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Impact of Selected Environmental Factors on Variation in Leaf and Branch Traits on Endangered Karst Woody Plants of Southwest China

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Abstract: We explored the adaptability of endangered plants in degraded karst habitats through functional trait variation, using three endangered woody plants (*E. cavaleriei*, *H. bodinieri* and *K. septentrionalis*) in karst peak-cluster depression. We investigated the variation decomposition and correlation analysis of 13 branch and leaf functional traits using a mixed linear model, variance decomposition, Pearson's correlation analysis, random forest regression, and generalized linear regression. The degree of variation in phosphorus concentration in the branches was the highest, while that in the carbon concentration in the leaves was the smallest. The variation in the carbon concentration in the branches and leaves, and the dry matter concentration in the leaves was mainly within species, while the variation in other functional traits was mainly between species. We found significant correlations among leaf traits, branch traits, and leaf–branch traits to different degrees; however, there were no significant correlations among branch traits in *H. bodinieri*. The significant correlations were higher in *E. cavaleriei* and *K. septentrionalis* than in *H. bodinieri*. Plant functional traits were influenced by soil and topographic factors, and the relationship between them varied by species. Our findings will enhance our understanding of the variation in leaf and branch traits in karst endangered plants and the adaptive strategies of endangered plants in degraded habitat, and will provide a scientific basis for vegetation conservation in the karst region of southwest China.

Keywords: endangered plants; leaf trait; random forest; community assembly; karst ecosystem



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1. Introduction

Plant traits refer to the ecological and physiological indicators related to the use of light, heat, water, and other external resources by plants. As a link between plants, the environment, and the ecosystem, plant traits can reflect physiological or evolutionary trade-offs among different plant functions and adaptation strategies to different environments [1,2]. Leaf, stem, and root traits do not only show the variation in traits among species, habitat, and resource use, but also the association or combination of traits that show the trade-off strategy of “investment income” in environmental adaptation [2–9]. Studies on plant traits from the individual to the global scale have found that intraspecific and interspecific trait variation within functional groups and communities, and that between communities can strongly reflect the response of different species to limited resource competition and

changes in environmental factors [3]. Interspecific variation and intraspecific trait variation are important factors affecting species coexistence and community composition [10,11].

Variation in plant traits is also influenced by the interaction between the habitat and organisms. A series of species with similar functional traits suitable for a specific environmental condition can be filtered out through environmental screening, leading to the convergence of traits of the coexisting species in the community. Meanwhile, competitive exclusion of highly similar species in communities reduces niche overlap between species. It can also alleviate resource competition pressure, leading to character divergence of community species in similar habitats [12]. The range of variation in functional trait values is the result of a combination of environmental filtering with a reduced range of trait change and limiting co-existing species, and niche differentiation with an increased range of trait change that is induced by competition [13,14]. Previous research has demonstrated that light and water are the main limiting factors in tropical and arid forests, respectively, and their community assembly mechanisms differ completely [15]. Therefore, it is necessary to examine the mechanisms of community assembly in different regions.

The karst region in southwest of China is approximately 540,000 km², and primarily comprises evergreen broad-leaved forest and seasonal rainforest. Due to human disturbance, most of the evergreen and deciduous broad-leaved mixed forests and seasonal rainforests growing on limestone and dolomite in the region have been degraded into secondary forest and shrubland vegetation [16]. In recent years, with the implementation of large ecological projects such as the Grain for Green Program (GGP) by the government of the People's Republic of China, a reduction in stony desertification and an increase in vegetation restoration has been achieved [17]. However, agricultural activities of the local farmers have led to the continued loss of soil nutrients and soil water in the karst region [18]. Meanwhile, the rate of shrubland succession to climax forest is decreasing due to severe seasonal drought and supply constraints from soil nutrients [19]. Endangered plant species in the karst region have attracted considerable attention because of their narrow distribution ranges, small viable population sizes, and their high social, economic, and scientific value. The ecophysiological characteristics and population regeneration of endangered species has been extensively studied [20,21]. However, studies on the variation in plant traits and the correlation among traits of endangered species in karst regions have been limited, restricting the development of conservation measures for endangered plant populations. Improving the understanding of endangered plant traits in karst microhabitats is fundamentally important for plant conservation in degraded karst ecosystems of southwest China.

Although some previous studies by our research group which mainly engaged in karst ecological restoration and community dynamics research have examined the relationship between vegetation and karst environmental factors [18,22–24], there are few reports on variation in traits of endangered plant. In long term evolution, plants reduce the adverse effects from the environment by forming specific combinations of functional traits [25]. We hypothesized that (1) the interspecific variation (caused by species identity) is greater than intraspecific variation (site specific); (2) the trade-offs of leaf and branch functional traits varied by different endangered species in karst degraded habitats. Therefore, in this study, we examined the degree of variation in leaf and branch traits and the relationship between plant traits of different endangered species to address the following questions: (1) What is the degree and proportion of interspecific and intraspecific trait variation in endangered species? (2) What are the plant traits and their interrelationships in endangered species? (3) What is the relationship between the functional traits of endangered species and environmental factors? We aim to reveal the adaptability of endangered plants to degraded habitat in karst regions and to provide a scientific basis for in situ conservation of endangered plants.

