Postprint: Plant Diversity and Soil Physicochemical Characteristics Across Different Topographies in Maolan Karst Forest

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Abstract

This study investigated the differences in plant diversity and soil physicochemical properties across different terrains in the Maolan karst forest, as well as the relationship between them, to provide a scientific basis for understanding the species diversity maintenance mechanisms in karst forests. The results showed that: (1) The species composition of woody plants differed among terrains. Slope areas had 35 families, 65 genera, and 78 species of woody plants; trough valleys had 38 families, 64 genera, and 89 species; and funnel depressions had 35 families, 61 genera, and 84 species. Meanwhile, the richness index, diversity index, and evenness index exhibited the pattern trough valley > funnel depression > slope, whereas the dominance index showed the pattern slope > funnel depression > trough valley. (2) Soil physical properties differed significantly among terrains ($P<0.05$). Soil bulk density and non-capillary porosity exhibited the pattern slope > trough valley > funnel depression, while natural water content, field water capacity, total porosity, capillary porosity, and other indicators all showed the pattern funnel depression > trough valley > slope. (3) Except for total K, most soil nutrient indicators were significantly higher in funnel depressions than in trough valleys and slopes, following the pattern funnel depression > trough valley > slope. (4) Redundancy analysis indicated that plant diversity was correlated with soil physicochemical properties, and plant diversity indices across different terrains were significantly influenced by soil physicochemical properties. The research findings corroborate that the complexity of terrain conditions and the heterogeneity of soil physicochemical properties in the Maolan karst forest constitute one of the reasons for the diverse microhabitats and rich species composition in this region.

Full Text

Preamble

Differences in Plant Diversity and Soil Physicochemical Properties Across Terrain Types in Maolan Karst Forest

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Abstract: This study investigates variations in plant diversity and soil physicochemical properties across different terrain types in Maolan karst forest and examines their interrelationships, providing a scientific basis for understanding species diversity maintenance mechanisms in karst forest ecosystems. The results show: (1) Species composition of woody plants differs among terrain types, with slopes containing 78 species from 65 genera and 35 families, trough valleys containing 89 species from 64 genera and 38 families, and funnels containing 84 species from 61 genera and 35 families. Richness, diversity, and evenness indices follow the pattern trough valley > funnel > slope, while dominance index shows the opposite trend: slope > funnel > trough valley. (2) Soil physical properties vary significantly among terrain types ($P<0.05$). Bulk density and non-capillary porosity follow the pattern slope > trough valley > funnel, whereas natural water content, field water holding capacity, total porosity, and capillary porosity show the reverse: funnel > trough valley > slope. (3) Except for total potassium, most soil nutrient indicators are significantly higher in funnels than in trough valleys and slopes, following the pattern funnel > trough valley > slope. (4) Redundancy analysis reveals correlations between plant diversity and soil physicochemical properties, with plant diversity indices in different terrain types being significantly influenced by soil properties. These findings corroborate that the complex topographic conditions and differential soil physicochemical properties in Maolan karst forest contribute to habitat diversity and rich species composition.

Keywords: karst forest, topographic condition, plant diversity, soil physicochemical properties, Maolan

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Introduction

Soil provides essential environmental conditions for plant survival and influences community structural characteristics. Variations in soil physicochemical properties drive changes in plant diversity, which in turn affects soil properties (Wu et al., 2001). The close relationship between soil and plant communities has long been a focal point in ecological research, forming the foundation of community ecology and biodiversity conservation and management. Numerous studies have examined the relationship between soil physicochemical properties and plant diversity across different vegetation types (Wang et al., 2010), successional stages (Wang et al., 2007), restoration stages (Liu et al., 2018), degradation stages (Liu et al., 2016), and varying degrees of rocky desertification (Sheng et al., 2015). While these studies have established a foundation for understanding plant diversity-soil relationships, research on how terrain influences plant diversity and soil properties in karst forests remains limited. Further investigation into terrain effects on plant diversity in karst forests is crucial for elucidating species diversity maintenance mechanisms.

