Journal of Environment and Earth Science
ISSN 2224-3216 (Paper) ISSN 2225-0948 (Online)
Vol.4, No.8, 2014

The Response of Plant Species Diversity to the Interrelationships between Soil and Environmental Factors in the Limestone Forests of Southwest China

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Abstract

An understanding of the spatial patterns of plant diversity is essential in deciding conservation priorities. Identifying these patterns may rely on our ability to predict how species respond to environmental variables. The present study examined plant species diversity variations and their ecological correlates in the limestone forest of Longhushan Nature Reserve, SW China. Species diversity was examined using statistical analyses and modellings to establish its response to the single or combined influence of the environmental habitat factors. The results showed that variations in diversity were dependent on complex relationships between karst habitat factors. The geological factor played an important role as its inclusion in the analysis with soil and environmental factors greatly improved the overall predictability of plant diversity. Species diversity was significantly predicted ($F=13.330$, $p<0.001$) with over 79% of its variance explained by the model (adjusted $R^2=0.794$). Trends in diversity were mainly related to moisture, rock type in association with slope gradient and temperature. The influence of rock type was related to dolomite as diversity had a positive trend in high dolomite percentage areas and the inverse trend in calcium rich areas. The dominant species responded differently to the significant factors, but a number of those species were found typically well adapted to the special karst habitats. *Sterculia nobilis*, *Albizia chinensis*, *Ficus oligodon*, and *Psychotria rubra* were found adapted to all habitats conditions, suggesting they could be appropriate species for restoration and forest amelioration measures. It was clearly demonstrated that the evidence of significant variations in species diversity was provided after combining variables from soil, geological, and environmental factors, suggesting their interactions influence on plants.

Keywords: plant species diversity, rock type, soil characteristics, environmental factors, interactions, karst forest

1. Introduction

The Earth's geology, landforms, soils and the natural processes that sustain them represent the corner stone upon which terrestrial biodiversity is dependent, as it is fundamental to the functioning of all natural terrestrial ecosystems. This is particularly essential to understand in karst areas like those of southeast Asia recognized as major foci for speciation and important biodiversity arks (Clements *et al*. 2006), were forests are becoming increasingly disturbed and fragmented (Sodhi *et al*. 2004; Laurance 2007).

Southeast Asian forests containing limestone karst systems are internationally recognized as areas of huge biological importance, with aesthetic qualities and groundwater value (Wong *et al*. 2003; Gillieson 2005). These areas support very high level of endemic species of plants, vertebrates and invertebrates (Vermeulen & Whitten 1999; Schilthuizen *et al*. 2005; Clements *et al*. 2006, 2008) and are recognized as a global priority for biodiversity conservation, containing four of the twenty-five biodiversity hotspots (Myers *et al*. 2000). However, plant diversity is threatened by rapidly changing land use patterns in tropical Asia (Sodhi *et al*. 2010) and it has been said that more effort should be made to document biodiversity in the region (Webb *et al*. 2010).

Plant community and biodiversity are believed to have a high degree of spatial variability that is controlled by both abiotic and biotic factors. Species diversity is an important component of the concept of biodiversity as it is a measure of the diversity within an ecological community that incorporates both species richness and the evenness of species' abundances. Many types of environmental changes may influence the processes that can both augment or erode diversity (*Sagar et al*. 2003). Hence, in searching to understand the factors that govern plant diversity and productivity, it makes sense to examine environmental variables that have direct influence on plant physiology and resource availability (Pausas & Austin 2001), or the effects of their interactions on plants. Many studies have suggested that soil properties have an important role in controlling the spatial patterns of vegetation (Sanford & Isicheir 1986; Jafari *et al*. 2004; Zuo *et al*. 2009). It has also been reported that the topographic features may explain most part of the species spatial variation in a particular climatic region (Palmer

& Dixon 1990; Shen *et al*. 2000; Liu *et al*. 2003; Ma *et al*. 2010). Topography is also known to have an important role in controlling the distribution of light, heat, moisture, and the strength and frequency of disturbance (McDonald *et al*. 1996; Shen *et al*. 2000). However, most researches have mainly focused on the relationships between soil and plants or plants and topography (Wu *et al*. 2001; Gong *et al*. 2007; Yue *et al*. 2008), while further studies of their interrelationships is required (Liu *et al*. 2003; Ye *et al*. 2004).

Another important factor that can be considered in examining the environmental variables that have influence on plant species is the geology. Studies have shown associations between geological substrates and tree species distribution and community composition (Reiners 2002; Tuomisto *et al*. 2003; Phillips *et al*. 2003; terSteege *et al*. 2006; Fayolle *et al*. 2012). However, there are limited examples showing the significance of the direct influence of rock type (its chemistry) on plant distribution (Cottle 2004). Nevertheless, it is obvious that properties of bedrock, soil, and topography are interrelated and associated with plant communities, but the problem is to define what this association is and at what level. This could be useful in the prediction of species response to changes in environmental factors in a particular geological environment like karst ecosystem.

Karst are considered as severely understudied (Vermeulen & Whitten 1999; Dennis & Aldhous 2004), while other studies have highlighted the importance of investigations directed to improve our understanding of tree diversity in tropical limestone forests, especially those in Central and South America (Kelly *et al*. 1988; Brewer *et al*. 2003; Felfili *et al*. 2007; Perez-Garcia *et al*. 2009). Yet information is still scarce regarding even such basic aspects as the range of environmental conditions in which they grow and the levels and patterns of species diversity of such ecosystems. Karst ecosystem is described as the ecosystem that is restrained by karst environment (Yuan 2001), especially by karst geological setting (Cao *et al*. 2003). It is also recognized as a highly complex interactive system which incorporates component landforms, life, energy flows, water, gases, soils and bedrock. Perturbation of any one of these elements is likely to impact upon the others (Yuan 1988; Eberhard 1994). Recognition and understanding of the importance and vulnerability of this dynamic interaction must underpin the effective management and conservation of karst forest biodiversity.

The present study examined plant species diversity variations and their ecological correlates in the limestone forest of Longhushan Nature Reserve (LNR) SW China. Located at the northern edge of tropical Asia, the karst landscape of southwest China (SW China) is one of the most typical landscapes developed on limestone in the world (Yuan 1993; Liu 2009). These mountains have unique types of vegetation (Zhang *et al*. 2010) and evolved into a cluster of distinctive mini-hotspots, each with its own unique flora and fauna. However, due to the excessive exploitation of the region's natural resources, SW China karsts are subject to serious degradation sequences resulting in forest deterioration to shrubs or grasses and even to rock desertification in some areas (Wu *et al*. 2008; Song *et al*. 2008).

The area is an ideal research habitat to study plant diversity, the range of environmental conditions in which species develop, and the patterns of species diversity in such ecosystems. Our objectives were to examine: i) plant communities' composition and dominant species in the reserve; ii) soil characteristics, rock type, environmental factors, and their single effects on species diversity; iii) species diversity responses to the combined effects of rock type, soil and environmental factors, and determine which variables have the most significant impact; and iv) the influence of significant environmental factors on dominant species distribution.

2. Materials and methods

2.1Study area

LNR is located in the subtropical area of southern China, Nanning, Guangxi Zhuang Autonomous Region (Fig 1). The reserve covers an area of 2255.7 hectares and is bounded between 22°56′ to 23°00′N latitudes and 107°27′ to 107°41′E longitudes. It has a monsoonal climate characteristic of the subtropical zone and is influenced by the regulation of a maritime climate. LNR belongs to Guangxi which has one of the key forest areas in southern China, ranking first among the Chinese provinces being home to rare plant species, and Longhushan as a microcosm of Guangxi, reflects this rich diversity. However, divided by a highway, the status of the area is that of a nature reserve and tourist attraction with an estimated 100,000 visitors per annum. Longhushan is also a primate reserve with an increasing impact from both primate population density and anthropogenic impacts through agriculture, facilities and infrastructure developed for tourism. Hence, the public road running through the reserve in addition to the development of tourism infrastructures, the influence of local inhabitants, and the excessive increase of primate population, may exceed its environmental carrying capacity, making species protection and conservation difficult.

