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# Effects of Topographical and Edaphic Factors on the Distribution of Plant Communities in two Subtropical Karst Forests, Southwestern China

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**Abstract**: Relationships between topography, soil properties and the distribution of plant communities on two different rocky hillsides are examined in two subtropical karst forests in the Maolan National Natural Reserve, southwestern China. Surveys of two 1-ha permanent plots at each forest, and measurements of four topographic and thirteen edaphic factors on the slopes were performed. Two-way Indicator Species Analysis (TWINSPAN) and Detrended Canonical Correspondence Analysis (DCCA) were used for the classification of plant communities and for vegetation ordination with environmental variables. One hundred 10 m×10 m quadrats in each plot were classified into four plant community types. A clear altitudinal gradient suggested that elevation was important in community differentiation. The topography and soil explained 51.06% and 54.69% of the variability of the distribution of plant species in the two forest plots, respectively, indicating both topographic factors (eg. elevation, slope and rock-bareness rate) and edaphic factors (e.g. total P, K and exchangeable Ca) were the important drivers of the distribution of woody plant species in subtropical karst forest. However, our results suggested that topographical factors were more important than edaphic ones in affecting local plant distribution on steep slopes with extensive rock outcrops, while edaphic factors were more influential on gentle slope and relatively thick soil over rock in subtropical karst forest. Understanding relationships between vegetation and environmental factors in karst forest ecosystems would enable us to apply these findings in vegetation management strategies and restoration of forest communities.

**Keywords:** Karst forest; Classification; Ordination; Edaphic factor; Topography; Rock outcrop

## Introduction

The relationships between plant communities and environmental factors are among the most fundamental questions contributing to understanding plant species composition and structure in a particular habitat, landscape and region (Burke 2001; John et al. 2007; Yavitt et al. 2009; Lennon et al. 2011). Plant ecologists have been successful at defining the changes in species composition along environmental gradients at the differing spatial scales (Basnet 1992; Porembski et al. 1995; Chen et al. 1997; Härdtle et al. 2005; Wang et al. 2009; Pajunen et al. 2010; Zhuang et al. 2012). In the regional or global scales, many species responses are well correlated with climate

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factors (Jarema et al. 2009). But at the local scale, topographic variability plays a critical role in determining plant species distribution (Itoh et al. 2003; Cui et al. 2009), sometimes acting through soil microclimate or nutrient availability (Chen et al. 1997; Potts et al. 2002; John et al. 2007; Yavitt et al. 2009). Therefore, these environmental factors are important not only in detecting plant species distribution variations with spatial scale, but also for providing insight into the environmental requirements of the species needed for successful ecological restoration and the establishment of plantations (Toledo et al. 2012).

Karst is a distinctive topography created by the rainfall and groundwater acting on carbonate bedrock such as limestone and dolomite (Xu 1995). China has the largest and widest karst regions in the world, which is mainly distributed in the subtropical mountainous regions of southwestern China (Yuan 1991; Wang et al. 2004) where a unique type of karst vegetation grows. Limestone outcrop soils in this area are typically shallow and often have rapid drainage, high levels of Ca and Mg, and a relatively high pH and high organic matter content compared with many other subtropical or tropical forest soils (Nie et al. 2011; Zhang et al. 2011). These formations harbour several types of microhabitats (e.g. soil surface, rocky surface, rocky gully, rocky-soil surface and rocky crevice), which can be selectively exploited by different plant species with different ecological requirements and therefore have particularly high levels of plant diversity (Long 2007; He et al. 2008). Consequently, the role of preserving a large number of endemic and rare species has been attributed to these habitats, owing to their peculiar topography and soil characteristics (Zhang et al. 2010). However, few studies so far have intensively investigated the subtropical forests on the karst terrain of the world because of the restricted distributions of this substrate and the difficulty of working in karst terrain.

