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Beta Diversity Patterns and Determinants among Vertical Layers of Tropical Seasonal Rainforest in Karst Peak-Cluster Depressions

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Abstract: Karst peak-cluster depressions in tropical China are characterized by high habitat heterogeneity, supporting complex seasonal rainforest communities, and harboring a rich abundance of endemic and endangered plants. However, for these rainforests, species and phylogenetic beta diversity and their limiting factors are poorly understood. In this study, the relationships between the beta diversity of three vertical layers (herb, shrub, and tree), environmental factors, and physical distance in China's tropical karst seasonal rainforest were studied. The results showed that each layer exhibited high species and beta diversity, with species turnover being the dominant contributing factor. Environmental filtering and dispersal limitations were significant drivers of community assembly. Environmental filtering exerted a strong influence, with slope position, soil availability of phosphorus and potassium, pH, and organic matter being the key factors. These findings elucidate seasonal rainforest species and beta diversity spatial patterns within karst peak-cluster depressions, providing a foundation for developing karst ecosystem forest management and vegetation restoration measures.

Keywords: karst seasonal rainforest; beta diversity; species turnover; richness difference; community assembly

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1. Introduction

Understanding the mechanisms that underlie the formation, maintenance, and loss of biodiversity is central to community ecology, as they play a crucial role in promoting sustainable development and effective conservation of biodiversity [1,2]. Beta diversity, which reflects variation in species composition among communities along spatial, temporal, or environmental gradients, is an important aspect of biodiversity [3]. Species beta diversity, specifically, captures differences in community composition over larger distances and species turnover across small-scale environmental gradients [4]. Phylogenetic beta diversity, however, involves measuring evolutionary relationships among species and how they change along environmental gradients, thus influencing community assembly [5,6]. Loss of beta diversity can lead to biological homogenization and a decline in ecosystem functioning [7]. Therefore, there has been increasing interest in the analysis of community assembly processes that drive patterns of beta diversity [8,9].

Beta diversity, which comprises measurements of variation in species composition among communities, can be divided into two processes: species turnover (or replacement) and richness differences (or nestedness) [10]. These processes differ and influence the spatiotemporal distributions of species, resulting in complex patterns of community similarity [11]. However, previous studies have often paid little attention to the different processes contributing to species-level differences between communities [12]. Understanding the mechanisms driving these patterns depends crucially on differentiating the underlying processes that contribute to beta diversity [13].

Species turnover, reflecting the replacement of species between different locations, is influenced by mechanisms including habitat filtering, competition, and geographic isolation [14]. For instance, natural selection along an environmental gradient can lead to different species occurring in habitats that are suitable for their survival [14], whereas geographic isolation caused by mountain uplift can result in population isolation and the formation of allopatric species [15]. In contrast, differences in richness reflect variation in species composition between communities and can be caused by species loss or gain along an environmental gradient or across the entire study area. The mechanisms influencing such differences include the diversity of available ecological niches and ecological processes leading to nestedness [16,17]. To gain a comprehensive understanding of the processes driving beta diversity and to implement effective biodiversity conservation strategies, assessing the relative contributions of species turnover and richness differences to the overall patterns of beta diversity is important.

Traditionally, beta diversity quantifies community diversity based on species classification, abundance, and differences in species composition between ecological communities [18,19]. However, a limitation of this approach is that communities may contain species with redundant evolutionary relationships, and changes in species composition often overlook species-level phylogenetic relationships [20]. Phylogenetic beta diversity provides a complementary perspective by addressing differences in evolutionary relationships between communities and highlighting the impact of historical processes on community assembly [21]. Therefore, to accurately capture the ecological processes and mechanisms underlying beta diversity, understanding it from both taxonomic and phylogenetic perspectives is essential [20].

When considering the ecological processes influencing beta diversity, there are two main perspectives. Some researchers argue that stochastic processes such as random speciation, dispersal, and extinction are sufficient to explain beta diversity patterns [22,23], whereas others contend that differences in species' ecological niches play crucial roles in shaping beta diversity patterns, with deterministic processes such as habitat filtering and competitive exclusion being important factors in aggregating species diversity into deterministic states [24]. Community assembly is thus driven by both deterministic and stochastic processes, although quantifying the relative importance of each type of process is challenging owing to potential variation with spatial scale and to the quality and quantity of environmental data available [25]. To a certain extent, understanding the spatial patterns of beta diversity in relation to geographic distance and environmental differences can provide insights into the relative importance of deterministic and stochastic processes, currently a hot topic in ecology [26]. Karst regions, comprising approximately 15% of the world's total land area [27], have received limited attention in terms of vegetation science compared to other ecosystems [28]. Northern tropical karst seasonal rainforest is a notable forest vegetation type found in the karst regions along the northern boundary of the tropics [29]. This forest type possesses distinctive features, such as a diverse community structure, rich tree species composition, and a prominent presence of endemic elements, primarily because of its geochemical background characterized by high levels of calcium and alkalinity, its diverse habitat types, and the influence of the monsoon climate [25]. Previous research has identified an aggregated distribution pattern among numerous tree species in karst regions; this may be attributed to limited dispersal distances or a narrow ecological niche [30]. Furthermore, the composition of plant species within communities varies across different habitats, and most karst tree species exhibit a stronger association with a particular habitat [31]. The interaction between species and the environment drives substantial shifts in species assemblages among diverse habitats, consequently influencing alterations in beta diversity. By assessing plant species composition and distribution in biodiversity hotspots influenced by environmental gradients, we can considerably advance our understanding of the local plant community and the effects of environmental factors on these communities [32]. Nevertheless, the mechanisms driving the formation of karst forest communities, which are undergoing notable microhabitat changes, are poorly understood.

