

Article

What Drives Understory Plant Functional Diversity in Karst Plantations? Critical Roles of Canopy Gap and Soil Nitrogen

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Abstract

Establishing plantations in areas characterized by fragile natural vegetation emerges as a crucial approach to ecological restoration in karst regions. However, strong environmental filtering in karst regions constrains the ecological functions of understory plant communities. As the key stand structure and soil environmental factors driving community assembly remain elusive, variations in functional diversity are highly unpredictable, hindering the full realization of community functional potential. Based on a two-year investigation across 3 plantation types (36 plots) in the Liujiang River basin, we recorded stand structure and understory species abundances, quantified soil physicochemical properties, measured 8 leaf traits of understory plants encompassing leaf morphological, physiological, and chemical traits, and calculated community-weighted mean trait values to represent community-level leaf traits. Mixed-effects models were employed to elucidate the key drivers of understory leaf functional diversity. Results showed that *Eucalyptus grandis* × *urophylla* plantations supported the highest understory species diversity (10 species), temporally increased community-level leaf traits, and increased function diversity over other stands by 20.53%. In *Pinus massoniana* plantations, community-level leaf traits remained stable, but functional dispersion significantly increased by 24.47% temporally. In *Bauhinia purpurea* plantations, understory plants exhibited thicker, smaller leaves and significantly higher C:N ratios, accompanied by a 37.77% decline in functional evenness and an 11.42% decline in dispersion. Canopy gap and soil total nitrogen were the critical drivers for understory leaf functional diversity. Under light-nitrogen co-limitation, intensified environmental filtering suppressed relative abundance of subordinate species. Conversely, leveraging high trait plasticity, *Bidens pilosa* and *Miscanthus floridulus* dominated community-level trait trade-offs, determining functional variation approaches. Therefore, a synergistic management strategy, optimizing aboveground light and supplementing belowground nitrogen, should be considered to break single-species dominance and maintain functional diversification.

Keywords: understory plant adaptation strategy; functional diversity; canopy gap; soil total nitrogen; environmental filtering



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1. Introduction

In plantation ecosystems, understory plant communities account for a relatively small proportion of total biomass, yet they play a pivotal role in sustaining forest biodiversity, enhancing community productivity, and mitigating soil and water loss [1,2]. Plant growth

and community assembly are sensitive to environmental factors such as light availability and soil nutrients. Under light stress or nutrient limitation, plants adapt by modifying their functional traits to optimize resource acquisition [3]. Harsh environments may lead to trait convergence, where surviving species occupy similar stress-tolerant niches [4]. Conversely, to avoid intense competition for relatively abundant resources, plants may exhibit trait divergence to partition ecological niches. These trait-based niche shifts ultimately dictate which species can coexist, thereby shaping community assembly pathways [4]. In plantation environments, stand structural characteristics (e.g., tree species, stand density, and canopy gaps) reshape the distribution patterns of understory light intensity [5]. Meanwhile, the developments of different afforestation species result in significant variations in soil physicochemical properties and nutrient status [6]. Currently, studies investigating the effects of environmental changes in plantations on understory plant functions predominantly focus on the species level, mainly emphasizing the morphological adaptations, physiological adjustments, and individual growth responses of single species or a few dominant species to reduced light availability and soil nutrient fluctuations [7,8]. However, how understory community assembly responds to these factors within the heterogeneous habitats of different plantations remains unclear.

Constrained by the unique carbonate rock geological background, the soil environment in karst regions exhibits extreme fragility [9]. Poor soil physical structure and slow turnover of available nutrients in this region lead to severe belowground resource limitations for vegetation [10,11]. To improve the degraded environment and promote vegetation recovery, this region extensively established multi-type plantations. While these plantations primarily serve ecological purposes, portions located in areas with abundant rainfall are also managed as timber forests to provide concurrent economic benefits [12]. The plantation coverage rate in karst regions of China increased by up to 11.47% [13]. However, current research on the plant ecology of karst plantations predominantly focused on the growth adaptability of afforestation tree species, carbon sequestration functions, and community species diversity [14–16]. Furthermore, existing studies on the species diversity of understory plant communities were mostly concentrated in temperate or conventional subtropical forests in non-karst regions, and their conclusions were difficult to directly apply to the highly heterogeneous karst environment [17,18]. Few studies revealed how the diverse stand structure and the soil physicochemical environment synergistically influence the assembly pathways of understory plant communities in karst plantations. In fact, the harsh conditions in karst plantations subjected understory plants to a more complex and severe living environment than those in non-karst regions [19]. Therefore, during the critical period when ecological restoration in karst regions is transitioning from “scale expansion” to “high-quality development” [20], it is urgent to explore the mechanisms of understory plant community assembly in these plantations.

Functional diversity reflects the responses of plant communities to environmental changes and community assembly processes more accurately than traditional species diversity [21]. Leaves are the primary organs for material and energy exchange, and their specific traits reflect plant adaptation strategies. The composition, range, and variation in these traits across different species reveal how environmental factors filter these adaptation strategies during community assembly [22]. Such environmental filtering effects are effectively characterized by leaf functional diversity [23]. The Environmental Filtering Hypothesis emphasizes that abiotic environmental conditions function as a filter, permitting only species with functional traits to survive and colonize a given habitat [24]. In karst plantations, the filtering effects of light and soil resource limitations are likely to drive plants to adopt specific resource trade-off strategies [25]. It may prompt directional changes in leaf functional trait combinations at the community level, and consequently lead

to variations in community functional diversity. Therefore, exploring the mechanisms by which environmental conditions drive understory functional diversity can elucidate their fine-scale assembly rules in karst regions. This understanding holds significant scientific implications for the high-quality development of plantations in karst regions under the context of global change.