The Maolan National Natural Reserve (MNNR) in southern Guizhou Province is an intensively distributed, uniquely original and relatively stable karst forest ecosystem remained in subtropical China (Zhang et al. 2010). The topography there is characterized by typical karst fengcong-depression (a combination of clustered peaks with a common base) and funnel landscape. The topography and soil properties showed clear variations along a hillslope in typical karst peak-cluster depression (Zhou and Pan 2001; Peng et al. 2010). Previous studies on karst forest in southwestern China concentrated on quantitative floristic surveys (Jiang 1995; Zhu 2002; Song et al. 2010a; Liu et al. 2011), stand development (Liang 1992; Zhang et al. 2010) and degraded forest restoration (Yu et al. 2002; Wang et al. 2004; Guo et al. 2011). However, most of these studies are rather descriptive and little is still known about the relationships between the distribution of plant species and environmental factors in subtropical karst forest.

In this study, we analyzed the ecological relationships between the distribution of plant communities and their environmental factors in two subtropical karst forests in MNNR. The objectives of this study were: (1) to reveal the forest community types and its distribution patterns along the slope gradient on two different karst hillsides, (2) to ascertain the major environmental factors (e.g. topographical and edaphic variables) that determine the distributions of the plants communities in two subtropical karst forests in MNNR.

## 1 Methods

### 1.1 Study site

The study site was located in Maolan National Nature Reserve (25°09'20" N to 25°20'50"N, 107°52'10"E to 108°05'40"E), Libo County, Guizhou Province in southwestern China (Figure 1). This reserve, which is ca. 20,000 ha in size, was established in the 1985 and joined the World Biosphere Reserve Network under the Man and the

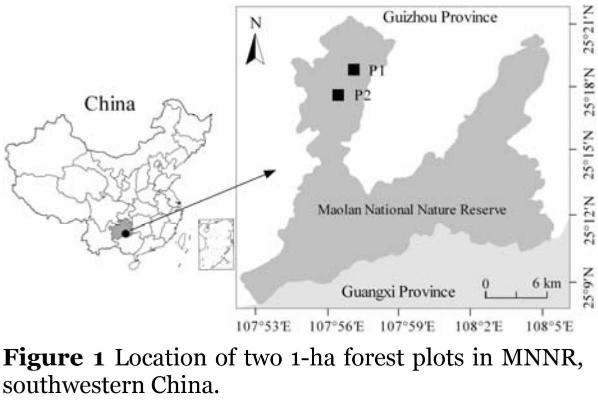

**Figure 1** Location of two 1-ha forest plots in MNNR, southwestern China.

Biosphere Project in 1996. The elevation of the reserve ranges from 430 to 1,078.6 m with an average of ca. 800 m. This region is characterized by a subtropical monsoon climate, with a mean annual rainfall of 1,320.5 mm, a mean annual temperature of 15.3 °C and a mean annual evaporation of 1,343.6 mm. The carbonate rocks are usually exposed on the surface, and soils are thin and discontinuous in the studied area. The shallow black limestone soil is rich in organic matter and nutrients such as N, P, K and Ca.

## 1.2 Field sampling

The two 1-ha (100 × 100 m) permanent plots (named P1 and P2, respectively) were established in two kinds of old-growth mixed evergreen-deciduous broadleaved forests in summer of 2008 in MNNR (Figure 1). Plot P1 was established on a steep southeast-facing slope (the mean slope is 45°) from valley-bottom to hill top at an elevation range of 835-912 m. Rock outcrops occur on almost the entire plot (ca. 85% of the ground surface). Plot P2 is situated near the top of another low mountain spanning an altitudinal range of 895 to 938 m. Two slopes facing southeast and northeast are included. The plot is gently sloping in the lower and higher altitudes, rather moderate or steep in the middle altitude, and with numerous outcrop rocks in the mid-lower part of the plot. The slope ranges from 5° to 48° with a mean value of 30°. The average rock-bareness rate cross the entire plot is ca. 40%. Each plot was divided into one hundred 10 m × 10 m contiguous quadrats as the basic unit of vegetation survey, using the forest compass (DQL-1, Harbin Optical Instrument Factory, China). All free-standing trees at least 1 cm in diameter at breast height (DBH; 1.3 m above ground) were tagged, measured and identified to species. We documented 4,281 living individuals with ≥1 cm DBH (belonging to 199 species, 140 genera and 65 families) in plot P1, and 3,857 individuals (191 species, 121 genera and 58 families) in plot P2, respectively.

