Karren Habitat as the Key in Influencing Plant Distribution and Species Diversity in Shilin Geopark, Southwest China

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Abstract: Karst rocky desertification (KRD) is one of the biggest challenges in the karst ecological restoration of Southwest China, and a thorough understanding of the plant community characteristics in various karren habitats provides a basis for mitigating KRD and restoring the degraded ecosystem. To improve our knowledge of the detailed characteristics and impact mechanisms of karren habitats on the species distribution and species diversity patterns of woody and herbaceous plants to benefit sustainable management and planting design for revegetation establishment in the karst region, a field investigation was carried out in the natural restoration vegetation of Shilin Geopark. The results indicated that karren habitats apparently determine the species diversity and composition. At the arbor layer, the habitat with the highest $\alpha$ diversity was solution corridor (SC), and at the shrub layer, grikes (GR) were the karren habitats with the most diverse communities. At the herb layer, solution rock debris (SRD) showed the highest richness of herbaceous species. The karren habitat features and topographic factors significantly influence plant $\alpha$ diversity and distribution. Soil area (SA) and canopy density (CD) were the dominant factors influencing plant diversity at the arbor, shrub and herb layers, soil thickness (ST) was significantly effective at the arbor and herb layers. Karren habitat height (KHH), litter thickness (LT), and slope gradient (SG) were significantly influential at the herb layer. The impacts of the karren habitat width (KHW), slope aspect (SAS), and SG on woody species distribution were significant. Knowledge obtained from this study will be helpful guidance for future sustainable restored vegetation design and management with high biodiversity and regional characteristics in the karst area of Southwest China and other fragile karst ecosystems in the world.

Keywords: karren habitat; species distribution; alpha diversity; Shilin Geopark; karst ecosystems

1. Introduction

The karst landscape, which covers approximately 22 million km$^2$ and 15% of the total terrestrial area, is one of the most crucial natural landscapes in the world [1]. This unique geomorphological environment features contiguous distribution of bare and shallow carbonate rock, which determines the high fragility of the karst ecosystem, especially in the context of climate change [2–4]. Some karst landscapes have gradually degraded into karst rocky desertification (KRD) landscapes...
because of intensive unreasonable human activities and the vulnerable carbonate environment. Vegetation destruction is the primary and direct cause for the occurrence and development of KRD, which led to serious soil erosion, extensive bedrock exposure, drastic decrease in biodiversity, landscape degradation, and the deterioration of ecosystem services in recent decades [5,6]. KRD landscapes have occurred in northern and central Vietnam, the islands of Java, Indonesia, southwest Cambodia, and Southwest China, among which Southwest China is the most acute KRD region [7,8].

Since the late 1990s, China has approved and implemented a series of ecological restoration projects with two major strategies to mitigate the rapid degeneration of the karst landscape and restore ecosystem services in eight Southwest provinces based on the degree of degradation [9–12]. In places of slight or moderate degradation, strategies of conservation area establishment in peri-urban areas were adopted to promote positive natural succession, while in areas where severe degradation was observed, reforestation, including aerial seeding and planting, was adopted to construct plant communities [13]. Following reforestation, the vegetation coverage generally increases significantly [14]. However, due to the lack of knowledge or the only short-term perspective of that time, many reforested areas that have been restored by the latter method were occupied with monocultures of needle-leaved trees or rapid-growing exotic species, such as Eucalyptus sp. from Australia, which exhaust water and nutrients in the soil and inhibit understory growth and succession. These problems resulted in increasing vegetation quantity rather than improving vegetation quality, which means that some rehabilitated forests could not achieve high ecosystem services over the long term [15]. However, endemic plant communities in conservation areas have overcome insufficient water supplies, shallow surface soil layers, and habitat fragmentation, and have developed relatively stable population compositions and community structures; this was partly explained by the fact that plants regrow rapidly in the microhabitats of KRD conservation areas because the diverse microhabitats protect seedlings and sprouts and provide relatively sufficient soil and nutrition for plant growth [16,17].

