Postprint: Relationship Between Plant Diversity and Environmental Factors in a Typical Mid-Subtropical Karst Forest

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Abstract

To gain an in-depth understanding of the relationships between species diversity and functional diversity of forest vegetation and environmental factors in karst hills, this study conducted comparative analyses of species diversity and functional diversity among deciduous broad-leaved forest, evergreen-deciduous broad-leaved mixed forest, and evergreen broad-leaved forest in the karst hills of Guilin through community surveys, measurements of functional traits and environmental factors, combined with statistical methods including variance analysis, multiple comparison, and redundancy analysis, to explore the influence mechanisms of environmental factors on species diversity and functional diversity across different vegetation types. The results showed that: (1) The Patrick richness index of evergreen broad-leaved forest was significantly higher than that of deciduous broad-leaved forest and evergreen-deciduous broad-leaved mixed forest; the Pielou evenness index was highest in evergreen-deciduous broad-leaved mixed forest, followed by deciduous broad-leaved forest, and lowest in evergreen broad-leaved forest. (2) The functional richness index of evergreen broad-leaved forest was significantly higher than that of evergreen-deciduous broad-leaved mixed forest and deciduous broad-leaved forest; the functional evenness index was highest in evergreen-deciduous broad-leaved mixed forest, followed by deciduous broad-leaved forest, and lowest in evergreen broad-leaved forest. (3) Results from redundancy analysis combined with Monte Carlo random permutation tests indicated that species diversity of deciduous broad-leaved forest was primarily influenced by canopy openness and soil water-soluble calcium; functional diversity was affected by soil water-soluble calcium and rock exposure rate; rock exposure rate and soil thickness were the main limiting factors for both species diversity and functional diversity in evergreen-deciduous broad-leaved mixed forest, in addition, species diversity was also significantly affected by soil available nitrogen; species diversity and functional diversity of evergreen broad-leaved forest were mainly significantly influenced by rock exposure rate, soil water content, and soil thickness. These findings reveal the responses of species diversity and functional diversity of different forest vegetation types to abiotic environmental changes, expand our understanding of species diversity and functional diversity in karst hills, and provide further reference for biodiversity conservation in karst hill regions.

Full Text

Preamble

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Title: Relationship Between Plant Diversity and Environmental Factors of Typical Subtropical Karst Forests in China

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Abstract

To gain deeper insight into the species diversity and functional diversity of forest vegetation in karst hills and their relationships with environmental factors, this study conducted comparative analyses of species diversity and functional diversity across three forest types in Guilin's karst hills: deciduous broad-leaved forest, mixed evergreen and deciduous broad-leaved forest, and evergreen broad-leaved forest. Using community surveys, functional trait measurements, and environmental factor assessments combined with statistical methods including one-way analysis of variance, multiple comparisons, and redundancy analysis, we investigated the mechanisms through which environmental factors influence species and functional diversity in different vegetation types. The results revealed: (1) The Patrick richness index was significantly higher in evergreen broad-leaved forest than in both deciduous broad-leaved forest and mixed evergreen and deciduous broad-leaved forest, while the Pielou evenness index was highest in mixed evergreen and deciduous broad-leaved forest, followed by deciduous broad-leaved forest, and lowest in evergreen broad-leaved forest. (2) Functional richness index was significantly higher in evergreen broad-leaved forest compared to the other two forest types; functional evenness index followed the same pattern as species evenness, being highest in mixed evergreen and deciduous broad-leaved forest, intermediate in deciduous broad-leaved forest, and lowest in evergreen broad-leaved forest. (3) Redundancy analysis combined with Monte Carlo permutation tests demonstrated that species diversity in deciduous broad-leaved forest was primarily influenced by canopy openness and soil water-soluble calcium, while functional diversity was affected by soil water-soluble calcium and rock exposure rate. Rock exposure rate and soil thickness were the main limiting factors for both species and functional diversity in mixed evergreen and deciduous broad-leaved forest, with species diversity also significantly affected by soil available nitrogen. In evergreen broad-leaved forest, both species and functional diversity were significantly influenced by rock exposure rate, soil water content, and soil thickness. These findings reveal how species and functional diversity in different forest vegetation types respond to abiotic environmental changes, expand our understanding of biodiversity patterns in karst hills, and provide a scientific basis for biodiversity conservation in these ecosystems.

