Microhabitats on Exposed Rock Surfaces in Tropical Karst Forests and Their Colonizing Plant Post-Colonization Imprint

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Abstract

Rock outcrops are a typical feature of karst ecosystems that develop diverse microhabitats and host diverse plants, yet the relationship between colonizing plants and microhabitats remains unclear. This study examined a tropical seasonally moist forest developed on a limestone mountain in Xishuangbanna, measuring the intrinsic characteristics and external environmental factors of 586 rock outcrop microhabitats and investigating the species composition of colonizing plants thereon. Pearson correlation analysis and redundancy analysis (RDA) were employed to reveal the effects of rock outcrop microhabitat characteristics and environmental factors on colonizing plants. The results showed that: (1) Characteristic values of rock outcrop microhabitats in tropical karst forests, such as soil depth (4.92$±4.00)*cmandarea*(532.28±1, 575.10)*cm*^{2}$, exhibited high variability. (2) A total of 1,518 individuals of trees, shrubs, and herbaceous plants belonging to 90 species, 82 genera, and 44 families were surveyed in the microhabitats, among which suitable species with advantages in karst substrates accounted for 35.6% of the total species number. (3) The area and soil depth of microhabitats explained more than 70% of the variation in colonizing plant species composition and richness. (4) A significant decreasing exponential species-area relationship existed between colonizing plant species richness and area within rock outcrop microhabitats. In summary, rock surface microhabitats within tropical karst forests exhibit high heterogeneity, area and soil depth are key factors influencing plant colonization, and the species-area relationship dominates the species richness pattern of rock surface microhabitats.

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Microhabitats and Their Colonized Plants on Rock Outcrop Surfaces in Tropical Karst Forests

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Abstract: Rock outcrops are typical features of karst ecosystems that support diverse microhabitats and various colonizing plants, yet the relationship between these plants and their microhabitats remains unclear. This study examined a tropical seasonal humid forest developed on limestone hills in Xishuangbanna, measuring the intrinsic characteristics and environmental factors of 586 rock outcrop microhabitats and investigating the species composition of colonizing plants. Pearson correlation analysis and redundancy analysis (RDA) were employed to reveal the influence of microhabitat characteristics and environmental factors on colonizing plants. The results showed: (1) Microhabitat characteristics such as soil depth [(4.92$±$4.00) cm] and area [(532.28$±1, 575.10)cm^{2}$] exhibited high variability in tropical karst forests. (2) A total of 1,518 individuals of 90 species belonging to 82 genera and 44 families of trees, shrubs, and herbs were recorded, with karst-preferent species adapted to limestone substrates accounting for 35.6% of total species. (3) Microhabitat area and soil depth explained over 70% of the variation in colonizing plant species composition and richness. (4) A clear decreasing exponential species-area relationship existed between colonizing plant species richness and microhabitat area. In conclusion, rock outcrop surface microhabitats in tropical karst forests exhibit high heterogeneity, with area and soil depth being key factors affecting plant colonization, and the species-area relationship dominates the species richness pattern on these microhabitats.

Keywords: karst, rock outcrop, microhabitat, habitat heterogeneity, karst characteristic species, species-area relationship

Introduction

Carbonate rocks in tropical and subtropical China have formed diverse karst landforms through hydraulic processes (Ford & Williams, 2007; De Waele et al., 2009; Parise, 2011). Exposed rock bodies (such as stone teeth, karst peaks, and scattered fragments) are common in natural forests, plantations, and desertification sites in such landforms, referred to as “rock outcrops” by Shen et al. (2018). Under differential dissolution conditions, various microhabitats with distinct external morphologies form on and between karst outcrops, measuring only tens of centimeters to several meters in length and width, including rock surfaces, crevices, grooves, caves, and pits (Zhu et al., 2002). Rock outcrop surface microhabitats are typically small in area and have often been overlooked in phytocoenological studies.

These microhabitats can intercept atmospheric deposits, litterfall, and some rock weathering products, forming lithic humus that provides a material foundation and living space for plant colonization (Hou & Jiang, 2006; Zhu et al., 2016). When seeds and spores of plants arrive through various dispersal pathways, they may germinate, survive, and establish in these microhabitats, becoming colonizing plants. Rock outcrop microhabitats host rich plant communities, including mosses, algae, and vascular plants, contributing to local ecosystem biodiversity maintenance (Wang et al., 2003; Cao et al., 2022). Colonizing plants on rock outcrops are typically regarded as lithophytes. Xu et al. (2006) documented 16 families and 17 species of epiphytic vascular plants on rock surfaces in a semi-humid evergreen broad-leaved forest in Yunnan's Stone Forest, while Zhu et al. (2016) recorded 15 families, 21 genera, and 21 species in desertified areas, 15 families, 25 genera, and 25 species in plantations, and 28 families, 39 genera, and 41 species in natural forests within 60 rock outcrop quadrats (2 m × 2 m each) in Yunnan's Stone Forest.

The humid tropical and subtropical karst regions of southwestern China represent the world's largest and most intensively developed karst area and constitute one of China's four major ecologically fragile zones (Li et al., 2002; Wang et al., 2019). The relationship between habitat and plants is fundamental for explaining biodiversity formation and maintenance mechanisms in karst regions and for exploring desertification control strategies (Ge, 2008; Cao et al., 2022). Environmental characteristics of karst regions—such as drought, thin and infertile soils, and calcium enrichment—become further extreme on rock outcrop surface microhabitats, imposing stricter requirements for karst adaptation in colonizing plants (Chen et al., 2018).