Collectively, we formulated the hypothesis that the stand structure and soil environment of different plantations are two “environmental filters”, and they exert cooperative effects in determining the leaf functional diversity of understory vegetation. To test the above hypothesis, this study systematically analyzes the effects of stand structure and soil environmental factors on the leaf functional diversity of understory plant communities in karst plantations, and explores their potential driving factors, with the aim of providing a scientific basis for structural optimization and comprehensive enhancement of ecological service functions in karst plantations.

2. Materials and Methods

2.1. Study Area

This study was conducted in the Liujiang River Basin, Guangxi Zhuang Autonomous Region, China ($109^{\circ}20'28.92''$ E~ $109^{\circ}44'23.38''$ E, $24^{\circ}16'4.22''$ N~ $24^{\circ}20'6.18''$ N) (Figure 1). This area is a typical karst catchment basin, where the exposed proportion of limestone and dolomite exceeds 80%, and karst fissures and underground conduits are widely distributed [26]. The karst development has reached a mature stage, characterized by a typical peak forest plain landform [27]. The region has a subtropical monsoon climate with concurrent rainfall and heat. The mean annual precipitation exceeds 1800 mm, and the maximum monthly mean precipitation exceeds 370 mm (Table S1). The monthly mean temperature ranges from a minimum of 6.7 °C in winter to a maximum of 29.4 °C in summer [28].

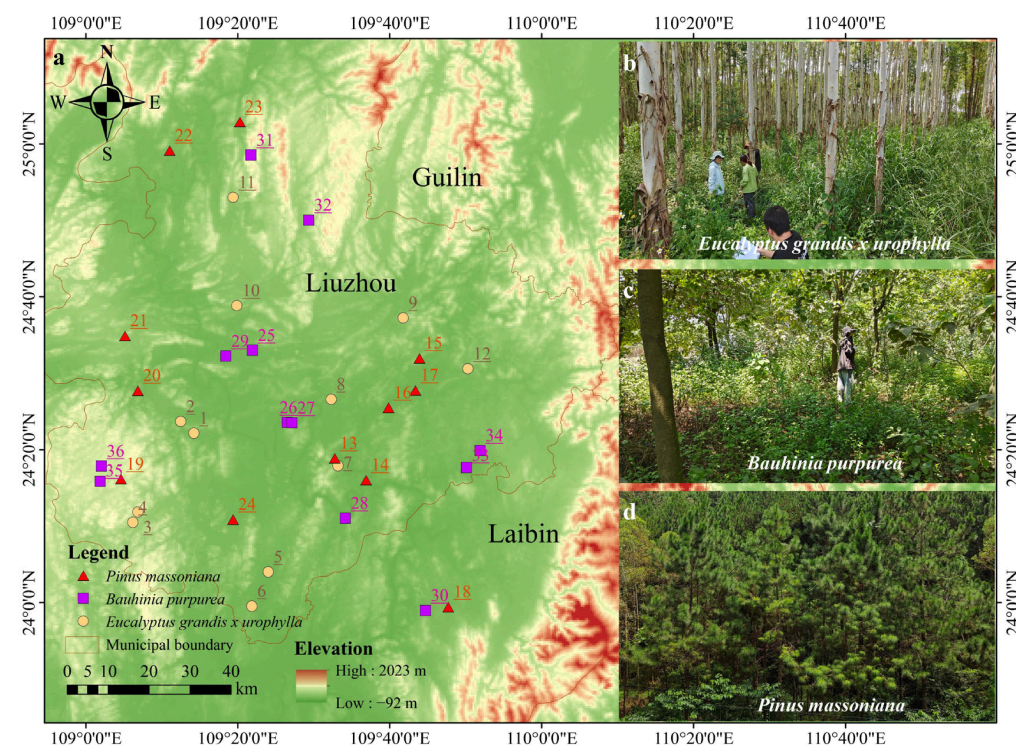


Figure 1. The study area is in the Liujiang River Basin, GuangXi Zhuang Autonomous Region, China (a). Three types of plantations, namely *Eucalyptus grandis* × *urophylla*, *Pinus massoniana*, and *Bauhinia purpurea*, were selected for this investigation (b–d). For each plantation type, 12 plots were established and selected to ensure spatial independence and adequate coverage across the river basin.

The original vegetation in this area consisted of shrubs and herbs. These natural shrub-herb communities were highly adapted to the barren and shallow soils typical of karst regions [22]. Despite their tolerance to poor soil conditions, the community structure remained simple and faced a continuous risk of degradation [22]. However, the combination of abundant precipitation and vegetation fragility led to severe soil erosion and a significantly increased risk of rocky desertification. Consequently, the local government introduced the exotic fast-growing species (*Eucalyptus grandis* × *urophylla*) and the native pioneer species (*Pinus massoniana* and *Bauhinia purpurea*) [29]. These species are characterized by their rapid biomass accumulation and quick canopy closure. They were specifically selected for planting as monocultures because these characteristics facilitate rapid soil and water conservation, thereby accelerating early-stage vegetation restoration while simultaneously providing economic forestry benefits [29]. According to publicly available data released by the local government, the area of planted forests has exceeded 1.271 million hectares, and the total forestry output value has reached 4.584 billion yuan [30].

2.2. Field Investigation

The surveys were conducted across 36 plantation plots within the Liujiang River Basin in July 2025 and July 2026, respectively. The two-year survey interval helped reduce the contingency of single-year environmental fluctuations and ensured the reliability of community data.

To ensure spatial independence among plots, all sampling sites were evenly distributed throughout the Liujiang River Basin. Spatially, the distance between any two plots was strictly controlled to be greater than 3 km [31]. Plots of the same plantation type had to differ by at least one dominant understory species. Additionally, to avoid statistical bias caused by uneven sample sizes, the number of plots for each plantation type was kept consistent. This sampling design effectively avoided the influence of spatial autocorrelation and community homogenization on the study results.

