Plant species richness responses to the interactions between karst environmental factors, southwest China

[1,] *Dado TOURE [1]Jiwen GE,

[1]Institute of Ecology and Environmental Sciences, School of Environmental Studies, China University of Geosciences (Wuhan)
***Corresponding** author: Dado TOURE
Institute of Ecology and Environmental Sciences, School of Environmental Studies, China University of Geosciences, Wuhan, Hubei, 388 Lumo Lu, 430074, Foreign Students Building: Oriental Garden, P.R. China. E-mail: touredado@yahoo.fr

Abstract

A good understanding of the spatial patterns of plant diversity is essential in deciding management and conservation priorities. This may rely on our ability to predict how species respond to environmental variables. Understanding this response requires examining essentially environmental factors or their interactions that have influence on plant and resource availability. The present study examined plant species richness patterns and their ecological correlates in the karst forest of Longhushan Nature Reserve southwest China. The analysis concerned a representative sample of vegetation plots from a systematic sampling that combines measurements of plant species richness for all trees DBH≥10 cm, with extensive information on rock type, environmental and soils parameters, allowing for the consideration of the interaction between different environmental habitat factors. Species richness was examined using analyses of variance and covariance (ANOVA, ANCOVA), correlation, and multiple regressions modellings to establish the single or combined effects of these environmental factors. The results showed that examining these factors separately, no evidence of significant variation in richness was proved. However, when considered for their combined effects there were significant mean differences in richness ($F = 16.373$, $p < 0.001$) and the model accounted for about 87% of its variance. Trends in species richness were mainly related to rock type, moisture, elevation, and slope degree in association with temperature and nutrients status, although slope degree and rock type were found with the greatest impacts followed by moisture and elevation. It was clearly demonstrated that the evidence of significant variation in richness 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 rock type may be an important factor influencing the relationships between plant species and other environmental habitat factors in karst areas. The influence of rock type was related to the percentage content of dolomite and calcite. There was positive trend of richness in high dolomite percentage areas but the inverse trend in calcite dominated areas. Since the predictable variation in species richness is important in determining areas of conservation, we may postulate for instance that this geological factor is an indicator of high species richness areas in the Longhushan karst forest, which could be used for assigning priority sites for conservation or restoration.

Keywords: Interactions, rock type, soil characteristics, environmental factors, plant **s**pecies richness, karst forest

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Introduction

The ability to measure biodiversity has become essentially important nowadays, given the increasing rates of species extinction and human alteration of natural habitats. Plant community and biodiversity are believed to have a high degree of spatial variability that is controlled by both abiotic and biotic factors. Hence, many types of environmental changes may influence the processes that can both augment or erode diversity (Sagar et al. 2003). The understanding of patterns and processes of biological diversity in space is thus, a fundamental problem in ecology and conservation (Rosenzweig 1995; Barnosky et al. 2001; Moritz 2002), and general relationships between plant biodiversity, environmental conditions, and biological conservation have been examined by Primack (1993) and Spellerberg (1995).

One of the important components of the concept of biodiversity is species diversity as it is a measure of the diversity within an ecological community that incorporates both species richness and the evenness of species' abundances. 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 and Austin 2001), or the effects of their interactions on plants. Species richness, the number of species per unit area, is a simple and easily interpretable indicator of biological diversity (Peet 1974). Plant richness is likely to be governed by two or more environmental factors (Margules et al. 1987; Pausas 1994; Austin et al. 1996), and variations in species richness are often linked to various environmental gradients (Huston, 1994; Wang et al., 2002; Sharma et al., 2009). For instance, different altitudes and slopes were found to influence species richness and dispersion behavior of tree species (Ellu and Obua 2005). It has also been pointed out that altitude and climatic variables like temperature and rainfall are the determinants of species richness (Kharakwal et al. 2005). Elevation gradients are thus, one of the most commonly discussed determinative factors in shaping the spatial patterns of species richness (Lomolino 2001; Chawla et al. 2008; Acharya et al. 2011), but topography is also commonly correlated with other important environmental variables, notably the ground water regime and the physical and chemical properties of the soils. At local scales, species associations with topography and soil factors have been reported in tropical forests worldwide (Webb and Peart 2000; Harms et al. 2001; Phillips et al. 2003; Palmiotto et al. 2004; Russo et al. 2005; John et al. 2007). Topography is 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). Also, studies on the variations in species richness along elevation gradients have at least resulted in five patterns and all trends have been discussed in relation to different environmental variables (Körner 2002; Grytnes 2003b; Rahbek 2005). 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).