2. Materials and Methods

2.1. Research Site

The research site is in Bannan, Xiabai, and Dongjiang village ($107^{\circ}51'–108^{\circ}43'$ E, $24^{\circ}44'–25^{\circ}33'$ N, 400–600 m above sea level), Chuanshan town, Huanjiang county, west of Guangxi province, which is the location of the Mulun National Nature Reserve, China (Figure 1). According to the records from the weather station in Huanjiang county from 1961 to 2020, the average annual temperature is 15.7°C , and that in January and July is 10.1 and 28.0°C , respectively. The annual precipitation is 1389 mm and the annual sunshine time is 4422 h. The parent rock is limestone. Karst is mainly distributed in the southwest of the county. The soil is mainly dark or brown calcareous soil with well-developed carbonate rocks. The region is characterized as a subtropical mixed evergreen deciduous broadleaf forest, that the plot contained 6754 living, woody plant individuals belonging to 34 families, 87 genera, and 109 species dominated by *Itoa orientalis* Hemsl., *Cornus macrophylla* Wall. and *Bridelia tomentosa* Blume. Importantly, *Eurycorymbus cavaleriei* (H. Lévl.) Rehder and Hand-Mazz., *Handeliodendron bodinieri* (H. Lévl.) Rehder and *Kmeria septentrionalis* Dandy belong to the families Sapindaceae, Sapindaceae, Magnoliaceae and genera *Eurycorymbus*, *Handeliodendron*, *Kmeria*, respectively, which are endemic to China (Figure 1, Table S1). It is a rare and endangered species distributed in karst regions in southwest China (transition from subtropical to subtropical). In 1999, they were listed as key protected plant in China [26–28].

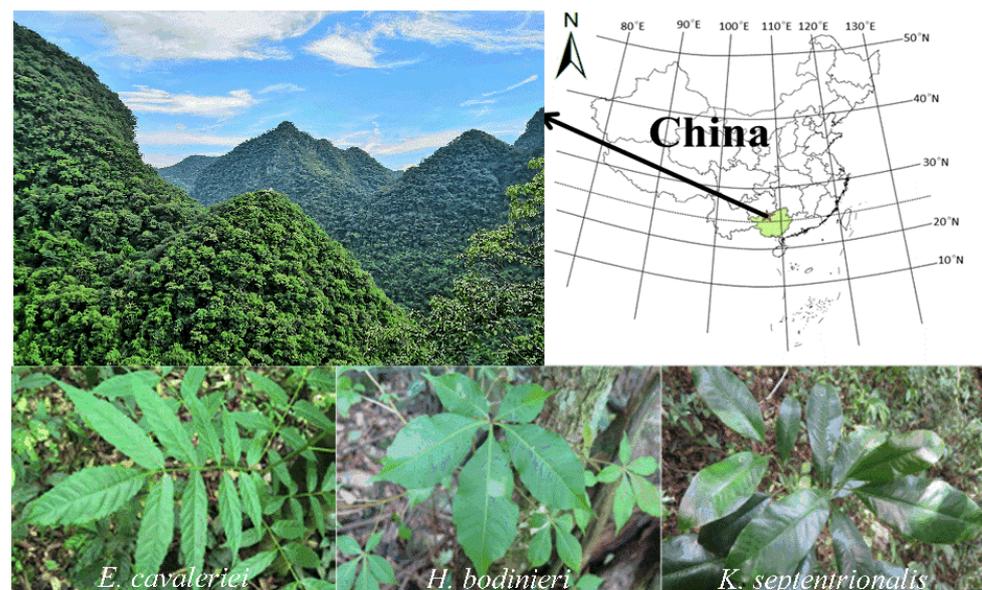


Figure 1. The field site in this research (the Mulun National Nature Reserve, China; Photo by Hu Du).

2.2. Field Survey

From July to September 2021, 42 ($20\text{ m} \times 20\text{ m}$) quadrats were set up in karst peak-cluster depression (Figure 1) and each quadrat was further divided into 16 sub-quadrats of $5\text{ m} \times 5\text{ m}$. Based on the standard field protocol of the Center for Tropic Forest Sciences (CTFS), the diameter at breast height (DBH), height, and the crown width of all woody plants with $\text{DBH} \geq 1\text{ cm}$ in the quadrat were investigated and the species, quantity, height, and growth status of the shrubs and herbs were recorded. The global positioning system (GPS) (E640 + MobileMapper) was used to record the longitude, latitude, altitude, and other geographic information of the inner center of the sample square, as well as to record the slope direction, slope position, slope, rock exposure rate, and soil thickness [29].

2.3. Measurement of Leaf and Branch Traits

A total of 126 individuals of three endangered species (*E. cavaleriei*, *H. bodinieri* and *K. septentrionalis*) formed the research focus, with four intact branches and 20–30 leaves being collected from each tree. Thirteen traits reflecting the ecological strategies of the woody plant species were measured, namely the (i) leaf area (LA, cm²), which is crucial for leaf energy, water balance, as well as tolerance to environmental stress, with smaller leaves generally being observed in drier and more exposed conditions. (ii) Leaf thickness (LTH, mm) reflects the strategies of the species for resource acquisition and use, especially of light, water, and nutrients. (iii) Specific leaf area (SLA, cm²·g⁻¹) indicates a trade-off between an investment in the leaf surface area to capture light for photosynthesis and an investment in constructing more protective tissues to avoid dehydration and herbivory. (iv) Leaf dry matter concentration (LDMC, g·g⁻¹) reflects plant resource acquisition ability and leaf tissue construction. (v) Leaf aspect ratio (L/D) is associated with photosynthesis. (vi) Leaf tissue density (LTD, g·cm⁻³) characterizes the trade-off between water transport and structural input of the leaf network. (vii) Wood density (WD, g·cm⁻³) is associated with nutrient transport. (viii) Leaf nitrogen concentration (LTN, mg·g⁻¹) is the total amount of nitrogen per unit of leaf dry mass. (ix) Leaf phosphorus concentration (LTP, mg·g⁻¹) is the total amount of phosphorus per unit of leaf dry mass. (x) Leaf carbon concentration (LTC, mg·g⁻¹) is the total amount of carbon per unit of leaf dry mass. (xi) Branch nitrogen concentration (BTN, mg·g⁻¹) is the total amount of nitrogen per unit of branch dry mass. (xii) Branch phosphorus concentration (BTP, mg·g⁻¹) is the total amount of phosphorus per unit of branch dry mass. (xiii) Branch carbon concentration (BTC, mg·g⁻¹) is the total amount of carbon per unit of branch dry mass. The concentrations of carbon, nitrogen, and phosphorus are directly involved in biochemical and geochemical cycles.