Based on the above criteria, a total of 12 *Eucalyptus grandis* × *urophylla* plantation plots, 12 *Pinus massoniana* plantation plots, and 12 *Bauhinia purpurea* plantation plots were selected (Figure 1). These plantations were selected because they shared a mature, closed-canopy developmental stage, which ensured comparable understory environments despite their different stand ages (Table S1). The coordinates and elevation of each plot were recorded using a GPS device (WS-009), and the slope direction was measured using a slope inspection tool (MNom) (Table S1). Three 20 m × 20 m quadrats were randomly selected for investigation within each plot. In each quadrat, the number of planted trees was recorded, and the diameter at breast height, tree height, and crown width of the planted trees were measured following the methods described in Tan et al., 2024a [31]. Following the method proposed by Franceschi et al. 2022 [32], canopy gap was determined by subtracting the total horizontally projected canopy cover from the quadrat area. For understory species, the crown width and crown height were measured using a ruler with a precision of 0.1 cm [22]. The abundance of each understory species was recorded. Within each quadrat, the understory vegetation coverage was defined as the horizontal projection area covered by shrubs and herbs per unit area [31].

2.3. Sample Collection and Determination

In each quadrat, 1.0 kg soil samples were collected from a depth of 0–20 cm using the five-point sampling method. At the same sampling points, soil core samples were collected using a cutting ring [30]. The 1.0 kg soil samples were air-dried and sieved through a 0.15 mm sieve. Soil available nitrogen was determined by the alkaline hydrolysis diffusion method. Total nitrogen was measured using the Kjeldahl method after digestion with

sulfuric acid and catalysts. Available phosphorus was extracted with sodium bicarbonate-sodium fluoride-hydrochloric acid solution and quantified via the molybdenum-antimony anti-colorimetric method. Total phosphorus was determined by the NaOH alkali fusion combined with molybdenum-antimony anti-spectrophotometry.

The perforated side of each cutting ring was immersed in shallow water to allow the soil to absorb water spontaneously for 12 h, after which the weight was measured. The soil-filled cutting rings were then oven-dried at 105 °C for 48 h, and the dry weight of the soil was recorded. The soil saturated water content was determined based on the weight difference. Soil bulk density was calculated by dividing the dry weight of the soil by the volume of the cutting ring (100 cm³) [22].

Following Cornelissen et al. (2003) [33], five standard individuals of each understory species were selected in per quadrat for leaf sample collection, based on the average plant height and crown width of that species within the quadrat. 10 healthy leaves were collected from individuals for functional trait measurement. The following leaf functional traits were measured according to the standard protocols described by Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013) [33,34]. Prior to transporting the leaf samples back to the laboratory, leaf chlorophyll content (SPAD) was measured using a SPAD-502 m (Konica Minolta, Tokyo, Japan), and leaf thickness was determined by a 0.1 mm vernier caliper. Upon arrival at the laboratory, the leaf samples were scanned using an EPSON V19 scanner (Seiko Epson Corporation, Suwa, Japan), and leaf area was determined using AutoCAD 2022 (Autodesk, Inc., San Rafael, CA, USA). Subsequently, leaf fresh weight was measured by electronic balance. The leaf samples were immersed in distilled water for more than 12 h until constant weight to record leaf saturated weight. Afterwards, all leaves were oven-dried at 80 °C for over 48 h to a constant mass, and leaf dry weight was recorded. Specific leaf area was calculated as the ratio of leaf area to leaf dry weight. The dried leaf samples were ground and sieved through a 0.15 mm mesh. Leaf carbon content was determined using the potassium dichromate oxidation method [35]. Following catalytic digestion, leaf nitrogen content was quantified with an automatic discrete chemical analyzer (Smartchem200) (KPM Analytics, Westborough, MA, USA) [35]. The leaf carbon-to-nitrogen ratio was calculated as leaf carbon content divided by leaf nitrogen content. Leaf dry matter content and leaf relative water content were calculated as follows:

$$LDMC = \frac{LDM}{LSM}$$

$$RWC = \frac{LFM - LDM}{LSM - LDM}$$

where *LDMC* is leaf dry matter content, *RWC* is relative water content, *LDM* is leaf dry weight, *LFM* is leaf fresh weight, and *LSM* is leaf saturated weight.

Consistent with previous studies, increases in leaf dry matter content, leaf thickness, and carbon-nitrogen ratio, accompanied by reductions in specific leaf area, leaf relative water content, chlorophyll content, and leaf nitrogen content, indicate a conservative adaptation strategy, which enhances resource use efficiency [36]. The opposite trends indicate an acquisitive adaptation strategy, which maximizes resource acquisition [36].

2.4. Data Analysis

Normality was tested for each data group using the Kolmogorov–Smirnov test. When the data deviated from a normal distribution, a Box–Cox transformation was performed to ensure normality [37]. Paired *t*-tests were performed to detect significant differences in stand structure factors, soil nutrient variables and understory leaf functional traits between different years within the same plantation type, given the paired data structure. For comparisons among different plantations in the same year, one-way analysis of variance

(one-way ANOVA) was adopted to test the intergroup differences in the above indicators. The confidence level was set at 0.95.

Community-weighted means were calculated for leaf functional traits in each plot to obtain community-level trait values [38], ensuring that functional traits could be compared on the same scale as other indicators at the community level.

$$T_c = \sum_{i=1}^s P_i T_i$$

where T_c is the community-level trait value, P_i is the relative abundance of the i -th species, T_i is the trait value of the i -th species in the community, and s is the total number of species within the community.

Understory leaf functional diversity was assessed using three indicators: functional richness, functional evenness, and functional dispersion, which were calculated based on understory species, species abundance, and leaf functional trait values. Functional richness characterizes the range of functional trait space occupied by the community [39]. Higher values indicate greater resource utilization potential, reflecting the effective use of resource space by species in the environment [39]. This index is equivalent to the volume of the multidimensional convex hull formed by the multiple functional traits of species in the community. Due to its computational complexity, functional richness was calculated using the FD package in R version 4.5.0 [40].