Small-scale differences within plant habitats, known as habitat heterogeneity, constitute an important foundation determining plant diversity within local ecosystems (Heidrich et al., 2020). The diverse combinations of morphological characteristics and environmental factors of rock outcrop microhabitats create high horizontal spatial heterogeneity (Guo et al., 2011; Chen et al., 2013), presumably affecting the growth and survival of colonizing plants and thereby influencing species composition and distribution (Shen et al., 2018). However, few studies have examined the relationship between habitat heterogeneity and colonizing plants within local karst systems.

This study investigated rock outcrop surface microhabitats in a tropical karst forest in Xishuangbanna, using plot survey methods to obtain species data of colonizing plants. Pearson correlation analysis and redundancy analysis were employed to explore how external environmental factors (canopy density, altitude, slope position, aspect, slope gradient, height, rock-habitat ratio) and microhabitat morphological characteristics (area, depth, depth-width ratio, and circular coincidence) affect colonizing plant species composition and diversity. We addressed two questions: (1) To what extent do external environmental factors and intrinsic morphological characteristics of rock outcrop surface microhabitats influence colonizing plant species richness? (2) How do responses of species richness to these factors vary among different life forms and karst adaptability groups? This research aims to provide data support for revealing biodiversity patterns and maintenance mechanisms in karst regions.

1.1 Study Area Overview

The study area is located within the Menglun Subreserve of Xishuangbanna National Nature Reserve, covering approximately 300 hm^2 of Permian carbonate rocks at 600–800 m elevation, with bedrock exposure exceeding 90% in some areas. The region experiences a northern tropical monsoon climate with an annual average temperature of 21.5 °C, annual precipitation of 1,557 mm, and annual relative humidity of 86%, featuring distinct wet and dry seasons (Wu, 2019).

The forest community experiences minimal anthropogenic disturbance, with forest coverage exceeding 95%. The vegetation type is tropical seasonal humid forest. The lower tree layer has >80% coverage, dominated by *Cleistanthus sumatranus*, followed by *Lasiococca comberi* var. *pseudoverticillata*, accompanied by *Celtis philippensis* and others. In the understory shrub layer, *Cleistanthus sumatranus* saplings dominate. The forest contains abundant woody lianas and common thick-leaved vascular epiphytes (Zhu et al., 2015).

In the study area, rock outcrops and plants coexist harmoniously, forming a typical "rock-soil-plant" karst forest ecosystem (Shen et al., 2018). The soil is leached humus carbonate soil developed on limestone substrates (Yang et al., 2018), neutral to slightly acidic, with thin and discontinuous horizons. In contrast, the lithic humus in microhabitats consists primarily of black and brown limestone soils, neutral to slightly alkaline.

1.2 Survey Methods

The study region has distinct rainy and dry seasons with intense karstification. To avoid interference from excessively high moisture and temperature conditions during the rainy season, fieldwork was conducted during the dry season (November–December). Surveys were performed in two phases: first locating and marking microhabitats, then recording habitat and plant information two weeks later. We selected areas with concentrated rock outcrops and minimal anthropogenic disturbance to reduce variations in topography, microgeomorphology, forest canopy density, and surrounding plant community composition caused by human activity. A total of 586 microhabitats were surveyed [Figure 1: see original paper]A, all selected as closed habitats with plant growth and root systems confined within them [Figure 1: see original paper]B,C. Microhabitats with root systems extending beyond boundaries or with unclear borders were excluded. Additionally, control plots (5 m × 5 m) without rock outcrops were established in concentrated microhabitat areas to survey environmental characteristics and species composition.

Habitat heterogeneity can be assessed through two approaches: estimating the types and quantities of habitats within a given area (Triantis et al., 2006; Sfenthourakis & Triantis, 2009), or using environmental factor proxies since they affect plant spatial distribution (Sheng et al., 2018). Commonly used proxies include altitude and slope gradient for topographic heterogeneity, and normalized difference vegetation index (NDVI) for heterogeneity formed by plant community differences (Yan et al., 2023). This study focused exclusively on rock outcrop surface microhabitats within a single tropical karst forest with uniform and stable vegetation. Therefore, we defined habitat heterogeneity using the microhabitats' intrinsic characteristics and their environmental indicators within the forest.

We measured canopy density above each rock outcrop microhabitat, topographic factors (altitude, slope position, aspect, slope gradient, height, rock-habitat ratio), and morphological characteristics (area, depth, depth-width ratio, and circular coincidence). Canopy density was calculated by comparing average photosynthetically active radiation between 12:00–14:00 at survey sites and open areas without shade. Portable GPS was used to measure latitude, longitude, and altitude. Slope position was classified as lower, middle, upper, or summit based on mountain profiles. Aspect was measured with a compass and categorized as shady (337.5°–67.5°), semi-shady (67.5°–112.5° and 292.5°–337.5°), semi-sunny (112.5°–157.5° and 247.5°–292.5°), and sunny (157.5°–247.5°). Slope gradient was measured with a clinometer. Rock outcrop height was measured with a tape, and the ratio of microhabitat position height to outcrop height (rock-habitat ratio) was calculated to determine relative position on the outcrop.

Microhabitat morphological characteristics were evaluated using ImageJ software (Liu et al., 2018). Each microhabitat was photographed vertically with a scale bar [Figure 1: see original paper]C. Photographs were imported into the software, and unit length was calibrated using pixel counts of the scale bar. The microhabitat outline was selected with the lasso tool to obtain length, width, area, and circular coincidence (the degree of shape similarity to a standard circle). To reduce human error, each image was processed three times and averaged. Soil depth was measured at 3–5 points with a graduated rod and averaged. The depth-width ratio was calculated as average soil depth divided by the microhabitat's long axis length, and volume was the product of area and soil depth.