## 1.3 Environmental variables collection

Each quadrat was characterized by four topographic factors: elevation (ELE), slope degree (SLO), slope aspect (ASP) and the rock-bareness rate (RBR). Elevation was measured by a portable GPS receiver (GPSMAP 60CSx, Garmin Ltd., Taiwan, China). Slope degree and aspect were measured by the DQL-1 Forest Compass (Harbin Optical Instrument Factory, China). The percentage of rock-bareness within each 10 m×10 m quadrat was visually estimated. The descriptive variable slope aspect was converted to quantitative data (slope aspect: 1 for east-north aspects, 2 for east-south aspects and 3 for south aspect). Soil samples at a depth of 0-10 cm from three locations chosen randomly within each 10 × 10 m quadrat. Then each bulk soil sample was air-dried and passed through a 2 mm sieve to separate the fine and coarse soil fractions. All subsequent analyses were performed on the fine fractions. Soil pH was measured in a 1:2.5 soil to water suspension. Soil organic matter (OM) was measured by the $K_2Cr_2O_7$-capacitance method and total nitrogen (TN) by the micro-Kjeldahl method; total phosphorus (TP) was measured by NaOH fusion and Mo-Sb colorimetric procedures; total potassium (TK) was measured by NaOH fusion and flame photometry; total calcium (TCa) and magnesium (TMg) by atomic absorption spectrometry. The available nitrogen (AN) of soils was determined by diffusion-absorption method. Available phosphorus (AP) was extracted using $NaHCO_3$ solution and its content was determined by Mo-Sb colorimetric method. Available potassium (AK) was extracted with neutral ammonium acetate and measured by flame photometry. Cation exchange capacity (CEC) was determined by replacement of exchangeable cations by ammonium acetate (1 M, pH 7). Exchangeable Ca (ECa) and Mg (EMg) were extracted with DTPA and measured by atomic absorption spectrometry. All soil analysis was conducted following the procedures described by Lu (2000).

## 1.4 Data analysis

Quantitative classification and ordination methods were used to detect discontinuous and continuous variation in forest composition and to relate this to variation in environmental factors (Franklin et al. 2006). An importance values (IVs) for each woody plant with ≥1 cm diameter at breast height (DBH) in each quadrat was calculated as the average of relative density and relative dominance.

Two-way Indicator Species Analysis (TWINSPAN) (Hill 1979) was applied on the data matrix (100 subplots × 199 species and 100 subplots × 191 species for plot P1 and P2, respectively) using their IVs for plant group classification. A standardization analysis was conducted in the species matrix used in TWINSPAN and the classifications were carried out by the cut-off levels of 0, 2, 5, 10, and 20 for TWINSPAN. To support the TWINSPAN analyses and to describe relationships between woody plant distributions and environmental variables, a multivariate gradient analysis—Detrended Canonical Correspondence Analysis (DCCA) was used. DCCA has some advantages over other ordinations because it enables easier interpretation of the figure axes (ter Braak and Šmilauer 2002). The vegetation data matrix consisted of IVs for each species in each quadrat in plot P1 and P2. The environmental data matrix consisted of topographical variables (elevation, slope degree, slope aspect and the rock-bareness rate) and edaphic variables (soil pH, organic matter, total N, P ,K ,Ca, Mg, available N, P ,K , exchangeable Ca, Mg and cation exchange capacity). A Monte Carlo permutation test (499 randomizations) was performed to determine the significance of the eigenvalues. Species which occurred once only were omitted from the analysis and data were not transformed (Burke 2001). In order to examine the respective contribution of the explanatory variables, the partial detrended canonical correspondence analysis (partial DCCA) was implemented to partition the species variation into independent components: (a) topographical variables, (b) soil variables, (c) covariation of topographical and soil variables, and (d) unexplained variation. TWINSPAN classification and DCCA ordinations were carried out using the software package PC-ORD 4.41 (McCune and Mefford 1999) and CANOCO 4.5 (ter Braak and Šmilauer 2002), respectively.