In this study, for the seasonal rainforests in karst peak-cluster depressions in southwestern China, we analyze the spatial patterns of species and phylogenetic beta diversity, and their determinants, among vertical layers (herb, shrub, and tree). We aim to address the following questions: (1) Is the formation of the patterns of beta diversity in these layers driven primarily by turnover or richness differences? (2) Considering both species and phylogenetic diversity, what is the relative importance of environmental filtering and dispersal limitations in community assembly? This study will contribute to a better understanding of the mechanisms underlying the formation and maintenance of plant diversity patterns and provide insight into the conservation and management of forest in the tropical karst region.

2. Materials and Methods

2.1. Study Area

The study site is located in the Nongang National Nature Reserve, Longzhou County, Guangxi Province, southwestern China (22°13′56″–22°39′09″ N, 106°42′28″–107°04′54″ E) (Figure 1). The forest in this reserve has remained almost undisturbed by humans for over a century and thus preserves the most pristine karst seasonal rainforest in China and even globally [25]. The terrain consists of typical karst peak-cluster depressions, composed of clustered mountain peaks and funnel-shaped landscapes with a common base (Figure 1). The elevation ranges from 150 to 600 m. The climate is tropical monsoon, with abundant but unevenly distributed rainfall. The rainy season occurs from March to August, whereas the dry season lasts from September to February. The average annual temperature is approximately 22 °C, with the temperature of the coldest month (January) exceeding 13 °C and that of the hottest month (July) exceeding 28 °C. Annual precipitation ranges from 1200 to 1500 mm. The main soil type is limestone soil, characterized by high alkalinity, thin soil layers, and discontinuous soil cover, making it susceptible to erosion and flushing by precipitation. The area is rich in plant resources, with common tree species including *Radermachera sinica*, *Camellia petelotii*, *Cephalomappa sinensis*, *Garcinia paucinervis*, and *Deutzianthus tonkinensis*.

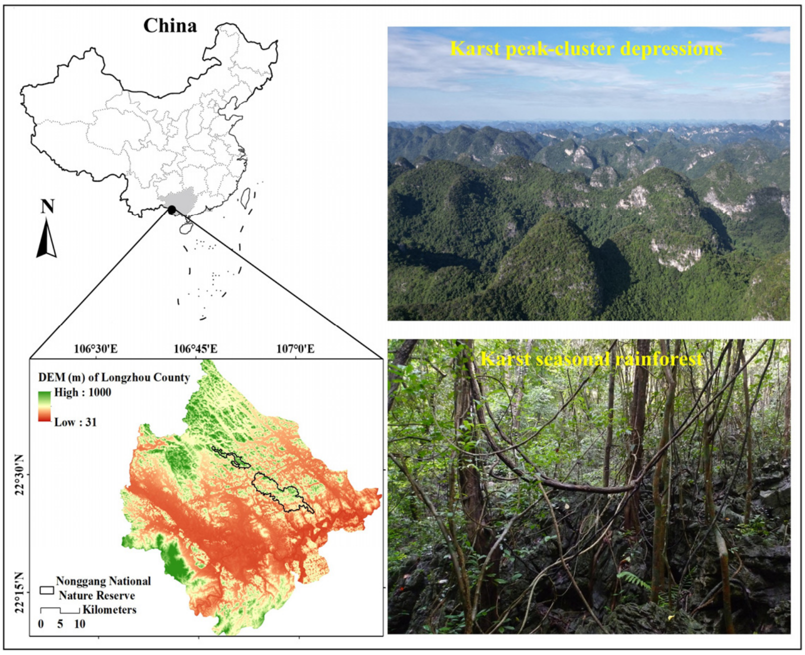

Figure 1. Location of the study area and the landscape of karst peak-cluster depressions in tropical China.

2.2. Plot Survey

Among the typical landform units of peak-clustered depressions in the study area, we selected four slope positions (depression, lower slope, middle slope, and upper slope) based on variation in relative elevation. We established plots in these four slope positions to conduct community-based surveys and sampling focused on the herb, shrub, and tree layers. First, we established 10 plots each measuring 20 m × 20 m in the tree layer at each slope position, with a minimum spacing of 30 m between plots. In total, we established 40 plots on four hills, recording the species present, diameter at breast height (DBH), height (h), and crown width of trees (at $h \geq 3$ m). Within each plot, two random subplots each measuring 5 m × 5 m were designated for the shrub layer survey, and we recorded the species present, average height, canopy coverage, individual count, and average shrub DBH ($1 \text{ m} \leq h < 3 \text{ m}$). Each plot was further subdivided into four 10 m × 10 m quadrats. Within each quadrat, one 1 m × 1 m subplot was established for the herb layer survey, and we recorded species present, individual count, average height, and canopy coverage of herb plants and woody plant seedlings ($h < 1$ m). Simultaneously, additional measurements were taken for each plot, including latitude and longitude, slope aspect, slope degree (SD), and rock outcrop rate (ROR). Geographic coordinates and slope aspect (SA) were determined using a handheld GPS device (Garmin GPSMAP 60CSx). SD and ROR were estimated visually by the consensus of three trained observers who often participated in plot-based data collection work in karst aeras. Basic information on environmental factors and species richness is shown in Table S1.