Microhabitats in the karst region are relatively small-scale habitats whose formation is related to the development and dynamics of karst landforms, which are affected by environmental forces, including anthropogenic activities [18,19]. Zhu et al. [18] categorized the microhabitats into six types based on their formation mechanisms and external morphological characteristics. Yu et al. [16] used “karren habitats” to describe microhabitats based on the geographic features of the Shilin Geopark and divided karren habitats into five types, including grike, deep solution pit, solution corridor, solution rock debris, and solution well. Microhabitats/karren habitats have been discussed in a few studies that primarily focus on the heterogeneity of soil properties, soil microbial diversity, the diversity of woody species, seedlings, and sprouts, and the effects of microclimate regulation in different succession stages [16,20–22]. Relevant studies revealed that karren habitats facilitate the persistence of biodiversity. These habitats are known as “refugia”, which are essential for conservation planning because those may offer many species the only opportunity for in situ survival[23–25].

Shilin Geopark provides a unique karst geography and forest landscape, which represents the karst landscape in Southwest China. KRD occurred in the Shilin Geopark at the end of the 19th century. Since 1931, the severely destroyed zonal natural vegetation has been protected to promote positive natural succession. After decades of protection, the forest was gradually restored, and Shilin Geopark was valued as a UNESCO World Heritage site, which was credited for its ecological, aesthetic, and social values in 2002. The complex community structure, abundant native species, biodiversity, and high karren habitat heterogeneity of the mixed evergreen–deciduous broadleaf forest made Shilin Geopark an ideal site to reveal the plant community characteristics of nature-restored vegetation. Previous studies showed that simulation of the characteristics of native vegetation is an effective sustainable restoration strategy for the degraded vegetation, similar to the restoration of “native forests by native trees” [26,27]. However, few studies have been reported on the detailed characteristics and impact mechanisms of karren habitats on species distribution and species diversity patterns. This partly resulted in the previously mentioned monoculture of the revegetation. Therefore, we identified a nature-restored forest from Shilin Geopark as the research site to analyze the plant composition
and diversity in different karren habitats and explored the main environmental factors that influenced their colonization. Specifically, we expect to answer the following questions: (1) What the plant species composition characteristics are in various karren habitats; (2) how the $\alpha$ diversity of the plant community varies between various karren habitats; (3) how environmental factors affect the plant distribution and $\alpha$ diversity; and (4) what the dominant influencing factors on the $\alpha$ diversity of arbor, shrub, and herb layers are, in an attempt to fill the knowledge gap in the understanding of the vegetation characteristics in the diverse karren habitats and to provide a reference for plant selection and planting strategies in KRD restoration areas to improve the ecological sustainability of karst restoration areas in Southwest China.

2. Methodology

2.1. Study Area and Site Description

This study was performed in the buffer area of the Shilin Geopark (24°38′–24°58′ N, 103°11′–103°29′ E, alt. 1600–2203 m) located in central Yunnan Province, Southwest China (Figure 1a,b). This area has a subtropical monsoon climate that is characterized by two different seasons: A dry season (November to May) with 20% of annual precipitation, and a rainy season (June to October) with 80% of annual precipitation. The mean annual temperature is 16.2 °C, with an average minimum of 8.2 °C and maximum of 20.7 °C [28]. The moderate temperature period, from late spring to early autumn, coincides with the wet season, which favors plant growth. The main landform in Shilin is the hilly plateau with a few towering mountains [29].

Figure 1. Study site and sampling design. (a) China (b) Yunnan Province (c) Shilin Geopark (d) Study site.

The zonal native vegetation of this area is semi-evergreen broad-leaved forests, which are dominated by *Cyclobalanopsis glauoides*, *Neolitsea homilantha*, and *Olea yunnanensis*. Historical agricultural activities outside the Shilin Geopark were fundamentally based on the cultivation of flat areas and moderate slopes. However, intensive forest clearing for fuel, animal grazing, and wood harvesting occurred primarily because of rapid population growth, which eventually turned most karst forests into KRD areas since the 1910s. Only a few primary forests were preserved, with slight disturbance in the Mizhi mountain, because of the protection of the local ethnic villages. The natural restoration forest we selected is located in the Moon Lake village in the northeastern park (Figure 1c), where slopes are 10–30%
and the ratio of soil/rock is approximately 2:3; it has been regenerating for 40 years after the stopping of intense, but short, human disturbance.