The Maolan Nature Reserve features well-preserved primary karst forest with minimal anthropogenic disturbance, making it an ideal site for studying karst forest ecosystems and geomorphological development. Compared to forests on normal landforms, karst forests exhibit distinct differences in ecological environment, community appearance, composition, vertical structure, successional dynamics, and the influence of high habitat heterogeneity on vegetation (Long, 2009). Previous research has yielded substantial findings on soil microorganisms (Long et al., 2004), litter dynamics (Zhao et al., 2018), soil moisture (Liu et al., 2012), nutrient cycling (Yu et al., 2015), plant diversity (Hou et al., 2011), community structure (Qin & Long, 2016), and spatial distribution patterns (Qin & Long, 2016) in Maolan karst forest. However, most studies have focused on single ecological processes, with limited attention to relationships between these components.

Maolan karst forest contains various negative landforms including sinkholes, funnels, depressions, trough valleys, blind valleys, and basins. The spatial combination of these negative landforms with cone peaks creates geomorphic assemblages such as peak-cluster depressions, peak-cluster funnels, and peak-cluster basins—the three most widely distributed geomorphic types in the region (Zhou, 1987). Under relatively uniform soil formation conditions, topographic variations can create diverse microhabitats with differences in light, temperature, moisture, and nutrients, significantly influencing soil formation and plant evolution processes. This study examines woody plants and soils across three terrain types—slopes, trough valleys, and funnels—in Maolan karst forest, analyzing community species diversity and soil physicochemical characteristics and exploring their interrelationships to provide theoretical insights into species diversity maintenance mechanisms.

1.1 Study Area Overview

Maolan Karst Forest Nature Reserve is located at the border between Guizhou and Guangxi provinces in southern China (107°52' -108°05' E, 25°09' -25°20' N). The reserve features typical karst peak-cluster landforms, with elevations ranging from 430 to 1,078.6 m (average ~800 m). The mean annual temperature is 15.3°C with accumulated temperature of 5,727.9°C. Precipitation concentrates between April and October, with an annual average of 1,320.5 mm and mean annual relative humidity of 83%. Parent materials consist primarily of carbonate rocks such as dolomite and limestone, forming weakly alkaline calcareous soils with pH values of 7.5-8.0. The main vegetation type is evergreen-deciduous broadleaf mixed forest. Dominant tree species include *Cyclobalanopsis glauca*, *Carpinus pubescens*, *Photinia davidsoniae*, and *Litsea verticillata*. Shrub layer dominants include *Mahonia fortunei*, *Euonymus dielsianus*, *Pittosporum crispulum*, *Nandina domestica*, and *Sinosideroxylon wightianum*. Common herbaceous species include *Selaginella uncinata*, *Cyrtogonellum fraxinellum*, and *Elatostema stewardii*.

The three terrain types exhibit distinct habitat characteristics: (1) **Slopes** are located in the middle-upper slope positions with high rock exposure and numerous rock fragments. Soils are black calcareous with low total coverage (~40%). Water conditions are poor but light is abundant, making vegetation establishment difficult. Most plants grow directly in rock fissures with well-developed root systems. (2) **Trough valleys** have flat bottoms with black calcareous soils and high coverage (~60%). Soil depth ranges 2-6 cm, with good moisture and moderate light conditions. (3) **Funnels** are typical negative landforms with dense vegetation and high canopy closure. Soils are black calcareous with the highest coverage (85%) and depths of 5-20 cm. Thick surface litter layers impede water infiltration, causing waterlogging, while poor light conditions prevail due to shading from surrounding slopes (Qin et al., 2018).

1.2 Methods

1.2.1 Field Survey

In May 2018, plot surveys were conducted in the buffer zone of Limingguan Shui Autonomous Township within Maolan Nature Reserve. The study area primarily comprises slopes, trough valleys, and funnels. Ten continuous plots (20 m × 20 m each) were established for each terrain type, yielding 4,000 m^2 per terrain type and 1.2 ha total. Geographic coordinates were recorded using GPS, along with elevation, slope, and aspect. Each plot was subdivided into 5 m × 5 m subplots to record species name, individual count, diameter at breast height, height, crown width, and canopy closure for all woody plants.

1.2.2 Soil Sampling

Based on the plot survey, three standard plots (20 m × 20 m) were selected per terrain type. Within each plot, five-point sampling was conducted in the four cardinal directions and center, yielding 15 soil samples per terrain type (45 total). Due to shallow soils (<20 cm at some points), 1 m × 1 m surface soil samples were collected.