Keywords: forest community, species diversity, functional diversity, karst hills, environmental factors

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Introduction

As human activities intensify, the impact of biodiversity on ecosystem functioning has become one of the most critical areas of ecological research (Naeem et al., 2008). Species diversity represents a core component of biodiversity research, as changes in species composition and richness can characterize the structural complexity of biological communities and ecosystems, reflecting community structure, organizational levels, developmental stages, stability, and habitat differences—forming the ecological foundation for understanding vegetation organization (马克平等, 1995). The relationship between environmental factors and species diversity has long been a central ecological question (许涵等, 2013; Weigel et al., 2019). For instance, Huang et al. (2016) found that in karst seasonal rainforests, species diversity peaked at mid-elevations due to gradually improving light conditions, but declined at higher elevations where water availability became limiting. Pan et al. (2021b) demonstrated that shrub diversity in karst hills varied with slope aspect, with shady slopes supporting greater diversity than sunny slopes due to differences in light, moisture, and nutrient conditions.

Functional diversity, which quantifies the diversity of species traits and functions, reflects functional differences among plants and their distribution ranges through various trait characteristics. By considering complementarity and redundancy among coexisting species (Sandra et al., 2001), functional diversity better links species functional traits to ecosystem services and processes (Petchey & Gaston, 2006). Research indicates that functional diversity, like species diversity, is closely related to ecosystem functioning (Flynn et al., 2011). Quantifying changes in community functional diversity across habitats can indicate the degree of convergence or divergence in trait distributions, providing crucial insights into how environmental changes shape community trait distributions and functions (赵耀等, 2018). Functional diversity analysis primarily encompasses three components: functional richness, functional evenness, and functional divergence (Mason et al., 2005). Widely used indices include functional richness index (FRic), functional evenness index (FEve), and functional divergence index (FDiv) (韩涛涛等, 2021). Functional richness and evenness are often linked to community assembly processes and ecosystem functioning (Mouchet et al., 2010; Mouillot et al., 2011). Low functional richness or evenness suggests that species cannot survive under certain environmental conditions, resulting in underutilized niche space, reduced community productivity and ecosystem stability, and diminished buffering capacity against environmental fluctuations or disturbances.

Karst hills represent unique terrain formed by the action of precipitation and groundwater on carbonate bedrock (Zhang et al., 2010). Located in southwestern China's karst region, Guilin features typical and intensive karst development, rich biodiversity, and distinctive vegetation types. Deciduous broad-leaved forest represents a major vegetation type in subtropical karst hills with obvious seasonal characteristics. Mixed evergreen and deciduous broad-leaved forest, composed of both evergreen and deciduous species, serves as the dominant ecosystem in Guilin's karst hills and plays an irreplaceable role in restoration and conservation of karst forest ecosystems. Evergreen broad-leaved forest, a zonal forest vegetation type in subtropical humid regions composed of evergreen species, maintains its green appearance year-round and performs important ecological functions in maintaining karst hill environments. While numerous studies have examined species coexistence and biodiversity patterns in karst ecosystems (李瑞等, 2016; 盘远方等, 2021a; 谭卫宁等, 2022), most have focused on single vegetation types or single dimensions of diversity (species or functional) in relation to environmental factors. Comprehensive research integrating both species and functional diversity characteristics across different forest vegetation types and their coupling relationships with environmental factors remains scarce. Based on this background, our study examined deciduous broad-leaved forest, mixed evergreen and deciduous broad-leaved forest, and evergreen broad-leaved forest in Guilin's karst hills. Using variance analysis, multiple comparisons, and redundancy analysis, we explored differences in species and functional diversity among vegetation types and their driving factors, addressing two key questions: (1) How do species diversity and functional diversity vary across different vegetation types? (2) What are the main environmental factors influencing species and functional diversity in each forest type? Our results enrich the theoretical framework for conservation and management of forest vegetation and biodiversity in Guilin's karst hills and provide scientific references for ecological restoration of degraded karst vegetation.