Vascular plant species and individuals colonizing each microhabitat were identified and recorded, classified into three life forms: tree, shrub, and herb. Species were categorized by karst adaptability through literature review and consultation with experts at Xishuangbanna Tropical Botanical Garden. Colonizing plants were divided into three groups: exclusive species (restricted to carbonate substrates, not growing in other habitats), preferent species (showing high selectivity for carbonate substrates, thriving in karst habitats but poorly developed in acidic or other substrates), and indifferent species (showing no substrate preference with no clear geographic boundaries in phytogeographic terms) (Tu, 1995; Zhu et al., 2003; Zhu et al., 2007).

1.3 Data Processing

Species count represented species richness; individual count represented abundance. Based on life form and karst adaptability classifications, we counted microhabitats containing each plant type and calculated their colonization rate as the percentage of total microhabitats. Preliminary data organization and analysis were conducted using Excel. Due to non-normal distribution of environmental factor data between microhabitats and control plots and the small control dataset, Mann-Whitney variance analysis was performed using Origin 2023's non-parametric test function to assess significant differences (Yuan et al., 2014). Pearson correlation analysis in Origin 2023 was used to create correlation matrices between environmental/morphological factors and species composition/richness. Constrained ordination was applied to explore karst habitat heterogeneity effects on colonizing plant distribution patterns.

Using R package vegan, detrended correspondence analysis (DCA) of species composition and richness matrices yielded first-axis gradient lengths of 1.23 for life forms and 1.27 for karst adaptability groups, indicating linear relationships rather than unimodal models suitable for canonical correspondence analysis (CCA). Therefore, redundancy analysis (RDA) based on linear models was selected to analyze relationships between microhabitat environmental factors and species composition/richness, test significance of each factor's influence, conduct hierarchical analysis of effect sizes to determine model explanatory power, and generate RDA ordination diagrams (Long et al., 2012). The species-area relationship (SAR) curve for rock outcrop microhabitats was fitted using Origin 2023's exponential fitting function, and SAR scatter plots were generated.

2.1 Rock Outcrop Surface Microhabitats and Their Environmental Characteristics

Non-parametric comparison of 586 rock outcrop microhabitats and control plots revealed no significant differences in altitude, slope position, aspect, slope gradient, or canopy density , with low coefficients of variation for these environmental characteristics. In contrast, morphological characteristics showed high variability, with coefficients of variation exceeding 100% for area, volume, length, and depth-width ratio. Volume showed the highest variability (611.89%), followed by area (295.92%), ranging from 0.14 to 20,154.41 cm^2. Overall, rock surface microhabitats were relatively small, resembling "flower pots" with average depth of only 4.92 cm, average length of 24.02 cm, average area of 532.28 cm^2, and average circular coincidence of 0.52. Pearson correlation analysis between morphological and environmental factors showed strong correlations between altitude and slope position, area and volume, and area and length [Figure 2: see original paper], with moderate or weak correlations among other characteristics.

2.2 Characteristics of Colonizing Plants

In the 586 rock outcrop microhabitats, 1,545 vascular plant individuals were surveyed (average 2.6 per microhabitat). Twenty-seven seedlings that could not be identified were excluded, leaving 1,518 individuals belonging to 90 species, 82 genera, and 44 families. Herb species richness (36 species) exceeded shrubs (31) and trees (23), but tree abundance (763 individuals) > shrubs (494) > herbs (261), with tree abundance approximately double that of shrubs. Colonization rates were highest for shrubs (66.0%), followed by trees (55.3%) and herbs (30.5%) . Only one exclusive karst species was found: *Ornithoboea henryi* (1 individual). Indifferent species (34 families, 54 genera, 57 species) exceeded preferent species (20 families, 30 genera, 32 species) in taxonomic diversity, but preferent species abundance (986 individuals) was approximately double that of indifferent species (531), with preferent species colonization rate (86.0%) exceeding indifferent species (65.5%) . Trees were dominated by preferent species, shrubs by indifferent species, and herbs showed relatively greater indifferent species dominance .

Among colonizing plants, Euphorbiaceae and Urticaceae had the highest species richness (6 species each). The three most abundant species were *Cleistanthus sumatranus* (33.5%, tree, preferent), *Pseuderanthemum polyanthum* (7.4%, shrub, indifferent), and *Lasiococca comberi* var. *pseudoverticillata* (7.3%, tree, preferent). The three species with highest colonization rates were *Cleistanthus sumatranus* (29.4%, tree, preferent), *Pseuderanthemum polyanthum* (15.5%, shrub, indifferent), and *Reissantia arborea* (9.2%, shrub, preferent).

2.3 Relationship Between Rock Outcrop Microhabitats and Colonizing Plants

Pearson correlation results showed that microhabitat morphological characteristics (soil depth, area, volume, length, depth-width ratio, circular coincidence) had more significant effects on species richness across life forms and karst adaptability groups than external environmental factors (altitude, slope position, aspect, slope gradient, canopy density, height, rock-habitat ratio) [Figure 3: see original paper], with area, length, volume, and soil depth showing strong positive correlations with species richness.

High collinearity was observed between length and area, volume and area, and slope position and altitude. After sequentially excluding length, volume, and slope position, RDA of microhabitat environmental factors and species composition/richness was performed [Figure 4: see original paper]. The first RDA axis explained over 90% of variation, with area contributing most to RDA1 . Area showed the highest model explanatory power (approximately 50%), followed by soil depth (>20%), with both factors far exceeding other microhabitat characteristics and showing highly significant effects.