In addition to soil, topography and climate, another important factor that should be considered in examining the environmental variables that have influence on plant species is the geology. The influence of geology on species can be split into the direct influence of rock type itself (its chemistry and physical structure), and the indirect role that it plays in soil formation as well as the development of structures that influence the distribution of plants at a range of scales (Cottle 2004). Pausas and Carreras (1995) found that of all the variables they studied in Pyrenean forests, only bedrock type was significantly related to species richness. When they studied the species richness of different life forms, temperature and moisture also became significant. Many studies have reported strong associations between underlying geological substrates and tree species distribution and community composition (Reiners 2002; Tuomisto et al. 2003; Phillips et al. 2003; ter Steege et al. 2006; Fayolle et al. 2012). Yet there are limited examples showing the significance of the direct influence of rock type (its chemistry) on plant distribution (Cottle 2004). Hence, it is obvious that properties of bedrock, soil, and topography are interrelated and also associated with plant species, but the problem is to define what this association is and at what level. Therefore, examining separately and simultaneously their relationships with plant may be a useful way for a better prediction of species responses to changes in environmental factors in a particular geological environment such as a karst ecosystem.

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 are major foci for speciation and important biodiversity arks (Clements et al. 2006), supporting very high level of endemic species of plants, vertebrates and invertebrates (Vermeulen and Whitten 1999; Schilthuizen et al. 2005; Clements et al. 2006, 2008). They are also 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) where, forests are becoming increasingly disturbed and fragmented (Sodhi et al. 2004; Laurance 2007), so it has been said that more effort should be made to document biodiversity in the region (Webb et al. 2010). Limestone forests are typically rich in endemic flora and have high environmental heterogeneity due to large scale variability in substrate solubility (Perez-Garcia et al. 2009). However, few studies have intensively investigated tropical forests over limestone partly due to the difficulty of working in tropical karst terrain (Kelly et al. 1988; Brewer et al. 2003). While karst are considered as severely understudied (Vermeulen and Whitten 1999; Dennis and Aldhous 2004), 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; 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 in such ecosystems.

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 have 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). Karst ecosystem described as the ecosystem that is restrained by karst environment (Yuan 2001), especially by karst geological setting (Cao et al. 2003), is 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 mountain ecosystems.

The present study examined plant species richness patterns and their ecological correlates in the karst forest of Longhushan Nature Reserve (LNR) SW China, by analyzing a representative sample of vegetation plots from a systematic sampling that combines measurements of plant species richness for all trees DBH≥10 cm, with extensive information on rock type, environmental and soils parameters, allowing for the consideration of the interactions between different environmental habitat factors. LNR, unlike some other karst areas in a region well known to be subject to rapid rock desertification processes, has the advantage of relatively high vegetation coverage even retaining the arbor layer, though undergoing significant anthropogenic influence, which may exceed its environmental carrying capacity and put it at risk of degradation. This makes the area an ideal research habitat to study plant richness, the range of environmental conditions in which species develop, and the patterns of species richness in such ecosystems. The information could be significant in the development of management and conservation strategies of karst forest biodiversity in the region. Our objective was to analyze the trends in plant species richness related to the interactions among environmental habitat factors (including rock type, soil and other environmental factors). In the analysis we first explored plant communities and dominant species in the reserve. Then we examined rock type, soil characteristics, environmental factors, and their single effects on species richness. We finally tested plant richness responses to the collective effects of rock type, soil and environmental factors, and determined which variables have the most significant impact on species.

Materials and methods

Site location and description

Located in the subtropical area of southern China, Long'an County, Nanning, Guangxi Zhuang Autonomous Region (Fig 1), LNR is approximately 90 kilometers away from Nanning city, the provincial capital. 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. Longhushan has a monsoonal climate characteristic of the subtropical zone and is influenced by the regulation of a maritime climate. It has abundant sunshine combined with high rainfall, but with little frost and no snowfall. The annual average temperature is 21.8Cº, with the annual average precipitation of 1500 mm which is mostly centralized in summer. The reserve is divided into three sectors by two landscape barriers: the highway from Nanning to Daxin and the "Green River". 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, the status of the area is that of nature reserve and tourist attraction with an estimated 100,000 visitors per annum. Longhushan is also a primate reserve with increasing impact from both primate population density and anthropogenic effects through agriculture, facilities and infrastructures developed for tourism. The public road running through the reserve in addition to the development of tourism infrastructures, the influence of local inhabitants living around it, and the increasing of primate population over the last 20 years (estimated to be thousands), may exceed its environmental carrying capacity, making species protection and conservation difficult. The lack of floral and faunal information has also led to the belief that some aspects of its ecology are not well known, thus need to be studied. The protected area though not very big as opposed to others in the region, may represent an important resource in Guangxi in term of vegetation formation in a karst ecosystem. The site could become an interesting research habitat to study karst plant species, forest sustainable management, karst ecological system and the geomorphological interaction with vegetation establishment.