The measurement methods for these plant traits were as follows: With the petioles cut off, LA and L/D were measured using a scanner (Yaxin-1241, Yaxin, China) and image processing software (ImageJ, MD, USA). The LTH was measured using vernier calipers (SF2000, Guilin, China). During the measurement, the edges of the five leaves were aligned, and the main and secondary veins were avoided as far as possible. The values of the upper, middle, and lower parts of the leaves were recorded and then the mean values of the thickness at different positions of the five leaves were estimated as LTH. The fresh weight of the leaves was weighed using a balance (BSM-220.4, Zhuojing, China) with an accuracy of 1/1000. The dry weight of the leaves was weighed after subsequently drying the leaves in an oven at 105 °C for 30 min, and then dried till they reached a constant weight at 70 °C for 48 h. The ratio of the leaf dry weight to the leaf fresh weight was recorded as LDMC, the ratio of leaf area to leaf dry weight was denoted as SLA, and the ratio of leaf fresh weight to leaf volume (product of LA and LTH) was denoted as LTD. The ratio of dry weight to the volume of the branches was denoted as WD. The carbon, nitrogen, and phosphorus concentrations of dried leaves and branches were measured in a laboratory.

2.4. Soil Sampling and Measurement

We measured 12 environmental factors, including soil organic matter (SOM), soil pH (pH), soil total nitrogen (STN), soil available nitrogen (SAN), soil total phosphorus (STP), soil available phosphorus (SAP), soil total potassium (STK), soil available potassium (SAK), altitude (Ele), aspect (Asp), slope (Slo), and rock exposure (Roc). The soil was sampled using the “plum flower pattern”. After removing the surface litter and humus layer from the four vertices and centers of each 20 m × 20 m quadrat, 1 kg of surface soil sample (0–20 cm depth) was drilled using an earth drill and then mixed evenly using the quartering method. The samples were put into sealed bags and taken back to the laboratory to determine the soil chemical properties. Following collection, the fresh soil samples were placed in a cool and ventilated condition indoors for natural air drying. After air drying, the roots, stones, animal and plant residues, and other sundries were removed and the soil sample was finely grinded using a mortar. Soil samples with different pore sizes (0.15, 0.25, and 1.4 mm) were analyzed and measured. Soil pH was determined in a 1: 5 soil-water

slurry using a combination glass electrode, SOM was determined by the chloride potassium dichromate volumetric-external heating method, STN was determined by the semi-micro Kjeldahl determination of nitrogen method, STP was determined by sodium hydroxide (NaOH) fusion-ammonium molybdate spectrophotometry, STK was determined by NaOH fusion-flame spectrophotometry, SAN was determined by the diffusion-absorption method, SAP was determined by NaHCO₃ extraction-ammonium molybdate spectrophotometry, and SAK was determined by (NH₄)₂CO₃ extraction-flame spectrophotometry [30]. Each soil sample was repeated three times and its average was used for data analysis.

2.5. Statistical Analysis

The coefficient of variation ($CV = (\text{standard deviation } SD / \text{mean } M) \times 100\%$) was used to calculate the degree of interspecies and intraspecies variation in plant traits. The LTH was taken as an example to illustrate the calculation of the intraspecific and interspecific variation coefficient. The first step was to calculate LTH mean and LTH standard deviation for each species, and then obtain the intraspecies coefficient of variation using the variation calculation formula. The mean and standard deviation between the species was calculated using the results from the first step, and the interspecies coefficient of variation was subsequently calculated.

All the variables were checked for normality and transformed by applying logarithms or square roots where required. To explore the variance components of the plant traits at two different scales (species and individual), we fitted a linear mixed model using a restricted maximum likelihood method to quantify the variance of plant traits across two scales nested with each other using nested analysis of variance [ANOVA] with random error at the individual and species scales. We used a variance component analysis on this model based on the varcomp function of R. The ratio between the variance components represents the proportional contribution of the change at each scale. Pearson's correlation analysis was used to test the correlation between the plant traits in the three endangered species, and Student's T test was used to analyze the correlation.

The relationship between the plant traits and the environmental factors was analyzed using a generalized linear model and a random forest model. Twelve environmental indicators were used as independent variables and thirteen traits were used as dependent variables. The optimal model was selected according to the AIC value, the model determination coefficient (R^2), and p -value. All the statistical analyses were computed on R 4.1.1, using the libraries nlme, ade, and randomForest.

3. Results

3.1. Variation in the Leaf and Branch Traits of Karst Endangered Plants

The general characteristics of the three endangered woody plants in the karst region are shown in Table 1. The LA, WD, BTP, and LP varied considerably, ranging from 4.496 to 167.336 cm², 0.073 to 0.764 g·cm⁻³, 0.034 to 0.348 mg·g⁻¹, and 0.011 to 0.273 mg·g⁻¹, respectively. For the species, LN, LP, LC, BTN, and BTP among different plants were as follows: *E. cavaleriei* > *H. bodinieri* > *K. septentrionalis*, while LA and LTH in three endangered species showed the opposite trend (*K. septentrionalis* > *H. bodinieri* > *E. cavaleriei*). Among the three endangered plants, LTD, L/D, and LDMC were the highest in *E. cavaleriei* and the lowest in *H. bodinieri*. The BTC and WD were the highest in *H. bodinieri* and the lowest in *K. septentrionalis* (Figure 2).