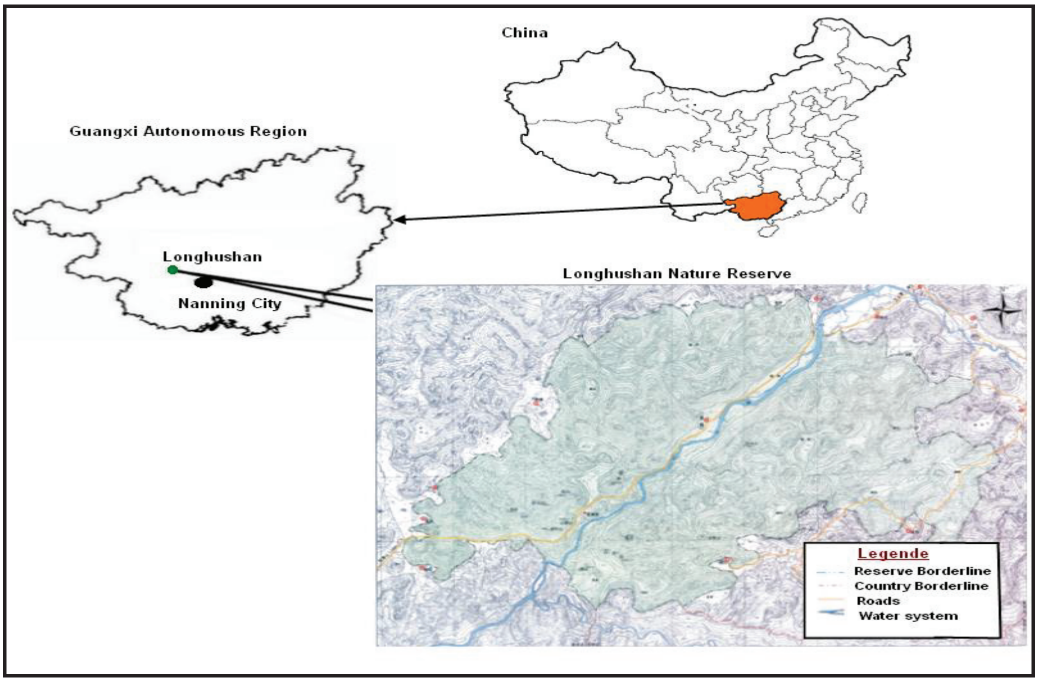


Figure 1. Location map of Longhushan Nature Reserve

2.2 Sampling and data collection

A systematic survey was implemented in the reserve and data was collected from 17 quadrats (30m×30m) randomly located along 4 south-north transects lines. For each quadrat, dominant canopy and sub-strata species, endangered and endemic plant species were recorded. In addition, the stem girth at breast height (GBH-1.3 m) was measured for each tree greater than 10 cm DBH (diameter at breast height) and all individuals were identified to species and plotted. Geological and soil samples respectively for rock type (RT) and soil characteristics were also collected. In each 30m×30m quadrat, $1m^2$ quadrats were randomly placed in order to make soil sampling and assess the percentage of ground cover (GC) including litter and vegetation. Several environmental variables were recorded such as latitude and longitude of the quadrat, elevation (E), slope degree (Sd), canopy cover (CC), soil depth (SDp), ground temperature (GT), and ground cover (GC). Rock samples were collected from the rocky outcrop on the surface of each quadrat, while soil samples were collected from the topsoil layer (0–10 cm) after the removal of leaf litter.

2.3 Experimental design

Soil samples were analyzed for some major characteristics that can influence other soil properties in the habitat and affect nutrients availability for plants. Hence, samples were tested for texture, moisture (M), pH, and organic matter (OM) content. Soil M was obtained by the oven-dry method calculated from soil sample weights before and after drying and expressed as a percentage of the mass of the oven-dried soil. Soil-water suspension method was used to test pH, while the Walkley-Black Method was applied to determine soil organic carbon and the results expressed as percent OM. Soil type was examined using the United State Department of Agriculture (USDA) method to determine soil textural classes based on percentage content of sand, silt, and clay. Karst areas are characterized by a thin soil layer, where plant species can be in contact with the rocks and even grow through their fissures. The influence of RT was examined through its main chemical components and samples were analyzed for their percentage content of calcite and dolomite by a chemical staining method using alizarin-red test (Friedman 1959; Warne 1962). The botanical specimens were identified within two weeks in the South China Herbarium Guangxi Botanical Garden IBK, Guilin and were preserved for future reference. The botanical nomenclature of the Southern China Botanical Garden, Chinese Academy of Sciences (1987, 1991, and 1995) was adopted. The status of rare plant species were established by illustrated handbooks of Guangxi Vegetation and China high vegetation, as well as the Red Book. The endangered species list published by Chinese Government was also referenced.

2.4 Data processing and statistical analysis

In order to examine plant communities and species diversity, plant indices such as importance value index and diversity were calculated. Simpson's Reciprocal Index was used to measure species diversity through the following formula (equation 1):

$$Simpson's\ Reciprocal\ Index = 1/D \quad D = \sum n\,(n-1) / N\,(N-1) \qquad (1)$$

Where D is the Simpson's Index of diversity; n, is the total number of individuals of a particular species; and N, the total number of individuals of all species. Species importance value index (IVI) based on trees DBH≥10cm was calculated according to Curtis (1959), from the sum of their relative frequency, relative density, and relative dominance (relative basal area). Basal areas for trees ($BA=\pi r^2$), species and quadrats ($BA=\sum \pi r^2_{/A}$) were calculated from the DBH of tree stems. Where: *BA* is the basal area; *r* is the radius of tree stem (r=DBH/2); and *A* is the area in which the trees/species were recorded. Tree DBH was obtained using tree GBH divided by π (pi, π = 3.1415). Species frequency was obtained from the number of quadrats in which species occurred divided by total number of quadrats. Density was calculated for species and quadrats through the number of individuals of the species or quadrat divided by the area from which species were recorded. Statistical analysis was conducted with IBM SPSS Statistics 19 using Correlation, one way analysis of variance (ANOVA), General Linear Model (two way ANOVA, ANCOVA) and Multiple Regression analyses, at 95% confidence interval (CI, $p<0.05$). Data were divided into four groups including one group of response variables (plant index: species diversity), and three groups of independent variables (IV) (Table 1). ANOVA was applied to examine the single or combined effects of RT and soil texture (ST) on plant by comparing the average species diversity across different RT and ST groups. ANCOVA examined the effect of ST or RT on plant diversity while including covariates. Pearson's simple correlation was used to test the bivariate correlations between diversity and each predictor as well as the correlations among the predictors. Furthermore, predictors from all three groups of factors (soil indicators, environmental and geological factors) were included separately and then collectively in three standard multiple regression models using the enter method to find the best fit for diversity. In each model, the following values were mainly produced: the multiple correlation coefficient (R), represents the linear correlation between the observed and models predicted values of plant species diversity; the coefficient of determination (R^2), represents how much of the variance in diversity was accounted for by each model; the adjusted coefficient of determination (Adj. R^2), same as the R^2; The ANOVA F-statistics or null hypothesis, tests the model's ability to explain variations in plant diversity and determines the model fit with its overall significance (P); the coefficient (B) represents the estimated values of the regression weight for each predictor; the impact of each predictor variable (t), tests the null hypothesis for each predictor of the model with its significance level (P). Note that R^2 and adj. R^2 both indicate the proportions of variance in plant diversity accounted for by the models. Since we have a limited sample size (N=17) and several predictors, we reported the values of adj. R^2 to avoid over-estimation of the success of the models. Adj. R^2 is more restrictive and takes into consideration not only the number of predictor variables, but also the number of observations the model is based on. In addition, for the significant models the partial regression plots between diversity and each significant predictor showing their linear relationships and the residuals plots to validate the regression assumptions (normality and constant variance) were produced. The equation that calculated the predicted value of plant diversity for the significant model was also established following the general form of the multiple linear regression function (equation 2).

$$Predicted\ plant\ diversity = B_0 + (B_1V_1) + (B_2V_2) + \ldots (B_nV_n) + E \qquad (2)$$

Where B_o is the constant of the regression slope (y-intercept); B_1, B_2,…B_n represent the unstandardized coefficients of the model's predictors (regression slope); V_1, V_2,…Vn are the different environmental variables used as predictors in each model; and E is the random error.