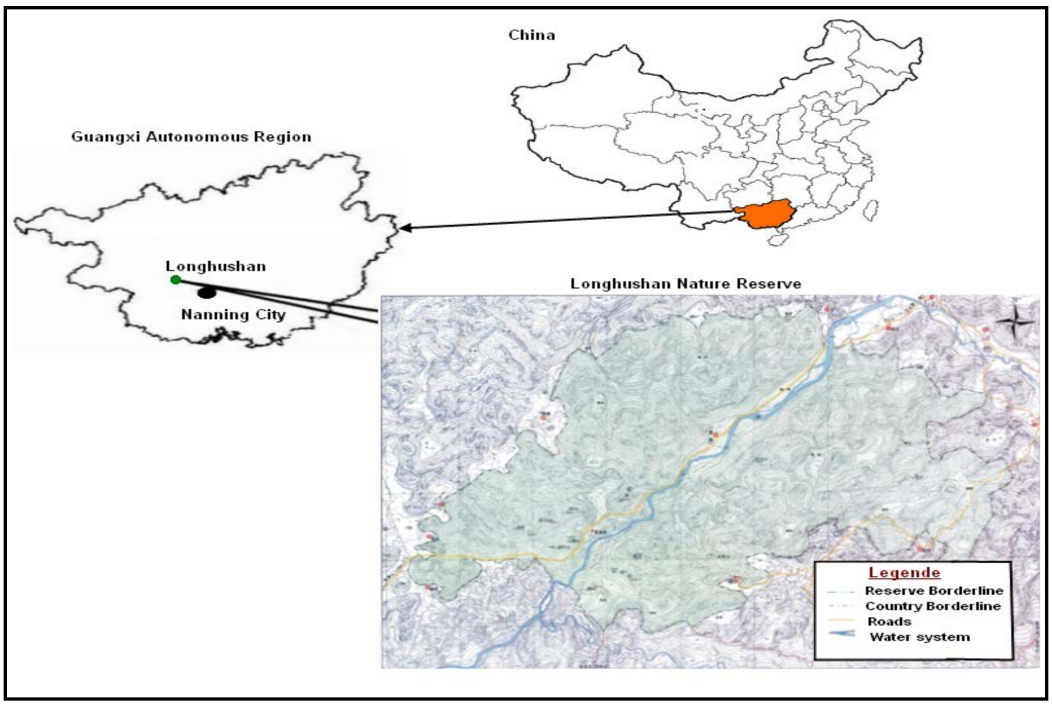

Figure 1: Longhushan Nature Reserve location map.

Sampling design and data collection

Data was collected from 17 quadrats (Q1, Q2,…, Q17) through a systematic survey implemented in the reserve using 30m × 30m quadrats randomly located along 4 south-north transects lines equidistant apart. Geological and soil samples respectively for rock type (RT) and soil characteristics were collected from each quadrat. The number of species for trees greater than 10 cm diameter at breast height (DBH) was recorded for each quadrat and all individuals were identified to species and plotted. 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 including topographical factors were also 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 outcrops on the surface of each quadrat, while soil samples were collected from the topsoil layer (0–10 cm) after the removal of leaf litter.

Lab experiment

Since the site is in a karst area characterized by a thin soil layer, where plant species can be in contact with the rocks and even grow through their fissures, we tried to evaluate the direct influence of RT through its main chemical components. The material basement of karst areas is carbonate rock, which major types are limestone (mainly composed of calcite – $CaCO_3$), and dolostone (compose of dolomite – $CaMg\,(CO_3)_2$). Hence, to examine the trends of plant richness in relation to carbonate RT, geological samples were analyzed for their percentage content of calcite and dolomite. Rock specimens were examined using first diluted HCl acid on the samples, followed by a staining method with alizarin-red test, then dolomite and calcite percentage determined under microscopic observation (Friedman 1959; Warne 1962). Soil samples in this research were examined for some major characteristics that can influence other soil properties in the habitat and affect nutrients availability for plants. Samples were tested for texture, moisture (M), pH, and organic matter (OM) content. Soil M content was obtained by the standard Gravimetric method or oven-dry method calculated from soil samples' 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. To determine soils organic carbon the classic rapid dichromate oxidation technique (Walkley-Black Method) was used, then OM content was quantified by back titration with 0.5 FeSO4 solution with a few drops of ferroin indicator, and the results expressed as percent OM. To examine soil type, the United State Department of Agriculture (USDA) method was used to determine soil textural classes based on percentage content of sand, silt, and clay.

Statistical analysis

Data were afterward divided into four groups including one group of dependent variable (DV) or response variables (plant index), and three groups of predictors or independent variables (IV) (Table 1). Statistical analysis was conducted with IBM SPSS Statistics 19 using Correlation, one way analysis of variance (ANOVA), General Linear Model (two way ANOVA, ANCOVA-analyses of covariance), and Multiple Regression analyses, at 95% confidence interval (CI, $p<0.05$). ANOVA was applied to examine the single or combined effects of RT and soil texture (ST) on plant by comparing the average species richness across different RT and ST groups. Unlike RT, ST was not included in the regression analysis since it was not a dichotomous factor. However, ANCOVA examined the single effect of ST (one-way ANCOVA) or its joint effect with RT (two-way ANCOVA) on plants, while controlling the effects of influential variables (covariates) selected from soil indicators and environmental parameters. Using different tests in

ANCOVA, several parameters were produced: the F-Ratio, compares the mean differences in richness between and within RT or ST groups' variance; the significance (P) of the F-Ratio gives its confidence level; the partial eta squared (P. Eta^2) indicates how much of the total variance in richness was explained by each IV and covariate; and the observed power (OP) presents the probability of finding significant effects (at 0.05 level) with our sample size.

