Niche of Dominant Tree Populations in Different Topographic Positions in Maolan Karst Forest Postprint

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Abstract

The niche characteristics of species are influenced by interspecific interactions and the degree of environmental adaptation. To understand the niche characteristics of dominant arbor populations in Maolan karst forest, community surveys were conducted across three terrain types (slope, sinkhole, and funnel) in the Maolan National Karst Forest Nature Reserve, and the niche breadth, niche overlap, and other characteristics of dominant arbor populations in these three terrain positions were calculated. The results showed that although the ranking order of niche breadth Bi and Ba values for dominant arbor populations varied slightly among different terrain positions, they were generally consistent. Litsea verticillata exhibited greater niche breadth in slope and sinkhole terrains, with Bi/Ba values of 0.782/0.416 and 0.891/0.703, respectively; Clausena dunniana showed larger niche breadth in slope and funnel terrains, with Bi/Ba values of 0.788/0.518 and 0.963/0.826, respectively. The highest niche overlap value (Lhi) was observed between Celtis sinensis and Carpinus pubescens in the funnel terrain (0.138), while the lowest values were found between Triadica rotundifolia and Viburnum henryi/Boniodendron minus in the slope terrain (0.002), and between Litsea verticillata and Cyclobalanopsis glauca in the sinkhole terrain (0.002). Species with similar ecological characteristics and habitat requirements typically exhibit larger niche overlap values, and vice versa; species with larger niche breadth also tend to have larger niche overlap values, and vice versa. The study indicates that niche overlap among dominant community populations across the three terrain types is relatively low, and the Maolan karst forest is in a stable climax community stage, but competition among populations within the community is intense due to limited environmental resources, with the intensity of competition in different terrain habitats following the order: funnel > sinkhole > slope, and differences in light availability represent the primary factor influencing the natural distribution of dominant arbor populations across terrain positions. This study reveals the niche characteristics of dominant community populations across different terrains and can provide a reference basis for the conservation of dominant arbor populations in karst forests.

Full Text

Niche Characteristics of Dominant Tree Populations in Maolan Karst Forest Across Different Topographic Positions

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Abstract

Niche characteristics of species are influenced by interspecific interactions and environmental adaptation. To understand the niche features of dominant tree populations in Maolan karst forest, we conducted community surveys across three topographic positions (hillside, valley, and funnel) in the Maolan National Karst Forest Nature Reserve and calculated niche breadth and niche overlap indices for dominant tree populations. The results revealed that while the ranking of niche breadth (Bi and Ba values) varied slightly across topographic positions, the overall patterns were consistent. *Litsea verticillata* exhibited large niche breadth in hillside and valley habitats, with Bi/Ba values of 0.782/0.416 and 0.891/0.703, respectively. *Clausena dunniana* showed large niche breadth in hillside and funnel habitats, with Bi/Ba values of 0.788/0.518 and 0.963/0.826, respectively. The highest niche overlap value (Lhi) occurred between *Celtis sinensis* and *Carpinus pubescens* (0.138) in funnel habitats, while the lowest values (0.002) were observed between *Triadica rotundifolia* and *Viburnum henryi*/*Boniodendron minus* in hillside habitats, and between *Litsea verticillata* and *Cyclobalanopsis glauca* in valley habitats. Generally, species with similar ecological characteristics and habitat requirements exhibited greater niche overlap, while those with dissimilar traits showed less overlap. Populations with broader niche breadth tended to have higher niche overlap values, and vice versa. Our findings indicate that niche overlap among dominant populations remains relatively low across the three topographic positions, suggesting that Maolan karst forest represents a stable climax community. However, intense competition for limited environmental resources exists among populations within the community, with competition intensity varying as funnel > valley > hillside across topographic habitats. Variation in light availability represents the primary factor influencing the natural distribution of dominant tree populations across different topographic positions. This study elucidates the niche characteristics of dominant populations across topographic gradients and provides a scientific basis for the conservation of karst forest tree populations.