2.3. Environmental Factor Measurements

In each 20 m × 20 m plot, five soil samples from 0–20 cm depth were collected using the five-point method [33]. After mixing the samples, they were transported back to the laboratory for analysis of soil chemical indicators. The measured indicators included soil pH, soil organic matter (SOM), exchangeable magnesium (EMg), available phosphorus (AP), available potassium (AK), and ammonium nitrogen (NH_4^+-N). Soil pH was determined using the potentiometric method, SOM content using the potassium dichromate external heating method, AP content using the molybdenum antimony anti-coloration method, AK content via sodium hydroxide fusion flame photometry, and EMg via atomic absorption spectrophotometry. The soil water content (SWC) of the topsoil in each plot was determined using a soil moisture meter (WET-2, Delta-T Devices Ltd., Cambridge, UK).

2.4. Data Analysis

To examine the differences in species composition and the environmental factors influencing them among different slopes, we conducted analyses using the species composition similarity index and non-metric multi-dimensional scaling (NMDS). We used Jaccard's similarity index (I) to determine the similarities in species composition between plant communities as follows:

$$I = j/(a + b - j)$$

where j is the number of plant species existing at both slope positions, a is the number of species recorded in one slope position, and b is the number recorded in the second slope position. Classification was as follows: I = 0–0.25, very dissimilar; 0.25–0.5, dissimilar; 0.5–0.75, similar; and 0.75–1.0, very similar [34].

We used NMDS analysis to examine the changes in species composition and their influencing factors in the herb, shrub, and tree layers. We calculated the Bray-Curtis similarity index based on species abundance data and performed NMDS ordination using this index. To assess the correlation between environmental factors and the first two axes of the NMDS ordination, we employed the envfit function and adjusted the p-values using the false discovery rate (FDR) method [32]. The quality of the ordination fit was evaluated based on the stress coefficient. A stress value ≤ 0.2 indicates an acceptable fit, whereas a stress value > 0.2 suggests a relatively poor fit with relatively low explanatory power. In the NMDS ordination plot, sample points are represented by circles, and the closer the points are, the greater the similarity in species composition. The size of the ellipses in the plot represents the similarity in species composition at each slope, with smaller ellipses indicating a higher degree of similarity. Environmental factors were represented by arrows in the plot, where the length of the arrow represents the magnitude of the correlation between the environmental factor and the sample points. The angles between the arrows and the ordination axes or between different arrows indicate the strength of the correlation between the environmental factors or between an environmental factor and an ordination axis. When the angle is obtuse, it indicates a negative correlation [35]. Jaccard's similarity index and NMDS analysis were performed using the "vegan" package [36].

We used the V. PhyloMaker package [37] to construct a complete phylogenetic tree for the vascular plants sampled. Phylogenetic beta diversity was calculated using the branch lengths obtained from this tree. The "BAT" package [38] was used to compute species and phylogenetic beta diversity based on the Jaccard dissimilarity index. Overall beta diversity (β_{total}) was decomposed into species turnover (β_{repl}) and species richness difference (β_{rich}). B_{repl} represents the dissimilarity between communities caused by one-to-one replacement of species in terms of species composition or phylogenetic evolution. B_{rich} reflects the differences between communities caused by differences in species composition or phylogenetic evolution in terms of the absolute difference in the number of unique species among communities, regardless of species composition nestedness [12]. These are calculated as follows:

$$\beta_{total} = \beta_{repl} + \beta_{rich} \tag{1}$$

$$\beta_{total} = \frac{b+c}{a+b+c} \tag{2}$$

$$\beta_{repl} = \frac{2 \times min(b,c)}{a+b+c} \tag{3}$$

$$\beta_{rich} = \frac{|b-c|}{a+b+c} \tag{4}$$

where a represents the number of shared species (for species beta diversity) or branch length based on the common ancestry between the two communities (for phylogenetic beta diversity), and b and c represent the number of species or branch length specific to each community.

The "geosphere" package [39] was used to calculate geographical distances based on latitude and longitude coordinates and to examine the effects of dispersal limitation and environmental filtering on beta diversity. The "vegan" package [36] was used to calculate environmental distances. Initially, Spearman correlation coefficients were computed among the environmental variables to assess collinearity, and variables with $r^2 > 0.6$ were removed. The remaining environmental variables were transformed into a distance matrix; slope position was transformed into Gower distance, and the other environmental variables into Euclidean distance. Mantel and partial Mantel analyses were performed by evaluating the correlation between the distance matrix and beta diversity, aiming to assess the relative importance of the various environmental factors on beta diversity. Subsequently, permutational MANOVA analysis was conducted to identify the key environmental factors influencing beta diversity. Slope position was represented by categorical variables 1, 2, 3, and 4, indicating depression, lower slope, middle slope, and upper slope, respectively [40]. SA was transformed using a formula to convert azimuth angles 0 to 360° into values ranging from 0 to 1 [41].