Pearson's simple correlation was used to test the bivariate correlations between each predictor and richness 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 tree standard multiple regression models using the enter method to find the best fit for richness. 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 richness; the coefficient of determination (R^2), represents how much of the variance in richness 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 richness 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 richness 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 our 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 richness 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 richness for the significant model was also established following the general form of the multiple linear regression function:

$$\text{Predicted plant richness} = B_0 + (B_1V_1) + (B_2V_2) + \ldots (B_nV_n) + E$$

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 SPSS analysis

	Groups variables			
	Soil indicators	**Environmental parameters**	**Geological factor**	**Plant index**
Variables	Soil depth Texture Moisture pH Organic matter	Elevation Slope degree Canopy cover Ground cover Ground temperature	Rock type	Richness
Variables description	Predictors/Independent variables/Explanatory variables			Response variables

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

Results

Characteristics of soils, rock type, and plant communities

The basic statistical description of all target variables from plant index, soil properties, environmental and geological factors is presented in table 2. Based on dolomite and calcite percentage of surface rock collected from the 17 plots, high dolomite percentage was found 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%). Plant communities in the reserve were generally evergreen with delimitation between arbor layers, shrubs and grasses, and richness varied from 3 to 12 different species. A total of 59 species (DBH≥10cm) were identified across the 17 quadrats from which *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*, and *Beilschmiedia delicate* were the most dominant, based on their importance value index. Together they represented 64.25% of the total importance value and *Sterculia nobilis* was by far the most abundant species representing alone 13.60% of the total importance value.

Table 2: Descriptive statistics of all target variables from the four groups of factors (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
Species richness (Individual species)	3	12	7.18	3.11

Effects of soil texture and rock type on plant species richness

In both one-way and two-way ANOVA procedures there were no significant changes in plant species richness related to ST or RT, meaning there was no evidence to reject the null hypothesis that there is no relation between richness and ST or RT since the significance values were all above our alpha level of 0.05 ($p > 0.05$). Also, in ANCOVA the only significant association was found when the joint effects of ST and RT were examined (two-way ANCOVA) after controlling the effects of M and GC. ST was found significantly related to richness ($F = 3.978$, $p = 0.047$) and accounted for 57% of its variance (P. $Eta^2 = 0.570$), with near 64% chance of finding a significant difference in our case (OP = 0.638).

Correlation and multiple regression analysis results for the influence of the interaction between rock type, soil and environmental factors on species richness

According to Pearson's simple correlation, there was no significant association between richness and any other predictor except Sd ($r = 0.542$, $p<0.05$). But few inter-correlations were found among some of the predictors with the highest between M and OM ($r = 0.760$, $p<0.01$), SDp 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 or greater than 0.8 to fear for serious multicollinearity problem.

Influence of soil characteristics on species richness

Table 3 summarizes the analytical results of regression model 1 in which the fit of soil characteristics (SDp, M, pH, OM) as predictors of plant species richness was examined. The results showed that despite the multiple correlation coefficient R and the coefficient of determination R^2 values (table 3a), no significant model emerged in predicting plant richness. The model failed to explain any significant variation in richness, since the null hypothesis (F-ratio) that there is equal variance in the mean species richness was not rejected ($F = 0.494$, $p = 0.741$) as the significance p-value was greater than 0.05. In addition, from the coefficients and t-tests (table 3b), no single variable was found with significant impact, indicating that the fit of the observed values to those predicted by the multiple regression equation was no better than what we would expect by chance. This suggests there was not sufficient evidence of strong association between the four soil factors and plant richness.

Influence of environmental factors on species richness

Model 2 was designed to predict plant species richness response based on its linear relationship to the environmental factors (E, Sd, CC, GC, GT). The correlation coefficient indicates there was strong linear relation between richness and the five environmental variables (table 4a). However, although E and Sd seem to have some effects (table 4b), this model also failed to explain variation in plants since it was still just marginally significant ($F = 2.860$, $p = 0.068$, $0.05 < p < 0.1$). Hence, as for the previous model, with significance $p > 0.05$ there was insufficient evidence to reject the null hypothesis of no significant difference in mean level.