Functional evenness describes the evenness of the distribution of plant functional traits within the niche space, and reflects the efficiency of resource exploitation by coexisting species [39]. A higher functional evenness value indicates that species and their functional traits are evenly distributed across the niche space of the community. This index was calculated using the following formula [36]:

$$Feve = \frac{\sum_{b=1}^{S-1} \min \left(PEW_b \times \frac{1}{S-1} \right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

$$PEW_b = \frac{EW_b}{\sum_{b=1}^{S-1} EW_b}$$

$$EW_b = \frac{d_{ij}}{w_i + w_j}$$

where $Feve$ is functional evenness; S is the number of species; PEW_b is the locally weighted mean evenness; EW_b is the weighted mean evenness; w_i is the relative abundance of species i ; and d_{ij} is the Euclidean distance between species i and species j .

Functional dispersion characterizes the degree of functional differentiation among species [35]. High functional dispersion indicates greater functional complementarity among species [38], reflecting a high degree of trait divergence and thus high resource use efficiency. It is calculated using the following formula:

$$c = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j}$$

$$F_{dis} = \frac{\sum a_j z_j}{\sum a_j}$$

where F_{dis} is functional dispersion; a_j is the relative abundance of species j , x_{ij} is the i -th functional trait of species j , and z_j is the distance from species j to the weighted centroid c .

Linear mixed-effects models are effective for analyzing nested data. By incorporating random effects, these models eliminate biased standard error estimates and false positive results caused by non-independent sampling plots [41]. Therefore, to accurately identify the key environmental drivers of understory leaf functional diversity, linear mixed-effects models were constructed in this study. Understory leaf functional diversity indicators were treated as response variables, stand structure factors and soil properties were set as fixed effects, and plantation type was included as a random effect. Prior to modeling, variance inflation factors (VIF) of all environmental predictors were calculated to avoid estimation bias induced by multicollinearity among explanatory variables. Redundant variables with VIF values greater than 10 were removed from the dataset. All analyses were performed in R 4.5.0. Firstly, the full set of mixed-effects models were constructed using the lme4 package (v2.0). The MuMIn package (v1.48.19) was then applied for model selection to screen the optimal mixed-effects model. Finally, significant influencing variables were identified based on the *p*-values derived from the best-fit model at a confidence level of 0.95. Standardized regression coefficients were extracted to compare the relative contributions of each environmental factor to leaf functional diversity.

3. Results

3.1. Changes in Stand Structure Under Different Plantations

During 2025–2026, *Eucalyptus grandis* × *urophylla* were characterized by the highest tree height, canopy gaps, and understory vegetation coverage, but had significantly lower crown width and diameter at breast height compared to the other plantations (Table 1). *Pinus massoniana* exhibited the largest crown width and diameter at breast height (Table 1). *Bauhinia purpurea* exhibited the lowest canopy gaps and understory vegetation coverage, both of which experienced further significant decreases in 2026 (Table 1).

Table 1. Stand structure parameters of different plantations.

Plantation	Year	Crown Width/m	Diameter at Breast Height/cm	Tree Height/m	Number of Trees per Square Meter	Canopy Gap/%	Understory Vegetation Coverage/%
<i>Eucalyptus grandis</i> × <i>urophylla</i>	2025	2.1 ± 0.1 Ac	12.1 ± 2.5 Ac	11.3 ± 1.7 Aa	16.2 ± 2.1 Aa	45.4 ± 8.3 Aa	85.6 ± 6.1 Aa
	2026	2.1 ± 0.1 Ac	13.0 ± 2.6 Ac	12.1 ± 1.9 Aa	16.2 ± 2.1 Aa	46.3 ± 8.5 Aa	81.4 ± 5.9 Aa
<i>Pinus massoniana</i>	2025	3.4 ± 0.3 Ba	25.3 ± 8.4 Aa	9.1 ± 2.2 Ab	12.1 ± 2.3 Ab	31.4 ± 4.2 Ab	75.6 ± 6.0 Ab
	2026	3.5 ± 0.2 Aa	26.0 ± 8.2 Aa	9.3 ± 2.0 Ab	12.1 ± 2.3 Ab	33.8 ± 8.5 Ab	70.0 ± 5.8 Bb
<i>Bauhinia purpurea</i>	2025	2.9 ± 0.2 Ab	15.6 ± 1.8 Ab	9.9 ± 1.2 Ab	12.3 ± 1.8 Ab	21.3 ± 6.4 Ac	56.2 ± 5.1 Ac
	2026	2.9 ± 0.1 Ab	16.7 ± 1.9 Ab	10.7 ± 1.3 Ab	12.3 ± 1.8 Ab	15.5 ± 4.7 Bc	46.0 ± 4.2 Bc

Different capital letters indicate significant differences in stand structure parameters between different years in the same plantation (*p* < 0.05). Different lowercase letters indicate significant differences in stand structure parameters among different plantations within the same year (*p* < 0.05).

3.2. Changes in Understory Species Composition Under Different Plantations

The *Eucalyptus grandis* × *urophylla* plantation had the highest number of understory plant species, reaching 10 species (Table 2). The *Bauhinia purpurea* plantation had the lowest richness, with only 5 understory species recorded (Table 2). The abundances of *Bidens pilosa* and *Miscanthus floridulus* increased significantly in the second year compared with the first year in both the *Eucalyptus grandis* × *urophylla* and *Pinus massoniana* plantations (Table 2). By contrast, the total number of understory species declined in the *Bauhinia purpurea* plantation across the two sampling years (Table 2).

Table 2. Number and abundance of understory species per 100 square meters.