Optimal model fitting revealed a decreasing exponential species-area relationship for microhabitats (e^{96}.7, $R^2 = 0.56$), where species richness increased rapidly at first, then slowly, and finally stabilized with increasing area [Figure 5: see original paper]. The maximum colonizing species number on rock outcrop microhabitats was 10, similar to the average 9.6 species in control plots (5 m × 5 m). Approximately 88% of data points clustered at species richness values of 1 and 2, while about 93% of data fell within areas <2,000 cm^2, and 70% within areas <200 cm^2.

3.1 High Heterogeneity of Karst Rock Outcrop Surface Microhabitats

Habitat heterogeneity is a key factor for rich species formation in karst regions (Ben-Hur & Kadmon, 2020). Most studies have qualitatively or quantitatively explored habitat heterogeneity-plant diversity relationships at macroscales using quadrats (Tan, 2021), neglecting rock outcrops as extreme habitats that host rich plant communities (Shen et al., 2018). Zhu et al. (2002) first classified karst microhabitat types based on external morphological characteristics of karst surfaces, a framework widely applied in southwestern subtropical karst microhabitat research. This study used small-area rock outcrop surface microhabitats in karst forests as a model to explore relationships between habitat heterogeneity and species richness.

Previous research has revealed relationships between karst surface microhabitat heterogeneity and differences in topographic, soil, and climatic factors among microhabitats (Wang et al., 2007; Liao et al., 2010; Liu et al., 2016; Wu et al., 2018). In summary, heterogeneity of karst rock outcrop microhabitats manifests in high variability of intrinsic characteristics (depth, length, area, volume, shape parameters like depth-width ratio and circular coincidence) and environmental differences among microhabitats. Our microhabitats were located in a tropical karst forest with only ~100 m altitude difference, mature stable climax communities, and >95% forest coverage, resulting in minimal local-scale differences in hydrothermal conditions and relatively small contributions of environmental factors to microhabitat heterogeneity. Consequently, no significant differences were found in environmental factors between control plots and microhabitats. Therefore, heterogeneity of rock outcrop surface microhabitats in this study was primarily determined by intrinsic characteristics, especially area and depth. When spanning different vegetation types, environmental factor differences among rock outcrop microhabitats might increase, potentially enhancing their contribution to heterogeneity.

3.2 Species Composition Characteristics of Colonizing Vascular Plants

In this study, the genus-to-species ratio of colonizing vascular plants on rock outcrop microhabitats was 1.1, compared to 2.2 for vascular plants in the same region's tropical karst forest (Zhu et al., 2007) and 2.2 in Guangxi's Nonggang northern tropical karst forest (Huang et al., 2013). This indicates that colonizing vascular plants on rock outcrops show significantly lower genus-to-species ratios and pronounced oligotypic genus characteristics.

In terms of life form composition, forest-dominant tree and shrub species and lianas showed colonization advantages on microhabitats. This composition resembles that on zonal soils, where *Cleistanthus sumatranus* and *Lasiococca comberi* var. *pseudoverticillata* saplings dominate the understory (Zhu et al., 2015). Seeds of forest-dominant species appear well-adapted to karst environmental stresses (Ye et al., 2023), enabling successful germination and seedling establishment even in soil-poor rock outcrop microhabitats, providing abundant seed sources for forest regeneration. Although herb species richness was highest, colonization rates and abundance proportions were far lower than for trees and shrubs, likely due to high forest canopy density limiting light and heat resources for low-growing herbs. Trees and shrubs dominated microhabitats, possibly because woody plants in tropical karst forests have well-developed root systems that can penetrate rock crevices to absorb nutrients and water (Xu et al., 1997). Lianas were widespread both regionally and within microhabitats, comprising nearly 58% of colonizing shrubs. These climbing species can tenaciously grow on steeply sloped microhabitats (Wei et al., 2014). Studies indicate that during early stages of desertification restoration, lianas can effectively cover rock surfaces, crevices, and grooves, maximizing utilization of limited microhabitat resources (Wu et al., 2015).

Karst habitats are harsh, and plants have developed unique water and nutrient absorption and utilization strategies to adapt (Huang et al., 2011), achieving coexistence by occupying specific resources and spaces (Nakashizuka, 2001) and developing distinct environmental preferences (Hu et al., 2017). This study found that karst characteristic species better adapted to and dominated rock outcrop microhabitats. Although exclusive karst species proportion was very low (1.1%), possibly due to historical anthropogenic disturbance, preferent species proportion was high (35.6%). For example, on outcrops at higher elevations in karst hills, numerous karst preferent species such as *Paraboea rufescens* and *Pilea plataniflora* occurred. The proportion of karst characteristic species in our rock outcrop microhabitats was significantly higher than in other floristic studies: Zhu et al. (2003) reported 10.1% exclusive and 12.2% preferent karst species in Xishuangbanna, while Zhu et al. (2007) reported karst characteristic species (exclusive + preferent) comprising 20–30% of southern China's karst flora. This higher proportion may relate to the extreme environmental constraints of rock outcrop microhabitats, where karst characteristics like drought, rocky thin soils, and calcium enrichment become further extreme, intensifying plant selection so that only species and individuals adapted to these conditions can establish and grow normally (Su & Li, 2003).

3.3 Tropical Karst Rock Outcrop Surface Microhabitats and Plant Colonization

Formation of microhabitats with colonizing plants on rock outcrop surfaces is a challenging process, requiring sufficient karstification to create grooves that can effectively intercept water, soil, and nutrient resources, followed by arrival of viable seeds/spores from nearby sources that can adapt to the harsh microhabitat conditions (Li et al., 2007). For such fragile microhabitats, even minor external disturbances could cause collapse, suggesting they should be highly sensitive to environmental differences.