As shown in Table 1, the overall variation coefficient of the 13 plant traits ranged from 4.12 to 85.06%, and the degree of variation for different plant traits was different. Among these traits, the degree of variation for BTP was the largest, while that for LC was the smallest. The mixed effects model was used to analyze the relative contribution of species to the variation in the 13 plant traits. The interspecific and intraspecific effects on the variation in the 13 plant traits were different (Figure 3). The main sources of interspecific variation in WD, LA, LN, LP, L/D, LTH, SLA, BTN, and BTP were 94.31%, 88.26%, 74.19%, 84.32%, 60.04%, 67.72%, 55.80%, 58.24%, and 67.17%. Among these traits, the variation in

BTC, LC, and LDMC were mainly derived within the species, which were 61.44%, 59.52%, and 52.54%, respectively. The LTD variation was similar between species (43.39%) and within species (48.94%). Interspecific variation (60.98%) was higher than intraspecific variation (33.25%), and interspecific variation was the main source of the variation in the plant traits.

Table 1. Descriptive statistics characteristics for functional traits of three endangered plants.

Traits	Mean \pm SD	Minimum	Maximum	Coefficient of Variation (%)
Leaf area (cm ²)	64.440 \pm 47.842	4.496	167.336	74.24
Specific leaf area (cm ² ·g ⁻¹)	147.120 \pm 56.114	57.940	463.125	38.14
Leaf thickness (mm)	0.193 \pm 0.064	0.080	0.378	32.92
Leaf tissue density (g·cm ⁻³)	0.416 \pm 0.134	0.130	0.825	32.23
Leaf length–width ratio	2.712 \pm 0.490	1.688	5.164	18.07
Leaf dry matter content (g·g ⁻¹)	0.402 \pm 0.087	0.229	1.175	21.73
Leaf nitrogen concentration (mg·g ⁻¹)	1.992 \pm 0.723	1.140	4.970	36.28
Leaf phosphorus concentration (mg·g ⁻¹)	0.098 \pm 0.055	0.034	0.348	56.20
Leaf carbon concentration (mg·g ⁻¹)	40.690 \pm 1.678	36.100	44.800	4.12
Branch nitrogen concentration (mg·g ⁻¹)	0.875 \pm 0.399	0.380	2.230	45.64
Branch phosphorus concentration (mg·g ⁻¹)	0.061 \pm 0.052	0.011	0.273	85.06
Branch carbon concentration (mg·g ⁻¹)	45.016 \pm 2.697	37.800	49.500	5.99
Wood density (g·cm ⁻³)	0.288 \pm 0.189	0.073	0.764	65.70

3.2. Trade-Off in the Plant Traits of Karst Endangered Plants

Our research found that there were different significant correlations among leaf traits, branch traits, and leaf–branch traits. Pearson’s correlation showed that, in *E. cavaleriei*, for leaf traits, LA was significantly correlated with LTH, SLA, LTD, and LP (Figure 4A). LTH had a significant negative correlation with LTD. SLA had a significant positive correlation with LP, and a significant negative correlation with LTH. For the branch traits, BTN was positively correlated with BTP. The WD had a significant negative correlation with BTN and BTP. For the leaf and branch traits, SLA had a significant positive correlation with BTN and BTP. BTC had a significant positive correlation with LC and LDMC. WD was significantly or extremely significantly correlated with LN, LP, and LA. There was a significant negative correlation between LN and BTC. LP had a significant positive correlation with BTN and BTP.

In *H. bodinieri*, for the leaf traits, LA was positively correlated with LTH only (Figure 4B). There was no significant correlation between the branch traits. For the leaf and branch traits, there was a significant negative correlation between LDMC and BTN. LN was only negatively correlated with BTP.

In *K. septentrionalis*, for the leaf traits, LA was positively correlated with SLA only (Figure 4C). There was a significant negative correlation between LTH and LTD. SLA was negatively correlated with LDMC and LTD. There was a significant positive correlation among LN, LP, and LC. For the branch traits, BTN was positively correlated with BTC and WD. There was a significant negative correlation between BTP and BTC. For the leaf and branch traits, BTC was significantly positively correlated with LTH, and negatively correlated with LTD, L/D, LP, and LC. There was a significant positive correlation between LP and BTP, and a significant negative correlation between LTD and BTN.