Understory Species	Family	Year	Individual Number/100 m ⁻²		
			<i>Eucalyptus grandis</i> × <i>urophylla</i> Plantation	<i>Pinus massoniana</i> Plantation	<i>Bauhinia purpurea</i> Plantation
<i>Bidens pilosa</i>	Asteraceae	2025	133.47 ± 21.02 Bc	188.92 ± 25.91 Bb	209.31 ± 14.67 Aa
		2026	172.53 ± 18.79 Ab	218.39 ± 22.60 Aa	161.47 ± 13.33 Bb
<i>Miscanthus floridulus</i>	Poaceae	2025	51.44 ± 19.38 Ba	42.92 ± 12.67 Bab	33.94 ± 18.53 Ab
		2026	74.11 ± 14.05 Aa	68.19 ± 11.03 Aa	19.61 ± 8.75 Bb
<i>Ageratum conyzoides</i>	Asteraceae	2025	57.75 ± 20.49 Aa	66.50 ± 15.53 Aa	13.53 ± 6.71 Ab
		2026	24.56 ± 11.12 Ba	20.94 ± 7.02 Ba	6.78 ± 3.38 Bb
<i>Erigeron sumatrensis</i>	Asteraceae	2025	20.90 ± 14.40 Aa	12.27 ± 8.28 Ab	
		2026	9.97 ± 5.90 Ba	6.87 ± 4.21 Ba	
<i>Spermacoce pusilla</i>	Rubiaceae	2025	25.67 ± 17.49 Aa	9.83 ± 5.01 Ab	
		2026	10.17 ± 5.46 Ba	9.17 ± 6.09 Aa	
<i>Digitaria sanguinalis</i>	Poaceae	2025	27.00 ± 10.85 Aa	15.01 ± 4.08 Ab	
		2026	15.83 ± 7.20 Ba	11.01 ± 4.97 Aa	
<i>Ageratina adenophora</i>	Asteraceae	2025	19.83 ± 10.32 A		
		2026	12.83 ± 3.44 B		
<i>Nephrolepis cordifolia</i>	Nephrolepidaceae	2025	48.67 ± 7.36 A		
		2026	5.33 ± 0.47 B		
<i>Stephania japonica</i>	Menispermaceae	2025			4.00 ± 0.81 A
		2026			4.00 ± 0.82 A
<i>Dicranopteris pedata</i>	Gleicheniaceae	2025	20.33 ± 5.31 A		
		2026	7.33 ± 2.87 B		
<i>Commelina communis</i>	Commelinaceae	2025			6.67 ± 1.24 A
		2026			5.33 ± 1.25 A
<i>Oxalis corniculata</i>	Oxalidaceae	2025	10.67 ± 5.37 A		
		2026	5.17 ± 1.07 B		

Different capital letters indicate significant differences in the number of understory plant individuals between different years within the same plantation ($p < 0.05$). Different lowercase letters indicate significant differences in the number of understory plant individuals among different plantations within the same year ($p < 0.05$).

3.3. Variation in Community-Level Leaf Functional Traits and Leaf Functional Diversity

The interannual comparison of understory leaf functional traits within each plantation revealed that specific leaf area increased significantly over time in the *Eucalyptus grandis* × *urophylla* plantation, while the rising trend was non-significant in the *Pinus massoniana* plantation (Table 3). By contrast, specific leaf area decreased significantly in the *Bauhinia purpurea* plantation (Table 3). Similarly, the leaf carbon-nitrogen ratio significantly decreased over time in the *Eucalyptus grandis* × *urophylla* plantation, but the change in the *Pinus massoniana* plantation was not significant, while it significantly increased in the *Bauhinia purpurea* plantation (Table 3).

Table 3. Community-level leaf functional traits of understory plant communities.

Functional Traits	<i>Eucalyptus grandis</i> × <i>urophylla</i> Plantation		<i>Pinus massoniana</i> Plantation		<i>Bauhinia purpurea</i> Plantation	
	2025	2026	2025	2026	2025	2026
Leaf thickness/mm	22.23 ± 1.55 Ac	21.27 ± 1.77 Ac	24.79 ± 1.66 Ab	24.54 ± 2.03 Ab	27.77 ± 2.71 Aa	28.33 ± 2.80 Aa
Leaf dry matter content/%	29.90 ± 1.10 Ac	29.23 ± 0.99 Ac	31.01 ± 1.12 Ab	30.05 ± 1.07 Ab	33.55 ± 0.85 Aa	34.74 ± 0.92 Aa
Specific leaf area/g·cm ⁻²	169.90 ± 9.67 Ba	183.97 ± 6.65 Aa	148.44 ± 10.03 Ab	149.14 ± 9.67 Ab	138.48 ± 9.80 Ac	106.62 ± 10.42 Bc
Leaf relative water content/%	72.91 ± 1.29 Aa	73.81 ± 1.07 Aa	71.06 ± 0.84 Aa	71.58 ± 0.98 Ab	68.89 ± 0.96 Ab	67.42 ± 0.94 Ac
chlorophyll/SPAD	44.82 ± 1.79 Ba	46.10 ± 2.04 Aa	42.64 ± 1.71 Ab	43.09 ± 1.96 Ab	39.5 ± 2.81 Ac	37.14 ± 2.94 Ac
Leaf carbon content/mg·g ⁻¹	454.67 ± 7.67 Aa	450.24 ± 9.26 Aa	445.96 ± 8.27 Ab	436.32 ± 8.63 Bb	435.94 ± 7.19 Ac	421.58 ± 9.26 Bc
Leaf nitrogen content/mg·g ⁻¹	21.32 ± 1.00 Aa	22.43 ± 0.98 Aa	19.92 ± 1.06 Ab	20.60 ± 1.13 Ab	17.73 ± 0.99 Ac	15.42 ± 1.04 Bc
Leaf carbon-nitrogen ratio	21.46 ± 0.93 Ab	20.22 ± 0.94 Bb	22.54 ± 1.02 Ab	21.35 ± 1.20 Ab	24.71 ± 1.22 Ba	27.49 ± 1.87 Aa

Different capital letters indicate significant differences in traits between different years in the same plantation ($p < 0.05$). Different lowercase letters indicate significant differences in traits among different plantations within the same year ($p < 0.05$).