1.1 Study Area Overview

The study area is located in Guilin City, Guangxi Zhuang Autonomous Region, China, at 110°14 –110°42 E, 24°43 –25°20 N. Guilin's karst hills feature typical karst landforms with complex and variable topography, low environmental capacity, high rock exposure, slow soil formation, shallow soil layers, poor water retention capacity, and high habitat heterogeneity. The climate is classified as mid-subtropical humid monsoon, with abundant rainfall and mild temperatures. The mean annual temperature is 18–19 °C, with average temperatures of 8 °C in the coldest month (January) and 28 °C in the hottest month (August). The frost-free period extends to 309 days annually. Mean annual precipitation is 1,856.7 mm, unevenly distributed throughout the year with dry conditions in autumn and winter. Mean annual evaporation is 1,458.4 mm (盘远方等, 2023). Dominant tree species include *Quercus glauca*, *Celtis sinensis*, *Zelkova schneideriana*, *Boniodendron minus*, *Choerospondias axillaris*, and *Mallotus philippensis*. Common shrubs include *Alchornea trewioides*, *Murraya exotica*, *Mallotus repandus*, and *Sageretia thea*. Herbaceous species include *Arachniodes aristata*, *Teucrium pernyi*, and *Ophiopogon bodinieri*.

1.2 Sample Plot Setup and Community Survey

From 2019 to 2021, we established one 1 hm^2 sample plot in karst hills at each of three locations: Maocun in Lingchuan County, Longcun in Yongfu County, and Beitou Village in Yangshuo County, Guilin. Each plot was divided into 25 basic quadrats of 20 m × 20 m for community surveys. Sample quadrat sizes were 20 m × 20 m for the tree layer, 5 m × 5 m for the shrub layer, and 1 m × 1 m for the herb layer. Shrub and herb quadrats were positioned at the four corners and center of each tree quadrat. During surveys, all woody plants with diameter at breast height (DBH) or basal diameter $\geq$ 1 cm were measured, recording species name, relative coordinates, height, DBH/basal diameter, and crown width. For herbaceous plants, we recorded species name, individual count, average height, and coverage.

1.3 Environmental Factor Measurements

Using each 20 m × 20 m quadrat as a sampling unit, we collected soil samples from 0–20 cm depth using a five-point sampling method after removing surface litter. Samples were air-dried for nutrient analysis. Soil available nitrogen (AN, $mg \cdot kg^{-1}$) was measured using the alkali diffusion method. Soil water-soluble calcium (Ca, $mg \cdot kg^{-1}$) was determined by the strontium chloride-flame spectrophotometry method. Soil water content was measured using the oven-drying method with ring knife samples. Soil thickness was measured using a steel rod insertion method, recording the length of rod penetrating the soil. Elevation was measured using a Touch 35 dual-satellite navigator. Soil sampling and measurements of thickness and elevation were conducted at the four corners and center of each quadrat, with data averaged across these points. Slope was calculated from elevation data (盘远方等, 2023). Rock exposure rate was calculated as the ratio of bedrock area to total quadrat area (林红玲等, 2021). Canopy openness was measured using hemispherical photography: a Canon EOS 5D camera with a 180° fisheye lens was positioned 1.3 m above ground at each quadrat center to capture upward-facing canopy images, which were analyzed using Gap Light Analyzer (GLA) software to obtain canopy openness data. Environmental characteristics of different forest vegetation types are summarized in Table 1 .