The Shilin Geopark is famous for its fabulous stone forest landforms, which cover approximately 400 km² and are underlain by Permian carbonate substrates that are mainly limestone [30]. The karren are small-scale features on the upland surface due to dissolution on the exposed limestone, and karren habitats are karren that contain soil and organisms (e.g., plants, animals, and microbes) [16,31]. Based on the formation mechanism, the size of the karren, and the proportion of soil distributed in, between or on various karren, karren habitats are divided into five typical types, including the grike (GR), deep solution pit (DSP), solution corridor (SC), solution rock debris (SRD), and solution well (SW) [16,32]. The characteristics (e.g., length, width, and area) of the five types of karren habitats in Shilin were different due to their irregular shapes in addition to the size (Table 1, Figure 2). GR is a linear karren formed by structural fractures with a width of 0.1–0.2 m, and most GRs are rectangles. DSP is formed by the increasing dissolution of irregular, small, or round pits, and the straight diameter of DSP is mostly within 1 m. SC is a type of structural fissure between clint or stalagnate, which is a strip or square section with a length of 0.6–10 m. SRD is caused by natural or human activities and is formed due to the accumulation of rocks after the collapse of a clint. Some small gaps between the rocks range from 0.01 to 0.20 m, and the soil is distributed along the gaps. SWs occur on the exposed rock surfaces due to the dissolution of small pits, which are round or nearly round with the diameter greater than 0.3 m.

**Table 1. Karren habitat types [16].**

| Karren Habitat Types         | Formation         | Shape          | Characteristics of Soil and Litter | Surface Soil Thickness/cm | Litter Thickness/cm |
|------------------------------|-------------------|----------------|-----------------------------------|--------------------------|--------------------|
|                              |                   | Length/m       | Width/m                          | Proportion/%             |                    |
| Grike (GR)                   | Structural fractures | 0.20–20.00     | 0.10–0.20                        | 20–60                    | 1.00–52.00         |
| Deep solution pit (DSP)      | Dissolution       | 0.40–5.00      | 0.10–0.30                        | ≥40                      | 9.00–38.50         |
| Solution corridor (SC)       | Structural fractures | 1.35–10.00     | 0.60–10.00                      | ≥70                      | 10.00–65.30        |
| Solution rock debris (SRD)   | Collapse of the clint | 1.15–10.00     | 0.25–10.00                      | ≤15                      | 15.00–46.00        |
| Solution well (SW)           | Dissolution       | 0.65–10.00     | 0.30–2.30                       | ≥40                      | 19.00–64.00        |

The white dotted line outlined the karren.

(b) Top view of the karren habitats

**Figure 2.** Illustration of karren habitat types. (a) Perspective of the karren habitats; (b) Top view of the karren habitats.
2.2. Sampling Design

The field survey was performed during the period of April to May 2019, which has been proved to have the highest species richness [33]. The 1-ha forest plot, which formed a square of 100 × 100 m (24°50′2″–24°49′59″ N, 103°25′37″–103°25′34″ E), was established according to the standards of the Center for Tropical Forest Science [34], and it was divided into 25 quadrats of 20 × 20 m (Figure 1d). We used a Global Positioning System (GPS) device (HOLUX M-241) to locate all the quadrats and marked them with an alpha-numeric label (from 1 to 5 and from A to E). All of the karren habitats in each quadrat were identified according to Table 1, and 197 karren habitats were obtained in total. Then, all of the woody and herbaceous plants in each karren habitat were documented.

2.3. Data Measurements

Data on the individual number, diameter at breast height (DBH) (including all stem stumps), average height, and crown width of each woody species of the arbor and shrub layers were recorded in each karren habitat. Saplings of the arbor (DBH < 3 cm) were recorded in the shrub layer. For the herb layer, data on the average coverage and height of each herbaceous species and woody seedlings (H < 30 cm) were recorded.

For each karren habitat, according to previous theory and practice [16,35], the environmental factors, which may have potential influences, including topographic factors and karren habitat features, were documented. Topographic factors, including slope aspect (SAS) and slope gradient (SG), were measured in each karren habitat. Slope aspect (SAS) was converted into quantitative data, such as 0, 1, 2, 3, 4, 5, 6, 7, and 8 for a flat, northern slope, northeast slope, northwest slope, eastern slope, western slope, southeast slope, southwest slope, and southern slope, respectively [35]. Karren habitat features, including length, width, height, and area of the karren habitats, soil area (SA), soil thickness (ST) (from the surface soil to the rocks) and litter thickness within the karren habitats, and canopy density (CD), were recorded.

Species identification was based on the flora specific to the Yunnan region [36] and Flora Reipublicae Popularis Sinicae website (http://www.iplant.cn/frps).