In the same year, the overall functional diversity indicators followed the order: *Eucalyptus grandis* × *urophylla* plantation > *Pinus massoniana* plantation > *Bauhinia purpurea* plantation (Figure 2). The inter-plantation differences exceeded 20.53%, with a maximum gap reaching 429.65% (Figure 2). Interannual comparison within the same plantation type showed that functional evenness and functional dispersion of the *Bauhinia purpurea* plantation significantly decreased by 37.77% and 11.42%, respectively (Table 3). In contrast, functional dispersion of the *Pinus massoniana* plantation significantly increased by 24.47% (Figure 2).

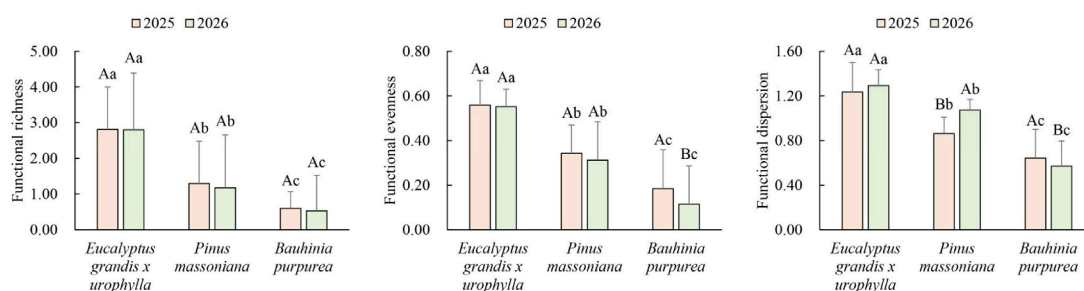


Figure 2. Plant functional diversity of understory plant communities. Different capital letters indicate significant differences in understory functional diversity between different years in the same plantation ($p < 0.05$). Different lowercase letters indicate significant differences in understory functional diversity among different plantations within the same year ($p < 0.05$).

3.4. Variations in Soil Properties Under Different Plantations

In the same plantation, no significant interannual differences were detected in soil bulk density, soil saturated water content and soil total nitrogen (Table 4). However, available soil nutrients decreased significantly over time in the *Eucalyptus grandis* × *urophylla* plantation (Table 4). Across different plantation types in the same year, the order of soil nutrients and soil saturated water content was *Eucalyptus grandis* × *urophylla* plantation > *Pinus massoniana* plantation > *Bauhinia purpurea* plantation, whereas soil bulk density followed the opposite trend (Table 4).

Table 4. Soil properties of different plantations.

Plantation	Year	Soil Bulk Density/g·cm ³	Soil Saturation Water Content/%	Soil Available Nitrogen/mg·kg	Soil Available Phosphorus/mg·kg	Soil Total Nitrogen/g·kg	Soil Total Phosphorus/g·kg
<i>Eucalyptus grandis</i> × <i>urophylla</i>	2025	1.00 ± 0.03 Ab	58.07 ± 1.76 Aa	141.11 ± 19.83 Aa	12.53 ± 1.54 Aa	1.35 ± 0.19 Aa	0.76 ± 0.16 Aa
	2026	1.01 ± 0.06 Aa	57.24 ± 7.43 Aa	126.13 ± 26.68 Ba	10.98 ± 1.69 Ba	1.36 ± 0.26 Aa	0.73 ± 0.18 Aa
<i>Pinus massoniana</i>	2025	1.04 ± 0.03 Aa	53.48 ± 1.88 Ab	123.52 ± 19.16 Ab	10.01 ± 1.73 Ab	0.99 ± 0.17 Ab	0.52 ± 0.13 Ab
	2026	1.04 ± 0.05 Aa	52.38 ± 6.49 Ab	108.34 ± 27.05 Ab	9.49 ± 1.55 Aab	0.98 ± 0.23 Ab	0.48 ± 0.15 Ab
<i>Bauhinia purpurea</i>	2025	1.09 ± 0.06 Aa	52.94 ± 1.78 Ab	116.11 ± 27.43 Ab	9.21 ± 1.81 Ab	0.97 ± 0.16 Ab	0.48 ± 0.11 Ab
	2026	1.09 ± 0.07 Aa	51.52 ± 6.59 Ab	106.65 ± 33.35 Ab	8.22 ± 1.62 Ab	0.95 ± 0.16 Ab	0.46 ± 0.10 Ab

Different capital letters indicate significant differences in soil properties between different years in the same plantation ($p < 0.05$). Different lowercase letters indicate significant differences in soil properties among different plantations within the same year ($p < 0.05$).

3.5. Response Factors of Functional Diversity in Understory Plant Communities

Canopy gap was a significant factor driving the understory plant functional diversity among different plantation types, with an explanatory contribution exceeding 53.52% and reaching up to 93.55% (Figure 3). Soil total nitrogen was also identified as an important driving factor. The joint explanatory contribution of soil total nitrogen and soil bulk density to functional richness exceeded 22.08% (Figure 3). The contributions of soil total nitrogen and soil total phosphorus to functional evenness and functional dispersion were no less than 19.96% and 6.45%, respectively (Figure 3).