1.2.3 Soil Physicochemical Analysis

Soil bulk density (Bb), natural water content (Nc), field water holding capacity (Fc), and capillary porosity (Cp) were measured using the ring knife method. Total porosity (Tp) was calculated as Tp = 93.947 - 32.995 × Bd, and non-capillary porosity (Np) as Np = Tp - Cp (Sheng et al., 2015). Soil pH was determined potentiometrically (2.5:1 water:soil ratio). Organic matter was measured by K Cr O volumetric oxidation. Total nitrogen was analyzed using a Kjeldahl apparatus. Total phosphorus and potassium were determined by molybdenum-antimony colorimetry after NaOH fusion. Available nitrogen was measured by alkali diffusion, available phosphorus by 0.5 mol $\cdot$ L ^{1} NaHCO extraction, and available potassium by CH COONH extraction, following standard soil agrochemical analysis methods (Bao, 2006).

1.2.4 Data Processing

Data were preprocessed in Excel. ANOVA and multiple comparisons (LSD test) were performed using SPSS 25.0. Redundancy analysis (RDA) was conducted using Canoco 4.5. Plant diversity indices were calculated following Qin et al. (2018).

2 Results and Analysis

2.1 Floristic Composition of Woody Plants

As shown in , floristic composition varied among the three terrain types. Slopes supported 78 woody species from 65 genera and 35 families, trough valleys had 89 species from 64 genera and 38 families, and funnels contained 84 species from 61 genera and 35 families. Dominant families on slopes were Lauraceae (6 genera, 9 species), Rosaceae (5 genera, 5 species), Cornaceae (3 genera, 4 species), and Euphorbiaceae (3 genera, 3 species). In trough valleys, dominant families were Lauraceae (6 genera, 9 species), Rosaceae (4 genera, 5 species), Verbenaceae (3 genera, 4 species), and Rutaceae (3 genera, 3 species). Funnel dominants included Lauraceae (6 genera, 11 species), Rosaceae (6 genera, 7 species), Cornaceae (3 genera, 4 species), and Anacardiaceae (3 genera, 3 species). Lauraceae and Rosaceae were dominant across all three terrains.

A total of 43 families were recorded, with 30 families present in all three terrain types (69.8% of total families). Dominant families primarily included Lauraceae, Rosaceae, Cornaceae, Euphorbiaceae, Verbenaceae, Rutaceae, and Anacardiaceae. Trough valleys exhibited the richest and most complex species composition, followed by funnels, while slopes had the simplest composition with fewest species.

2.2 Plant Diversity Across Terrain Types

As shown in , richness index did not differ significantly among terrains (range: 5.76–6.41), while diversity and evenness indices showed significant differences (ranges: 2.69–3.03 and 0.81–0.88, respectively). These three indices followed the pattern trough valley > funnel > slope. Dominance index differed significantly (range: 0.87–0.93) and showed the opposite trend: slope > funnel > trough valley. Richness, diversity, and evenness indices were highest in trough valleys and lowest on slopes, while dominance index was highest on slopes and lowest in trough valleys.

2.3 Soil Physicochemical Properties

2.3.1 Physical Properties As shown in , soil physical properties differed significantly among terrain types. Bulk density was highest on slopes (1.12 g·cm^{3}), intermediate in trough valleys (1.03 g·cm^{3}), and lowest in funnels (0.99 g·cm^{3}). Natural water content was highest in funnels (52.34%), intermediate in trough valleys (44.76%), and lowest on slopes (34.22%). Field water holding capacity followed the same pattern: funnels (52.15%) > trough valleys (43.50%) > slopes (34.55%). Total porosity was highest in funnels (62.68%), intermediate in trough valleys (60.98%), and lowest on slopes (57.49%). Capillary porosity showed the same trend: funnels (51.53%) > trough valleys (44.95%) > slopes (38.91%). Non-capillary porosity exhibited the opposite pattern: slopes (18.58%) > trough valleys (16.03%) > funnels (11.15%). Thus, except for bulk density and non-capillary porosity (slope > trough valley > funnel), all other physical properties showed funnel > trough valley > slope.