1.4 Plant Functional Trait Sampling and Measurement

For all woody individuals with DBH/basal diameter $\geq$ 1 cm, we collected three sun-exposed, intact, mature leaves from the canopy top and three non-current-year branches approximately 10 cm long and 1 cm in diameter. Samples were sealed in plastic bags and transported to the laboratory. Functional trait measurements followed standardized protocols (Pérez-Harguindeguy et al., 2013). Chlorophyll content (SPAD) was measured using a SPAD-502 chlorophyll meter (SPAD-502 Plus, Konica Minolta, Japan). Leaf thickness was measured using electronic calipers (SF 2000, Guilin, China) with 0.01 mm precision, taking measurements at the leaf tip, middle, and base (avoiding the main vein) and averaging the three values. Leaf dry matter content (LDMC) was determined by weighing fresh leaves on an electronic balance (BSM-220.4, Zhuojing, China) with 0.0001 g precision, then oven-drying at 80 °C to constant weight and reweighing; LDMC was calculated as the ratio of dry weight to fresh weight. Wood density was estimated using branch density: after removing bark, branch volume was measured by water displacement, then samples were oven-dried at 80 °C to constant weight and weighed; wood density was calculated as the ratio of dry weight to volume ($g \cdot cm^{-3}$).

1.5.1 Important Value Calculation

Important values for tree and shrub layers were calculated as follows (林红玲等, 2021):

Tree important value = (relative abundance + relative dominance + relative frequency) / 3

Shrub important value = (relative abundance + relative frequency) / 2

1.5.2 Species Diversity

Species diversity was assessed using the Patrick richness index and Pielou evenness index (张金屯等, 2004):

(1) Patrick richness index: Patrick = S

(2) Pielou evenness index: Pielou = -Σ(P lnP) / lnS

where S is the number of species in each quadrat and P is the proportion of individuals of species i in the community (i = 1, 2, 3, …).

1.5.3 Functional Diversity

Functional diversity indices were calculated based on four traits—leaf dry matter content, chlorophyll content, leaf thickness, and wood density—weighted by species abundance. Indices included functional richness (FRic) and functional evenness (FEve), calculated as follows (Petchey & Gaston, 2002):

(1) Functional richness index (FRic):

FRic = ΣSFc

where SFc represents the niche space occupied by species i in the community, and Rc represents the range of trait |c|.

(2) Functional evenness index (FEve):

PEW = Σdist(i,j) × (w + w) / (S - 1)

EW = PEW / ΣPEW

FEve = Σmin(EW) / (S - 1)

where S is the number of species in the community, EW is the evenness weight, dist(i,j) is the Euclidean distance between species i and j, w is the relative abundance of species i, i represents branch length, and PEW is the weighted evenness of species i.

1.5.3 Statistical Analysis

We used one-way analysis of variance (ANOVA) and Tukey HSD tests to analyze differences in species diversity and functional diversity indices among forest vegetation types. Redundancy analysis (RDA) was employed to examine relationships between diversity metrics and environmental factors. The significance of each explanatory variable was determined through RDA ordination and Monte Carlo permutation tests. All statistical analyses and figures were generated using R version 4.0.5.

2.1 Community Species Composition

A total of 151 plant species belonging to 47 families and 105 genera were recorded across the three forest vegetation types in Guilin's karst hills. Deciduous broad-leaved forest contained 63 species (41.72% of total) from 33 families (70.21%) and 58 genera (55.24%). Dominant tree species included *Celtis sinensis*, *Mallotus repandus*, *Choerospondias axillaris*, and *Chimonanthus nitens*. Dominant shrubs were *Alchornea trewioides*, *Murraya exotica*, and *Mallotus repandus*, while major lianas were *Phanera championii* and *Pterolobium punctatum*.

Mixed evergreen and deciduous broad-leaved forest comprised 91 species (60.26%) from 38 families (80.85%) and 67 genera (63.81%). Dominant trees included *Quercus glauca*, *Zelkova schneideriana*, and *Boniodendron minus*. Dominant shrubs were *Alchornea trewioides*, *Callicarpa bodinieri*, and *Mallotus philippensis*, with *Phanera championii* as the main liana.

Evergreen broad-leaved forest contained 84 species (55.63%) from 35 families (74.47%) and 66 genera (62.86%). Dominant tree species were *Quercus glauca*, *Mallotus philippensis*, *Pittosporum planilobum*, and *Decaspermum parviflorum*. Dominant shrubs included *Mallotus philippensis*, *Alchornea trewioides*, and *Pittosporum planilobum*, with *Phanera championii* as the primary liana. Main woody plant species are illustrated in Figure 1 [Figure 1: see original paper].