Keywords: karst forest, different topography, dominant population, niche, Maolan

Introduction

Niche represents a core concept in population ecology research, reflecting not only a population' s adaptive capacity and resource utilization ability within its environment, but also its functional role and position within the community or ecosystem. As an important tool for evaluating interspecific and intraspecific relationships, niche research has been widely applied in studies of biodiversity and its formation and maintenance mechanisms, community structure and succession, and forest resource conservation and utilization. Scholars have conducted extensive research on plant population niches across various ecosystems, including alpine meadows, tropical forests, subtropical forests, and temperate forests, encompassing trees, shrubs, herbs, and lianas. Studies on karst forest plant population niches have also been reported, such as research on niche characteristics of dominant populations in *Sinosideroxylon* communities in Mulun, Guangxi, and analyses of dominant arbor populations across different successional stages in Maolan karst forest. However, comprehensive niche studies in karst forests remain relatively scarce, necessitating further investigation.

As a unique subtropical forest ecosystem, Maolan karst forest differs significantly from forests on normal terrain in terms of habitat conditions, floristic composition, population dynamics, and community characteristics. Previous research has examined quantitative characteristics of plant communities, interspecific segregation patterns, interspecific associations, and spatial distribution patterns of tree species in Maolan karst forest, laying a foundation for deeper investigation of community characteristics in karst regions. The complex and diverse topography of Maolan karst forest includes depressions, funnels, and valleys, with substantial variation in soil, moisture, and light conditions across different landforms. Through long-term adaptation to these heterogeneous microhabitats, plant populations have developed differential resource utilization strategies, resulting in distinct niche characteristics. Trees, which are widely distributed across all topographic positions and exhibit rich species diversity and abundance, play crucial roles in forest community succession, population evolution, and community stability. To investigate the differential adaptive capacities of dominant tree populations to highly heterogeneous habitats and their resource utilization patterns, and to understand their positions within communities across different topographic positions, this study analyzes the niche characteristics of dominant tree populations in Maolan karst forest across three topographic habitats, providing a scientific basis for conservation and restoration of degraded karst forest vegetation.

1 Study Area

The study was conducted in Maolan National Karst Forest Nature Reserve, located at the border between Guizhou and Guangxi provinces in Libo County, Guizhou Province (107°52 10 -108°05 40 E, 25°09 20 -25°20 50 N). The reserve covers approximately 20,000 ha and features a mid-subtropical monsoon humid climate. The annual accumulated temperature 10°C is 5,767.9°C, with mean annual temperature of 15.3°C and annual temperature range of 18.3°C. The growing season extends 315 days, with annual precipitation of 1,752.5 mm and mean relative humidity of 80%. Abundant rainfall and high humidity create favorable conditions for forest development. The parent rock is primarily limestone and dolomite, with soil types dominated by black calcareous soil rich in organic matter, nitrogen, and phosphorus, exhibiting weak alkaline properties. The main vegetation type is evergreen-deciduous broad-leaved mixed forest, with some coniferous-broadleaved mixed forest. Dominant tree species in the canopy layer include *Litsea verticillata*, *Cyclobalanopsis glauca*, *Cornus kousa* subsp. *chinensis*, and *Machilus rehderi*, while the shrub layer comprises *Pittosporum crispulum*, *Euonymus dielsianus*, *Sinosideroxylon wightianum*, and *Nandina domestica*.

2 Methods

2.1 Plot Setup and Community Survey

Field community surveys were conducted during the growing season in June 2016. Ten discontinuous 20 m × 20 m sample plots were established in typical locations across three topographic positions (hillside, valley, and funnel) in the reserve, totaling 30 plots with a combined area of 1.2 ha. Environmental factors including elevation, aspect, slope, soil thickness and coverage, moisture conditions, and light availability were recorded for each plot. Using standard community survey methods, each plot was subdivided into sixteen 5 m × 5 m subplots to survey all trees and shrubs, recording species names, individual counts, height, diameter at breast height, and crown width.