3. Results

3.1. Community Similarity

The results of species similarity analyses in the three layers were less than 0.5 between slope positions. Concurrently, with an increase in the distance between slope positions, the similarity gradually decreases (Table 1). The NMDS ordination results (Figure 2) show a higher overall similarity in species composition within the same slope, with plots on adjacent slopes exhibiting a greater similarity in species composition than those on non-adjacent slopes. Most environmental factors show significant correlations with the NMDS ordination axes ($p < 0.05$) (Table 2), indicating their strong explanatory power on the species composition of the herb, shrub, and tree layers. SD, SP, SWC, and ROR are important driving forces influencing species composition, and the remaining factors play important roles (Figure 2).

Table 1. Similarity in plant species composition between different slope positions.

Layer	Slope Position	Depression	Lower Slope	Middle Slope	Upper Slope
Herb layer	Depression		56	38	31
	Lower slope	0.306		46	33
	Middle slope	0.217	0.277		37
	Upper slope	0.141	0.152	0.198	
Shrub layer	Depression		26	14	16
	Lower slope	0.313		23	21
	Middle slope	0.169	0.377		18
	Upper slope	0.139	0.216	0.205	
Tree layer	Depression		49	41	28
	Lower slope	0.308		50	39
	Middle slope	0.225	0.318		44
	Upper slope	0.132	0.211	0.226	

The number of common species is shown on the upper side of the diagonal, whereas Jaccard similarity values are on the lower side.

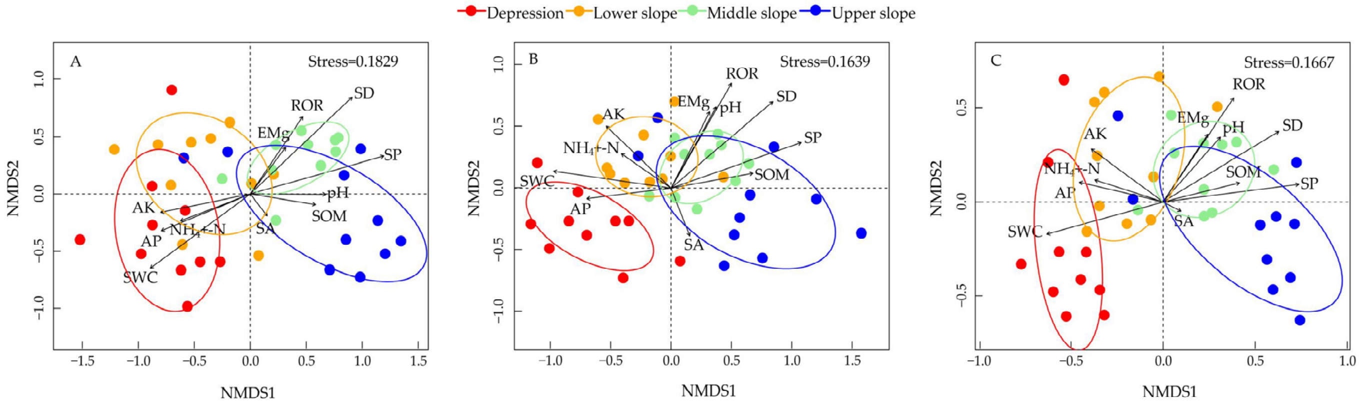

Figure 2. Non-metric multi-dimensional scaling (NMDS) ordination of 40 forest plots and environmental factors in karst peak-cluster depressions. (**A**) Herb layer; (**B**) shrub layer; and (**C**) tree layer. AP, available phosphorus; AK, available potassium; EMg, exchangeable magnesium; NH_4^+-N, ammonium nitrogen; pH, soil pH; SOM, soil organic matter; SWC, soil water content; SA, slope aspect; SD, slope degree; SP, slope position; ROR, rock outcrop rate.

Table 2. Correlation coefficients of non-metric multi-dimensional scaling (NMDS) ordination axes and environmental factors of different layers of tropical seasonal rainforest in karst peak-cluster depressions.

Explanatory Variables	Herb Layer				Shrub Layer				Tree Layer			
	NMDS1	NMDS2	R^2	*p*	NMDS1	NMDS2	R^2	*p*	NMDS1	NMDS2	R^2	*p*
SP	0.963	0.268	0.652	0.005	0.946	0.325	0.652	0.008	0.992	0.125	0.726	0.007
AP	−0.926	−0.377	0.313	0.005	−0.993	−0.121	0.248	0.009	−0.975	0.223	0.287	0.007
AK	−0.981	−0.195	0.283	0.005	−0.729	0.684	0.271	0.009	−0.811	0.585	0.303	0.007
NH_4+-N	−0.936	−0.353	0.189	0.040	−0.828	0.561	0.124	0.106	−0.954	0.300	0.199	0.025
EMg	0.614	0.790	0.114	0.140	0.459	0.888	0.244	0.009	0.560	0.828	0.249	0.007
pH	1.000	−0.006	0.194	0.045	0.494	0.869	0.288	0.009	0.670	0.742	0.284	0.007
SOM	0.988	−0.155	0.149	0.072	0.984	0.176	0.238	0.010	0.972	0.236	0.240	0.007
SWC	−0.808	−0.589	0.519	0.005	−0.990	0.141	0.484	0.008	−0.965	−0.263	0.563	0.007
SA	0.621	−0.784	0.025	0.632	0.372	−0.928	0.087	0.189	0.893	−0.450	0.016	0.741
SD	0.732	0.681	0.658	0.005	0.769	0.639	0.604	0.008	0.858	0.513	0.704	0.007
ROR	0.570	0.822	0.288	0.017	0.507	0.862	0.490	0.008	0.570	0.822	0.597	0.007