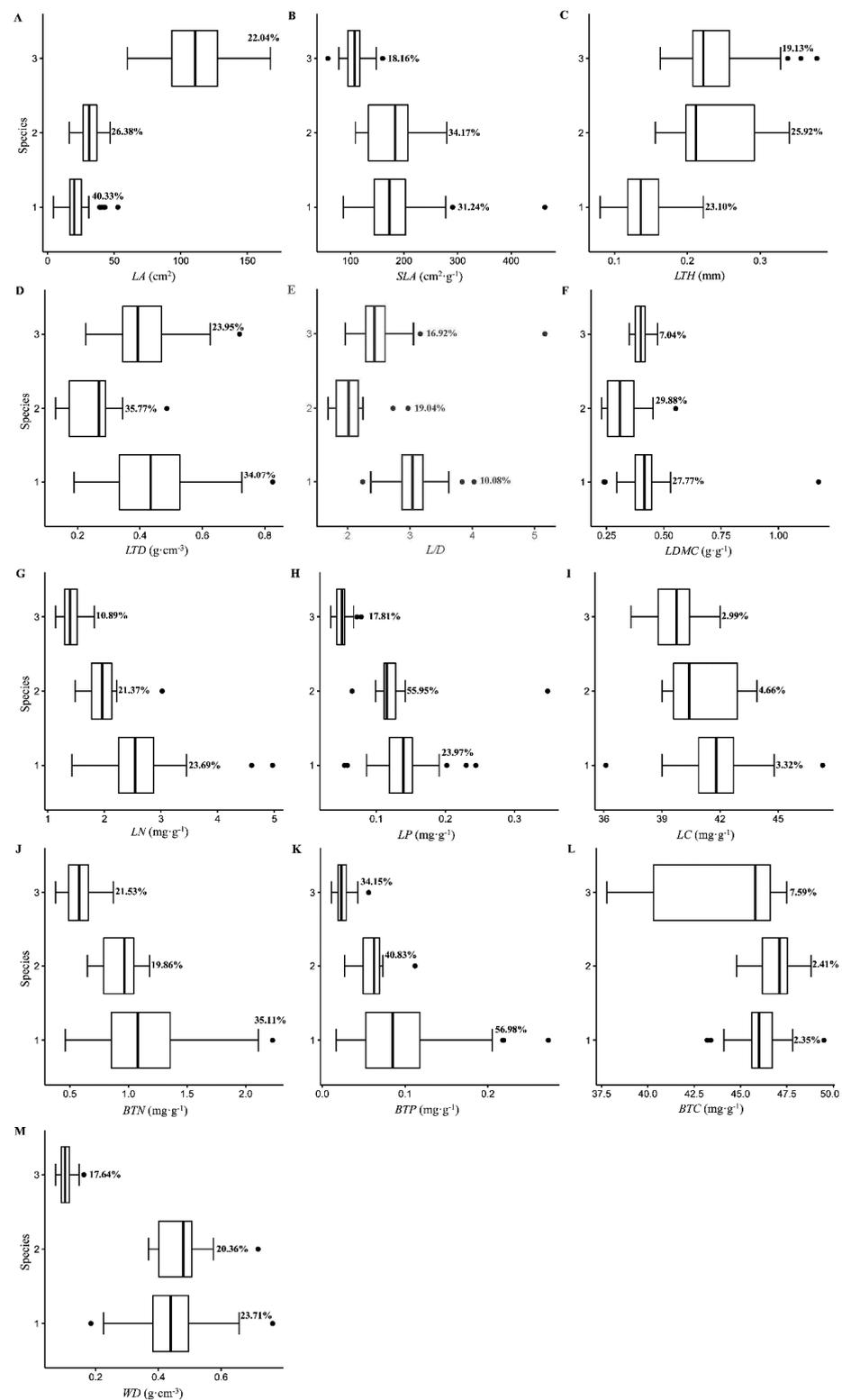


Figure 2. Boxplot of plant functional traits value of karst endangered plants, southwest China. (A) LA, leaf area; (B) SLA, specific leaf area; (C) LTH, leaf thickness; (D) LTD, leaf tissue density; (E) L/D, leaf aspect ratio; (F) LDMC, leaf dry matter content; (G) LN, leaf nitrogen concentration; (H) LP, leaf phosphorus concentration; (I) LC, leaf carbon concentration; (J) BTN, branch nitrogen concentration; (K) BTP, branch phosphorus concentration; (L) BTC, branch carbon concentration; (M) WD, wood density. The ordinate represents the name of the species, the species number: 1, *E. cavaleriei*; 2, *H. bodinieri*; 3, *K. septentrionalis*.

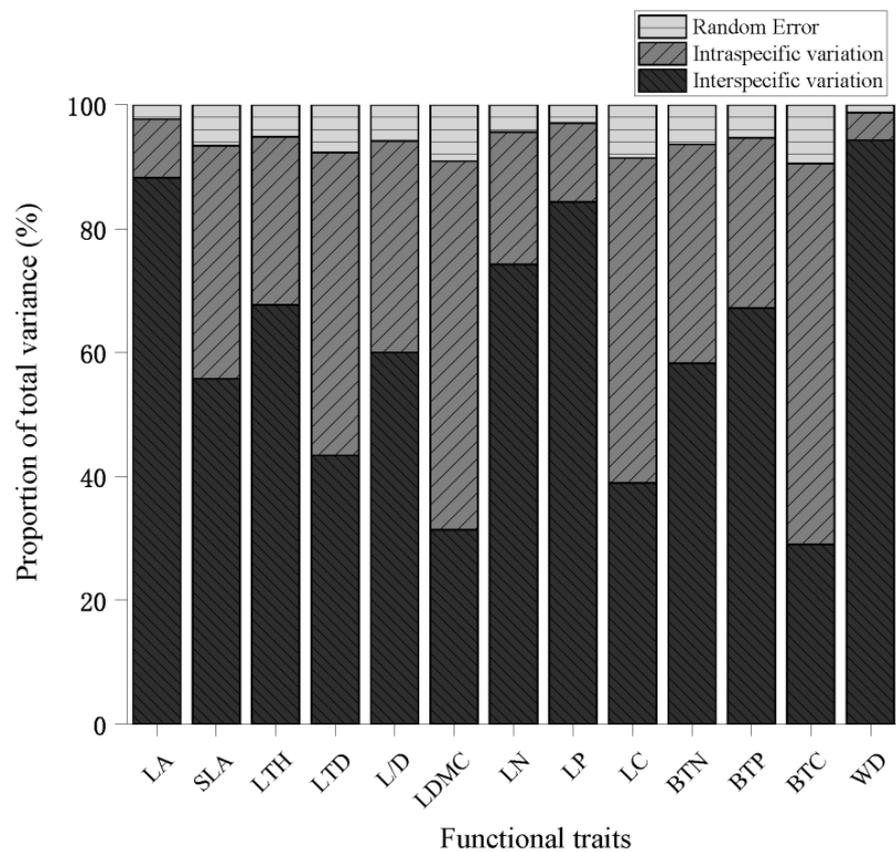


Figure 3. Variance partitioning of different functional traits at interspecific and intraspecific scales. The abbreviations of plant functional traits are shown in Figure 2.