Table 3: Multiple linear regression model 1 between species richness as response variable and the single effect of soil characteristics as predictors, before combining variables from all three groups (95% CI; N=17)

a- Model fit

Model	Predictors (IV)	Plant Index (DV)	Model summaries			ANOVA (F-statistics)	
			R	R^2	Adj. R^2	F-ratio	P
1	SDp, M, pH, OM	Richness	0.376	0.141	-0.145	0.494	0.741

b- Coefficients

Model	Dependent variables	Predictors	B	Beta	t	p
1	Richness	Constant	6.546		0.573	0.578
		Soil depth	-0.017	-0.200	-0.524	0.610
		Moisture	0.129	0.487	1.071	0.305
		PH	-0.196	-0.050	-0.128	0.900
		Organic matter	-0.322	-0.345	-0.790	0.445

SDp: soil depth; M: moisture; OM: organic matter; IV: Independent variables also called predictors; DV: Dependent variables

Table 4: Multiple linear regression model 2 between species richness and the single effect of environmental factors, before combining variables from all groups (95% CI; N=17)

a- Model fit

Model	Predictors (IV)	Plant Indices (DV)	Model summaries			ANOVA (F-statistics)	
			R	R^2	Adj. R^2	F-ratio	P
2	E, Sd, CC, GC, GT	Richness	0.752	0.565	0.368	2.860	0.068

b- Coefficients

Model	Dependent variables	Predictors	B	Beta	t	p
2	Richness	Constant	-2.110		-0.169	0.869
		Elevation	0.057	0.646	2.570	0.026
		Slope degree	0.097	0.520	2.414	0.034
		Canopy Cover	-0.081	-0.429	-1.701	0.117
		Ground Cover	0.022	0.149	0.621	0.547
		Ground Temperature	0.082	0.038	0.165	0.872

E: elevation; Sd: slope degree; CC: canopy cover; GC: ground cover; GT: ground temperature

Effects of the interactions between rock type, soil characteristics, and environmental factors on species richness

In model 3, influential variables (E, Sd, M, OM, RT, CC, GT) selected from soil, geological and environmental factors were included to test their fit as predictors of plant richness. The high R value (Table 5a) suggest the existence of very strong correlation between the seven predictors and richness (R = 0.963). Unlike the previous models, the null hypothesis was rejected this time as the model was able to explain significant variation in richness (F = 16.373, $p < 0.001$), and accounted for over 87% of its variance (adj. $R^2 = 0.871$). This value indicates that compared to model 1 and 2, the amount of variation explained by model 3 in richness increased significantly by respectively over 100% and 50.3%, suggesting that the overall prediction model was greatly improved. The coefficients and t-tests (Table 5b) show that richness was significantly predicted by positive effects of E, Sd, M, and a negative effect of RT. Since RT was coded as 1=dolomite and 2=calcite, this suggests that richness increased with increasing E, Sd, M, and in high dolomite percentage areas. The t-tests also indicate that Sd and RT were found as the greatest contributors to richness (respectively: t = 6.734, $p < 0.001$; and t = -6.328, $p < 0.001$) followed by M (t = 3.291, $p < 0.01$) and E (t = 3.252, $p < 0.05$), while OM, CC, and GT were found with no significant impacts. Although OM (nutrients store for plants), CC, and GT contributed less to the fit of the regression equation, their presence in the model was however essential for the predictability of plant richness, suggesting they should be considered in examining the environmental factors that impact plant species richness in karst habitats.

Table 5: Regression model 3 between species richness as dependent variable and the collective effects of soil, environmental and geological factors as predictors, after combining influential variables selected from all three groups of factors (95% CI; N = 17)

a- Model fit

Model	**Predictors (IV)**	**Plant Indices (DV)**	**Model summaries**			**ANOVA (F-statistics)**	
			R	**R^2**	**Adj. R^2**	**F-ratio**	**P**
3	E, Sd, M, OM, RT, CC, GT	Richness	0.963	0.927	**0.871**	16.373	**0.000**

b- Coefficients

Model	**Dependent variables**	**Predictors**	**B**	**Beta**	**t**	**p**
3	Richness	Constant	1.424		0.218	0.833
		Elevation	0.039	0.441	3.252	**0.010**
		Slope degree	0.121	0.653	6.734	**0.000**
		Moisture	0.128	0.482	3.291	**0.009**
		Organic Matter	-0.239	-0.256	-1.538	0.158
		Rock Type	-4.032	-0.639	-6.328	**0.000**
		Canopy Cover	-0.028	-0.150	-1.221	0.253
		Ground Temperature	0.146	0.067	0.619	0.552

E: elevation; Sd: Slope degree; M: Moisture; OM: Organic Matter; RT: Rock Type.; CC: canopy cover; GT: ground temperature

The partial regression plots (Fig 2) indicate the existence of strong linear relationships between each significant predictor and richness in the presence of the other variables of the model. The R^2 Linear values confirm that Sd and RT had the greatest impacts on richness as they accounted for respectively over 83% and near 82% of the variance in richness (respectively: R^2 Linear = 0.834, and 0.816) (Fig 2b, d). M explained near 55% of the variation (R^2 Linear = 0.546) (Fig 2c) while E accounted for 54% (R^2 Linear = 0.540) (Fig 2a). The normal plots of the model residuals (Fig 3a) showed no major deviations from standard normal distribution, and the scatterplots of residuals by predicted values (Fig 3b) seem to have no tendency in the distribution. Hence, since there was no strong evidence to support the violation of homoscedasticity and normal distribution it is safe to assume that these regression assumptions were approximately met, suggesting we can have confidence in the ANOVA and t-tests of the coefficients of regression slope. Therefore, using the unstandardized coefficients of the explanatory variables, the relationships between model 3 and plant species richness could be expressed by the following regression equation.