However, this study found low explanatory power of external environmental factors for colonizing plant species composition and richness on rock outcrop surfaces. Commonly, factors like altitude, aspect, slope gradient, canopy density, and height indirectly affect plant composition and distribution by influencing redistribution of light, water, and soil nutrients (Huang et al., 2016; Zhu et al., 2016; Zhang et al., 2023). Because our study area lies within a tropical karst forest with favorable hydrothermal conditions, even microhabitats with poor site conditions can support seed germination and seedling survival. The massive and seasonally indistinct seed rain supply (Dou et al., 2018) ensures effective seed replenishment, greatly enhancing plant colonization survival rates and buffering against environmental factor differences.

Microhabitat intrinsic characteristics (area, soil depth, depth-width ratio, circular coincidence) showed more significant effects and higher explanatory power for colonizing plant composition and distribution. Area overwhelmingly explained more variation in species richness than other environmental factors, followed by soil depth, indicating these are the primary determinants of species diversity on rock outcrop microhabitats. Larger area and greater soil depth enhance water and mineral nutrient retention capacity (Belcher et al., 1995; Li et al., 2012), support richer soil microbial communities and higher soil quality (Zhou et al., 2018), and provide more space for root growth (Liu, 2020), thereby supporting more plant colonization, consistent with our results.

Further simulation revealed a species-area relationship following island biogeography theory (MacArthur & Wilson, 1967; Lomolino & Weiser, 2001). Thus, rock outcrops and their surface microhabitats can be viewed as habitat islands embedded in karst soil matrices, with each island being isolated. The species-area relationship implies complex ecological processes related to speciation, extinction, and dispersal (Chave et al., 2002; Zurlini et al., 2002; Ricklefs & Bermingham, 2004). Our results demonstrate that area serves as a good indicator of colonizing vascular plant species richness in microhabitats. As internal and external forces enlarge microhabitat area, they gradually connect with surrounding soil patches, and colonizing species richness stabilizes. Additionally, most data points clustered at low species richness (1–2) and small areas ($<2{,}000\ cm^2$), primarily because selection was limited to microhabitats that could be clearly delineated. As area increases, microhabitats more easily connect with surrounding soil patches, and colonizing plants become larger with roots penetrating rock crevices, making it difficult to identify the microhabitat area supporting their growth, so such cases were excluded.

Most habitat heterogeneity studies are landscape-scale, using altitude and slope gradient as heterogeneity metrics (Yan et al., 2022). Our results suggest that for small-scale karst rock outcrop microhabitats, morphological characteristics should be considered as heterogeneity proxies, with area and soil depth as primary evaluation indicators. However, this study did not quantify spatiotemporal variability of nutrients and water in microhabitats, various carrying capacities, seed rain supply and effectiveness variations within forests, or include surveys across different vegetation types. Future research incorporating these aspects and linking them more comprehensively to colonizing plant biomass, richness, and density will provide more robust evidence for unraveling relationships between karst plant diversity and habitat heterogeneity.

Based on surveys and correlation analyses of 586 rock outcrop surface microhabitats and their colonizing plants in a tropical karst forest, we conclude: (1) Rock outcrop surface microhabitats in tropical karst forests exhibit high habitat heterogeneity, particularly in morphological characteristics with extremely high variability in volume and area. (2) Colonizing plants on rock outcrop surfaces show rich tree, shrub, and herb species richness, characterized by oligotypic genera and numerous karst characteristic species, with forest-dominant and karst-preferent species occupying dominant positions. (3) Area and soil depth on rock outcrop surfaces have extremely significant effects with high explanatory power for colonizing plant species composition and richness. (4) A clear decreasing exponential relationship exists between species richness and area, indicating that microhabitat area serves as a good indicator of species richness.

References

BELCHER JW, KEEDY PA, TWOLAN SL, 1995. Root and shoot competition intensity along a soil depth gradient[J]. J Ecol, 84(4): 673-682.

BEN-HUR E, KADMON R, 2020. Heterogeneity-diversity relationships in sessile organisms: a unified framework[J]. Ecol Lett, 23(1): 193-207.

CAO JH, YUAN DX, YANG H, 2022. Karst ecosystem and its plants[J]. Carsol Sin, 41(3): 365-377. [Cao Jianhua, Yuan Daoxian, Yang Hui, et al., 2022. Plants in karst ecosystems[J]. Carsologica Sinica, 41(3): 365-377.]

CHAVE J, MULLER-LANDAU HC, LEVIN SA, 2002. Comparing classical community models, theoretical consequences for patterns of diversity[J]. Amer Naturalist, 159(1): 1-23.

CHEN HS, NIE YP, WANG KL., 2013. Spatio-temporal heterogeneity of water and plant adaptation mechanisms in karst regions: a review[J]. Acta Ecol Sin, 33(2): 317-326. [Chen Hongsong, Nie Yunpeng, Wang Kelin, 2013. Research progress on spatio-temporal heterogeneity of water and plant adaptation mechanisms in karst mountainous areas[J]. Acta Ecologica Sinica, 33(2): 317-326.]

DOU LN, HANG WF, DENG XB, et al., 2018. Nine-year seed rain dynamics in Parashorea chinensis forest in Xishuangbanna, Southwest China[J]. Biodivers Sci, 26(9): 919-930. [Dou Lina, Zhang Wenfu, Deng Xiaobao, et al., 2018. Nine-year dynamics of seed rain in Parashorea chinensis forest in Xishuangbanna[J]. Biodiversity Science, 26(9): 919-930.]

DE WAELE J, PLAN L, AUDRA P, 2009. Recent developments in surface and subsurface karst geomorphology: An introduction[J]. Geomorphology, 106(1-2): 1-8.

FORD D, WILLIAMS PM, 2007. Karst Hydrogeology and Geomorphology[M]. England: John Wiley & Sons Ltd. : 9-36.

