degree remained unchanged from 2007-2017. The maximum tree number occurred at Wi = 0.50 and Mi = 1.00. The most common stand structure in this study was clumped distribution with strong mixing, with this trend becoming increasingly evident, consistent with results from Xue et al. [?, ?] and Lai et al. [?, ?]. Generally, spatial distribution patterns of natural mixed forests tend toward random distribution as community succession progresses [?, ?], with mingling degree gradually approaching 1, indicating that this forest community still has some distance from ideal conditions. In bivariate distributions of uniform angle index and size inequality index, frequencies of the same size inequality index showed normal distribution as uniform angle index classes changed, consistent with previous results [?, ?]. At the same uniform angle index class, relative frequencies across size inequality index classes showed small differences, indicating that stand spatial distribution is not a decisive factor affecting tree superiority levels, consistent with results from Xue et al. [?, ?] and Mao et al. [?, ?]. In bivariate distribution models of mingling degree and size inequality index, frequencies of trees suppressed by four conspecific neighbors with larger DBH became increasingly lower from 2007-2017, interspecific competition decreased, and communities gradually evolved toward subdominant and very strong mixing states. Over time, values of all three structural parameters (uniform angle index, size inequality index, and mingling degree) for the same diameter class structure showed increasing trends, with communities gradually evolving toward clumped, suppressed, and very strong mixing states. Small-diameter individuals showed clumped distribution, while large-diameter individuals showed clumped patterns at small scales with occasional random distribution, and aggregation intensity decreased with increasing spatial scale [?, ?]. Mingling degree showed an increasing trend, with lowest values at 0–5 cm and maximum values at DBH $\geq$ 15 cm, indicating that as tree diameter class increases, trees are mostly surrounded by heterospecific species due to interspecific density-dependent effects [?, ?].

This study analyzed spatial distribution patterns of five dominant species within the community. All dominant species except *R. sinica* (which showed random distribution in 2017) exhibited clumped distribution. Conspecific trees rarely aggregated together. Mingling degree values for *B. minus* and *H. bodinieri* even reached 0.908 and 0.906 in 2017. Light tolerance is an important indicator of plant regeneration requirements and niche differentiation. The Mulun evergreen broad-leaved forest has relatively high canopy closure, meeting regeneration requirements for shade-tolerant species. *S. pedunculatum* and *B. minus* have stronger habitat adaptability and shade tolerance compared with other dominant species, enabling better utilization of environmental resources. *H. bodinieri* showed gradually decreasing importance values, increasing uniform angle index, and a trend toward uneven distribution during succession. As a light-demanding species, *H. bodinieri* mainly grows at forest edges, roadsides, sparse forests, and sunny slopes, with straighter trunks in sunny locations and crooked trunks in dense forests. Uneven distribution of light resources within karst evergreen-deciduous broad-leaved forests leads to uneven distribution of *H. bodinieri*. *R. sinica* prefers warmth, tolerates dry heat and poor soil, and grows vigorously in moist, fertile sites. During this ten-year period, *R. sinica* showed significantly increased importance values, random distribution, and some reduction in mixing degree, likely due to the warm and humid climate of karst forests providing suitable growth conditions. Previous studies have shown that as succession progresses toward climax communities, stands become increasingly stable, with higher relative frequencies of strong and very strong mixing [?, ?], and stand spatial distribution gradually tends toward random distribution [?, ?]. Conspecific individuals experience intense competition due to convergent environmental resource utilization during growth, with weaker competitive individuals experiencing sharp population reductions. To better utilize environmental resources and promote more favorable growth, conspecific individuals tend toward dispersed distribution. Mean size inequality index values for the five dominant species mostly ranged from 0.25–0.50, with fewer neighboring trees with larger DBH than reference trees in structural units composed of reference trees. All five dominant species were between subdominant and moderate status, with a trend toward moderate status. In 2017, the ranking of dominant species changed slightly, with *B. minus* replacing *S. pedunculatum* as the main dominant species, though whether this dominance will continue requires further observation.

Using spatial structure parameters to analyze forests can provide clearer understanding of succession stages and facilitate progression toward more stable conditions. Based on local plant characteristics, natural site condition differences, and various influencing factors, rational optimization of forest spatial structure can increase stand diversity and make horizontal distribution more random. Scientifically and rationally controlling the number and spatial distribution of individuals in competitively advantaged and disadvantaged species groups can effectively enhance forest multifunctional benefits [?, ?]. During forest management, combining digital imagery for obtaining tree information with stand spatial structure analysis theory can achieve more cost-effective and effective sustainable forest management. In the future, spatial structure parameters can be combined with biotic and abiotic factors to explore factors influencing forest spatial structure, and can also be combined with productivity to explore productivity distribution under different spatial patterns, providing theoretical foundations for productivity research.

References

[?, ?] BEN HE, KADMON R, 2020. An experimental test of the area-heterogeneity tradeoff[J]. Proc Nat Acad Sci USA, 117(9): 4815-4822.