2.3.2 Chemical Properties As shown in , soil chemical properties varied significantly among terrain types. Soil pH did not differ significantly ($P>0.05$), with mean values of 7.32 (slope), 7.24 (trough valley), and 7.23 (funnel), following the pattern slope > trough valley > funnel. Organic matter was significantly higher in funnels (164.14 mg·kg^{1}) than in trough valleys (84.52 mg·kg^{1}) and slopes (46.23 mg·kg^{1}). Total nitrogen was significantly higher in funnels (8.40 g·kg^{1}) than in trough valleys (5.32 g·kg^{1}) and slopes (5.02 g·kg^{1}). Available nitrogen showed the same pattern: funnels (600.22 mg·kg^{1}) > trough valleys (272.71 mg·kg^{1}) > slopes (249.90 mg·kg^{1}). Total phosphorus was significantly higher in funnels (3.68 g·kg^{1}) than on slopes (1.44 g·kg^{1}). Available phosphorus was significantly higher in funnels (1.49 mg·kg^{1}) than in trough valleys (0.79 mg·kg^{1}) and slopes (0.79 mg·kg^{1}). Total potassium was significantly higher in trough valleys (12.16 g·kg^{1}) than in funnels (6.85 g·kg^{1}) and slopes (8.90 g·kg^{1}). Available potassium was significantly higher in funnels (130.73 mg·kg^{1}) and trough valleys (121.45 mg·kg^{1}) than on slopes (87.88 mg·kg^{1}). Thus, pH and total potassium showed patterns of slope > trough valley > funnel and trough valley > slope > funnel, respectively, while organic matter, total nitrogen, available nitrogen, total phosphorus, and available phosphorus all showed funnel > trough valley > slope.

2.4 Correlations Between Plant Diversity and Soil Properties

The RDA biplot ([Figure 1: see original paper]) shows that the first four ordination axes have eigenvalues of 0.084, 0.064, 0.008, and 0.003, respectively, accounting for 90.4% of total variance. The first two axes cumulatively explain 98.8% of species-soil relationship variance, with correlations to soil properties of 0.955 and 0.944, respectively, effectively capturing information from all 18 indicators. In the ordination diagram, arrow positions of diversity indices reflect their values along soil factor gradients, while arrows for soil properties indicate their relationships with ordination axes (positive/negative) and arrow length represents relationship strength.

As shown in and [Figure 1: see original paper], pH, bulk density, non-capillary porosity, and total potassium are positively correlated with Axis 1, while organic matter, total nitrogen, total phosphorus, available phosphorus, available potassium, capillary porosity, total porosity, and field water content are negatively correlated. pH, bulk density, and non-capillary porosity are positively correlated with Axis 2, while organic matter, total nitrogen, total phosphorus, total potassium, available nitrogen, available phosphorus, available potassium, capillary porosity, total porosity, and field water content are negatively correlated.

In the biplot, solid arrows represent soil properties and dashed arrows represent diversity indices. The angle between arrows indicates correlation: angles <90° represent positive correlation, >90° negative correlation, with smaller angles indicating stronger relationships. Evenness index appears in the upper right, positively correlated with organic matter, total nitrogen, total phosphorus, total potassium, available phosphorus, available potassium, total porosity, capillary porosity, natural water content, and field water capacity, but also positively correlated with pH, bulk density, and non-capillary porosity. Richness index appears in the upper left, positively correlated with organic matter, total phosphorus, total nitrogen, available phosphorus, available nitrogen, field water capacity, natural water content, capillary porosity, and total porosity, but negatively correlated with pH, bulk density, total potassium, available potassium, and non-capillary porosity. Diversity and dominance indices appear in the lower left, positively correlated with organic matter, total phosphorus, total nitrogen, available phosphorus, available potassium, capillary porosity, total porosity, field water capacity, and natural water content, but negatively correlated with pH, bulk density, and non-capillary porosity.