Table 1. Description of four groups of variables for statistical analysis

Groups of variables	Parameters/Variables	Type
Soil indicators	Soil depth	Predictors/Independent variables/Explanatory variables
	Texture (Categorical)	
	Moisture	
	pH	
	Organic matter content	
Environmental parameters	Elevation	
	Slope degree	
	Canopy cover	
	Ground cover	
	Ground temperature	
Geological factor	Rock type (Categorical)	
Plant index	Diversity	Predicted/Dependent variables/response variables

All variables but the two categorical were scale variables. RT was coded as 1 = dolomite, 2 = calcite; ST was coded as 1 = coarse textured soil, 2 = moderately coarse, 3 = medium, 4 = fine

3. Results

3.1 Description of plant communities, soil characteristics, and rock type

The basic statistical description of all variables is presented in table 2. Plant communities in the reserve were generally found to be evergreen dominated with delimitation between arbor layers, shrubs and grasses. Twelve species were identified in the reserve as rare or endangered (*Burretiodendron tonkinense, Camellia pubipetala, Canthium dicoccum, Desmos chinensis, Garcinia paucinervis, Habenaria ciliolaris, Zenia insignis, Hartia sinensis, Machilus salicina, Malania oleifera, Mallotus philippinensis, Hainania trichosperma*), among them 6 were included in the IUCN Red List for endangered species (*Burretiodendron tonkinense, Zenia insignis, Canthium dicoccum, Garcinia paucinervis, Malania oleifera, Camellia pubipetala*), and 3 were found endemic (*Malania oleifera, Hainania trichosperma, Camellia pubipetala*). A total of 411 trees belonging to 59 species including one unidentified species, were measured across the 17 quadrats, and species diversity varied from 2.78 to 15.79. Fig 2 compares the importance value indices (IVI) of the 59 species, which varied from 1.078 to 40.81 with the highest for *Sterculia nobilis*, the lowest for *Viburnum fordiae*. Hence, based on their importance values, *Sterculia nobilis, Ficus sp, Albizia chinensis, Liquidambar formosana, Teonongia tonkinensis, Bischofia javanica, Sterculia lanceolata*, *Ficus oligodon*, *Abarema clypearia*, *Psychotria rubra*, *Dalbergia hupeana*, *Ficus abelii*, *Syzgium jambus*, *Pyrus calleryana*, *Beilschmiedia delicata* were found as the dominant species in the reserve. Together they represented 64.25% of the total species importance value and *Sterculia nobilis* was by far the most abundant, constituting alone 13.60% of the total importance value (Fig 2). All the remaining species were found with their IVI less than the average IVI (5.085) obtained in the area. Based on the dolomite and calcite percentage of surface rocks collected from the 17 plots, dolomite was higher in 11 samples varying from 70 to 98% and representing about 65% of the studied plots, from which more than 90% had dolomite content ≥90%, while 35.3% of the sampled area was found with high calcite content. Soil type was classified as coarse, moderately coarse, medium, and fine textured soil. Fine and medium textured soil dominated in 75% of the studied area, while coarse and moderately coarse dominated in 25%. PH was found moderately acidic (ranging from 5.25 to 5.71) only in two plots representing 11.76% of the study site. However, about 88.24% of the surveyed area was found with soil pH ranging between near neutral to moderately alkaline (6.66-7.91), which supports the results of Liu *et al*. (2006) and Hu *et al*. (2009) in their studies of another karst area in southwest China (Guizhou province). OM ranged from 2.35 to 12.51% and interpreted according to Hartz (2007), near 53% of the study site was found with high OM content (>5%) and 47% with low OM content (<5%). The M content ranged from 14.14 to 57.49%, and considering the moisture interpretation chart of Harris and Coppock (1991), 88.23% of the sampled plots had insufficient available moisture (50% or less), while only 11.76% had sufficient available moisture (50 to 75%).

Table 2. Descriptive statistics of all variables of interest (N=17)

Parameters	Min	Max	Mean	Std. Deviation
Elevation (m)	109	243	150.82	35.16
Slope degree (°)	5	60	23.71	16.72
Canopy cover (%)	40	90	65.00	16.45
Ground cover (%)	20	95	63.53	20.82
Ground temperature (°C)	24.00	29.00	26.99	1.42
Soil depth (cm)	3	100	34.29	36.71
Rock type	-	-	-	-
Soil texture	-	-	-	-
Moisture (%)	14.14	57.49	38.13	11.69
pH	5.25	7.91	7.30	0.79
Organic matter content (%)	2.35	12.51	7.11	3.32
Simpson diversity Index	2.78	15.79	6.94	3.79
Importance value index	1.08	40.81	5.08	6.61