The total number of woody individuals across all quadrats was 11,546, including 5,784 trees, 5,312 shrubs, and 450 lianas. Individual counts varied substantially among forest types: 2,940 in deciduous broad-leaved forest, 1,605 in mixed evergreen and deciduous broad-leaved forest, and 7,001 in evergreen broad-leaved forest.

2.2 Species Diversity and Its Variation

As shown in Figure 2 [Figure 2: see original paper], the Patrick richness index was significantly higher in evergreen broad-leaved forest compared to both deciduous broad-leaved forest and mixed evergreen and deciduous broad-leaved forest ($P < 0.05$), with no significant difference between the latter two (Figure 2A). The Pielou evenness index differed significantly among all three forest types, following the pattern: mixed evergreen and deciduous broad-leaved forest > deciduous broad-leaved forest > evergreen broad-leaved forest (Figure 2B).

2.3 Functional Diversity and Its Variation

Figure 3 [Figure 3: see original paper] reveals that functional richness was significantly higher in evergreen broad-leaved forest than in the other two forest types ($P < 0.05$), with no significant difference between mixed evergreen and deciduous broad-leaved forest and deciduous broad-leaved forest (Figure 3A). Functional evenness was highest in mixed evergreen and deciduous broad-leaved forest, intermediate in deciduous broad-leaved forest, and lowest in evergreen broad-leaved forest (Figure 3B).

2.4 Effects of Environmental Factors on Species and Functional Diversity

RDA ordination combined with results from Table 2 showed that in deciduous broad-leaved forest, canopy openness and soil water-soluble calcium were the primary factors influencing species diversity, explaining 76.24% of variation (Figure 4A). Rock exposure rate and soil water-soluble calcium significantly affected functional diversity, explaining 48.22% of variation (Figure 4D). In mixed evergreen and deciduous broad-leaved forest, rock exposure rate, soil available nitrogen, and soil thickness influenced species diversity, while functional diversity was primarily affected by rock exposure rate and soil thickness, with explanatory rates of 30.71% and 24.10%, respectively (Figure 4B, E). In evergreen broad-leaved forest, rock exposure rate, soil water content, and soil thickness were the main factors affecting both species and functional diversity, explaining 46.09% and 49.90% of variation, respectively (Figure 4C, F).

3.1 Patterns of Species Diversity Across Forest Vegetation Types

Species diversity reflects species richness and evenness within a given spatial extent, closely related to species number and individual distribution while being influenced by microtopography, nutrient content, and distribution uniformity within communities (马志波等, 2016; 赵娜等, 2018; 林丽等, 2021). Karst hills feature fragmented terrain, severe rocky desertification, high rock exposure rates, shallow soil layers, and heterogeneous water and nutrient distribution. Our results showed that evergreen broad-leaved forest had significantly higher Patrick richness index than the other two forest types ($P < 0.05$). Field observations revealed that compared to the other forests, evergreen broad-leaved forest had relatively thicker soil layers, higher soil water content, lowest rock exposure rate, gentler slopes, and more uniformly distributed nutrients (Appendix A). These superior habitat conditions provided more abundant resources, allowing more species to coexist and resulting in the highest Patrick richness index.

Species evenness reflects the distribution pattern of individual numbers among species and is influenced only by the uniformity of individual distribution, not by total species number (刘俊等, 2007). Our study found that Pielou evenness index was highest in mixed evergreen and deciduous broad-leaved forest, intermediate in deciduous broad-leaved forest, and lowest in evergreen broad-leaved forest (Figure 2B). Although mixed evergreen and deciduous broad-leaved forest had the richest species composition (91 species), it also had the highest rock exposure rate, thinnest soil layer, and most complex microtopography with numerous small habitats such as fissures, rock pits, and gullies distributed unevenly. This created discontinuous soil cover that hindered plant growth and development, resulting in the lowest total number of individuals (1,607) across the 1 ha plot (25 quadrats of 20 m $\times$ 20 m). However, analysis of the 25 quadrats revealed relatively uniform distribution of individual numbers among quadrats. Despite other forests having superior habitat resources and higher total individual numbers, quadrat-to-quadrat variation was substantial; for example, in evergreen broad-leaved forest, some quadrats contained 538 individuals while others had only 184. Since the Pielou evenness index measures uniformity of species individual numbers among quadrats rather than total community abundance, the high variation among quadrats in other forests resulted in mixed evergreen and deciduous broad-leaved forest having the highest evenness index.