2.2 Calculation Methods

(1) Importance Value Calculation

Importance Value = (Relative Density + Relative Dominance + Relative Frequency) / 3

Community survey data from hillside (plots 1-10), valley (plots 11-20), and funnel (plots 21-30) were analyzed to calculate population importance values. Based on importance value rankings, 14 populations were identified as dominant tree populations across the three topographic positions in Maolan karst forest .

(2) Niche Breadth

Niche breadth was calculated using Levins’ and Hurlbert’ s formulas:

Levins' Niche Breadth

$$B_i = \frac{1}{\sum_{j=1}^{r} P_{ij}^2}$$

where B_i is the niche breadth of species i, P_{ij} is the proportion of species i' s use of resource j relative to its total resource use, calculated as $P_{ij} = \frac{n_{ij}}{\sum_{j=1}^{r} n_{ij}}$, with n_{ij} representing species i' s dominance in resource j (importance value in sample plots), and r is the number of resource states. This index ranges from 0 to log r.

Hurlbert' s Niche Breadth

$$B_a = \frac{1}{r\sum_{j=1}^{r} P_{ij}^2}$$

where B_a is the niche breadth, with P_{ij} and r as defined above. This index ranges from 0 to 1.

(3) Niche Overlap

Niche overlap refers to the degree to which two species share resources at the same level along a resource gradient, calculated as:

$$L_{ih} = \sum_{j=1}^{r} P_{ij} P_{hj} / \sum_{j=1}^{r} P_{ij}^2$$

where L_{ih} represents species i' s overlap with species h, and L_{hi} represents species h' s overlap with species i. $B(L)$ denotes Levins' niche breadth index, with $B(L)_i$ and $B(L)_h$ ranging from $1/r$ to 1, while L_{ih} and L_{hi} range from 0 to 1.

3 Results

3.1 Niche Breadth

Niche breadth values (Bi) for dominant populations are presented in Table 3 . In hillside habitats, *Cladrastis platycarpa*, *Clausena dunniana*, and *Litsea verticillata* exhibited the largest niche breadth values (0.847, 0.788, and 0.782, respectively). In valley habitats, *Litsea verticillata*, *Lindera communis*, and *Diospyros kaki* showed the greatest niche breadth (0.891, 0.847, and 0.800, respectively). In funnel habitats, *Clausena dunniana*, *Celtis sinensis*, *Machilus rehderi*, and *Cyclobalanopsis glauca* had the largest niche breadth values (0.963, 0.938, 0.904, and 0.895, respectively). Variation in niche breadth across topographic positions reflects differences in habitat characteristics, population size, distribution patterns, and ecological traits. For example, *Litsea verticillata*, with strong drought tolerance, occurred as large individuals in high numbers on hillsides, playing an important role in maintaining community stability in these drier environments. As a shade-tolerant species, *L. verticillata* seedlings could regenerate and persist in valleys with high canopy closure and favorable moisture and soil conditions, contributing to its large niche breadth in both hillside and valley habitats. The light-demanding deciduous species *C. platycarpa* occurred primarily as large canopy trees with few seedlings and saplings, mainly distributed on hillsides, resulting in large niche breadth there but small niche breadth in valleys and funnels.

3.2 Niche Overlap Analysis

3.2.1 Hillside Habitats In hillside habitats, 20 species pairs (11.0% of total) had niche overlap values 0.07, and 51 pairs (28.0%) had values 0.05. Species pairs with large niche breadth values, such as *Cladrastis platycarpa*–*Clausena dunniana*, showed high niche overlap (Lih/Lhi = 0.053/0.055), while species with small niche breadth values, such as *Celtis sinensis*–*Boniodendron minus*, exhibited low overlap (Lih/Lhi = 0.005/0.006). *Cladrastis platycarpa* is a light-demanding deciduous species, while *C. dunniana* exhibits sun-loving yet shade-tolerant and drought-resistant characteristics. Competition for light resources resulted in both species occupying upper canopy positions on hillsides, leading to high niche overlap. Although both *C. sinensis* and *B. minus* are sun-loving and shade-tolerant species with strong light requirements, *C. sinensis* occurred in low numbers primarily in the upper canopy, whereas *B. minus* was abundant but mainly distributed in the middle and lower canopy layers. This vertical stratification created niche separation, resulting in minimal competition between these two species on hillsides.