## 2 Results

### 2.1 TWINSPAN classification

The 100 quadrats in plot P1 and P2 were clustered into eight groups according to TWINSPAN. However, in view of the actual ecological significance, four groups (Group A-D) were adopted based on the third cut level of TWINSPAN, representing four forest communities in plot P1 and P2, respectively (Figures 2 and 3).

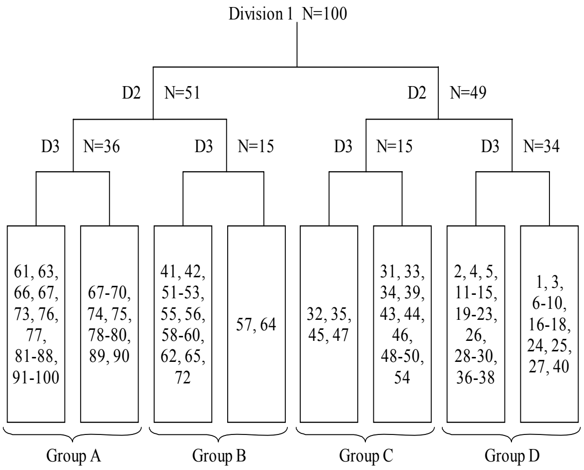

**Figure 2** Dendrogram of the TWINSPAN classification for 100 quadrats in plot P1 in MNNR, southwestern China. The numbers in the squares refer to quadrats.

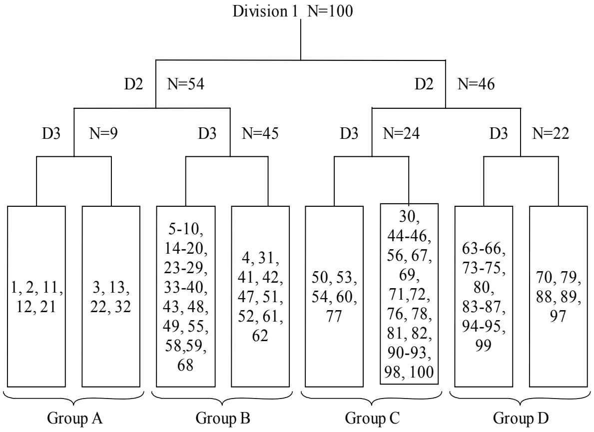

**Figure 3** Dendrogram of the TWINSPAN classification for 100 quadrats in plot P2 in MNNR, southwestern China. The numbers in the squares refer to quadrats.

Forest community types were named after the dominant species, followed by subdominant species. The four communities in plot P1 were: A) *Platycarya longipes* + *Clausena dunniana* + *Carpinus pubescens* + *Cyclobalanopsis glauca*; B) *C. dunniana* + *Celtis biondii* + *Acer wangchii*; C) *A. wangchii* + *C. dunniana* + *C. biondii*; D) Comm. *Viburnum brachybotryum* + *Swida parviflora* + *A. wangchii* + *Symplocos sumuntia* (Figure 2). The four communities in plot P2 were: A) *Lindera communis* + *P. longipes* + *Lindera nacusua*; B) *P. longipes* + *Cyclobalanopsis myrsinaefolia* +

*Distylium myricoides* + *Carpinus pubescens*; C) *C. myrsinaefolia* + *Castanopsis. carlesii* var. *spinulosa* + *Osmanthus fragrans* + *Rhododendron latoucheae*; D) *C. carlesii* var. *spinulosa* + *R. latoucheae* + *O. fragrans* (Figure 3). The environmental characteristics for the four forest community groups in plot P1 and P2 are shown in Table 1. It was obvious that each community group differs from the other in terms of its environmental needs.

## 2.2 DCCA ordination

For plot P1, the eigenvalues obtained for the first and second axes were 0.659 and 0.321, respectively. The species-environment correlations coefficients were 0.967 for axis1 and 0.829 for axis2. The cumulative percentage of variance explained by the first four axes accounted for 24.5% of the species data variation and 61.6% of the species-environment variation. A Monte-Carlo test showed that all ordination axes were significant ($p < 0.001$) (Table 2).