$$\text{Richness} = 1.424 + (0.039 \times \text{elevation}) + (0.121 \times \text{slope degree}) + (0.128 \times \text{moisture}) – (0.239 \times \text{organic matter}) – (4.032 \times \text{rock type}) – (0.028 \times \text{canopy cover}) + (0.146 \times \text{ground temperature})$$

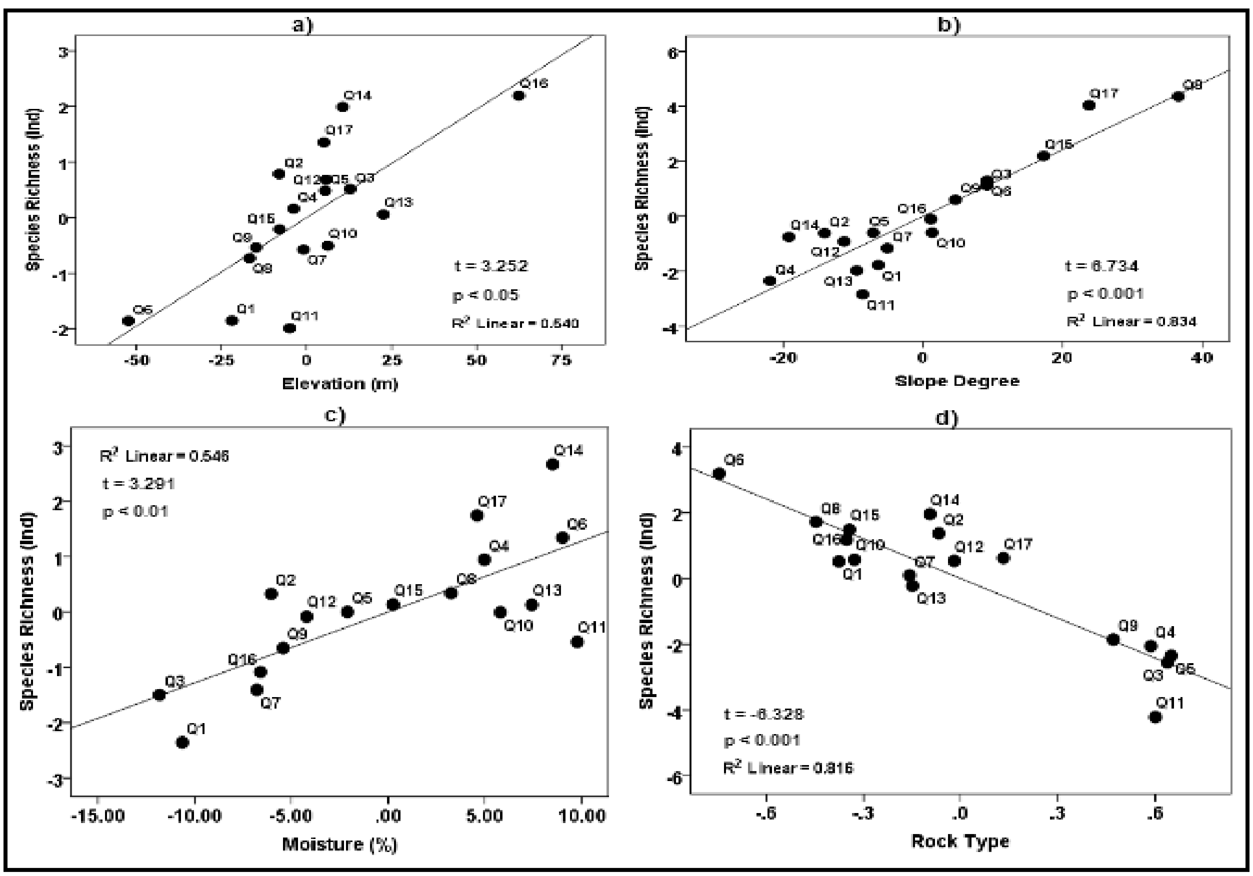

Figure 2: Model 3 partial regression plots displaying linear correlations between species richness and a) elevation, b) slope degree, c) moisture, and d) rock type, as significant predictors.