GE F, 2008. Modern ecology[M]. Beijing: Science Press: 36-47. [Ge Feng, 2008. Modern Ecology[M]. Beijing: Science Press: 36-47.]

GUO K, LIU CC, DONG M, 2011. Ecological adaptation of plants and control of rocky desertification on karst region of Southwest China[J]. Chin J Plant Ecol, 35(10): 991-999. [Guo Ke, Liu Changcheng, Dong Ming, 2011. Ecological adaptation of plants and rocky desertification control in karst regions of Southwest China[J]. Chinese Journal of Plant Ecology, 35(10): 991-999.]

HEIDRICH L, BAE S, LEVICK S, et al., 2020. Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests[J]. Nat Ecol Evol, 4(9): 1-9.

HOU MF, JIANG ZC, 2006. Species diversity of karst original forest in different geochemica environments in Maolan[J]. Ecol Environ Sci, 15(3): 572-576. [Hou Manfu, Jiang Zhongcheng, 2006. Plant species diversity of karst primary forest in different geochemical environments in Maolan[J]. Ecology and Environmental Sciences, 15(3): 572-576.]

HU G, ZHANG ZH, CHENG AY, et al., 2017. Characterizing and analyzing stand spatial structure of a northern subtropical karst secondary forest in Tianlong mountain of central Guizhou province, China[J]. Earth Environ, 45(1): 25-31. [Hu Gang, Zhang Zhonghua, Cheng Anyun, et al., 2017. Quantification and analysis of stand spatial structure of a typical karst secondary forest in Tianlong Mountain, central Guizhou[J]. Earth and Environment, 45(1): 25-31.]

HUANG FZ, DING T, LI XK, et al., 2016. Species diversity for various associations along an altitudinal gradient in the karst seasonal rainforest in Nonggang[J]. Acta Ecol Sin, 36(14): 4509-4517. [Huang Fuzhao, Ding Tao, Li Xiankun, et al., 2016. Changes in species diversity of different associations along an altitudinal gradient in Nonggang karst seasonal rainforest[J]. Acta Ecologica Sinica, 36(14): 4509-4517.]

HUANG YQ, LI XK, ZHANG ZF, et al., 2011. Seasonal changes in Cyclobalanopsis glauca transpiration and canopy stomatal conductance and their dependence on subterranean water and climatic factors in rocky karst terrain[J]. J Hydrol, 402(1/2): 135-143.

HUANG YS, WU WH, JIANG RH, et al., 2013. Primary study on species diversity of plant in Longgang national nature reserve of Guangxi[J]. Guihaia, 33(3): 346-355. [Huang Yusong, Wu Wanghui, Jiang Rihong, et al., 2013. Preliminary study on plant species diversity in Longgang National Nature Reserve, Guangxi[J]. Guihaia, 33(3): 346-355.]

LI CC, CHENG X, YANG SC, 2012. Study on the soil thickness factor of plant growth in karst mountains: Take the Guizhou Xiangbao Mountain as an example[J]. J Guizhou Norm Coll, 28(9): 38-41. [Li Chengcheng, Cheng Xing, Yang Shichao, 2012. Study on soil thickness factor for plant growth in karst mountainous areas: A case study of Xiangbao Mountain, Guizhou[J]. Journal of Guizhou Normal College, 28(9): 38-41.]

LI XS, PENG MC, DANG CL, 2007. Research progress of natural regeneration of plants[J]. Chin J Ecol, 26(12): 2081-2088. [Li Xiaoshuang, Peng Mingchun, Dang Chenglin, 2007. Research progress on natural regeneration of plants[J]. Chinese Journal of Ecology, 26(12): 2081-2088.]

LI YB, HOU JY, XIE DT, 2002. The Recent Development of Research on Karst Ecology in Southwest China[J]. Sci Geol Sin, 22(3): 365-370. [Li Yangbing, Hou Jianjun, Xie Deti, 2002. Recent progress in karst ecological research in Southwest China[J]. Scientia Geographica Sinica, 22(3): 365-370.]

LIAO HK, LONG J, LI J, et al., 2010. Preliminary study on spatial heterogeneity of soil mineral composition and organic carbon content at different microhabitats that under different vegetation types in karst region[J]. Carsol Sin, 29(4): 434-439. [Liao Hongkai, Long Jian, Li Juan, et al., 2010. Preliminary study on spatial heterogeneity of soil mineral composition and organic carbon content in microhabitats under different vegetation types in karst regions[J]. Carsologica Sinica, 29(4): 434-439.]

LIU F, WANG SJ, LUO HB, et al., 2008. Micro-habitats in karst forest ecosystem and variability of soils[J]. Acta Pedol Sin, 45(6): 1055-1062. [Liu Fang, Wang Shijie, Luo Haibo, et al., 2008. Microhabitats in karst forest ecosystems and soil heterogeneity[J]. Acta Pedologica Sinica, 45(6): 1055-1062.]

LIU J, SHEN YX, ZHAO ZM, et al., 2018. Method to measure surface rock ratio in rocky desertification areas[J]. MT Res, 36(6): 973-980. [Liu Juan, Shen Youxin, Zhao Zhimeng, et al., 2018. A method for measuring surface rock exposure rate in rocky desertification areas[J]. Mountain Research, 36(6): 973-980.]

LIU Y, 2020. Effects of soil depth on plant community structure and biomass in karst region [D]. Chongqing: Southwest University: 49-63. [Liu Yuan, 2020. Effects of soil depth on plant community structure and biomass in karst regions[D]. Chongqing: Southwest University: 49-63.]