2.4. Data Analyses

Five statistical analysis methods were used, and these values were computed in Microsoft Office Excel 2016 and R 3.6.1 [37]. The R script we used is provided in the supporting material (Supplementary Materials):

- The α diversity of plants was computed using the Patrick index, the Shannon–Wiener index, and the Pielou index.

  Importance value: \( P_i = \frac{(D_i + C_i + H_i)}{3} \),

  where \( D_i \), \( C_i \), and \( H_i \) indicate the relative density, coverage, and height, respectively, for the \( i \)th species.

  Shannon–Wiener index [38]: \( H = -\sum P_i \ln P_i \)

  Patrick diversity index [39]: \( P = N \)

  Pielou evenness index [40]: \( J = -\sum P_i \ln P_i / \ln N \)

  where \( P_i \) indicates the importance value for the \( i \)th species and \( N \) represents the number of species.

- One-way analysis of variance (ANOVA) was performed to compare plant α diversity between karren habitat types if the data of response variables complied with normal distribution. However, when the data did not show a trend of normal distribution, we performed variation analysis using non-parametric Kruskal–Wallis ANOVA (kruskal test and dunn test in R).

- Canonical correspondence analysis (CCA) was calculated with the R package vegan [41] to analyze the relationship between plant species distribution and environmental factors. A data matrix was constructed consisting of species and environmental variables. To investigate whether specific karren habitat types (KHT) differed in species distribution, these types were pooled into
the environmental variables as factor constraints. Occasional plant species with a frequency below 3% have been checked for whether they belong to the category of conservation species. If not, occasional species were omitted to eliminate the excessive effect. The statistical significance of species–environmental correlations was examined using 1000 distribution-free Monte Carlo permutations [41].

- Pearson correlation between all influencing factors and species α diversity was calculated by using the R package Hmisc [42].
- Stepwise linear regression was performed to further demonstrate the effects of dominant environmental variables on plant α diversity and examine the extent of effects.

3. Results

3.1. Plant Taxonomic Composition in Different Karren Habitats

In total, 118 species belonging to 41 families and 74 genera were recorded in this survey season. The most common karren habitat type was GR, which also recorded the most species (60), followed by DSP, SRD, and SC, with 52 species, 50 species, and 48 species, respectively. Only 11 species were recorded for SW. GR also contained the most woody plants, with 44 species recorded, while the most herbaceous species were found in SRD. The average number of species in each karren habitat type varied. The average number of plant species was greatest in SC (9.28 ± 3.57) and smallest in SW (1.55 ± 0.69) (Table 2). The species found in all karren habitat types were *Pistacia weinmanniifolia*, *Neolitsea homilantha*, and *Cyclobalanopsis glaucoides*, which demonstrated that these plants were the most common species in the karren habitats.

Table 2. Number of plant species in different karren habitat types.

| Karren Habitat Type | No. of Karren Habitat | Total No. of Species/Family Number | Mean No. of Species Number ± SE | No. of Woody Species/Family Number | No. of Herbaceous Species/Family Number |
|---------------------|-----------------------|-----------------------------------|--------------------------------|-----------------------------------|----------------------------------------|
| GR                  | 62                    | 60/28                             | 7 ± 2.69<sup>a</sup>            | 44/22                             | 16/8                                   |
| DSP                 | 54                    | 52/25                             | 6 ± 2.64<sup>c</sup>            | 36/19                             | 16/8                                   |
| SC                  | 39                    | 49/26                             | 9 ± 3.57<sup>b</sup>            | 35/21                             | 13/6                                   |
| SRD                 | 23                    | 50/26                             | 7 ± 2.32<sup>b</sup>            | 28/20                             | 22/11                                  |
| SW                  | 11                    | 11/10                             | 2 ± 0.69<sup>d</sup>            | 9/8                               | 2/2                                    |

Different lowercase letters (a, b, c, d) mean significant discrepancy on the 0.05 level in different karren habitats.

3.2. α Diversity Distribution of Plants in Different Karren Habitats

The α diversity was different between karren habitat types, and the differences were all remarkable for the Shannon–Wiener, Patrick, and Pielou indices. At the arbor layer, SC was the habitat with the highest diversity and evenness, but the diversity indices presented no significant differences among the GR, DSP, SRD, and SW. The karren habitat with the highest diverse and homogeneous communities at the shrub layer was GR, whereas at the herb layer, SRD contained the most herbaceous species and showed the highest diversity and evenness. The diversity indices of the SW were the lowest and least concentrated either in the shrub or herb layer (Figure 3).