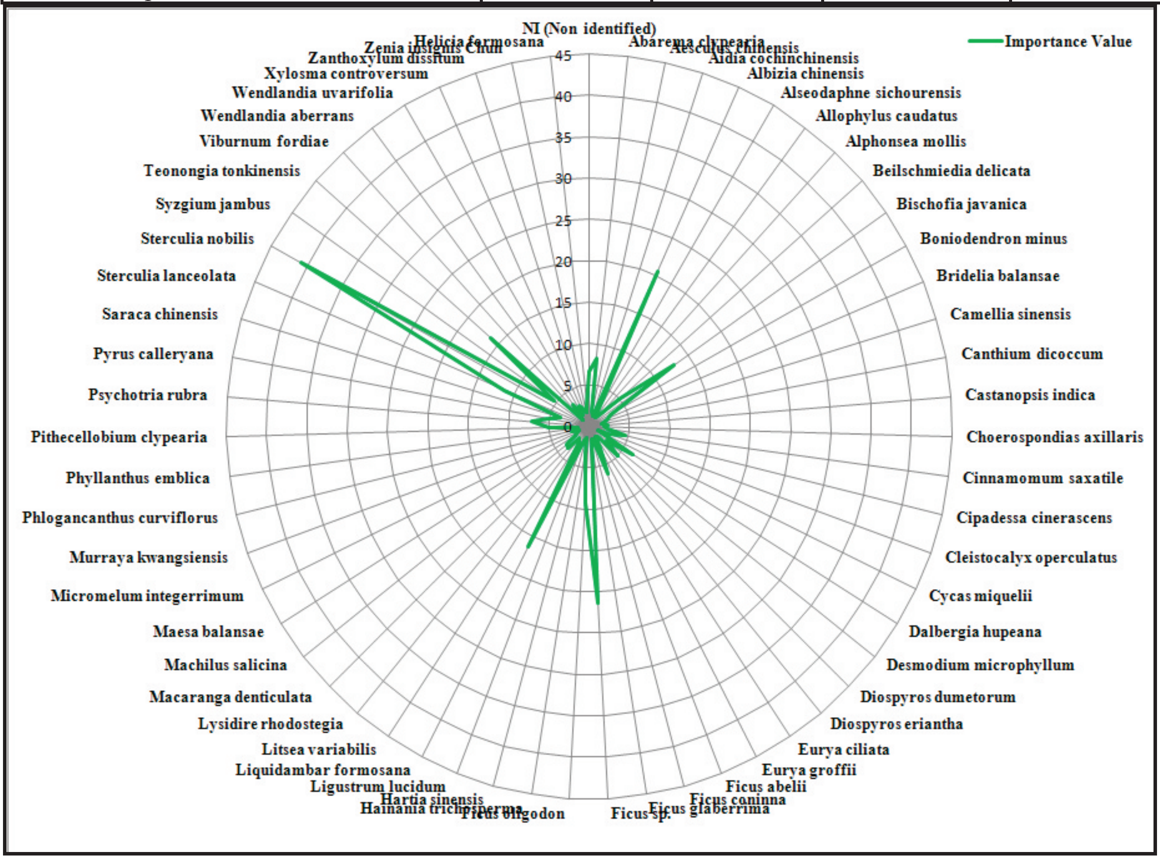


Figure 2. Comparison of the importance values of 59 plant species in the karst forest of LNR

3.2 ANOVA and ANCOVA results for the impact of soil texture and rock type on plant species diversity

Both one-way and two-way ANOVA established no significant variation in the mean species diversity related to RT or ST. There was no evidence to reject the null hypothesis that there is no relationship between diversity and ST or RT since the significance p-values were all above our alpha level of 0.05 ($p > 0.05$). ANCOVA also failed to prove any statistically significant relation between plant species diversity and ST or RT.

3.3 Correlation and multiple regression analysis for the impact of the interactions between rock type, soil characteristics, and environmental factors on plant species diversity

The Pearson's simple correlations between species diversity and each predictor variable, as well as the correlations among the predictors were examined. There was no significant association between diversity and any other predictor except Sd ($r = 0.644$, $p<0.01$). But there were inter-correlations among few of the predictors with the highest between M and OM ($r = 0.760$, $p<0.01$), soil depth and pH ($r = -0.661$, $p<0.01$). However, except these two associations, all correlation coefficients among the predictors were less than 0.6 and no correlation was equal to or greater than 0.8 to fear for serious multicollinearity problem

3.3.1 Regression models 1 and 2 for the single impacts of soil characteristics and environmental factors on species diversity

In regression model 1 plant species diversity response based on the linear relationship to four soil variables (SDp, M, pH, and OM) was examined and the analytical results are summarized in table 3. Despite the multiple correlation coefficient value ($R=0.314$), the model failed to explain any significant variation in diversity, since the p-value of the F-statistic was greater than 0.05 (table 3a). There was not sufficient evidence to reject the null hypothesis that there was no significant difference in the mean species diversity. Also, the p-values of the coefficients and t-tests were all above 0.05, indicating the fit of the observed values of diversity to those predicted by the multiple regression equation was no better than what we would expect by chance (table 3b), suggesting there was no significant relationship between the four soil variables and plant diversity established by model 1.

Environmental variables (E, Sd, CC, GC, GT) were included in model 2 to examine their relationships with species diversity. The results (table 3) showed there was strong linear relation between diversity and the five environmental parameters ($R=0.823$), and diversity was significantly predicted with more than 98% confidence that it did not occur by chance ($F=4.604$, $p=0.016$, $p<0.05$) (table 3a). Significant mean difference was observed as the null hypothesis was rejected, and 53% of the variance in diversity was accounted for by the model (adj. $R^2=0.530$). The estimated values of the regression coefficients (B or Beta) (table 3b) showed that the only statistical predictors of diversity with significant regression weights were Sd with a positive effect (Beta=0.594, $p=0.009$, $p<0.01$) and CC with a negative effect (Beta=-0.515, $p<0.05$). The t-tests suggest that adding those two variables contribute significantly to the prediction of diversity, while the other three (E, GC, and GT) in this model, do not improve the fit of the multiple regression equation any more than expected by chance. The partial regression plots (Fig 3) display and support the existence of linear relationships between diversity and both Sd and CC in the presence of the other predictors of the model. Sd explained about 48% of the variance in diversity (R^2 Linear = 0.481) (Fig 3a), while near 34% was accounted for by canopy cover (R^2 Linear = 0.338) (Fig 3b). The residuals plots requested to check the regression assumptions are presented in Fig 4. The normal P-P plot (Fig 4a) indicates that aside from minor deviations, the residuals seem close to normality. The scatterplot of residuals versus predicted values (Fig 4b) shows that overall the residuals at each predicted value do not appear to vary significantly. Considering our sample size, it is safe to assume that heteroscedasticity is not severe enough to warrant concern. We conclude that the regression assumptions of normality and equal variances (homoscedasticity) were approximately met, suggesting we can have confidence in the ANOVA and t-tests of the coefficients of regression line. Hence, from the constants and the coefficients (B or Beta) of each predictor, the regression equation that predicted plant species diversity in model 2 can be calculated following the equation (3):

$$\textit{Diversity} = -17.40 + (0.023 \times \textit{elevation}) + (0.135 \times \textit{slope degree}) - (0.119 \times \textit{canopy cover}) + (0.003 \times \textit{ground cover}) + (0.932 \times \textit{ground temperature}) \quad (3)$$

Table 3. Multiple regression models 1 and 2 showing the effects of soil characteristics and environmental factors (predictors) on species diversity (response variable) before including variables from all groups (N=17, 95% CI)

a) Model fit

Models	**Predictors (IV)**	**Plant Indices (DV)**	**Model summaries**			**ANOVA (F-statistics)**	
			R	R^2	Adj. R^2	F-ratio	P
1	SDp, M, pH, OM	Diversity	0.314	0.099	-0.201	0.329	0.853
2	E, Sd, CC, GC, GT	Diversity	0.823	0.677	0.530	4.604	0.016

b) Coefficients

Models	**DV**	**Predictors**	**B**	**Beta**	**t**	**p**
1	Diversity	Constant	7.467		0.521	0.612
		Soil depth	-0.013	-0.127	-0.326	0.750
		Moisture	0.134	0.413	0.887	0.393
		PH	-0.177	-0.037	-0.092	0.928
		Organic matter	-0.548	-0.480	-1.072	0.305
2	Diversity	Constant	-17.400		-1.324	0.212
		Elevation	0.023	0.215	0.992	0.343
		Slope degree	0.135	0.594	3.193	0.009
		Canopy Cover	-0.119	-0.515	-2.372	0.037
		Ground Cover	0.003	0.018	0.087	0.932
		Ground Temperature	0.932	0.347	1.767	0.105

IV: Independent Variables; DV: Dependent Variables; SDp: Soil Depth; M: moisture; OM: Organic Matter; E: elevation; Sd: slope degree; CC: canopy cover; GC: ground cover; GT: ground temperature.