3.2.2 Valley Habitats In valley habitats, 32 species pairs (17.6% of total) had niche overlap values 0.07, and 64 pairs (35.2%) had values 0.05. The three species with largest niche breadth values—*Litsea verticillata*, *Lindera communis*, and *Diospyros kaki*—showed variable overlap patterns: *L. verticillata*-*L. communis* and *L. verticillata*-*D. kaki* had Lih/Lhi values of 0.055/0.047 and 0.048/0.038, respectively, while *L. communis*-*D. kaki* showed higher overlap (Lih/Lhi = 0.075/0.070). Species with small niche breadth values, such as *Cyclobalanopsis glauca*–*Cornus hongkongensis*, exhibited low overlap (Lih/Lhi = 0.026/0.028). In valleys with high canopy closure, competition for light resources resulted in *L. verticillata*, *L. communis*, and *D. kaki* all occupying middle and lower canopy positions with strong light demands. However, *L. verticillata* occurred in low numbers as large individuals, while *L. communis* and *D. kaki* were abundant but smaller in size, leading to lower niche overlap between *L. verticillata* and the other two species but higher overlap between *L. communis* and *D. kaki*. *C. glauca* primarily occupied upper canopy positions, utilizing upper-layer space resources, whereas the evergreen shade-tolerant species *C. hongkongensis* occurred in middle and lower canopy layers. This vertical stratification created niche separation and low overlap between these two species.

3.2.3 Funnel Habitats In funnel habitats, 45 species pairs (24.7% of total) had niche overlap values 0.07, and 102 pairs (56.0%) had values 0.05. The three species with largest niche breadth values—*Clausena dunniana*, *Celtis sinensis*, and *Machilus rehderi*—all showed high pairwise overlap: *C. dunniana*-*C. sinensis* and *C. dunniana*-*M. rehderi* had Lih/Lhi values of 0.076/0.068 and 0.077/0.092, respectively, while *C. sinensis*-*M. rehderi* showed Lih/Lhi = 0.060/0.063. Species with small niche breadth values, such as *Cladrastis platycarpa*-*Carpinus pubescens*, exhibited low overlap (Lih/Lhi = 0.005/0.004). *C. dunniana* and *C. sinensis* are sun-loving species, while *M. rehderi* is shade-tolerant. Poor light conditions in funnel habitats intensified competition among these three species, all occupying upper canopy positions with strong light demands. In contrast, *C. pubescens* occurred in middle and lower canopy layers, creating niche separation from upper-canopy *C. platycarpa* and resulting in low overlap.

Overall, the highest Lih value (0.114) occurred between *Litsea verticillata* and *Viburnum henryi* in hillside habitats. Both species share sun-loving and drought-tolerant characteristics, primarily distributed in middle and lower canopy layers of well-lit hillside and valley habitats, leading to intense competition and high niche overlap. The highest Lhi value (0.138) occurred between *Celtis sinensis* and *Carpinus pubescens* in funnel habitats. Both are sun-loving species occurring in high densities in funnels, but the poorest light conditions in this habitat intensified competition for light resources. The lowest Lih and Lhi values (0.002) were recorded for several species pairs, including *Triadica rotundifolia*-*Viburnum henryi*/*Boniodendron minus* in hillside habitats and *Litsea verticillata*-*Cyclobalanopsis glauca* in valley habitats. Although *T. rotundifolia* is sun-loving and drought-tolerant, it primarily occurs in poorly lit funnels with thick soil and high moisture, creating substantial habitat requirement differences from *V. henryi* and *B. minus* and resulting in niche separation. In valleys, *L. verticillata* occupied middle and lower canopy layers while *C. glauca* occurred in the upper canopy, creating vertical separation and low overlap.