[?, ?] CHEN YN, YANG H, MA SY, et al., 2015. Spatial structure diversity of two coniferous broad-leaved mixed forests in Changbai Mountain[J]. J Beijing For Univ, 37(12): 48-58.

[?, ?] DU H, HU F, ZENG FP, et al., 2017. Spatial distribution of tree species in evergreen-deciduous broadleaf karst forests in southwest China[J]. Sci Rep: 7.

[?, ?] GUO L, YAO CL, CAO RF, et al., 2017. Community species composition, diameter class structure and spatial distribution pattern of secondary deciduous broad-leaved forest in Baiyun Mountain[J]. J Henan Agric Univ, 51(05): 647-652.

[?, ?] HUBBELL SP, 2006. Neutral theory and the evolution of ecological equivalence[J]. Ecology, 87(6): 1387-1398.

[?, ?] HUI GY, ZHANG GG, ZHAO ZH., et al. 2019. Methods of forest structure research: a review[J]. Curr For Rep, 5(3): 142-154.

[?, ?] HAN M, DONG XB, LIU H, et al., 2020. Spatial structure of natural larch secondary forests at different succession stages in the Greater Hinggan Mountains[J]. J NE For Univ, 48(6): 123-127.

[?, ?] HU YB, HUI GY, QI JZ, et al., 2003. Spatial structure analysis of natural red pine broad-leaved forest in Jiaohe, Jilin[J]. For Res (5): 523-530.

[?, ?] HU ZY, LIU P, 2017. Distribution structure and species diversity of spruce forest in the Western Tianshan National Nature Reserve[J]. For Res Mgmt (6): 67-71.

[?, ?] HUI GY, 1999. Angular scale-a structural parameter describing the distribution pattern of individual trees[J]. Sci Silv Sin (1): 39-44.

[?, ?] HUI GY, VON GADOW K , ALBERT M, 1999. A new spatial structure parameter of stand: size ratio[J]. For Res (1): 4-9.

[?, ?] HUI GY, HU YB, ZHAO ZH, 2008. Spatial measurement of tree species separation degree based on relationship between adjacent trees[J]. J Beijing For Univ (4): 131-134.

[?, ?] HUI GY, HU YB, ZHAO ZH, 2009. A review of "structured forest management" [J]. World For Res, 22(1): 14-19.

[?, ?] HUI GY, ZHAO ZH, ZHANG GQ, et al., 2021. Role of a random organism in forest stability maintenance based on angular scale[J]. Sci Silv Sin, 57(2): 22-30.

[?, ?] KWEON D, COMEAU PG, 2021. Climate, site conditions, and stand characteristics influence maximum size-density relationships in Korean red pine (Pinus densiflora) and Mongolian oak (Quercus mongolica) stands, South Korea [J]. For Ecol Manag, 502, 119727.

[?, ?] LI YF, HUI GY, ZHAO ZH, et al., 2012. The bivariate distribution characteristics of spatial structure in natural Korean pine broad-leaved forest[J]. J Veg Sci, 23(6): 1180-1190.

[?, ?] LI YF, LUO XQ, LI J, 2022. Habitat heterogeneity in karst environments influences the proportion and distribution of random framework[J]. Ecol Indic, 143: 109387.

[?, ?] LI BO, 2000. Ecology[M]. Beijing: Higher Education Press.

[?, ?] LAI AH, WU ZL, ZHOU XN, et al., 2015. Binary distribution characteristics of spatial structure of selective cutting of Chinese fir broad-leaved mixed forest[J]. J For Environ, 35(4): 337-342.

[?, ?] LIU BS, FU DG, WU XN, et al., 2013. Spatial pattern of dominant species in secondary evergreen broad-leaved forests in central Yunnan[J]. Chin J Ecol, 32(3): 551-557.

[?, ?] LIU L, SONG TQ, PENG WX, et al., 2012. Spatial pattern of soil microbial biomass in Mulon Karst Nature Reserve[J]. Acta Ecol Sin, 32(1): 207-214.

[?, ?] LIU Y, LI CX, WANG ZC, et al., 2020. Stand spatial structure characteristics of two main natural secondary forests in the Greater Hinggan Mountains[J]. J Northeast For Univ, 48(6): 128-134.

[?, ?] LU JY, WU ZF, ZHANG CY, et al., 2021. Effect of forest layer structure on productivity of mixed coniferous broad-leaved forest in Jiaohe, Jilin[J]. Acta Ecol Sin, 41(5): 2024-2032.

[?, ?] MAO YX, ZHANG HD, WANG RZ, et al., 2019. Spatial Structure Characteristics of Main Tree Species of Primitive Broadleaved Korean Pine Forest in Eastern Liaoning Mountains[J]. J Appl Ecol, 30 (09): 2933-2940.

[?, ?] QIU RH, CHEN H, 2005. Effects of selective cutting on tree structure and species diversity in an evergreen broad-leaved forest[J]. Chin J Eco-Agric (3): 158-161.