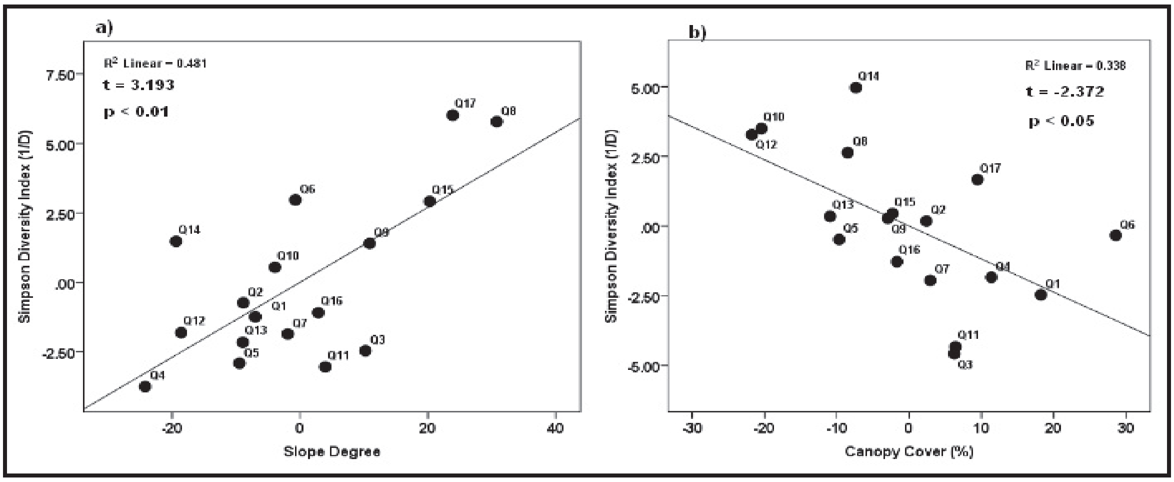


Figure 3. Model 2 partial regression plots displaying linear relationships between plant species diversity and a) slope degree, b) canopy cover, as significant predictors

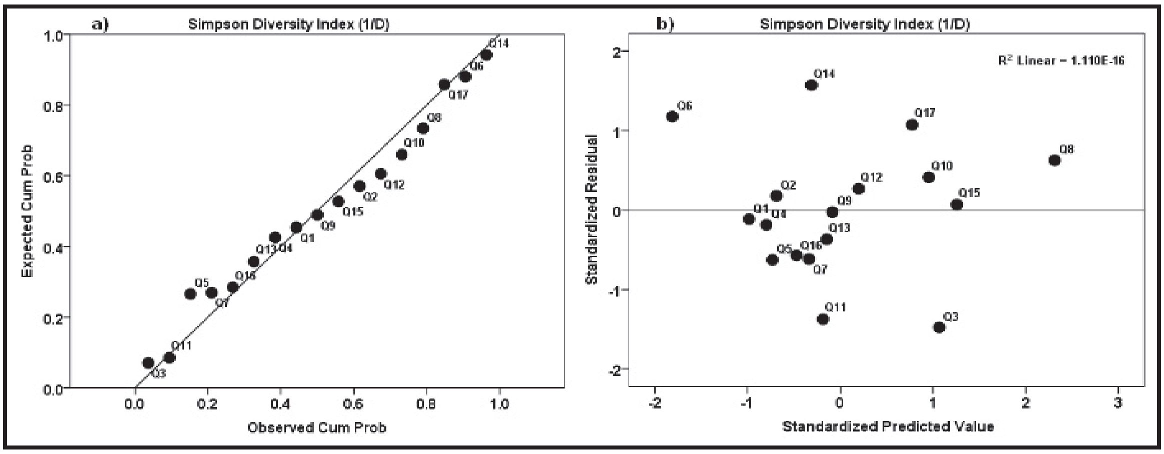


Figure 4. Model 2 residuals' plots in the prediction of species diversity for regression assumptions of normality and constant variance. a) Normal P-P plot is a plot of regression standardized residuals vs. standardized predicted values. It shows the residuals close to the reference line but with some small deviations in the distribution; b) the scatterplot of standardized residuals versus standardized predicted values also shows that the residuals have no strong tendency in the distribution, except perhaps for Q14 which is slightly higher, but no severe heteroscedasticity was observed.

3.3.2 Regression model 3 for the influence of the interactions between rock type, soil characteristics, and environmental factors on plant species diversity

In model 3, influential variables (Sd, CC, GT, M, RT) selected from all three groups of factors were examined to test their fit as predictors of species diversity (table 4). The results showed that there was strong correlation between the five variables and plant diversity ($R = 0.926$) (table 4a). Also, significant mean difference in diversity was observed ($F = 13.330$, $p < 0.001$) for which the model accounted for over 79% of the variance (adj.$R^2 = 0.794$). This proportion compared to model 2 suggests that the predictability of diversity was greatly improved since the amount of variation explained increased by 26.4%. The coefficients and t-tests (table 4b) suggest that all five predictors of the model were found with significant contribution to diversity, with the greatest effect from Sd followed by GT, M, CC, and RT. In fact, diversity was predicted by positive impacts of Sd ($t = 5.790$, $p < 0.001$), GT ($t = 3.551$, $p < 0.01$), M ($t = 3.265$, $p < 0.01$), and negative impacts of CC ($t = -3.099$, $p < 0.05$) and RT ($t = -2.812$, $p < 0.05$). Since RT was coded as 1=dolomite and 2=calcite, this suggests that species diversity increased with increasing Sd, GT, M, low canopy cover, and in dolomite areas. The scatter plots of partial regressions presented in Fig 5 indicate the existence of linear relationships between diversity and each predictor when the other variables are present in the model. They showed that over 75% of the variance in species diversity was accounted for by Sd (R^2 Linear = 0.753), 46.6% by CC (R^2 Linear = 0.466), over 49% by M (R^2 Linear = 0.492), near 42% by RT (R^2 Linear = 0.418), and over 53% by GT (R^2 Linear = 0.534). The normal plots and scatterplots of the residuals (Fig 6) show no evidence of significant deviation from normality or severe heteroscedasticity to support the violation of regression assumptions. Therefore, equation (4) expresses the association between model 3 and plant species diversity.

$$\textit{Diversity} = -25.844 + (0.158 \times \text{slope degree}) - (0.086 \times \text{canopy cover}) + (1.228 \times \text{ground temperature}) + (0.136 \times \text{moisture}) - (2.718 \times \text{rock type}) \quad (4)$$

Table 4. Regression model 3 showing the combined effects of soil properties, environmental and geological factors on species diversity after including influential variables selected from all three groups of factors (N=17; 95% CI)

a) Model fit

Model	Predictors (IV)	Plant Indices (DV)	Model summaries			ANOVA (F-statistics)	
			R	R^2	Adj. R^2	F-ratio	P
3	Sd, CC, GT, M, RT	Diversity	0.926	0.858	0.794	13.330	0.000

b) Coefficients

Model	Dependent variables	Predictors	B	Beta	t	p
3	Diversity	Constant	-25.844		-2.613	0.024
		Slope degree	0.158	0.694	5.790	0.000
		Canopy cover	-0.086	-0.375	-3.099	0.010
		Ground temperature	1.228	0.458	3.551	0.005
		Moisture	0.136	0.420	3.265	0.008
		Rock Type	-2.718	-0.352	-2.812	0.017