p, the significant correlation between the environmental factors and the NMDS axis, and the bold figure indicates that the p value remains significant after FDR correction; R^2 is the regression determination coefficient of multiple regression. AP, available phosphorus; AK, available potassium; EMg, exchangeable magnesium; NH_4^+-N, ammonium nitrogen; pH, soil pH; SOM, soil organic matter; SWC, soil water content; SA, slope aspect; SD, slope degree; SP, slope position; ROR, rock outcrop rate.

3.2. Beta Diversity Patterns

The herb, shrub, and tree layers of the community all exhibited high beta diversity, with mean values of 0.98, 0.96, and 0.94, respectively. These components played a significant role in shaping species diversity (Figure 3A). Comparing the slope positions, mean species beta diversity in the herb layer ranged from 0.94 in the depression to 0.97 on the upper slope; in the shrub layer, from 0.90 in the depression to 0.96 on the upper slope; and in the tree layer, from 0.90 in the depression to 0.92 on the upper slope. Species beta diversity in the different vegetation layers was predominantly driven by the turnover component (Figure 4A).

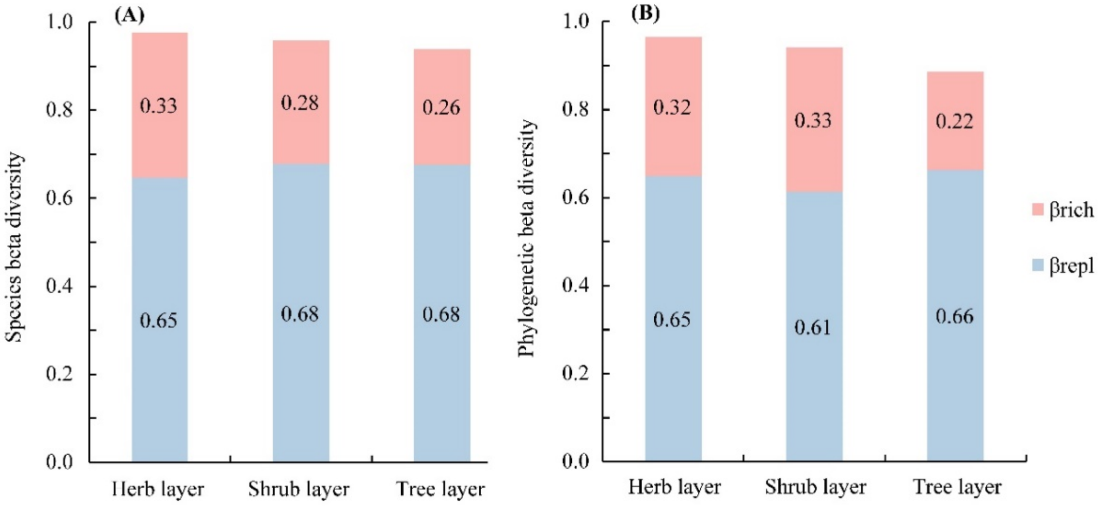

Figure 3. Species (**A**) and phylogenetic (**B**) beta diversity and their two components in the three layers. The data represent the average values of the replacement and richness components. B_{repl} represents the sum of the replacement components; β_{rich} represents the sum of the richness components for species or phylogenetic beta diversity.