All indices among the arbor, shrub, and herb layers in the same type of karren habitat presented significant differences in the GR, DSP, SC, and SRD, except the SW. In all five kinds of karren habitat types, the herb layer presented extremely and significantly higher diversity than the shrub and arbor layers, but it presented no significance in evenness (Figure 3).
homogeneous communities at the shrub layer was GR, whereas at the herb layer, SRD contained the most herbaceous species and showed the highest diversity and evenness. The diversity indices of the SW were the lowest and least concentrated either in the shrub or herb layer (Figure 3).

Figure 3. Variation in species α diversity in different karren habitats and different layers. *p < 0.05, **p < 0.01, ***p < 0.001. The different uppercase letters indicate notable discrepancy on the 0.05 level among karren habitats in the same layer, and different lowercase letters mean notable discrepancy on the 0.05 level among layers in the same karren habitat.

3.3. Effect of Environmental Factors on Woody and Herbaceous Species Distribution

Several environmental variables of topographic factors and karren habitat features have significant correlation with the ordination axes (Table 3). Specific karren habitat types were differentiated in woody plant species distribution. Woody species distribution was significantly negatively correlated with karren habitat width (KHW), karren habitat height (KHH), canopy density (CD), slope gradient (SG), and slope aspect (SAS) (p < 0.05), while being slightly positively correlated with soil thickness (ST) (p = 0.096) (Table 3). On the other hand, the correlations between herbaceous plant species composition and environmental variables showed a different pattern, with a significant negative correlation with canopy density, litter thickness (LD), and slope gradient (p < 0.05), but no relevance to karren habitat type (KHT). While canopy density primarily influenced woody and herbaceous plant species composition, slope gradient had a significant influence on woody plant species distribution (p = 0.001).

For woody and herbaceous plants, the species found in sites with smaller karren habitat width included Clematis fasciculiflora and Myrsine africana. Pistacia chinensis and Schizachyrium delavayi preferred places exposed to sunlight, whereas high canopy density was advantageous for Myrsine semiserrata. Zanthoxylum armatum grew on sunny slopes, and Neolitsea homilantha and Pilea pumila var. hamaii favored shady slopes. The moderate slope gradient was associated with Neolitsea homilantha, while small slope gradient was more associated with Cyclobalanopsis glauoides (Figure 4a,b). For herbaceous plants, Campylandra chinensis favored shady fields.
is significantly correlated with Shannon–Wiener diversity in all of the arbor, shrub, and herb layers. More specifically, *Myrsine africana* and **Myrtus communis** are associated with **GR**, while *Berberis pruinosa* and **Campylandra chinensis** are more preferred places exposed to sunlight, whereas high canopy density was advantageous for **hamaoi** while small slope gradient was more associated with **DSP**, and other species with low values on CCA axes grew in all kinds of karren habitats (Figure 4a, b). For references of karren habitat abbreviations, see Table 1.

### 3.4. Environmental Influence on Plant α Diversity

We determined several potential environmental factors that may greatly impact plant α diversity. In all of the factors, the karren habitat condition, represented by soil area (SA) and soil thickness (ST), is significantly correlated with Shannon–Wiener diversity in all of the arbor, shrub, and herb layers. The Shannon–Wiener diversity of different plant layers increased with the increase in soil area and thickness of the karren habitat, as shown in Figure 3a–f.
We determined several potential environmental factors that may greatly impact plant diversity and evenness, respectively (Table 6). For the topographic features, slope aspect (SAS) had an impact on Shannon–Wiener diversity in the arbor and herb layers, while slope gradient (SG) only contributed to plant diversity in the herb layer (Table 4).