LONG J, LIAO HK, LI J, et al., 2012. Relationships between soil and rocky desertification in typical karst mountain area based on redundancy analysis[J]. Chin J Environ Sci, 33(6): 2131-2138. [Long Jian, Liao Hongkai, Li Juan, et al., 2012. Study on soil-rocky desertification relationship in typical karst mountainous areas based on redundancy analysis[J]. Chinese Journal of Environmental Science, 33(6): 2131-2138.]

LOMOLINO MV, WEISER MD, 2001. Towards a more general species-area relationship: Diversity on all islands, great and small[J]. J Biogeogr, 28(4):

431-445.

MACARTHUR RH, WILSON EO, 1967. The theory of island biogeography[M]. New Jersey: Princeton University Press: 76.

NAKASHIZUKA T, 2001. Species coexistence in temperate, mixed deciduous forests[J]. Trends Ecol Evol, 16(4): 205-210.

RICKLEFS RE, BERMINGHAM E, 2004. History and the species-area relationship in Lesser Antillean birds[J]. Amer Nat, 163(2): 227-239.

RICKLEFS RE, LOVETTEL IJ, 1999. The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups[J]. J Anim Ecol, 68(6),

SHEN YX, ZHAO ZM, BI SC, et al., 2018. Rock outcrop and its ecological function in terrestrial ecosystem[J]. Adv Earth Sci, 33(4): 343-349. [Shen Youxin, Zhao Zhimeng, Bishengchun, et al., 2018. Rock outcrops and their ecological functions in terrestrial ecosystems[J]. Advances in Earth Science, 33(4): 343-349.]

SFENTHOURAKIS S, TRIANTIS KA, 2009. Habitat diversity, ecological requirements of species and the Small Island Effect[J]. Divers Distrib, 15(1): 131-140.

SHENG MY, XIONG KN, WANG LJ, et al., 2018. Response of soil physical and chemical properties to rocky desertification succession in South China Karst[J]. Carbonate Evaporite, 33(1): 15-28.

SU ZM, LI XK, 2003. The types of natural vegetation in karst region of Guangxi and its classified system[J]. Guihaia, 24(4): 289-293. [Su Zongming, Li Xiankun, 2003. Types of natural vegetation in Guangxi karst region and their classification system[J]. Guihaia, 24(4): 289-293.]

TANG QY, 2021. Distribution pattern of species and pedigree diversity of karst plant community based on habitat heterogeneity[D]. Guiyang: Guizhou University: 3-4. [Tan Qiyu, 2021. Distribution patterns of species and phylogenetic diversity of karst plant communities based on habitat heterogeneity[D]. Guiyang: Guizhou University: 3-4.]

TRIANTIS KA, VARDINOYANNIS K, Tsolaki EP, et al., 2006. Re-approaching the small island effect[J]. J Biogeogr, 33(5): 914-923.

TU YL, 1995. A analisis of flora and ecological characteristics of karst scrubs in Guizhou province[J]. J Guizhou Norm Univ, 13(3): 1-8. [Tu Yulin, 1995. Analysis of flora and ecological characteristics of karst scrub in Guizhou Province[J]. Journal of Guizhou Normal University, 13(3): 1-8.]

WANG DL, ZHU SQ, HUANG BL, 2003. Primary study on soft physical and chemical properties in rocky desertification process[J]. J MT Agric Biol，22(3): 204-207. [Wang Delu, Zhu Shouqian, Huang Baolong, 2003. Preliminary study on changes in soil physical and chemical properties during rocky desertification process[J]. Journal of Mountain Agriculture and Biology, 22(3): 204-207.]

WANG KL, ZHANG CH, CHEN HS, et al., 2019. Karst landscapes of China: patterns, ecosystem processes and services[J]. Landscape Ecol, 34(12): 2743-2763.

WANG SJ, LU HM, ZHOU YC, et al., 2007. Spatial variability of soil organic carbon and representative soil sampling method in Maolan karst virgin forest[J]. Acta Pedol Sin, 44(3): 475-483. [Wang Shijie, Lu Hongmei, Zhou Yunchao, et al., 2007. Spatial variability of soil organic carbon and representative soil sampling method in Maolan karst virgin forest[J]. Acta Pedologica Sinica, 44(3): 475-483.]

WEI XH, XU XZ, LEI LL, et al., 2014. Study on the featuresof vegetation in different landforms of peak forest plain in the North Guangdong[J]. Carsol Sin, 33(4): 441-448. [Wei Xinghu, Xu Xizhen, Lei Li, et al., 2014. Study on vegetation characteristics at different geomorphological positions of peak forest plain in northern Guangdong[J]. Carsologica Sinica, 33(4): 441-448.]

WU QS, LONG J, LI J, et al., 2019. Effects of different microhabitat types on soil microbial community composition in the Maolan karst forest in southwest China[J]. Acta Ecol Sin, 39(3): 1009-1018. [Wu Qiusheng, Long Jian, Li Juan, et al., 2019. Effects of different microhabitat types on soil microbial community composition in Maolan karst forest in Southwest China[J]. Acta Ecologica Sinica, 39(3): 1009-1018.]

WU Y, 2019. Biodiversity and ecological adaptability of epiphytes in the tropical karst forests in Xishuangbanna, Yunnan[D]. Beijing: University of Chinese Academy of Sciences: 23-27. [Wu Yi, 2019. Biodiversity and ecological adaptability of epiphytes in tropical karst forests of Xishuangbanna, Yunnan[D]. Beijing: University of Chinese Academy of Sciences: 23-27.]

WU YX, TAO DH, DENG PY, 2015. Problems and countermeasures of using vines for rocky desertification control[J]. S Chin For Sci, 43(2): 50-55. [Wu Yixiong, Tao Dihui, Deng Peiyi, 2015. Problems and countermeasures of using vines for rocky desertification control[J]. South China Forestry Science, 43(2): 50-55.]