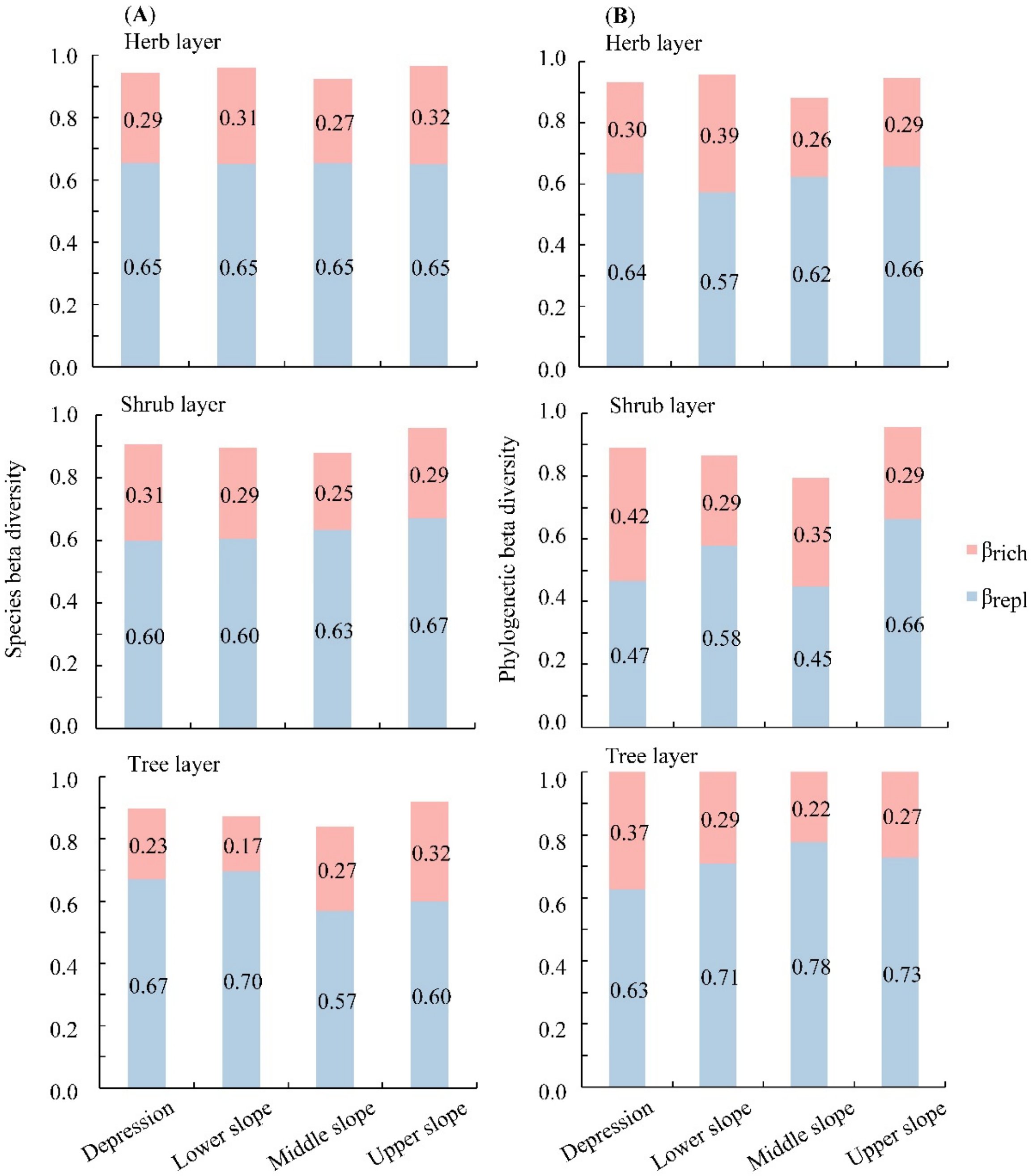

Figure 4. Species (**A**) and phylogenetic (**B**) beta diversity and their two components in the different layers at different slope positions. B_{repl} represents the sum of the replacement components for species or phylogenetic beta diversity; β_{rich} represents the sum of the richness components for species or phylogenetic beta diversity.

The mean phylogenetic beta diversity in the herb, shrub, and tree layers was 0.97, 0.94, and 0.89, respectively. Replacement was the main component contributing to the phylogenetic diversity (Figure 3B). Comparing the slope positions, the mean values of phylogenetic beta diversity in the herb layer ranged from 0.93 in the depression to 0.95 on the upper slope; in the shrub layer, from 0.89 in the depression to 0.96 on the upper slope; and in the tree layer, from 0.86 in the depression to 0.81 on the upper slope. Phylogenetic beta diversity in the three vegetation layers was primarily driven by the turnover component (Figure 4B).

3.3. Factors Influencing Species and Phylogenetic Beta Diversity

Slope position, environmental factors, and geographical distance all significantly affected species and phylogenetic beta diversity in the herb, shrub, and tree layers ($p < 0.05$) (Table 3). Geographical distance exerted relatively little influence on species and phylogenetic beta diversity. Controlling for environmental distance, geographic distance exerted a significant impact in all cases except that of phylogenetic beta diversity in the shrub layer ($p > 0.05$).

Table 3. Results of full and partial Mantel tests of the correlations between phylogenetic beta diversity and its two components, environmental factors, and geographic distance.

	Slope Position	**Environmental Factors**	**Environmental Factors (Geographic Distance)**	**Geographic Distance**	**Geographic Distance (Environmental Factors)**
$H\beta_{total}$	0.431 **	0.361 **	0.341 **	0.192 **	0.148 **
$S\beta_{total}$	0.412 **	0.325 **	0.310 **	0.142 **	0.099 *
$T\beta_{total}$	0.444 **	0.406 **	0.393 **	0.144 *	0.090 *
$HP\beta_{total}$	0.424 **	0.383 **	0.361 **	0.249 **	0.209 **
$SP\beta_{total}$	0.356 **	0.231 **	0.216 **	0.122 *	0.090
$TP\beta_{total}$	0.486 **	0.491 **	0.476 **	0.190 **	0.133 **

* $p < 0.05$; ** $p < 0.01$. Partial Mantel tests are indicated with the control variable in parentheses. $H\beta_{total}$, $S\beta_{total}$, and $T\beta_{total}$: total species beta diversity of the herb, shrub, and tree layers; $HP\beta_{total}$, $SP\beta_{total}$, and $TP\beta_{total}$: total phylogenetic beta diversity of herb, shrub, and tree layers.

We then analyzed the relative importance of the environmental factors on species and phylogenetic beta diversity: soil AP, AK, $NH4^+$-N, pH, SOM, and SD significantly affected species beta diversity in the herb layer ($p < 0.05$). Soil AP, AK, EMg, pH, SOM, and SWC were significantly correlated with species beta diversity in the shrub layer ($p < 0.05$). Similarly, soil AP, AK, EMg, pH, SOM, SWC, SD, and ROR significantly affected species beta diversity in the tree layer ($p < 0.05$). These environmental factors account for 31.76%–34.58% of the variation in species composition across each layer (Table 4).