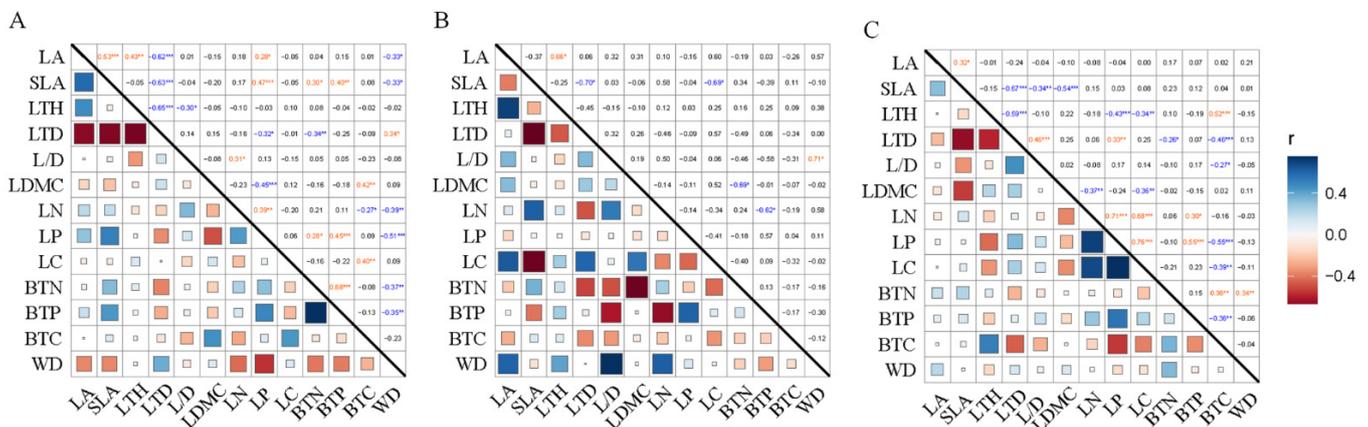


Figure 4. Pearson’s correlation coefficients between plant functional traits of the three endangered plants (A) *E. cavaleriei*, (B) *H. bodinieri* and (C) *K. septentrionalis*. The abbreviations of plant functional traits are shown in Figure 2. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

3.3. Relationship between the Karst Environment and Variation in Leaf and Branch Traits

The cumulative importance of different environmental factors on plant traits was obtained based on the random forest model. Plant functional traits were predominantly significantly affected by soil pH, STP, and Ele (Figure 5), and the order of importance was Ele (IncMSE = 227.73) > STP (IncMSE = 210.87) > soil pH (IncMSE = 210.46). The plant traits of the three endangered plants were affected differently by environmental factors (Figure S1). The cumulative importance of environmental factors on plant functional traits decreased. The plant traits in *E. cavaleriei* were mainly affected by STK (IncMSE = 77.07),

SOM (IncMSE = 77.04), STP (IncMSE = 73.61), and SAN (IncMSE = 72.91). The plant traits in *H. bodinieri* were predominantly affected by SAP (IncMSE = 11.16) and SAK (IncMSE = 13.70). The plant traits in *K. septentrionalis* were mainly affected by SAK (IncMSE = 47.62), STN (IncMSE = 47.27), STK (IncMSE = 45.81), and SOM (IncMSE = 42.32).

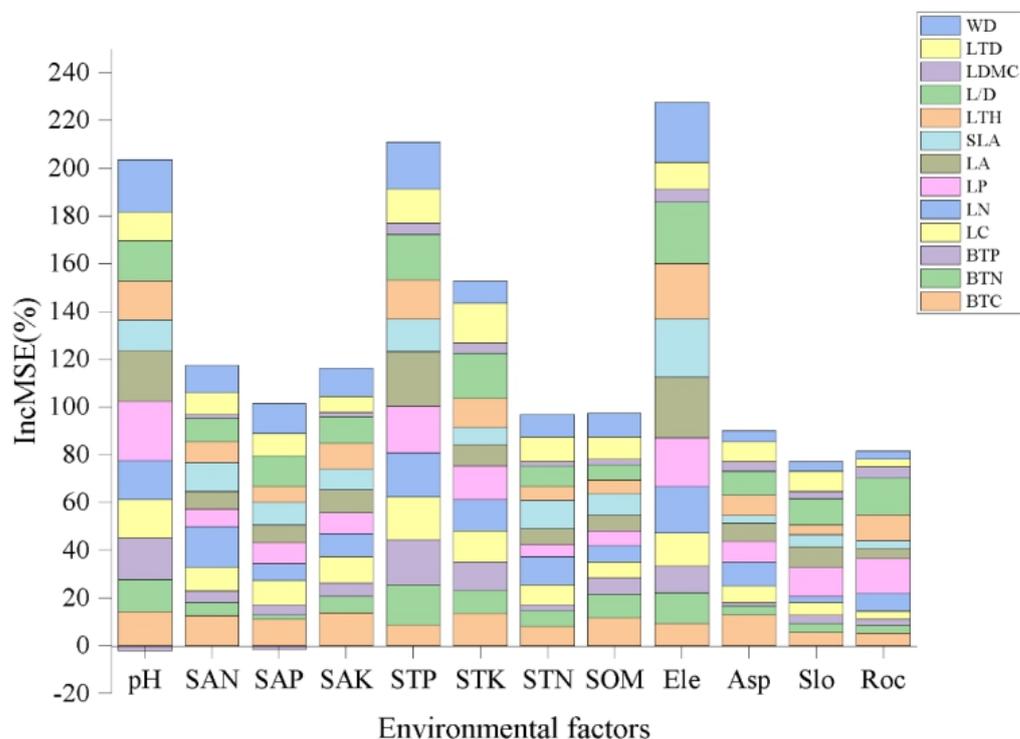


Figure 5. The relative accumulated importance of environmental factors in a random forest model.

Based on the generalized linear model, plant traits were affected by soil factors and topographic factors (Table 2). BTP and WD were affected by environmental factors. BTP was affected by STP ($R^2 = 0.49, p < 0.05$), and WD was affected by Ele ($R^2 = 0.79, p < 0.05$). Among leaf functional traits, LA was significantly affected by soil pH, SAN, STP, STK, Ele, Slo, and Asp ($R^2 = 0.92, p < 0.05$). LTH was affected by SAN and Asp ($R^2 = 0.62, p < 0.05$), and SLA was affected by STN, STK, and Ele ($R^2 = 0.42, p < 0.05$). LN was affected by soil pH, SAN, STN, STK, and Asp ($R^2 = 0.66, p < 0.05$). LP was affected by SAN, STN, STP, Ele, Asp, and Roc ($R^2 = 0.73, p < 0.05$).