Sd: slope degree; CC: canopy cover; GT: temperature; M: moisture; RT: rock type

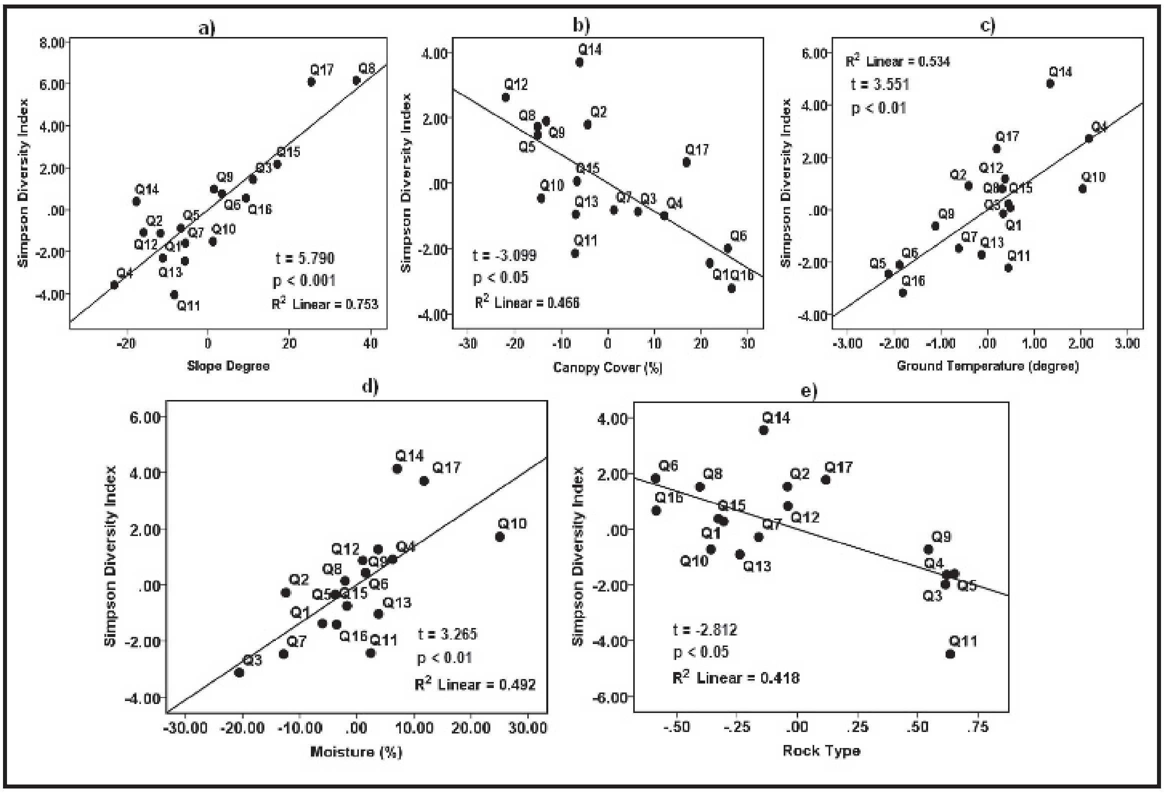


Figure 5. Model 3 partial regression plots showing the linear relationships between plant species diversity and a) slope degree, b) canopy cover, c) ground temperature, d) moisture, e) rock type, as significant predictors.

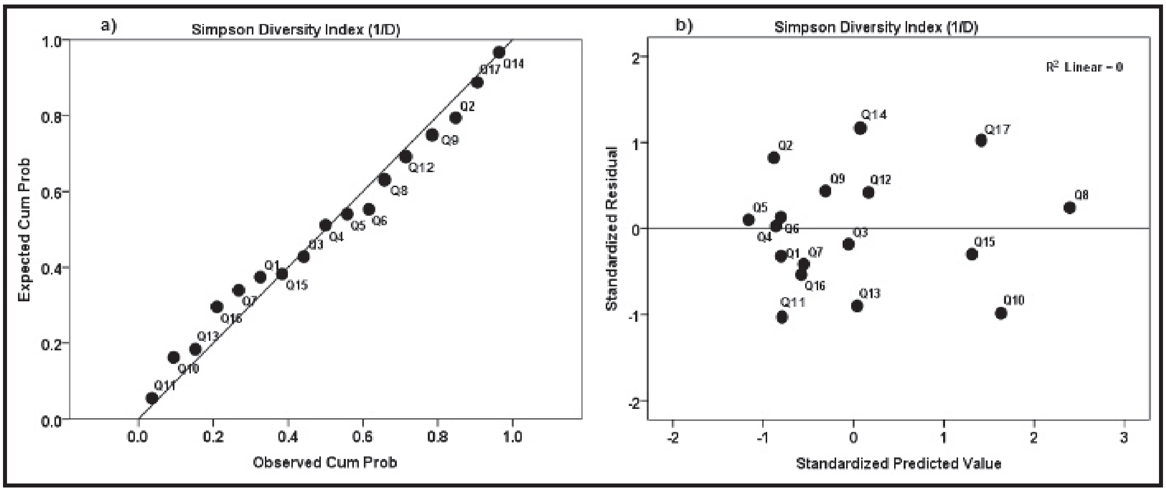
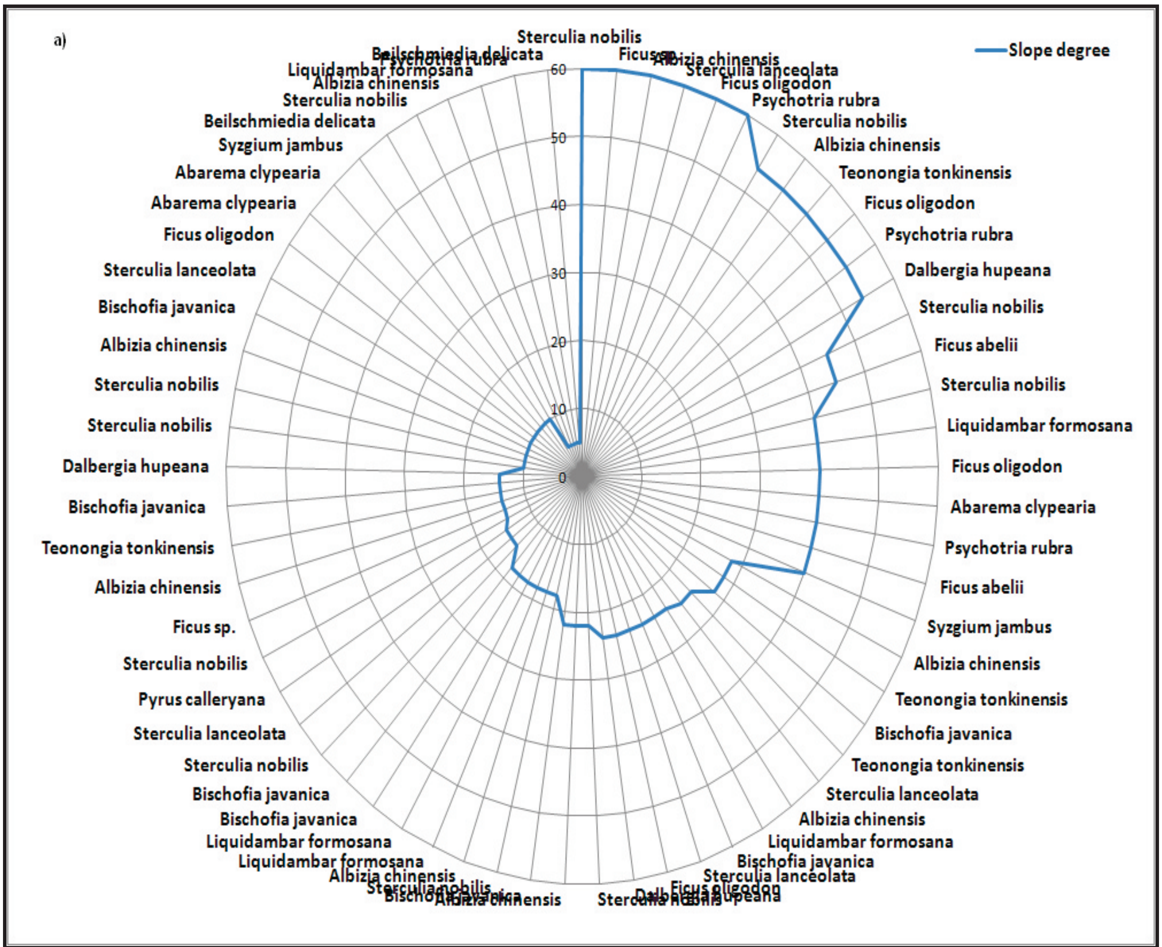
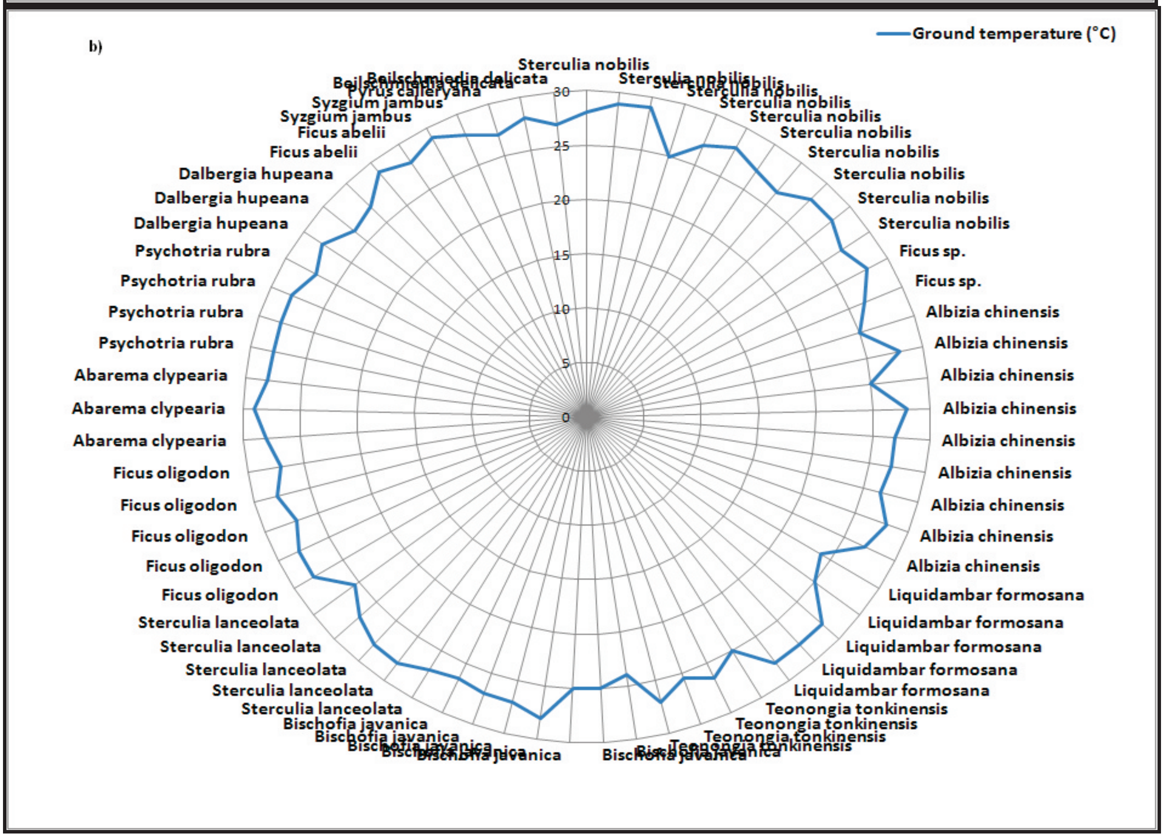