Table 4. Results of permutational MANOVA of the effects of environmental variables on species beta diversity.

Explanatory Variables	**Herb Layer**		**Shrub Layer**		**Tree Layer**	
	R^2	p (>F)	R^2	p (>F)	R^2	p (>F)
AP	0.044	***	0.046	***	0.050	***
AK	0.034	**	0.034	**	0.033	*
EMg	0.029	ns	0.034	*	0.034	*
NH_4^+-N	0.032	*	0.027	ns	0.029	ns
pH	0.036	**	0.035	**	0.039	**
SOM	0.030	*	0.039	**	0.036	**
SWC	0.029	ns	0.032	*	0.033	*
SA	0.025	ns	0.024	ns	0.027	ns
SD	0.031	*	0.028	ns	0.032	*
ROR	0.027	ns	0.029	ns	0.033	*
Residual	0.682		0.672		0.654	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, not significant. AP, available phosphorus; AK, available potassium; EMg, exchangeable magnesium; NH_4^+-N, ammonium nitrogen; pH, soil pH; SOM, soil organic matter; SWC, soil water content; SA, slope aspect; SD, slope degree; ROR, rock outcrop rate.

The environmental factors exhibited relatively high explanatory power for community phylogenetic diversity. Specifically, soil AP, AK, EMg, $NH4^+$-N, pH, SOM, SD, and ROR significantly influenced phylogenetic beta diversity in the herb layer ($p < 0.05$). Soil AP, AK, pH, SOM, and SWC significantly affected phylogenetic beta diversity in the shrub layer ($p < 0.05$). Soil AP, AK, EMg, $NH4^+$-N, pH, SOM, SWC, SA, SD, and ROR all significantly predicted phylogenetic beta diversity in the tree layer ($p < 0.05$). Overall, the environmental factors explained 33.46%–41.28% of the variation in species phylogenetic relationships within the three layers (Table 5).

Table 5. Results of permutational MANOVA of the effects of environmental variables on phylogenetic beta diversity.

Explanatory Variables	Herb Layer		Shrub Layer		Tree Layer	
	R^2	p (>F)	R^2	p (>F)	R^2	p (>F)
AP	0.048	***	0.041	**	0.066	***
AK	0.031	*	0.036	*	0.034	*
EMg	0.033	*	0.030	ns	0.036	*
NH_4^+-N	0.036	**	0.028	ns	0.035	*
pH	0.041	***	0.044	***	0.049	**
SOM	0.033	*	0.039	*	0.055	***
SWC	0.030	ns	0.039	*	0.040	**
SA	0.026	ns	0.025	ns	0.032	*
SD	0.036	**	0.027	ns	0.032	*
ROR	0.031	*	0.025	ns	0.034	*
Residual	0.656		0.665		0.587	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, not significant. AP, available phosphorus; AK, available potassium; EMg, exchangeable magnesium; NH_4^+-N, ammonium nitrogen; pH, soil pH; SOM, soil organic matter; SWC, soil water content; SA, slope aspect; SD, slope degree; ROR, rock outcrop rate.

4. Discussion

4.1. Patterns of Species and Phylogenetic Beta Diversity in Karst Seasonal Rainforests

This karst seasonal rainforest in southwestern China exhibited a complex community structure and rich species composition, resulting in high species and phylogenetic beta diversity in the herb, shrub, and tree layers. Species replacement was the major component contributing to this diversity, consistent with most findings [20,42,43]. Therefore, the high species beta diversity within each layer is driven primarily by high rates of species replacement. Typically, environmental filtering, competition, and geographic isolation are regarded as potential mechanisms leading to species turnover [14,44]. Alternatively, species replacement is influenced by environmental heterogeneity and variability in species traits [45]. Karst peak-clustered depressions exhibit environmental heterogeneity and geographic spatial gradients, with mountains acting as barriers, rugged terrain, and differences in microhabitats hindering species dispersal and causing most species to disperse only within nearby areas [46,47]. Consequently, there is significant variation in species composition across the different environmental gradients. Furthermore, this rainforest has prominent endemic components, suggesting that many species may have relatively narrow ecological niches and thus explaining the observed small effects of species and environmental characteristics on species richness.

Consistent with other findings [48,49], species beta diversity tended to be higher than phylogenetic beta diversity in our study area. Within the same community, species beta diversity is often higher than phylogenetic beta diversity; at smaller spatial scales, competition and exclusion among closely related species lead to higher species beta diversity between communities in similar habitats, even though phylogenetic beta diversity may be lower [50]. Our current findings are consistent with this trend. Therefore, our findings indicate the presence of redundant species that tend to share similar phylogenetic relationships in this karst seasonal rainforest community. A community that exhibits the replacement of redundant species has lower phylogenetic beta diversity than species beta diversity [20]. Within a community, changes in species composition and within individual plants reflect the environmental adaptability of species with different nutrient strategies. Such changes can alter ecosystem structure and functionality and impact its nutrient cycling processes [6]. Focusing on species dynamics within a community is therefore crucial for understanding the functional and structural aspects of the ecosystem.