Table 4. Pearson correlation coefficients with Shannon–Wiener diversity and Pielou evenness as dependent variables.

|                          | Arbor Layer | Shrub Layer | Herb Layer |
|--------------------------|-------------|-------------|------------|
|                          | Shannon–Wiener | Pielou | Shannon–Wiener | Pielou | Shannon–Wiener | Pielou |
| Karren habitat features  | SA 0.520 *** | 0.199 | 0.327 *** | 0.147 | 0.197 ** | -0.084 |
|                          | ST 0.848 *** | 0.274 * | 0.199 * | 0.094 | 0.303 *** | 0.021 |
|                          | KHH 0.391 *** | 0.013 | 0.157 | 0.016 | -0.011 | 0.030 |
|                          | LT 0.041 | -0.100 | 0.155 | 0.006 | -0.248 | 0.073 * |
|                          | CD -0.043 | -0.018 | -0.038 | 0.234 * | -0.134 | -0.064 |
| Topographic factors      | SAS -0.212 * | -0.062 | -0.083 | 0.068 | -0.157 * | 0.003 |
|                          | SG -0.124 | -0.063 | 0.025 | -0.034 | -0.151 * | -0.146 |

Two-tailed significance: $p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. SA—soil area, ST—soil thickness, KHH—karren habitat height, LT—litter thickness, CD—canopy density, SAS—slope aspect, SG—slope gradient.

3.5. Dominant Environmental Factors on a Diversity of Plants

As shown in the stepwise regression models of standardized $\alpha$ species diversity associated with environmental factors, karren habitat features had a dominant impact on $\alpha$ species diversity of arbor and shrub layers compared to topographic factors. In the arbor layer, canopy density (CD) was significantly negatively correlated with species diversity. Soil thickness (ST) and soil area (SA) were positively correlated, and soil thickness plays a more important role compared with soil area, with a standardized coefficient as high as 0.784. The influence of soil thickness was significant for species evenness, although the explanations of variation were not high (Table 5). In the shrub layer, soil area and canopy density were also significantly and positively correlated with plant species diversity and evenness, respectively (Table 6).
Table 5. Stepwise regression of the arbor layer species Shannon–Wiener diversity and Pielou evenness with environmental factors.

| Arbor Layer | Shannon–Wiener a | Pielou b |
|-------------|------------------|----------|
| β           | p-Value          | β        | p-Value |
| ST          | 0.784            | 0.000 ***| 0.371   | 0.021 * |
| SA          | 0.149            | 0.005 ** | ——      | ——      |
| CD          | −0.125           | 0.007 ** | ——      | ——      |
| LT          | ——               | ——      | −0.171 | 0.138 |

\( p < 0.1, ^* p < 0.05, ^{**} p < 0.01, ^{***} p < 0.001; \) β—standardized coefficient; ST—soil thickness, LT—litter thickness, CD—canopy density, KHH—karren habitat height, SA—soil area, SAS—slope aspect, SG—slope gradient; \( a R^2 = 0.752, \text{Adjusted } R^2 = 0.741, p = 0.000; \) \( b R^2 = 0.110, \text{Adjusted } R^2 = 0.079, p = 0.034. \)

Table 6. Stepwise regression of shrub layer species Shannon–Wiener diversity and Pielou evenness with environmental factors.

| Shrub Layer | Shannon–Wiener a | Pielou b |
|-------------|------------------|----------|
| β           | p-Value          | β        | p-Value |
| SA          | 0.327            | 0.000 ***| ——      | ——      |
| CD          | ——               | ——      | 0.228   | 0.028 * |

\( p < 0.1, ^* p < 0.05, ^{**} p < 0.01, ^{***} p < 0.001; \) β—standardized coefficient; \( a R^2 = 0.107, \text{Adjusted } R^2 = 0.11, p = 0.000; \) \( b R^2 = 0.055, \text{Adjusted } R^2 = 0.044, p = 0.028. \)

Compared to the woody layer, more variables showed significant connections in the herb layer. Increased karren habitat height (KHH) and canopy density decreased mean herb species diversity, but increasing soil area and soil thickness seemed to improve herb species diversity. Herb species evenness showed a reverse trend in which soil area was negatively associated with species evenness. Differently from the arbor and shrub layers, the topographic factors explained the species evenness of the herb layer, with slope gradient (SG) as a dominant influencing factor (Table 7).