Table 2. Relationship between endangered plant traits and environmental factors in karst region using a GLM model.

Traits	Enviornmental Factors	Wald χ^2	df	Sig.	R ²	p
LA	pH	20.366	1	0.000	0.92	<0.05
	SAN	10.007	1	0.002		
	STP	9.702	1	0.002		
	STK	10.813	1	0.001		
	Ele	19.379	1	0.000		
	Asp	39.77	6	0.000		
	Slo	14.432	1	0.000		

Table 2. Cont.

Traits	Environmental Factors	Wald χ^2	df	Sig.	R ²	p
SLA	STN	4.005	1	0.045	0.42	<0.05
	STK	5.47	1	0.019		
	Ele	5.914	1	0.015		
LTH	SAN	5.363	1	0.021	0.62	<0.05
	Asp	18.636	6	0.005		
LTD	SAN	6.483	1	0.011	0.28	<0.05
	STN	6.755	1	0.009		
	STK	8.663	1	0.003		
L/D	SAN	13.914	1	0.000	0.50	<0.05
	STN	10.535	1	0.001		
	STK	7.857	1	0.005		
	SOM	4.304	1	0.038		
	Asp	22.074	6	0.001		
	Slo	8.346	1	0.004		
LDMC	—	—	—	—	0.11	NS
LN	pH	5.243	1	0.022	0.66	<0.05
	SAN	12.446	1	0.000		
	STN	1.639	1	0.200		
	STK	4.972	1	0.026		
	Asp	16.392	6	0.012		
LP	SAP	9.774	1	0.002	0.73	<0.05
	STN	4.124	1	0.042		
	STP	20.765	1	0.000		
	Ele	13.888	1	0.000		
	Asp	17.929	6	0.006		
	Roc	16.881	1	0.000		
LC	—	—	—	—	0.49	<0.05
BTN	—	—	—	—	0.47	<0.05
BTP	STP	7.963	1	0.005	0.49	<0.05
BTC	—	—	—	—	0.17	NS
WD	Ele	13.737	1	0.000	0.79	<0.05

4. Discussion

4.1. Variation in Leaf and Branch Traits in Karst Endangered Plants

Results of linear mixed model analysis of all traits showed, the total variation range of 13 traits was 4%–85%, and the variation coefficient of carbon, nitrogen and phosphorus in the branches was higher than that in the leaves (Table 1). Chemical functional traits were related to photosynthetic rate and nutrient cycling [31]. The branches were used as nutrient transport organs to transport carbon, nitrogen, and phosphorus to the leaves. Empirical studies have reported on the response of chemical properties to high variability of nitrogen and phosphorus in the branches and leaves [32]. Our data also showed a high degree of variability in nitrogen and phosphorus, which is in line with previous research findings. In contrast, the variation in carbon in the leaves and branches was lower than that

in the nitrogen and phosphorus (Table 1). Plant traits are determined by genetic factors, environmental conditions, and their interaction. The low variability of carbon may be due to carbon being more stable in plants [33]. Our finding that, for the leaf traits, the leaf area had the highest coefficient of variation and the highest proportion of interspecific variation, which was consistent with previous results [34,35]. This indicates that the leaf area is closely related to photosynthesis and transpiration and is more variable than other traits as the main component of plant carbon sequestration and resource acquisition. For the branch traits, the proportion of interspecific variation in WD was higher than the intraspecific variation, which was consistent with the findings of Rosell et al. (2014) [36], but contrary to the findings of Zhang and Yu (2018) [37]. This indicates that interspecific variation and intraspecific variation are different under different conditions, and our results only reflect the adaptation of the three endangered plants to the environmental heterogeneity in karst areas.

A total of 13 functional traits in the three endangered plants were found to have varying degrees of intraspecific and interspecific variation (Figure 3). Interspecific variation has played a dominant role in the variation in plant functional traits; however, increasing evidence demonstrates that intraspecific variation should not be excluded, given that it accounts for 28%–52% of the total variation in plant functional traits [38,39]. Intraspecific variation in traits may be due to genetic variation between conspecifics or phenotypic plasticity under different environmental conditions [3,40]. The variance decomposition results in this research showed that the main source of variation in plant functional traits was interspecific, but there were still a few species where intraspecific variation was greater than interspecific variation (Figure 3). Intraspecific variation in SLA, LDMC, and LTD in the three endangered plants was higher than that of the karst woody plants, while LTH and LA were lower than that of the karst woody plants [41]. These differences between different research data may be due to the different plant species and heterogeneous habitats in karst areas. Therefore, if intraspecific variation is excluded and only interspecific functional traits are considered, the phenotypic plasticity resulting from intraspecific individual genotype variation and habitat heterogeneity will be severely underestimated.

4.2. Trade-Offs between Branch and Leaf Traits in Karst Endangered Plants

The effects of physiological, phylogenetic, environmental, and other factors likely play a key role in plant growth and long-term adaptation to the environment [42,43]. Plant traits have a certain correlation, which form a series of optimal functional trait strategies suitable for the specific environment. Due to the functional trade-offs in resource allocation, the strategy of each organ may lead to a combination of related traits [44]. In this study, the significant correlation of leaf traits was not consistent among the different species. In *E. cavaleriei* and *H. bodinieri* (Figure 4A,B), LA had a significant positive correlation with LTH. This may be because the leaves of *E. cavaleriei* and *H. bodinieri* are papery, and LTH should correspondingly increase when LA increases to make the leaf shape stretch and stay upright. LTH is related to defense, degradation, and nutrient cycling of the leaf. When LA increases, the corresponding LTH should also increase to satisfy the physiological and biochemical processes of the leaf [45]. However, in *K. septentrionalis*, LA had no significant correlation with LTH. Its leaves are leathery and have thick cell walls, which may not require an increase in LTH to maintain their leaf shape [46].