4.2. The Relative Importance of Dispersal Limitation and Environmental Filtering

Environmental factors and geographical distance both significantly affected species beta diversity at the three levels, indicating that filtering and dispersal limitations jointly drive tropical karst forest community assembly. The relative importance of these two processes varies across different vegetation types and locations [51]. Environmental filtering refers primarily to the filtering effects of non-biological factors (such as temperature, precipitation, topography, and soil nutrients), whereas under dispersal limitation, community structure and diversity are determined by the dispersal ability of each species [52]. Heterogeneity in resource distribution, owing to topography, plays a major role in the spatial distribution of plants, and the maintenance of plant diversity in tropical karst regions relies on the differentiation of plant ecological niches [29–31]. Consequently, the high habitat heterogeneity observed in karst regions is the primary driver of differences in species composition between communities. Our current findings support this. Environmental filtering plays a more important role in plant community assembly than geographical distance. Although the importance of environmental filtering in community assembly has been widely demonstrated, multiple ecological processes typically participate in constructing a community [53], and their relative importance varies depending on the location and vegetation type. Therefore, examining the species and phylogenetic diversity of different communities is essential.

Microhabitat conditions, such as light and soil properties (including soil depth), and large differences in water and nutrient availability along slopes are drivers of niche partitioning in plant community structure [54]. Here, SD, slope position, SWC, and ROR exert strong driving forces on species composition; species beta diversity also showed a strong correlation with slope position and with soil factors such as AP, AK, pH, and SOM. However, these environmental factors had a stronger driving effect on community phylogenetic diversity, potentially owing to the presence within the community of redundant species (i.e., those with shared phylogenetic relationships). Guo et al. [25] found that elevation, slope, and aspect were the main environmental drivers in the karst seasonal rainforest, consistent with the strong spatial heterogeneity of topographic conditions. The karst region in southern China is characterized by highly heterogeneous soils, with significant local variation in soil type owing to the large variation in the rock substrates from which the soil is formed [25]. In tropical karst peak-cluster depressions, the main soil types are black limestone soil on the upper slope, brown limestone soil on the slopes, and hydrated brown limestone soil in the depressions [55]. Levels of soil C, N, and P, and of other elements, are significantly correlated with elevation, and soil content and depth vary significantly along elevational gradients [31]. Soil serves as the primary source of nutrients for plants, and any change in soil parameters has a significant effect on the growth of plant communities [56]. Studies on mountain forest habitats around the world have also revealed the role of soil structure in species zonation. Soil has a great impact on plant species composition, and variations in primary influential factors may exist across different communities.

The transfer of soil nutrients and water along steep slopes and from upper slopes to depressions enhances the variation in plant community species composition along elevation gradients. Here, species and phylogenetic beta diversity were lower at higher elevations, indicating lower beta diversity in middle-slope plant communities. This phenomenon is attributed to the evident dominance of specific plant species on the middle slopes. These dominant species are the most powerful competitors for limited resources and may competitively exclude others, occupying the habitat and causing the disappearance of other species, thus leading to convergence of species composition in neighboring communities that are near one another in terms of elevation [57] and reducing beta diversity. However, in higher elevations, such as upper slope areas, endemic species richness peaks because of increasingly isolated habitats and smaller surface areas in mountainous ecosystems, which promote speciation, leading to an increase in beta diversity [58]. In other words, the higher beta diversity that we observed at higher elevations could be attributed to increased interspecific competition resulting from the strong habitat heterogeneity [59].

In karst peak-cluster depressions, upslope areas often contain different microhabitats (such as cliffs, rock surfaces, and soil surfaces), resulting in higher habitat heterogeneity. Although depressions exhibit more optimized soil conditions and water availability, they may intensify interspecific competition and thus increase community beta diversity at lower elevations. In conclusion, the karst peak-cluster depressions harbor plant communities with high beta diversity across different environmental gradients. The heightened habitat heterogeneity in this study has led to substantial variation in species composition within sites of the same slope position, consequently contributing to an increase in community beta diversity.

Our findings indicate that topographic and soil properties jointly influence species and the phylogenetic beta diversity of plant communities in the region. However, the explanatory power of these factors for community beta diversity is not particularly high, compared to the findings of Zhu et al. [60], who reported that environmental factors explained 12.4–74% of the variation in beta diversity. Therefore, community species and phylogenetic beta diversity may also be influenced by other factors, such as biotic and disturbance regimes, in karst peak-cluster depressions.

5. Conclusions

This study represents the first analysis of beta diversity and its drivers in the tropical seasonal rainforests in karst peak-cluster depressions in southwestern China. The herb, shrub, and tree communities exhibited high species and phylogenetic beta diversity, with species replacement being the primary driver of beta diversity. Community assembly was jointly driven by environmental filtering and dispersal limitations. Environmental filtering, owing specifically to slope position, soil AP, available potassium, pH, and soil organic matter, was more important than dispersal limitation in shaping community assembly. Based on these findings, effective plant conservation strategies for this forest type would involve improving the environmental conditions of plant communities and enhancing species dispersal between communities. By addressing these factors, conservation efforts may contribute to the preservation and management of the unique ecosystem of the tropical karst seasonal rainforest in southwestern China.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15020365/s1. Table S1: Basic information on environmental factors and species richness on different slopes in karst peak-cluster depressions.

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