3.2 Patterns of Functional Diversity Across Vegetation Types

Functional diversity emphasizes differences in species functional traits, determined by trait values, ranges, and distribution patterns (薛倩妮等, 2015). Functional richness reflects the functional space occupied by species traits, indicating the range of environmental resource utilization and community productivity (刘旻霞等, 2022). We found that functional richness was highest in evergreen broad-leaved forest, intermediate in deciduous broad-leaved forest, and lowest in mixed evergreen and deciduous broad-leaved forest (Figure 3A), showing consistent patterns with the Patrick richness index across the three forest types. This indicates that functional richness increases with species richness. Research has shown that species diversity promotes structural diversity, which in turn facilitates multi-species coexistence (Clark, 2010; Ali et al., 2016). Communities with high species diversity generally exhibit greater trait variation and lower niche overlap, expanding the range of functional space occupied by species. Therefore, the rich species composition in evergreen broad-leaved forest (i.e., highest Patrick richness index) enabled more effective utilization of niche space within the plot.

Functional evenness measures the uniformity of trait mean distribution within occupied trait space (盘远方等, 2021a). Our results showed that functional evenness in mixed evergreen and deciduous broad-leaved forest and deciduous broad-leaved forest was significantly higher than in evergreen broad-leaved forest (Figure 3B), consistent with patterns in Pielou evenness index. This suggests that functional traits in mixed evergreen and deciduous broad-leaved forest were evenly distributed within occupied trait space, enabling efficient resource utilization and reducing vulnerability to invasive species.

3.3 Coupling Relationships Among Species Diversity, Functional Diversity, and Environmental Factors

Our study revealed subtle differences in how environmental factors influence species and functional diversity across forest types, with explanatory power closely related to forest type and microhabitat conditions. In deciduous broad-leaved forest, canopy openness and soil water-soluble calcium were the dominant factors affecting species diversity (Table 2). Light is a crucial ecological factor influencing plant growth, survival, and distribution. Wang et al. (2019) found that heterogeneous light environments created by different canopy structures directly affected understory plant diversity. Our study showed that deciduous broad-leaved forest had the lowest canopy openness among the three forest types, resulting in weak light intensity that hindered survival of shade-intolerant species and individuals, thereby reducing both Patrick richness and Pielou evenness indices—consistent with findings by Huang et al. (2020). Soil water-soluble calcium was significantly negatively correlated with species diversity (Table 2), likely due to the unique habitat formation in karst hills. Limestone and dolomite bedrock, primarily composed of calcium carbonate, undergo long-term dissolution by groundwater, leading to high soil calcium carbonate content that significantly affects understory species diversity. According to limiting factor theory, when ecological factors fall below minimum requirements or exceed maximum tolerance limits for normal plant growth, they constrain growth, reproduction, and development. Evidently, excessive soil calcium carbonate content limited plant growth in deciduous broad-leaved forest, negatively constraining species diversity.