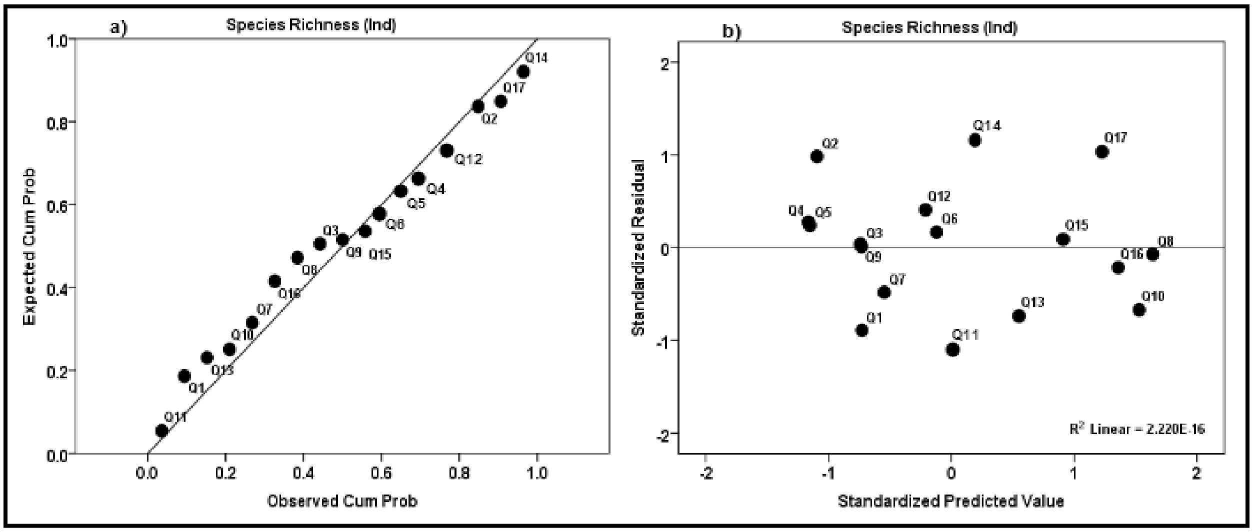

Figure 3: Model 3 residuals' plots in the prediction of species richness for regression assumptions of normality and constant variance. a) Normal P-P plot is a plot of regression standardized residuals vs. standardized predicted values. It shows the residuals close to the reference line; b) the scatterplot of standardized residuals versus standardized predicted values also shows that the residuals are roughly the same size for each predicted value of plant richness.

Discussion

Analysis of variables related to environmental and geological factors revealed some of their interactions with Longhushan soil upon which plants species depend. ANOVA failed to prove any significant effects of RT or ST on plant richness suggesting there was no sufficient evidence to detect such relations. However, when covariates from soil and environmental variables were included in ANCOVA analysis a slightly significant result was obtained. Richness was related to ST in the presence of RT, M, and GC, suggesting ST, RT, M, and GC have some interactions feedbacks on plant species richness. The influence of ST on richness found in this study supported the findings of Sala et. al (1997). This relation may be explained by the fact that soil texture affects soil behavior particularly its retention capacity for nutrients and water (Brown 2003), which availability have significant feedback on plant composition, distribution, and performance. Water availability is also reported as one of the most important environmental parameters controlling plant richness (Lavers and Field 2006), and it is said to be even more profound in environments where soil moisture is a major limiting resource like karst areas.

In our purpose to examine the trends in plant richness related to environmental habitat factors, Pearson's simple correlation analysis failed to establish the existence of bivariate association between richness and any predictor, except Sd. Multiple regression analysis also failed to prove that the four soil variables and the five environmental factors, each group examined separately, had any statistically significant relationship with richness. However, when influential variables selected from soil, environmental and geological factors were examined for their combined effects, strong associations were observed. The regression equation was very useful for making prediction of plant richness, since a great amount of its variance was explained, and the overall prediction model was greatly improved after combining variables from soil, geological, and environmental factors. There were positive trends of species richness with elevation, slope degree, moisture, and in dolomite areas in the presence of organic matter, canopy cover, and ground temperature. This suggests that moisture, organic matter content, temperature and rock type combined with topographic factors have some interactions influence on plant richness, supporting the conclusions of other studies (Specht 1989, 1993; Pausas and Carreras 1995; Leathwick et al. 1998; Hawkins et al. 2003).

The strong association between slope degree and richness was expected as first indicated by Pearson’s correlation. Our findings disagreed with several studies which found a decreasing trend in species richness with altitude (Hamilton 1975; Gentry 1988; Kitayama 1992; Stevens 1992; Pausas 1994; Rey Benayas 1995; Vazquez and Givnish 1998; Odland and Birks 1999). In fact, according to Rahbek (1995, 1997) there are three main patterns: a monotonic decline in species richness from low to high elevation, a hump-shaped pattern with a maximum at mid-elevations, or essentially a constant from the lowlands to mid-elevations followed by a strong decline further up. However, since the length of elevation gradient of our surveyed plots varied from 109 to 243 m, this might be insufficient altitudinal range to establish such patterns, further studies that cover higher elevations with bigger sample size in the area perhaps could help to address the exact trend. Nevertheless, the positive trend of species richness with elevation and slope degree may be attributed to several factors including limited access and disturbance at high elevations with steep slopes than at lower elevations, which sustained the findings of Song et al. 2008. In addition, Longhushan reserve is a karst area characterized by extremely complex topography, resulting in a wide range of climatic/microclimatic conditions and a variety of distinctive micro-habitats. Another reason may be the combination of topographic variables (elevation, slope degree, etc) and multiple environmental factors such as climate, soil type, texture, water and nutrients status, etc that influence species composition and distribution, sustaining the conclusion of previous researches (Holland and Steyn 1975; Austin et al. 1996; Ramsay and Oxley 1997).