LN and LP are important traits related to photosynthesis, which are highly coordinated among different species [47]. LN and LP were significantly positively correlated in *E. cavaleriei* and *K. septentrionalis*, (Figure 4A,C), which was consistent with recently studies on LN and LP in tropical rainforest and global plant species [44,47]. However, *H. bodinieri* showed no significant correlation between LN and LP. The different correlations between LN and LP in different species implies that different species have different nutrient requirements, which may due to the different biochemical structures and specific physiological metabolic processes among different species [48].

Additionally, SLA was significantly negatively correlated with LTD, and LA was significantly positively correlated with SLA in *H. bodinieri* and *K. septentrionalis* (Figure 4). Previous studies have shown that plants have a strategy of lower SLA, LA, and larger LTD under seasonal soil water conditions in karst areas. Lower SLA and LA in karst plants may reduce transpiration and retain water, thereby maintain a lower growth rate, and higher LTD may support nutrient storage.

Our finding has showed that LA was significantly negatively correlated with WD in *E. cavaleriei* (Figure 4A), which was consistent with previous studies [4]. Larger leaves may capture more nutrients; therefore, species with larger leaves can grow faster and have lower WD [5]. Meanwhile, the relationship between LN and BTP in *H. bodinieri*, *K. septentrionalis*, and *E. cavaleriei* was significantly negative, significantly positive, and no significant correlation, respectively. Endangered plants are more susceptible to the harsh karst habitat conditions. Different species may have different nutrient allocation strategies, leading to different synergistic relationships of branch and leaf traits [49]. LP and BTP were positively correlated in *E. cavaleriei* and *K. septentrionalis*. This indicates that the nutrient content of leaves needs to be kept relatively stable, and branches play an important regulatory role in stabilizing the nutrient content [31]. Therefore, when leaves grow rapidly, a large amount of phosphorus is needed to maintain their biochemical processes, and branches act as transport organs to satisfy the needs of leaves for phosphorus [50].

The traits in this study included both leaf and branch traits. However, root traits were not involved, mainly due to the plant species that formed the focus of this study being endangered. The roots of endangered plants cannot be destroyed for analysis to ensure their growth, development, and reproduction. The trade-off between the traits of different organ in endangered plant species will be investigated in future studies and will involve the development of a root sampling method that can be implemented with no or minimal damage to the plants.

4.3. Relationship between Endangered Plant Traits and Environmental Factors in the Karst Region

The difference in plant functional traits is not only related to their own growth characteristics, but is also closely related to external environmental factors. In this study, branch and leaf traits were closely related to environmental factors such as soil factors and terrain factors. Altitude, STP and soil pH were important factors affecting the branch and leaf traits (Figure 5). This result indicates that the change of altitude led to changes in the combination conditions of water and heat, which affected the light and water acquisition of plants, thereby affecting the variation in plant traits to ensure an efficient survival strategy [51,52]. Zeng et al. (2016) [53] studied the stoichiometric characteristics of plants in karst areas in northwest China and concluded that there was a phosphorus deficit in karst forests. The phosphorus in plants mainly comes from rock weathering. However, the seasonal drought in karst areas is not conducive to rock weathering, and reduces the phosphorus available to plants from the source, resulting in low soil phosphorus content. Therefore, STP is an important factor affecting the variation in plant functional traits [31,53]. Soil pH influences variation in functional traits, which is consistent with Both et al. (2019) [54] and Tao et al. (2019) [55]. This may be due to the direct effect of soil pH on the conversion of elements in the soil, affecting the turnover and availability of key mineral nutrients for plant growth, especially nitrogen and phosphorus [40,56].

Plant traits are strongly correlated with resource acquisition strategies and can be classified along important resource axes [57,58]. Our finding has showed that STN had no significant effect on LN and BTN. However, LP and BTP were significantly affected by STP (Figure S2). This may be due to the abundant nitrogen sources in plants, which may be obtained from the atmosphere and the soil, whereas most of the phosphorus in plants is only from the soil derived from rock weathering [32]. Additionally, LA and SLA were significantly affected by Ele, which was consistent with previous studies [33]. With the increase in altitude, plant functional traits tended to have smaller LA and lower SLA, and this strategy was beneficial to prevent water loss and resource consumption, making

plants well adapted to the resource-poor environment of karst areas [59]. Meanwhile, Sungpalee et al. (2009) [60] found that the altitude was more important, than the mean annual temperature and rainfall, in predicting the variation in WD. We also found that WD was significantly affected by altitude (Figure S2), which may be due to the direct influence of altitude on hydrothermal conditions. Different species have differences in the species' niches and adaptation strategies at different altitudes [61]. Plants become endangered due to internal and external factors. This study can be used to guide the scientific formulation of conservation measures for endangered plants by analyzing their biological characteristics and ecological adaptability.

5. Conclusions

The overall variation coefficient of the 13 plant traits ranged from 4.12 to 85.06%, and the degree of variation for different plant traits was different. Interspecific variation (60.98%) was higher than intraspecific variation (33.25%), and interspecific variation was the main source of the variation in the plant traits. There were different significant correlations among leaf traits, branch traits, and leaf–branch traits. Plant functional traits were predominantly significantly affected by soil (pH and STP) and topographic (Ele) factors, and the relationship between them varied by species. Our findings will enhance our understanding of the variation in leaf and branch traits in karst endangered plants and the adaptive strategies of endangered plants in degraded habitat, and will provide a scientific basis for vegetation conservation in the karst region of southwest China.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13071080/s1>, Figure S1, The relative accumulated importance of environmental factors among the 3 endangered plants; Figure S2, The relative importance of environmental factors in a random forest model; Table S1, The endangered plant catalogues.

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