XU L, HE XR, FANG ZJ, et al., 1997. Study on the community characteristics of the world's only walnut single leaf incense tree[J]. J NW For Univ, 12(4): 1-6. [Xu Liang, He Xinrong, Fang Zhijian, et al., 1997. Study on community characteristics of the world's only Juglandales single-leaf incense tree[J]. Journal of Northwest Forestry University, 12(4): 1-6.]

XU HQ, LIU WY, SHEN YX, et al., 2006. A preliminary study of epiphytes in semi-humid evergreen broad-leaved forest in Stone-forest Karst Region, Yunnan Province[J]. Guihaia, 26(1): 43-48. [Xu Haiqing, Liu Wenyao, Shen Youxin, et al., 2006. Preliminary study on epiphytes in semi-humid evergreen broad-leaved forest in Stone Forest Karst Region, Yunnan Province[J]. Guihaia, 26(1): 43-48.]

YAN YZ, JARVIE S, LIU QF, et al., 2022. Effects of fragmentation on grassland plant diversity depend on the habitat specialization of species[J]. Biol Conserv, 275: 109773.

YAN YZ, JARVIE S, ZHANG Q, et al., 2023. Habitat heterogeneity determines species richness on small habitat islands in a fragmented landscape[J]. J Biogeogr, 50(5): 976-986.

YANG L, YANG C, ZHU TB, et al., 2018. Contents and availability of trace elements in soils of natural forests in karst region[J]. Carsol Sin, 37(1): 59-66. [Yang Lin, Yang Cheng, Zhu Tongbin, et al., 2018. Content and availability characteristics of trace elements in soils of natural forests in karst regions[J]. Carsologica Sinica, 37(1): 59-66.]

YE TM, RONG L, WANG MJ ，et al., 2023. Relationship between aboveground biomass and in Tianlong Mountain, central environmental Guizhou[J]. Guihaia, 43(3): 484-493. [Ye Tianmu, Rong Li, Wang Mengjie, et al., 2023. Relationship between aboveground biomass and environmental factors in typical karst secondary forest of Tianlong Mountain, central Guizhou[J]. Guihaia, 43(3): 484-493.]

YUAN TX, ZHANG HP, OU ZY, et al., 2014. Effects of topography on the diversity and distribution pattern of ground plants in karst montane forests in Southwest Guangxi, China[J]. Chin J Appl Ecol, 25(10): 2803-2810. [Yuan Tiexiang, Zhang Heping, Ou Zhiyang, et al., 2014. Effects of topography on diversity and distribution patterns of ground plants in karst montane forests of Southwest Guangxi, China[J]. Chinese Journal of Applied Ecology, 25(10): 2803-2810.]

ZHANG T, ZHANG JL, YANG T, et al., 2023. Influence of topographic factors on plant diversity and spatial distribution of karst around FAST[J]. Guihaia，43(3): 473-483. [Zhang Ting, Zhang Jianli, Yang Tao, et al., 2023. Influence of topographic factors on plant diversity and spatial distribution of karst vegetation around FAST[J]. Guihaia, 43(3): 473-483.]

ZHOU W, YAN M, SU CH, et al., 2018. Study on soil microbial quantity and biomass developed from different carbonate-rock and soil thickness: A case study of Huaxi District in Guiyang[J]. Carsol Sin, 37(2): 168-174. [Zhou Wei, Yan Min, Su Chunhua, et al., 2018. Study on soil microbial quantity and biomass under different carbonate rocks and soil thickness: A case study of Huaxi District, Guiyang[J]. Carsologica Sinica, 37(2): 168-174.]

ZHU H, 2007. The karst ecosystem of southern China and its biodiversity[J]. Trop For, 35(S1): 44-47. [Zhu Hua, 2007. Characteristics of limestone (karst) ecosystems and biodiversity in southern China[J]. Tropical Forestry, 35(S1): 44-47.]

ZHU H, WANG H, LI BG, et al., 2003. Biogeography and floristic affinities of the limestone flora in Southern Yunnan, China [J]. Ann MO Bot Gard, 90(3): 444-465.

ZHU H, WANG H, LI BG, et al., 2015. Studies on the forest vegetation of Xishuangbanna[J]. Plant Sci J, 33(5): 641-726. [Zhu Hua, Wang Hong, Li Baogui, et al., 2015. Studies on forest vegetation of Xishuangbanna[J]. Plant Science Journal, 33(5): 641-726.]

ZHU SQ, HE JX, LU WM, et al., 2002. A study on microhabitats to karst forest in Maolan[M]// ZHU SQ, Ecological research on karst forest( ). Guiyang: Guizhou Science and Technology Press: 38-48. [Zhu Shouqian, He Jixing, Wei Luming, et al., 2002. Study on microhabitat characteristics of Maolan karst forest[M]// Zhu Shouqian. Ecological Research on Karst Forest (III). Guiyang: Guizhou Science and Technology Press: 38-48.]

ZHU XA, SHEN YX, HE BB, et al., 2016. Species diversity and biomass of vascular plant on rocky outcrops in karst area[J]. MT Res, 34(2): 165-172. [Zhu Xi'ai, Shen Youxin, He Beibei, et al., 2016. Species diversity and biomass characteristics of vascular plants on rocky outcrops in Yunnan Stone Forest[J]. Mountain Research, 34(2): 165-172.]

ZURLINI G, GROSSI L, ROSSI O, 2002. Spatial-accumulation pattern and extinction rates of Mediterranean flora as related to species confinement to habitats in preserves and larger areas[J]. Conserv Biol, 16(4): 948-963.

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