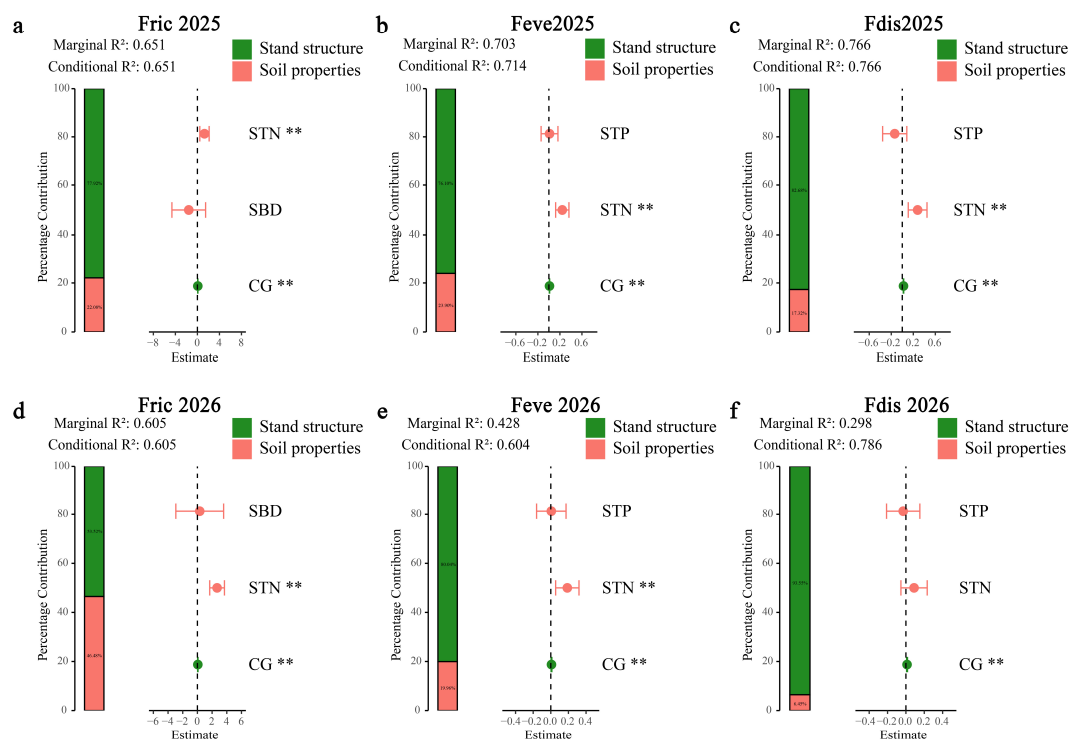


Figure 3. Mixed effects model results of driving factors for functional diversity of understory plant communities. SBD: soil bulk density, STN: soil total nitrogen, STP: soil total phosphorus, CG: Canopy Gap. “***” indicated $p < 0.01$. (a) Fric2025: effect of stand structure and soil properties on understory functional richness in 2025. (b) Feve2025: effect of stand structure and soil properties on understory functional evenness in 2025. (c) Fdis2025: effect of stand structure and soil properties on understory functional dispersion in 2025. (d) Fric2026: effect of stand structure and soil properties on understory functional richness in 2026. (e) Feve2026: effect of stand structure and soil properties on understory functional evenness in 2026. (f) Fdis2026: effect of stand structure and soil properties on understory functional dispersion in 2026.

4. Discussion

4.1. Assembly Mechanisms of Understory Plant Communities in Different Plantations

Variations in the abundance and functional traits of dominant species play a vital role in community assembly [42]. Over the two-year study period, dynamic changes in the understory community of *Eucalyptus grandis* × *urophylla* plantations revealed that *Bidens pilosa* and *Miscanthus floridulus* adopted an acquisitive adaptation strategy to achieve population expansion, whereas associated subordinate species adopted a conservative adaptation strategy to maintain survival (Tables 2 and S2). Due to the absolute dominance of the first two species, this strategy differentiation among species drove a shift in the community trait composition toward an acquisitive adaptation strategy (Table 3). However, owing to the high species richness and pronounced interspecific trait variation in this plantation type, the community exhibited high functional redundancy, which buffered against significant fluctuations in leaf functional diversity (Figure 2). These results indicated that the understory community of *Eucalyptus grandis* × *urophylla* plantations faces a potential risk of dominant species overexpansion, which may lead to community homogenization. Contrary to previous studies that suggest that the strong nutrient and water consumption of *Eucalyptus* suppresses understory diversity [43], the present study found that the understory community instead maintained high species richness and functional redundancy. By adopting a fast-acquisitive strategy, dominant species like *Bidens pilosa* and *Miscanthus floridulus* may mitigate the risk of abrupt biodiversity decline commonly observed in karst environments.

In the understory community of *Pinus massoniana* plantations, although *Bidens pilosa* and *Miscanthus floridulus* exhibited significant expansion in abundance, their adaptive strategies remained stable over the two-year period (Tables 2, 3 and S2). This stability maintained the original pattern of interspecific trait differentiation, resulting in no significant changes in functional richness or functional evenness (Figure 2). Notably, with the rapid expansion of these two dominant species, community-level leaf functional traits were dominated by *Bidens pilosa* and *Miscanthus floridulus* (Table 2). In contrast to the *Eucalyptus grandis* × *urophylla* plantations, this plantation type exhibited lower species richness and weaker functional redundancy. The absolute dominance of these species amplified the interspecific trait variation, thereby driving a significant increase in functional dispersion (Figure 2). These results indicated that the understory community of *Pinus massoniana* plantations has been dominated by a few dominant species.

The understory community of *Bauhinia purpurea* plantations was co-dominated by *Bidens pilosa*, *Miscanthus floridulus* and *Ageratum conyzoides*. All these species experienced population shrinkage over the two-year period, and leaf functional traits at both species and community levels consistently shifted toward a conservative resource strategy (Tables 2, 3 and S2). This indicated that the understory environment was subject to resource limitation.

The dynamics of the understory community were closely related to the strong functional trait plasticity of *Bidens pilosa* and *Miscanthus floridulus* (Tables 2 and S2). Previous studies on dominant species under strong environmental filtering emphasized that their high plasticity accelerates the formation of monodominant communities and leads to diversity loss [44,45]. However, this study revealed that while maintaining high abundance, these two dominant species broadened their adaptive thresholds to environmental filtering by virtue of their high functional trait plasticity. This trait dynamic adjustment, driven by environmental filtering, effectively alleviated competitive exclusion, thereby mediating their coexistence with companion species. Consequently, they were not merely “diversity excluders”; instead, by contributing most of the intraspecific trait variation within the

community, they dominated the maintenance of leaf functional diversity in the understory plant community.