The first axis was positively correlated with the elevation, slope and EMg, and negatively correlated with AK, TP and TK in plot P1. The second axis was associated with RBR, slope, TN and ECa (Table 3). As shown in the DCCA ordination diagram based on the first two axes, all of the plant communities generated by TWINSPAN had their own distribution ranges and limits (Figure 4). Group A was distinct for highest elevation, slope gradient, more rock outcrop and poor soil fertility and contained mostly light- demanding and drought-tolerant species such as *P. longipes*, *C. pubescens*, *Swida austrosinensis* and *C. dunniana*. Group B was mainly distributed in the medium elevation habitats with extensive rock outcrop and steep slope. Group C was located at low elevation, with the high soil fertility and moderate slopes. Group D was distributed cross lower elevation with low pH, nutrient rich soil, less rock outcrops, and was comprised of shade-tolerant species like *S. sumuntia*, *S. parviflora*, *V. brachybotryum* and

**Table 1** Mean of the environmental variables in the four plant community groups obtained by TWINSPAN in plot P1 and P2 in MNNR, southwestern China

| Variables | TWINSPAN groups | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | P1 | | | | P2 | | | |
| | A | B | C | D | A | B | C | D |
| Elevation (m) | 902 | 880 | 861 | 845 | 901 | 906 | 923 | 928 |
| Slope (°) | 48 | 53 | 44 | 25 | 25 | 32 | 24 | 20 |
| Aspect | ES | ES | ES | ES | ES | ES | ES,EN | ES,EN |
| Rock-bareness rate (%) | 88 | 93 | 85 | 70 | 40 | 60 | 35 | 8 |
| pH | 7.19 | 7.32 | 7.12 | 6.80 | 6.49 | 6.78 | 6.06 | 5.64 |
| OM (%) | 11.46 | 15.33 | 13.72 | 10.34 | 11.38 | 10.43 | 12.66 | 13.01 |
| TN (%) | 0.57 | 0.82 | 0.78 | 0.53 | 0.43 | 0.45 | 0.46 | 0.42 |
| TP (%) | 0.09 | 0.16 | 0.22 | 0.20 | 0.10 | 0.07 | 0.05 | 0.04 |
| TK (%) | 0.33 | 0.37 | 0.42 | 0.45 | 0.23 | 0.24 | 0.13 | 0.11 |
| TCa (%) | 1.10 | 1.61 | 1.09 | 0.78 | 0.60 | 0.87 | 0.19 | 0.07 |
| TMg (%) | 0.35 | 0.37 | 0.34 | 0.33 | 0.14 | 0.17 | 0.08 | 0.06 |
| AN($mg.kg^{-1}$) | 194.40 | 323.40 | 415.90 | 301.60 | 187.77 | 184.38 | 214.20 | 194.35 |
| AP($mg.kg^{-1}$) | 3.24 | 4.63 | 3.87 | 2.91 | 5.60 | 7.57 | 9.03 | 4.64 |
| AK($mg.kg^{-1}$) | 62.04 | 86.49 | 105.28 | 134.92 | 47.5 | 50.56 | 72.37 | 50.47 |
| ECa ($cmol.kg^{-1}$) | 14.46 | 15.94 | 15.45 | 12.23 | 9.08 | 11.55 | 5.12 | 3.34 |
| EMg ($cmol.kg^{-1}$) | 2.24 | 2.38 | 2.17 | 2.00 | 1.02 | 1.14 | 0.72 | 0.55 |

**Table 2** Eigenvalues and cumulative percentage variance of DCCA ordination

| | P1 | | | | P2 | | | |
|---|---|---|---|---|---|---|---|---|
| Axes | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| EI | 0.659 | 0.326 | 0.228 | 0.114 | 0.537 | 0.153 | 0.094 | 0.067 |
| SE | 0.967 | 0.829 | 0.731 | 0.688 | 0.942 | 0.806 | 0.711 | 0.699 |
| C (%) | 24.5 (four axes) | | | | 22.1 (four axes) | | | |
| CS (%) | 61.6 (four axes) | | | | 53.0 (four axes) | | | |

**Note:** EI = Eigenvalues, SE = species-environment, C = Cumulative variance of species, CS = Cumulative variance of species- environment relation