Redundancy analysis indicated that environmental factors affecting species diversity in mixed evergreen and deciduous broad-leaved forest and evergreen broad-leaved forest were similar, including rock exposure rate and soil thickness. Additionally, available nitrogen influenced mixed forest, while soil water content affected evergreen forest (Table 2). Mixed evergreen and deciduous broad-leaved forest had the thinnest soil layer and highest rock exposure rate (Table 1). This dual rock-soil structure reduced Patrick richness index. Furthermore, available nitrogen was significantly negatively correlated with species diversity, similar to findings by Cao et al. (2018). Increased available nitrogen content favors nitrophilic species, limiting distribution of nitrophobic species and reducing Patrick richness index. However, field surveys revealed rich microhabitats with high heterogeneity in mixed forest. Statistical analysis showed small differences in individual numbers among quadrats, leading to increased Pielou evenness index. In contrast, evergreen broad-leaved forest had the thickest, most continuous soil layer, lowest rock exposure, and relatively abundant, uniformly distributed nutrients, resulting in the highest Patrick richness index. The community was dominated by evergreen species adapted to shady, moist habitats, leading to positive correlations between soil moisture and species diversity indices.

Functional diversity in all three forest types was significantly negatively correlated with rock exposure rate (Table 2). Rock exposure rates differed markedly among forest types (Appendix A), with varying bedrock areas among quadrats creating aggregation effects on soil thickness, moisture, and nutrients. This influenced the uneven distribution of individuals and traits, driving patterns in FEve functional evenness index. High rock exposure rates also limited plant growth and development, reducing species numbers and constraining functional trait values and ranges, thereby decreasing FRic functional richness index in deciduous broad-leaved forest and mixed evergreen and deciduous broad-leaved forest. Soil water-soluble calcium was significantly negatively correlated with functional diversity in deciduous broad-leaved forest (Table 2). In high-calcium karst habitats, environmental filtering may facilitate coexistence of species with convergent functional traits, reducing both FRic functional richness and FEve functional evenness indices. Soil thickness was significantly positively correlated with functional diversity in mixed evergreen and deciduous broad-leaved forest and evergreen broad-leaved forest (Table 2). Mixed evergreen and deciduous broad-leaved forest had the highest rock exposure rate, thinnest and most discontinuous soil layer, and poorest habitat conditions. Under limited resources, strong environmental filtering caused trait convergence, resulting in the lowest FRic functional richness index. Evergreen broad-leaved forest had the thickest soil layer, highest soil moisture, and relatively uniform nutrient distribution, supporting higher plant diversity and more complete utilization of ecological space and limited resources. The 叠加 of species traits led to increased overall community functional traits, making FRic functional richness and FEve functional evenness indices closely related to soil thickness and water content.

3.4 Conclusion

This study revealed patterns of species diversity and functional diversity across different forest vegetation types in karst hills and identified key factors influencing these diversity metrics. Our findings provide empirical evidence for the relationship between species and functional diversity, elucidating environmental impacts on forest community diversity and offering important theoretical guidance for forest management. Guilin's karst hills face harsh habitat conditions that make plant growth and reproduction extremely difficult. Severe anthropogenic disturbance further hinders forest community development, necessitating effective protection and restoration measures. Due to the fragile ecology and weak disturbance resistance of karst environments, vegetation recovery is challenging once destroyed. Therefore, implementing forest closure for natural regeneration, strengthening protection of existing vegetation, reducing human disturbance, and combining natural recovery with artificial restoration and appropriate tending measures are essential strategies for conserving and restoring vegetation in karst hill regions.

Appendix: Variation in Environmental Factors Across Forest Vegetation Types

Environmental factors varied significantly among the three forest vegetation types in karst hills. Soil water content showed significant differences, following the pattern: evergreen broad-leaved forest > mixed evergreen and deciduous broad-leaved forest > deciduous broad-leaved forest (Figure S1A). Soil available nitrogen and rock exposure rate showed consistent patterns, being significantly lower in evergreen broad-leaved forest than in the other two forest types (Figure S1B, D). Soil water-soluble calcium was highest in mixed evergreen and deciduous broad-leaved forest but did not differ significantly from the other types (Figure S1C). Canopy openness was lowest in deciduous broad-leaved forest, with no significant difference between mixed evergreen and deciduous broad-leaved forest and evergreen broad-leaved forest (Figure S1E). Soil thickness was highest in evergreen broad-leaved forest, intermediate in deciduous broad-leaved forest, and lowest in mixed evergreen and deciduous broad-leaved forest (Figure S1F).

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