Figure 6. Model 3 residuals' plots in the prediction of species diversity. a) Normal P-P plot shows the residuals very close to the diagonal line suggesting normality in the distribution; b) the scatterplot also shows the residuals approximately the same size for each predicted value of diversity, indicating equal variance. Both plots present no evidence of violation.

3.4 Significant environmental factors and dominant species distribution in the Karst forest of LNR

Slope degree, ground temperature, moisture, canopy cover, and rock type were the most significant factors that affected plant species diversity. We analyzed how these significant environmental factors influenced the dominant species distribution in the reserve (Fig 7). Among the most abundant species, *Sterculia nobilis, Teonongia tonkinensis, Albizia chinensis, Sterculia lanceolata, Ficus oligodon, Psychotria rubra* were apt to live at both slight and steep slopes (Fig 7a), while *Bischofia javanica, Beilschmiedia delicata, Pyrus calleryana* grew only at slight slopes. In addition, *Abarema clypearia, Syzgium jambus, Ficus abelii* were adapted to high ground temperature, whereas *Teonongia tonkinensis, Pyrus calleryana* were apt to live in lower ground temperature and all the remaining dominant species were adapted to both conditions (Fig 7b). Most dominant species were adapted to both habitats with sufficient and insufficient moisture conditions, except *Ficus sp., Abarema clypearia, Ficus abelii, Syzgium jambus, Pyrus calleryana, Beilschmiedia delicata* recorded only in low moisture habitats (Fig 7c). Also, *Ficus sp., Sterculia lanceolata, Pyrus calleryana, Beilschmiedia delicata* were adapted to high dolomite percentage areas, while the remaining dominant species were all apt to survive in both habitats (dolomite or calcite dominated areas) (Fig 7d). Each of these species performed well in their habitats suggesting they could be appropriate for the restoration of degraded parts of the mountains with similar conditions, for instance the fragmented areas by tourist roads network, the denuded ground by primate damage, and the old plantations or abandoned agricultural lands. Therefore, based on the dominant species responses to the significant environmental factors, *Sterculia nobilis*, *Albizia chinensis*, *Ficus oligodon*, and *Psychotria rubra* were adapted to all karst environmental habitats conditions, suggesting they could be the most appropriate species for restoration and forest amelioration measures.


a)
Slope degree


b)
Ground temperature (°C)