**Table 3** Correlation coefficients between DCCA axes and environmental variables for the plant communities in plot P1 in MNNR, southwestern China. $^{*}p < 0.05$, $^{**}p < 0.01$

| Environmental variables | Correlation coefficient | | |
|---|---|---|---|
| | Axis 1 | Axis 2 | Axis 3 |
| Elevation | $0.942^{**}$ | 0.242 | 0.071 |
| Slope | $0.582^{**}$ | $0.425^{*}$ | -0.177 |
| Aspect | -0.199 | -0.165 | 0.027 |
| RBR | 0.280 | $0.562^{*}$ | -0.043 |
| pH | 0.154 | 0.245 | 0.049 |
| OM | 0.144 | 0.370 | 0.042 |
| TN | 0.088 | $0.464^{*}$ | 0.004 |
| TP | $-0.592^{**}$ | 0.232 | 0.214 |
| TK | $-0.558^{**}$ | 0.027 | 0.150 |
| TCa | 0.226 | 0.374 | 0.029 |
| TMg | 0.248 | 0.390 | -0.009 |
| AN | -0.397 | 0.260 | -0.039 |
| AP | 0.121 | 0.212 | -0.062 |
| AK | $-0.625^{**}$ | 0.037 | 0.019 |
| ECa | 0.314 | $0.475^{*}$ | 0.131 |
| EMg | $0.457^{*}$ | 0.305 | -0.008 |
| CEC | 0.077 | 0.385 | -0.177 |

RBR=Rock-bareness rate

**Table 4** Correlation coefficients between DCCA axes and environmental variables for the plant communities in plot P2 in MNNR, southwestern China. $^{*}p < 0.05$, $^{**}p < 0.01$

| Environmental variables | Correlation coefficient | | |
|---|---|---|---|
| | Axis 1 | Axis 2 | Axis 3 |
| Elevation | $0.754^{**}$ | 0.047 | 0.061 |
| Slope | -0.270 | 0.209 | -0.241 |
| Aspect | $-0.540^{*}$ | 0.017 | -0.477 |
| RBR | $-0.668^{**}$ | $0.479^{*}$ | -0.137 |
| pH | $-0.722^{**}$ | 0.222 | -0.037 |
| OM | 0.195 | -0.243 | 0.102 |
| TN | -0.256 | 0.016 | 0.143 |
| TP | -0.265 | 0.004 | -0.084 |
| TK | $-0.856^{**}$ | 0.133 | -0.179 |
| TCa | $-0.648^{**}$ | $0.423^{*}$ | -0.068 |
| TMg | $-0.753^{**}$ | 0.372 | -0.027 |
| AN | 0.041 | -0.025 | 0.176 |
| AP | -0.307 | 0.217 | 0.087 |
| AK | -0.007 | -0.152 | 0.172 |
| ECa | $-0.719^{**}$ | 0.191 | -0.068 |
| EMg | $-0.558^{*}$ | 0.147 | -0.023 |
| CEC | -0.390 | 0.001 | -0.049 |

RBR=Rock-bareness rate

*Brassaiopsis quercifolia* etc.

For plot P2, the eigenvalues obtained for the first and second axes were 0.537 and 0.153, respectively. The species-environment correlations coefficients were 0.942 for axis1 and 0.769 for axis2. The cumulative percentage of variance explained by the first four axes accounted for 22.1% of the species data variation and 53.0% of the species-environment variation. A Monte-Carlo test showed that all ordination axes were significant (p < 0.001) (Table 2).

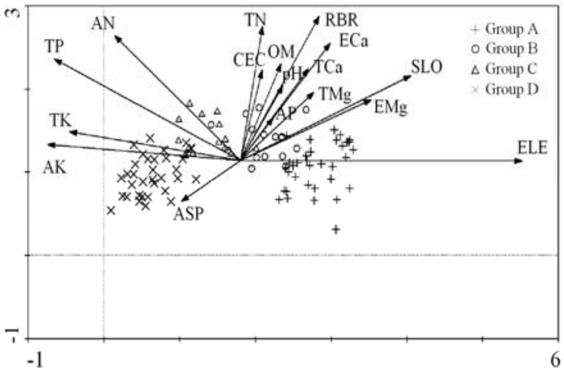

**Figure 4** DCCA ordination diagram of 100 quadrats in plot P1 in MNNR, southwestern China. The arrows in the diagram stand for the environmental factors, the length of each arrow indicates the contribution of the factor to ordination axes, and the angle between the arrows and the axes indicates the correlation between the variable and the ordination axes.