Table 7. Stepwise regression of the herb layer species Shannon–Wiener diversity and Pielou evenness with environmental factors.

| Herb Layer | Shannon–Wiener a | Pielou b |
|------------|------------------|----------|
| β          | p-Value          | β        | p-Value |
| KHH        | −0.160           | 0.045 *  | ——      | ——      |
| SA         | 0.162            | 0.058    | −0.149  | 0.063   |
| ST         | 0.289            | 0.000 ***| ——      | ——      |
| CD         | −0.180           | 0.014 *  | ——      | ——      |
| LT         | ——               | ——      | 0.257   | 0.002 **|
| SG         | ——               | ——      | −0.216  | 0.008 **|

\( p < 0.1, ^* p < 0.05, ^{**} p < 0.01, ^{***} p < 0.001; \) β—standardized coefficient; \( a R^2 = 0.145, \text{Adjusted } R^2 = 0.125, p = 0.000; \) \( b R^2 = 0.088, \text{Adjusted } R^2 = 0.070, p = 0.002. \)

4. Discussion

4.1. Plant Diversity Maintenance Mechanism in Karren Habitats

Complex terrain often leads to heterogeneous habitats where there may be more niches for more species to coexist, and microhabitats are a vital influencing factor of plant species diversity \([43–45]\). Our results demonstrate that karren habitat specialization plays a dominant role in the pattern of species diversity in the karst natural restoration area.
Soil area and soil thickness of karren habitats are positively correlated with the diversity of plants in all arbor, shrub, and herb layers, while the soil thickness mainly determined the arbor and herb species diversity. Specifically, arbor and shrub layers with higher species diversity were observed in karren habitats with a relatively larger area and deeper soil thickness, including solution corridors, grikes, and deep solution pits, while herbaceous layers with higher diversity were observed in a narrow habitat with relatively shallow soil, such as solution rock debris. Solution wells generally only had one layer of arbors, shrubs, or herbs due to the lack of soil.

This distribution pattern is similar to the findings from the research of Yu et al. [17], which was performed in the Suoyi Mountain, south of the Shilin Geopark. The previous study demonstrated that the soil thickness contributed to the diversified species composition and complex structure of the aboveground forest in the karst region [46]. The results of our study further confirmed the correlation of soil thickness, plant diversity, and the presence of karren habitats. The influence mechanism of soil thickness on different vegetation layers could apparently be partly explained by the different root distribution depths for various life forms. Previous studies found a two-layer model of plant root distribution: The roots of the arbors were distributed in deep soil, and the roots of herbaceous plants were distributed in shallow soil [46,47]. The thick soil layers in some karren habitats provide deep-rooted arbors and shrubs with sufficient water and nutrient resources for long-term stability, while the shallow soil in other kinds of karren habitats only supports the root growth of short-lived herbaceous plants.

We found that the species diversity of the herb layer was greater than that of the arbor and shrub layers in all types of karren habitats, but the herb species were not always dominant in the herb layer. Numerous woody seedlings and saplings were found in the herb layer, and several species have strong adaptability to karren habitats and may soon occupy the degraded area via residual piles. The succession in this area has demonstrated that once the external disturbance becomes weaker or disappears, species with high reproduction ability, such as *Neolitsea homilantha*, *Cyclobalanopsis glaucoides*, and *Olea tsoongii*, will dominate the herb layer.

The Pearson correlation analysis found that many environmental factors significantly affect plant diversity, but some factors were eliminated in the stepwise regression model, possibly due to the effect of collinearity among some factors. This suggests that plant diversity in karren habitats is the result of the interactions among multiple factors. Du et al. [35] demonstrated that the more complex the vegetation, the less the environmental factors explain community variations. This confirms that niche differentiation and the unified neutral theory of biodiversity are dominant in karst forest. However, the niche differentiation in our study may play a dominant role in species assemblage due to the karren habitat heterogeneity, which demonstrated that species coexistence might be maintained by a more complex combination of multiple mechanisms, on which further research might be performed in the future.

4.2. Environmental Interpretation for the Plant Species Distribution in Karren Habitats

Although plant species distribution did not show a high correlation with environmental factors in canonical correspondence analyses because of the extensive generalist species in all karren habitats and the substantial plots in our research, some environmental effects were significant. Numerous studies demonstrated that the topography of karst forests is closely related to the vegetation composition [44,45]. A topographical gradient may complicate the interpretation of the mechanism because it includes plenty of factors [48]. The slope gradient affected the distribution of woody and herbaceous species significantly in our study, which might have resulted from its effect on soil nutrients and relative humidity. The significant effect of canopy density on both woody and herbaceous plant distribution is obviously attributed to the light, which is a crucial factor affecting the plant distribution [49,50]. Heliophytes, or sun-loving species, increased with canopy exposure caused by canopy gaps and exposed rocks. A previous study has also demonstrated that canopy gaps impact plant distribution by increasing the light level, which influences the temperature and humidity of the air and soil [51].
The impacts of karren habitat width and height on woody species distribution and composition were more significant than for herbaceous species. The narrow width of the habitat may reduce the accessibility of humans and animals, since human activities and animal predation are major factors causing loss of woody seed and seedling bank replenishment. Karren habitat height may also influence the distribution of woody seedlings indirectly by influencing the accessibility of light. So far, no previous research concerns this aspect. Some research showed that litter thickness, litterfall production, and litter nutrient input had a positive impact on herbaceous species because plant litter production is an important process in the control of nutrient cycling within forest ecosystems, and litter coverage slows water evaporation and maintains the surface temperature [30]. However, litter thickness had a negative influence on herbaceous distribution in our study, which might be attributed to the fact that undecomposed litters limit the germination of herbaceous seeds with too much shading or prevent seed entry into the soil [52].