[?, ?] SONG TQ, 2015. Karst Plants and Environment in Southwest China [M]. BJ: Sci Pr, 2015:61-62.

[?, ?] WANG D, GUO Q, 2018. The influence of large trees on spatial distribution in broadleaved Korean pine forests[J]. Acta Ecol Sin, 38(23): 8400-8407.

[?, ?] WANG S, YAN Y, FU Z, et al., 2022. Rainfall-runoff characteristics and their threshold behaviors on a karst hillslope in a peak-cluster depression region[J]. J Hydrol, 605: 127370.

[?, ?] WU AC, TANG XL, LI AD, et al., 2022. Tree Diversity, Structure and Functional Trait Identity Promote Stand Biomass Along Elevational Gradients in Subtropical Forests of Southern China[J]. J Geophys Res-Biogeosci, 127(10): e2022JG006950.

[?, ?] WAN M, TIAN DL, FAN W, 2009. Community structure analysis of Quercus quercus in the southern foot of Taihang Mountain[J]. J Henan Agric Univ, 43(2): 139-144.

[?, ?] WANG ZC, DU H, SONG TQ, et al., 2015. Allometric growth models and forest biomass characteristics of major tree species (groups) in Guangxi[J]. Acta Ecol Sin, 35(13): 4462-4472.

[?, ?] WANG Q, ZHANG JC, TIAN YY, et al., 2012. Stand spatial structure analysis of natural mixed forest in Fengyang Mountain, Zhejiang province[J]. J Zhejiang A&F Univ, 29(6): 875-882.

[?, ?] WANG SS, YU XX, BAN JW, et al., 2006. Changes in community structure and species diversity during natural forest vegetation succession in the rocky mountainous areas of North China[J]. Res Soil Water Conserv (6): 48-50.

[?, ?] XIONG KN, CHI YK, 2015. Problems and countermeasures of karst ecosystem in southern China [J]. Ecolo Econ, 31(1): 23-30.

[?, ?] XUE WX, GUO QJ, AI XR, et al., 2021. Study on species composition and spatial structure of natural liriodendron liriodendron forest[J]. For Res, 34(2): 166-173.

[?, ?] YERJIANG BAKTURHAN, 2012. Study on plant diversity and spatial structure of Spruce natural forest in Tianshan Mountains [D]. Beijing:Beijing For Univ.

[?, ?] ZHANG ZH, HU G, ZHU JD, et al.,2011. Spatial heterogeneity of soil nutrients and their effects on tree species distribution in karst forests [J]. Chin J Plan Ecol,35(10):1038-1049.

[?, ?] ZHANG ZH, HU G, ZHU JD, et al., 2012. Stand Structure, Woody Sprcies Richness and Composition of Subtropical Karst Forests in Maolan,South-West China [J]. J Trop For Sci, 24(4): 498-506.

[?, ?] ZHANG LJ., DU H, YANG ZQ, et al., 2022. Topography and Soil Properties Determine Biomass and Productivity Indirectly via Community Structural and Species Diversity in Karst Forest, Southwest China [J]. Sustainability, 14(13): 7644.

[?, ?] ZHANG LJ, HUI GY, HU YB, et al., 2018. Spatial structural characteristics of forests dominated by Pinus tabulaeformis Carr[J]. Plos One, 13(4): e0194710.

[?, ?] ZHANG F, DU H, ZENG FP, et al., 2019. Community renewal dynamics of old-growth forest in karst cluster depression[J]. Acta Ecol Sin, 39(22): 8516-8525.

[?, ?] ZHANG GG, LIU RH, HUI GY, et al., 2019. Distribution and interpretation of spatial structure parameters of stand: A case study of natural mixed oak with sharp teeth forest Xiaolongshan[J]. J Beijing For Univ, 41(4): 21-31.

[?, ?] ZHANG GG, WANG DX, CHAI ZZ, et al., 2015. Distribution characteristics of spatial structure parameters of two typical natural forests in Xiaolongshan[J]. For Res, 28(4): 531-537.

[?, ?] ZHANG YH, DIAN YY, HUANG GZ, et al., 2021. Effects of stand spatial structure on species diversity in Pinus massoniana forest at different succession stages[J]. Chin J Ecol, 40(8): 2357-2365.

[?, ?] ZHANG YF, TANG MP, 2021. Dynamic characteristics of spatial structure of evergreen broad-leaved forest in Tianmu Mountain[J]. Acta Ecol Sin, 41(5): 1959-1969.

[?, ?] ZHAO ZH, HUI GY, HU YB, et al., 2013. Application of structured forest management methods in broad-leaved pine forests[J]. For Res, 26(4): 467-472.

[?, ?] ZHOU ML, ZHANG Q, KANG XG, et al., 2016. Stability of different forest communities based on spatial structure index[J]. Plant Sci J, 34(5): 724-733.

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