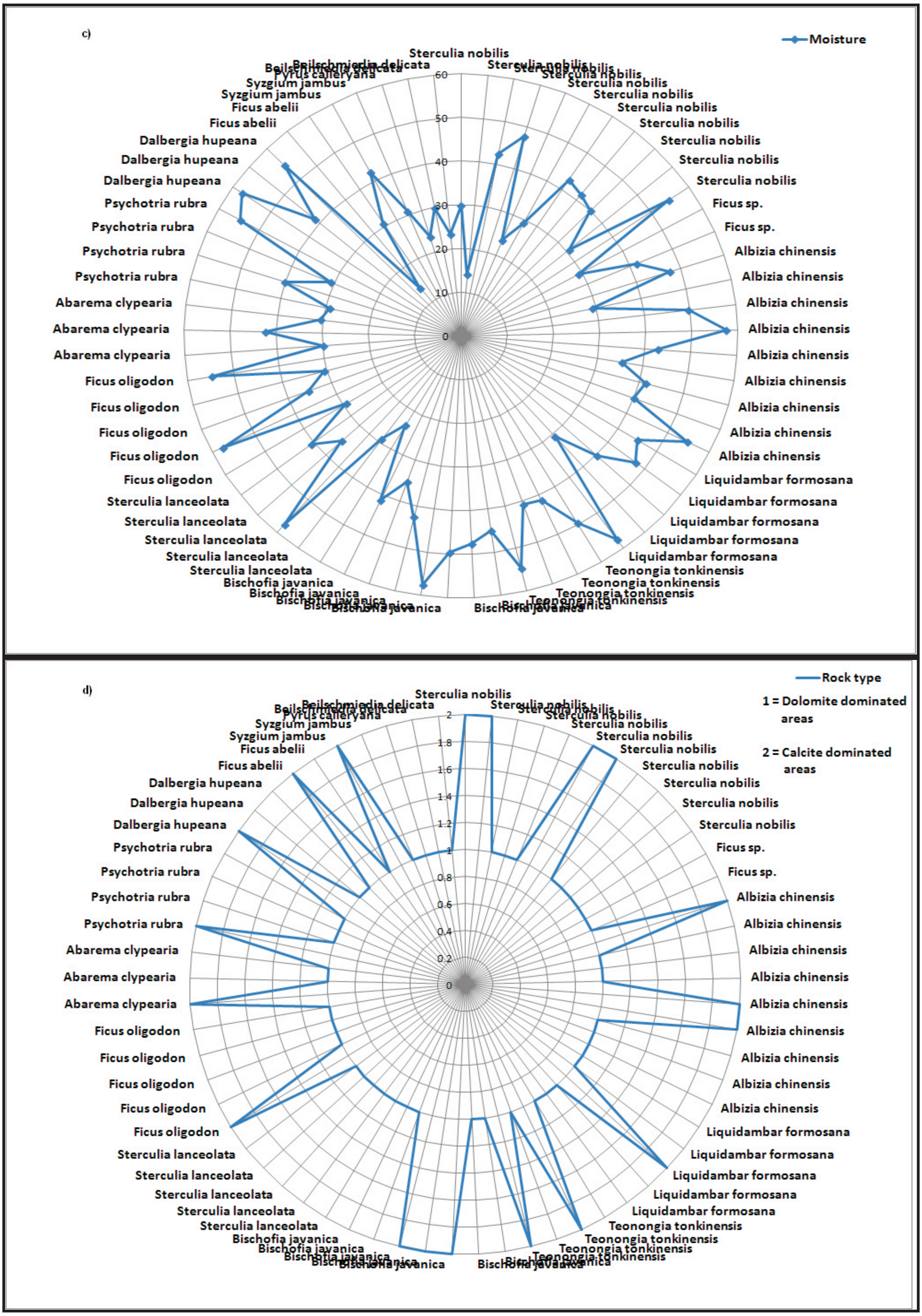


Figure 7. Distribution of dominant plant species along a) slope degree, b) ground temperature, c) moisture, and d) rock type, as significant environmental factors in LNR

4. Discussion

A combination of different environmental factors (soil, topography, temperature, and geology) forms diverse microhabitats leading to the heterogeneity of karst environments in LNR. Analysis of variables related to environmental and geological factors revealed some of their interactions with Longhushan soils upon which plant species depend. In this study ANOVA and ANCOVA both failed to prove any statistically significant effects of RT or ST on species diversity. Also of all the predictors, the only significant bivariate correlation established was between diversity and slope degree. Further, multiple regression analysis failed to prove that the four soil variables had any statistically significant relationship with diversity. For all these procedures we assumed there was not sufficient evidence to establish such associations. Although the five environmental factors significantly predicted diversity, but only slope degree and canopy cover were found with strong impacts. However, when influential variables were selected from soil, environmental and geological factors in combination as predictors to examine their joint effects on diversity, multiple associations were observed.

The results indicated that the regression equation was very useful for making prediction of diversity and a high amount of its variance was explained. It was also demonstrated that the overall prediction model was greatly improved for diversity after combining variables from soil, geological, and environmental factors. There were positive trends of species diversity with slope degree, ground temperature, moisture, low canopy cover, and in dolomite areas. These results corroborated those of previous studies including Knight *et al*. (1982) who found a positive linear relationship between South African tree species diversity and temperature; Fassnacht *et al*. (1994) estimated the foliage surface area index in forests and suggested that canopy cover is a key factor for predicting woody plant composition. Pausas & Carreras (1995) pointed out the significance of bedrock type, temperature, and moisture for species richness of Pyrenean Scots pine. The negative trend of species diversity with canopy cover may be explained by the fact that diversity was found to be positively related to ground temperature as supported by several other studies (Allen *et al*. 2002, 2006; Gillooly *et al*. 2007; Wang *et al*. 2009). Canopy cover as an index of light availability at the forest floor is determinant for variation in temperature. A decrease in canopy cover also increases ground temperature, which has a positive effect on diversity, suggesting that species diversity increases in low canopy cover. The positive association between diversity and moisture could be attributed to the fact that occurrence of plant species can be largely controlled by water availability as reported by several studies (Schupp 1995; Bahari *et al*. 1985; Woodward 1987; Engelbrecht 2007). Water availability is also reported as one of the most important environmental parameters controlling plant richness (Lavers & Field 2006), and it is said to be even more profound in environments where soil moisture is the major limiting resource like karst area.

The strong association between slope degree and diversity was expected as first indicated by Pearson's simple correlation. Topographic variation in slope of terrain can produce local differences in solar radiation, and this is most evident in mountains, but also occurs along hill slopes. In addition, changes in elevation alter temperature, precipitation, and winds. As a result, mountain climates are quite different from low elevations (Barry 1992; Whiteman 2000). On a local scale, different elevations correspond to different life zones, or areas of similar climate and vegetation. Hence, mountains can be used effectively as conservation reserves in a changing climate because they support a relatively broad distribution of possible climates and a high diversity of habitats within a small physical area.

In addition to soil, topography, and temperature, rock type was found among the important environmental factors which significantly influenced species diversity. This suggests that carbonate rock type may be a key factor in karst habitats since in addition to having strong influence on plant diversity, its inclusion in the analysis greatly improved the predictability of plant species. Plant diversity was found with a positive trend in high dolomite percentage areas and the inverse trend in calcite dominated areas. This suggests that plant species performed better in areas where carbonate rock had greater content of magnesium. Since the knowledge of correlates of species diversity can help to set up proxies that can help large-scale monitoring of plant species diversity (Austin 2002), and also the predictable variation in species diversity is important in determining areas of conservation, we may postulate that this geological factor is an indicator of high species diversity areas in the Longhushan Karst Mountains, which could be used for assigning priority sites for conservation or restoration.

5. Conclusion

The physical and chemical characteristics of karst geology and soil are of importance for plant species from the viewpoint of the karst ecosystem changeability. This study has shown that variations in species diversity in Longhushan are dependent on complex relationships between soil, environmental, and geological factors of karst ecosystems. It appeared that the geological factor played an important role in the distribution of plant species in the area, and its inclusion in the models greatly improved the overall predictability of diversity. The regression equation was very useful for making prediction of plant species and a high amount of the variance in diversity was explained. Trends in species diversity were mainly related to moisture, rock type in association with slope gradient and temperature. The dominant species responded differently to these significant factors, and a number of those species were found typically well adapted to the special karst habitats. *Sterculia nobilis*, *Albizia chinensis*, *Ficus oligodon*, and *Psychotria rubra* were found as the most appropriate species for restoration and forest amelioration measures. The rare and endangered species recorded in the reserve also require special protection.

In addition to its natural contribution to soil properties or influence on topography, the role of rock type was also related to its chemistry (dolomite percentage). Since karst areas are complex terrain with thin soil layers where plants can be in contact with rocks by growing through their fissures, this geological factor should be taken into consideration in addition to local environmental variations, in analyses of the factors that impact plant species in such ecosystem. It was clearly demonstrated that the evidence of significant variations in species diversity was provided after combining variables from soil, geological, and environmental factors, inferring their interactions influence on plants. Our findings have implications for the understanding of these interactions and suggest that not only plant species can be affected by this symbiosis, but also carbonate rock type may be an important factor influencing the relationship between plant species and environmental factors in karst areas. Therefore, effective and efficient management of karst biodiversity requires an elaborate data set and understanding of all the components and features, as well as the complex links and interactions between them and plant communities, if species and their habitats are to be managed in a way that can sustain their diversity. This knowledge can provide a reference for assigning priority sites for conservation, restoration, and the development of sustainable management strategies of karst forest biodiversity in southwest China.

Acknowledgements

This work was supported by the grants from the Natural Scientific Foundation of China (No. 40972218) and the Fundamental Research Founds for National University, China University of Geosciences (Wuhan) (No. G1323521125, No. G1323521225, G1323521325).

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