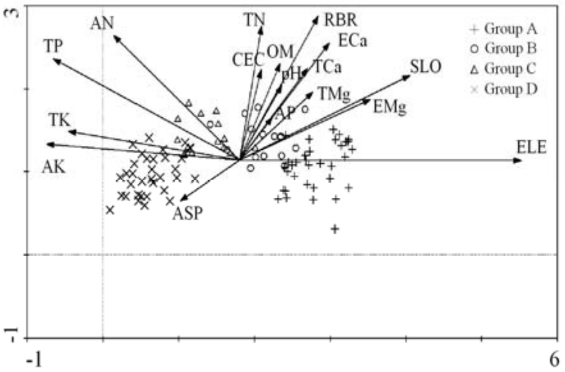

**Figure 5** DCCA ordination diagram of 100 quadrats in plot P2 in MNNR, southwestern China.

The first axis was mainly correlated with elevation, slope aspect, RBR, soil pH, TP, TK, TCa, TMg and ECa in plot P2. The main correlates of the second axis were RBR and ECa (Table 4). The DCCA axis revealed a composite gradient of elevation, slope aspect, RBR, TK, TCa, TMg, and ECa (Figure 5). The plant communities derived from TWINSPAN were superimposed onto the DCCA ordination (Figure 5). Group A was located in sunniest habitat and lowest elevation. Group B was located in drought habitats with the highest rock outcrop, soil pH, Ca and Mg content and contained mostly light-demanding and drought-tolerant species like *P. longipes*, *D. myricoides*, *L. communis* and *C. dunniana*. Group C and D were located at high elevation sites, mostly located on semi-shady or shady slopes, with less rock outcrop, comprising of shade-tolerant species such as *C. carlesii var. spinulosa*, *O. fragrans*, *Lasianthus japonicus var. lancilimbus*, *R. latoucheae* and *Ilex ficoidea*.

The partial DCCA illustrated that the overall amount of explained variation was 51.06% in plot P1 and 54.69% in plot P2 (Figure 6). For the plot P1, soil variables explained 17.52% of the variation in the species matrix, whereas 23.66% was predicted by the topographical variables. For the plot P2, edaphic variables seemed to be more important than topographical variables, accounting for 21.34% and 19.81%, respectively (Figure 6).

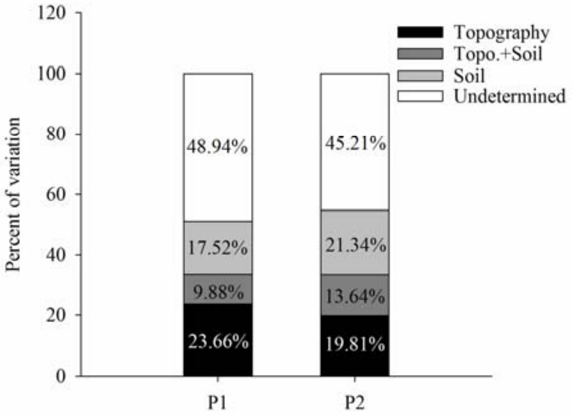

**Figure 6** Variation partitioning of the species data of the plot P1 and P2 in MNNR, southwestern China. Soil is the covariation of topographical and edaphic variables.

## 3 Discussion

The forest varies significantly in composition. TWINSPAN successfully distinguished them into different community types (Figures 2 and 3). An altitudinal gradient in TWINSPAN diagrams is clear which suggests that elevation is important in community differentiation. The effects of elevation on community variation are more obvious between four groups. Primary climax forest (Groups A and B), appear at high altitude in plot P1, and the species are mostly *P. longipes*, *C. dunniana*, *C. pubescens*, *C. biondii* and *S. austrosinensis* etc, and these species are mostly drought- and barren-resistant. Primary sub-climax forests (Group D) were widely spread throughout low elevation. In plot P2, however, at high altitude, the plant communities were dominated by shade-tolerant and moisture-loving species, such as *C. carlesii var. spinulosa*, *O. fragrans*, *L. japonicus var. lancilimbus* and *R. latoucheae* (Groups C and D). At the bottom of the slope, shade-intolerant and drought-tolerant forest dominated by *D. myricoides*, *L. communis* and *C. dunniana* was found.