Across all three topographic positions, 97 species pairs (17.8% of total) had niche overlap values 0.07, with values ranging from 0.002 to 0.138. The average Lih and Lhi values for all 14 dominant tree populations across the three habitats was 0.043, indicating low niche overlap and suggesting high stability of Maolan karst forest communities that have reached climax successional stages.

4 Discussion

Niche breadth reflects species' adaptation to habitats and resource utilization capacity. Under limited resource conditions, species with broader niche breadth can acquire more resources, demonstrating stronger environmental adaptation (Wu et al. 2016). Hillside habitats receive strong light but have steep slopes with high runoff, abundant shrubs, and mainly mature trees, favoring drought-tolerant species. The three species with largest niche breadth on hillsides—*Cladrastis platycarpa*, *Clausena dunniana*, and *Litsea verticillata*—are all mature trees with strong drought tolerance, indicating good adaptation to the dry, infertile hillside environment. Valley habitats offer the most favorable conditions with moderate light, moisture, and thick soil layers, supporting good growth of both trees and shrubs. *Litsea verticillata*, *Lindera communis*, and *Diospyros kaki* had the largest niche breadth values in valleys, likely related to their population densities and distribution patterns. While *L. verticillata* occurs mainly on hillsides, substantial populations also inhabit valleys, and seedlings of *L. communis* and *D. kaki* are concentrated in valley habitats. Funnel habitats have poorer environmental conditions, including short daylight hours, water accumulation in depressions, and thick but heavy soils, favoring seedlings, saplings, and lianas. *Clausena dunniana*, *Celtis sinensis*, *Machilus rehderi*, and *Cyclobalanopsis glauca* had the largest niche breadth values in funnels, all occurring primarily as seedlings and saplings. Considering both growth stages and environmental conditions, valleys represent the most suitable habitat for tree growth overall. However, for sun-loving yet shade-tolerant species such as *C. dunniana* and *C. glauca*, the moist, shaded funnel environment is suitable during seedling and sapling stages, whereas well-lit hillsides are more appropriate for mature trees.

Niche overlap occurs when two species share the same resource or occupy a particular resource factor (living space, food, etc.) along a resource gradient (Wang et al. 1995; Hu and Yu 2005). High niche overlap typically results from similar ecological characteristics or complementary habitat requirements among species (Lin et al. 2002; Ye et al. 2006). The relationship between niche breadth and niche overlap is complex; species with broad niche breadth generally exhibit high niche overlap, while narrow-niched species show low overlap. For example, *Cladrastis platycarpa* and *C. dunniana*, both with large niche breadth on hillsides, also showed high overlap there, whereas *Celtis sinensis* and *Bonioden-dron minus*, with small niche breadth, exhibited low overlap. This pattern aligns with findings from studies on *Quercus aliena* var. *acuteserrata* populations in the Qinling Mountains (Zhao et al. 2004). However, niche overlap also depends on species' biological and ecological characteristics (Zhang 2005), sometimes resulting in high overlap between narrow-niched species, such as the high overlap between *C. sinensis* and *Carpinus pubescens* in funnel habitats.

Competition arises under conditions of resource scarcity and niche overlap, with complex relationships determined by resource quantity, supply-demand ratios, and resource requirement satisfaction (Zhao et al. 2004). Overall, low niche overlap values among dominant tree populations in Maolan karst forest indicate high community stability, yet intense interspecific competition persists due to harsh habitats and resource limitation. Analysis of niche overlap across the three topographic positions revealed that 51 species pairs (28.0%) had overlap values 0.05 on hillsides, compared to 64 pairs (35.2%) in valleys and 102 pairs (56.0%) in funnels. This pattern indicates that competition intensity varies as funnel > valley > hillside across topographic habitats. Considering species growth characteristics, individual size, niche overlap, and environmental conditions, competition is strongest in funnels, moderate in valleys, and weakest on hillsides. Light intensity follows the opposite pattern, being strongest on hillsides, moderate in valleys, and weakest in funnels. Therefore, light availability represents the primary factor influencing the natural distribution of dominant tree populations in Maolan karst forest, consistent with findings for dominant shrub populations in the same region (Qin et al. 2018).

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