3 Discussion

3.1 Woody Plant Composition and Species Diversity Across Terrain Types

The Maolan karst nature reserve comprises three main landscape types: slopes, trough valleys, and funnels. Due to habitat diversity and topographic complexity, plant communities continuously adapt their ecophysiological characteristics to environmental changes, forming unique community structures and physiognomies (Qin et al., 2018). Slopes feature steep terrain, discontinuous soil distribution, and well-developed rock fissures where plants grow directly. Extreme water and nutrient deficiency intensifies competition, resulting in simple structure dominated by small drought-tolerant trees with few understory shrubs and pronounced dominant species. Trough valleys have flat bottoms with moderate water and light conditions, fertile soils, and equitable nutrient distribution, supporting good plant growth and high richness, diversity, and evenness indices, though dominant species are less pronounced (Long, 2009; Qin et al., 2018; Wu et al., 2018). Funnels are typical negative landforms with abundant moisture and humidity, supporting many shade-tolerant and cool-preferring species. Most funnel bottoms harbor dense forests with tall trees and high species richness. However, short duration and low intensity of light, combined with temporary waterlogging in some areas, affect plant growth, resulting in shade-tolerant seedlings and saplings with pronounced dominant species, though less extreme than on slopes.

3.2 Soil Physicochemical Characteristics Across Terrain Types

Soils in Maolan karst forest developed from carbonate rocks (limestone, dolomite) through dissolution processes, forming black calcareous soils rich in Ca and Mg with weak alkalinity. Consistent soil formation conditions result in non-significant pH differences. Funnels, as enclosed negative landforms, accumulate decomposing litter from surrounding slopes, forming thick humus layers with loose texture that facilitate organic matter accumulation. Thick litter layers impede water infiltration, causing waterlogging, while dense vegetation and high canopy closure reduce solar radiation, temperature, and wind speed, slowing evaporation and increasing soil moisture, resulting in heavy, poorly structured soils with low permeability. In contrast, slopes have poor habitat conditions with thin (2-6 cm), discontinuous soils, high rock exposure, and well-developed fissures that promote rapid water infiltration and poor water/nutrient retention. Longer and stronger solar radiation, higher surface temperatures, and greater wind speeds accelerate evaporation, reducing soil moisture. Surface litter is easily washed away, hindering organic matter accumulation and resulting in poor soil quality. Trough valleys, being flat and open, receive abundant solar radiation with balanced water and heat distribution, providing relatively ideal habitat conditions and higher nutrient content compared to slopes and funnels.

3.3 Relationships Between Plant Community Diversity and Soil Properties

Soil physicochemical properties influence plant community structure and species diversity, while plant communities reciprocally affect soils (Tang et al., 2016). Our results demonstrate correlations between species diversity and soil properties, corroborating that complex topography and differential soil properties contribute to habitat diversity and rich species composition in Maolan karst forest. Soil nutrients affect plant richness and diversity indices, while litter and organic residues accumulate, mineralize, and decompose in surface soils, with some nutrients absorbed directly by plants and the remainder retained in soils (Li & Wang, 2016). Due to the unique geographic environment of karst forests, plant community composition and types are constrained by terrain, leading to differences in litter composition, storage, and decomposition rates among terrain types. These differences create topographic variation in soil properties that subsequently affects plant communities. Among the three terrain types, funnels have the highest nutrient content but lower diversity indices than trough valleys, reflecting microhabitat diversity effects. Funnel bottoms support good plant growth and high species diversity, accumulating thick litter layers and abundant moisture that accelerate organic matter decomposition, providing superior soil conditions. However, despite dense forests, dominant species are prominent, resulting in diversity indices second only to trough valleys. Trough valleys, with flat terrain and favorable water-heat conditions, promote litter decomposition and uniform nutrient distribution, enabling plants to obtain relatively balanced nutrients and supporting high species richness. Slopes represent harsh habitats where soils and undecomposed litter are easily washed away by rain, slowing soil formation. Plants primarily rely on soils in rock fissures and humus from litter layers, resulting in low nutrient content, intense competition, and difficult establishment. Sparse vegetation consists mainly of drought-tolerant species, with pronounced dominant species and lowest species diversity. Jin et al. (2019) found that plant diversity increases with soil nutrient content, while Zeng et al. (2013) demonstrated that improving soil nutrients during vegetation restoration promotes plant growth and diversity, indicating positive soil-plant synergistic effects. Rosenzweig (1995) reported negative correlations between available soil nutrients and plant diversity at small spatial scales, contrary to our findings. Nevertheless, the influence of soil nutrient content on plant diversity is undeniable. These results provide a theoretical foundation for conservation and management strategies in Maolan Nature Reserve, offering important implications for protecting species diversity across different terrain types and for restoring degraded karst forests.

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