A particularity of our findings is that in addition to soil and topography, rock type was found as one of the most important environmental factors which significantly influenced plant species richness. Hence, carbonate rock type may be a key factor in karst habitats since it strongly affected richness by explaining a great amount of its variation, but also its inclusion in the model greatly improved the predictability of richness. Dolomite percentage was determinant as richness was found with positive trend in dolomite dominated areas but the inverse trend in calcite dominated areas, suggesting that the number of plant species was higher in areas where carbonate rock has 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 the predictable variation in species richness is important in determining areas of conservation, we may postulate for instance that this geological factor is an indicator of high species richness areas in the Longhushan karst forest, which could be used for assigning priority sites for conservation or restoration.

Another particularity is that although not statistically significant, OM was found negatively related to richness. The negative trend though may be explained by a slow decomposition of OM resulting in its accumulation and the tie up of nutrients that are held in it. As reported by Foth (2006), high organic matter contents in soils are the result of slow decomposition rates rather than high rates of organic matter addition. However, the slow decomposition could be due to several factors, as the rate of decomposition is mainly dependent on the abundance of soil microbes (e.g. bacteria, fungi), the substrate quality (nutrient content: C/N ratios, OM composition…), and soil environmental conditions (pH, moisture, texture, temperature…). Our analysis showed that over 88% of the sampled plots had insufficient available moisture, while soil biological activity requires sufficient air and moisture. In fact, it is said that optimal microbial activity occurs at near “field capacity”, which is equivalent to 60-percent water-filled pore space (Linn and Doran 1984). In addition to the insufficient moisture content, the results showed that about 75% of the sampled plots had fine and medium textured soil indicating high clay content, while clay particles are believed to protect some of the more easily decomposable organic compounds from rapid microbial breakdown through encrustation and entrapment (Paul and van Veen 1978; Anderson 1979; Tisdall and Oades 1982). Therefore, although the two factors (soil moisture and texture) may not suffice to totally explain the negative relation between richness and organic matter content, but the lack of adequate soil moisture combined with the dominance of finer textured soil may have contributed to limited microbial metabolisms, resulting in the accumulation of organic matter and the tied up of nutrients needed by plant to grow. This conclusion supports those of Woods and Raison (1983) who suggested that moisture was a major factor in controlling OM decomposition, and Killham et al. (1993) who showed that substrate utilization by microbes in soil was strongly affected by its location, both in terms of pore size and the matric water potential under which turnover takes place. Nevertheless, it should be noted that further studies in the reserve with greater number of observations might help to fully explain the different factors that affect OM decomposition in karst habitats and their impact on plant species. For instance, the microbial biomass, the substrate quality (OM composition, C:N ratios), and the anthropogenic disturbance on different ecological processes could represent interesting subjects for future studies to better understand the complexity of processes OM undergoes in karst habitats in order to establish suitable management strategies.

Conclusion

A good understanding of the spatial patterns of plant biodiversity is fundamental to deciding conservation priorities. In karst areas the physical and chemical characteristics of geology and soils are of importance for plant species from the viewpoint of the karst ecosystem changeability. This study has shown that variations in plant species richness in Longhushan were dependent on complex relationships between soil, environmental, and geological factors of karst habitats. Within this complexity of relationships it appears that the geological factor played an important role in the distribution of plant species in the area, and its inclusion in the analysis greatly improved the predictability of species richness. Trends in species richness were mainly related to rock type, moisture, elevation, and slope degree in association with temperature and nutrients status. In addition, a number of dominant species were found typically well adapted to the special karst environmental habitats. Based on their responses to the significant environmental factors, *Sterculia nobilis*, *Albizia chinensis*, *Ficus oligodon*, and *Psychotria rubra* were adapted to all environmental habitats conditions, suggesting they could be appropriate for restoration and forest amelioration measures. The results clearly demonstrated that the evidence of significant variation in richness was provided after combining variables from soil, geological, and environmental factors, inferring their interaction influence on plants. Evidence supports each of these degrees of interactions, and no single context explained all the associations between richness and soil characteristics, rock type, or environmental factors. 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 rock type may be an important factor influencing the relationship between plant species and other environmental habitat factors in karst areas. Thus, effective and efficient management of karst forest ecosystems requires an elaborate data set and understanding of all the components and physical 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 biodiversity conservation, the prevention of rock desertification, and the development of sustainable management, conservation, and restoration strategies of karst mountains resources in southwest China.

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