4.2. Driving Mechanism of Leaf Functional Diversity in Understory Plant Communities

The functional structure trajectories of understory communities differed significantly among plantation types. While traditional perspectives emphasized that extreme water scarcity and poor soil in karst regions limit understory vegetation development [46], our study not only supported this view from the perspective of leaf functional diversity, but further demonstrated that the coupling effect of canopy gaps and soil total nitrogen acted as core driving factors (Figure 3). Canopy gaps reflect the distribution pattern of light resources and determine the upper limit of light acquisition for dominant species [47]. In karst environments, nitrogen, which is highly prone to leaching, is not only a core factor limiting primary productivity and constraining leaf functional trait trade-off strategies, but also serves as a key material support regulating light resource use efficiency [48]. Considering that the soil total nitrogen content in our study area was lower than that in other subtropical regions [49,50], the synergistic effect of light and nitrogen was especially crucial. Under the synergistic regulation of above- and below-ground resources, the assembly of understory plant communities followed three distinct pathways. In the *Eucalyptus grandis* × *urophylla* plantation, sufficient light availability combined with relatively high soil total nitrogen generated a strong positive synergy, which effectively supported diversified survival strategies among different species and helped maintain the highest level of functional diversity and functional redundancy (Tables 1, 2 and 4). In *Pinus massoniana* plantations, despite low soil total nitrogen levels, moderate canopy gaps allowed the resource-acquisitive dominant species *Bidens pilosa* and *Miscanthus floridulus* to maintain high acquisitive traits, thereby widening the trait distance between these species and conservative subordinate species, and driving a significant increase in community functional dispersion (Figure 2). *Bauhinia purpurea* plantations underwent severe dual environmental filtering imposed by relatively low light and low nitrogen (Figure 3). Heavy aboveground shading coupled with infertile belowground soil forced plants to abandon fast-growth strategies and converge toward a resource-conservative strategy (Table S2). This ultimately resulted in simplified community structure and severe degradation of leaf functional diversity (Figures 2 and 3). Our results were consistent with previous theories that high-nutrient availability promoted trait divergence, while low-nutrient availability led to trait convergence [51], and that high canopy closure induced light competition, resulting in trait homogenization toward conservative strategies [52].

In summary, the leaf functional diversity of understory communities in karst plantations was not determined by a single factor, but by the coupled interaction between aboveground canopy structure and belowground nitrogen availability. This finding reflects the differing roles of plantations and natural vegetation in restoring karst regions. In complex karst environments, natural shrub-herb communities exhibit low resistance to soil erosion and nutrient leaching [53]. Therefore, their limited effectiveness in soil conservation often triggers a vicious cycle of progressive soil impoverishment and vegetation degradation, making their successional trajectories highly unpredictable [53]. Conversely, plantations establish a robust structural framework that effectively enhances soil and water conservation [54]. Furthermore, the understory community development in plantations is controllable, and forest managers can regulate these driving factors to guide the understory plant growth, ensuring a more stable and sustainable restoration trajectory.

Most studies conducted in karst regions regarded soil moisture or phosphorus availability as key drivers governing understory succession [55,56]. Nevertheless, the abundant annual precipitation in the study area largely alleviated surface water leakage and drought

stress induced by karst geological conditions (Table S1). Under sufficient water conditions, the focus of competition among understory plants shifts. Notably, the prolonged high rainfall input in the study area likely diminishes the spatial variation in the soil moisture gradient (Table S1). Such relatively homogeneous and sufficient water conditions masked the filtering effect of water as a potential environmental filter to a certain extent, making it difficult for the present study to accurately separate the actual weight of water limitation at the current research scale. Future research should span broader precipitation gradients or incorporate dry and rainy season dynamics to fully decouple the multi-dimensional filtering mechanisms in karst environments.

This study emphasizes that, within the highly heterogeneous environment of karst plantations, canopy gaps provide space for the expression of functional trait plasticity in dominant species. While soil total nitrogen, as a core belowground environmental filter, strongly constrains the divergence potential of community traits. Therefore, the management of karst plantations should consider implementing precise environmental regulation based on the successional trajectory of understory communities. On the one hand, plantation tending and thinning should focus on optimizing the spatial heterogeneity of canopy gaps. In light-limited *Bauhinia purpurea* plantations, moderate thinning may alleviate understory light competition and break the conservative trait convergence of understory plants. For open-canopy plantations such as *Eucalyptus grandis* × *urophylla* and *Pinus massoniana* plantations, maintaining a patchy light environment may constrain the excessive expansion of acquisitive dominant species, and avoid the intense competitive exclusion caused by simplified environmental filtering. On the other hand, given that low nitrogen availability acts as a strong environmental filter limiting acquisitive traits, targeted nitrogen addition may alleviate the resulting trait convergence. This synergistic regulation of aboveground light and belowground nitrogen is key to breaking single-species dominance and maintaining understory functional stability.

5. Conclusions

In the karst region of the Liujiang River Basin, *Bidens pilosa* and *Miscanthus floridulus* became dominant species in plantation understory communities by virtue of their trait plasticity in adapting to dual environmental filters. When understory light availability and soil total nitrogen became limiting factors, intensified environmental filtering limited the relative abundance of subordinate species, which further consolidated the dominant status of these two species. Community-level functional traits shift toward a conservative adaptive strategy, leading to a reduction in community functional diversity. Although a decline in functional diversity is generally regarded as negative feedback, such community dynamics possess certain ecological significance in resource-poor karst habitats.

In environments where the growth of other species is limited, the strong adaptability of *Bidens pilosa* and *Miscanthus floridulus* is critical for sustaining basic understory biomass and material cycling. Karst plantation management should optimize canopy gaps and apply targeted soil nitrogen. This approach helps break the absolute dominance of single species and sustains the functional stability of understory communities. Furthermore, future research should explore broader precipitation gradients to explore the complex environmental filters shaping understory community assembly in karst plantations.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f17091083/s1>, Table S1: Geographic information and stand age of different plantations; Table S2: Functional traits of various understory species.

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