Compared to species diversity, woody species distribution had slight correlations with soil thickness. Some generalist arbor species in the karst region have deep and elaborate cluster roots that help these species exploit the topsoil and the epikarstic and deep fissure water [53]. The surface soil could be washed along these fissures into the underground fissure network easily, which exacerbates soil erosion. However, water that reaches the deep fissures may not quickly evaporate, and it is easily absorbed by the deep roots of the arbor. Therefore, the roots of some deep-rooted arbor pass through the topsoil and fissures to reach deep groundwater and ensure normal growth [54]. However, herbs equipped with relatively shallow roots would only be able to utilize shallow water, as also found in previous studies [55].

The results of the variation partitioning demonstrated that both abiotic and biotic factors contribute to the plant species distribution in this karst region. This indicates that the choice of species in the late succession stage according to the different widths or heights of karren habitats will promote plant species renewal in karst areas. However, other factors that were not included in our research, such as soil properties, temperature, human disturbance, or plant competition, may also have important impacts on the distribution of plant species.

4.3. Implications for Planting Design and Management in the Karren Habitats of KRD Restoration Areas

This research aims to understand woody and herbaceous species diversity in karren habitats and environmental influence factors for biodiversity conservation in natural forests, and to eventually provide knowledge for plant restoration design in the karst Geopark. Several highly valued woody species were identified that are encouraged to be applied as sustainable restoration plant species in the planning and design of revegetation in karst rocky desertification restoration areas. For instance, *Olea tsoongii*, *Myrsine africana*, and *Pistacia weinmannifolia* (Figure 4) can grow in any karren habitat. However, planting designs for ecological restoration in the scenic karst region should pay attention to the differences in karren habitat types. The planting of arbors and shrubs may need to concentrate on grikes, deep solution pits, and solution corridors to make full use of the water and heat resources to enhance stability and sustainability, while herb planting should primarily focus on solution rock debris. It should be discreetly considered to use solution wells as the main type for karst forest restoration because of their limited space. The simulation of natural plant communities, including ferns, annuals, perennials, lianas, shrubs, and arbors, according to diversified succession stages in karren habitats, would also be an essential strategy [56,57]. Most plants and seeds used within the karren habitats should be of autochthonous origin to support local biodiversity and regional identity.

Nowadays, we use not only objective criteria (high biodiversity, endemism), but also subjective/emotional criteria (“landscape of our grandparents”, “wilderness beauty”) to positively evaluate the karst landscape [58]. The latter criterion can be seen as a kind of scenario that depicts sustaining of place-specific interactions between humans and nature [59]. In karren habitats, many species actually have high ornamental value, such as *Dalbergia minosoides*, *Cotoneaster vernae*, and *Photinia glomerate*, which present flowers or fruits in spring, summer, and autumn, respectively,
and also exhibit a type of wild beauty and regional identity that is authentic and reminds people of the memory or history of a site. Karren habitats with native plant species, instead of fast-growing exotics, reflect geological changes and human activities that occurred in the local area, which may improve the connection between people and true nature.

5. Conclusions

The present research revealed the distribution and diversity patterns of woody and herbaceous plant species in karren habitats. In general, karren habitat features and topographic factors were essential for explaining the patterns of species diversity and distribution. Our analyses provided an understanding of the relationship between plant species and special geological characteristics in karst areas. This research merits directions for future studies on indigenous features and high biodiversity, which are vital for sustainable planting design: (1) Revealing other environmental factors in karren habitats and relationships with plant community characteristics and (2) understanding the succession processes and dynamics in karren habitats of urban and rural karst forests.

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