Topographic factors are related to the vegetation communities, as found previously by many studies (Chen et al. 1997; Brewer et al. 2003; Cui et al. 2009). Elevation affects the vertical distribution of plant species and communities through differences in hydrothermal conditions. Changes in altitude, accompanied by variations in water, precipitation, and light conditions, alter vegetation distribution (Zhang et al. 2011). In the fengcong-depress landscape (a combination of clustered peaks with a common base) of Karst mountains, soil thickness, moisture and nutrient showed clear variations in different altitudinal zones (Zhou and Pan 2001). In plot P1, in medium and higher altitude zones, slope angle was found to be relevant at values greater than 45°. Higher slopes with rocky terrain are associated with shallow soils having low water-holding capacity, thereby, making the plant communities more dependent on atmospheric moisture (Nie et al. 2011). Therefore, upper elevation sites had droughty, shallow soils and strong winds, but more intense sunshine. Such harsh habitats would lead to dominance of shade-intolerant and drought-tolerant plants, such as *P. longipes*, *C. dunnian* and *C. biondii*. It was clear that slight shade-tolerant and drought-tolerant plants (e.g. *V. brachybotryum*, *S. parviflora* and *S. sumuntia*) had the ability to grow and dominate in low elevation habitats. Thus, elevation differences would lead to the distinction of the community type (Figure 4). In plot P2, however, the elevation range was comparatively small and high elevation sites had relatively gentle, semi-shady or shady slopes with less rock outcrop. Therefore, contrary to plot P1, the upper elevation sites of plot P2 had deep and moist soils, while low elevation had shallow soils and extensive rock outcrop. The shade-tolerant and moisture-loving species *C.*

*carlesii* var. *spinulosa*, *R. latoucheae*, and *O. fragrans* were positively associated with elevation, while the shade-intolerant and drought-tolerant species *P. longipes*, *D. myricoides*, *C. myrsinaefolia* and *C. pubescens* were negatively correlated with elevation, indicating that they occurred at low elevation (Figure 5). Our results indicated that elevation was a main influential factor. Besides elevation, other topographic factors, such as slope and BRB, were also significant to spatial variation of plant communities, because slope and RBR also affect soil water conditions and temperature, and aspect further affects isolation in the communities. In karst forest, extensive rock outcrops sites tend to have a shallow and patchy soil cover, forming a very limited capacity of soil water storage (Porembski and Barthlott 2000; Querejeta et al. 2007; Chen et al. 2010). Water leaching leads to potential drought. Thus, drought-tolerant species were positively linked to increasing rock outcrop, while moisture-loving plants were found in areas with deeper soils. Therefore, the RBR was the factor strongly related to plant distribution in two subtropical karst forests, a result also found in other studies (Song et al. 2010b; Zhang et al. 2010).

Topographic features associated with soil properties have been found to be strongly correlated with species distribution on a local scale (Johnston 1992; Chen et al. 1997; Cui et al. 2009). In our study, the community pattern in plot P1 was correlated with soil nutrients like AK, TP, TK and ECa. In plot P2, soil pH, TP, TK, TCa, TMg, and ECa increased with more RBR. Previous study has demonstrated that there existed a direct correlation between soil pH and RBR in karst forest (Ran et al. 2006). Weathering and dissolution of the calcareous rocks have contributed to increase in pH. Soils are often very alkaline, and the underlying bedrock provides a readily available source of Ca, Mg, K and P (Crowther 1987; John et al. 2007). Thus, most calcareous soils are often rich in P and K in addition to having high levels of Ca and Mg (Oliveira-Filho et al. 1998). The present results showed the drought-tolerant species were positively linked to increasing the soil pH, Ca and Mg content, while moisture-loving plants were linked to sites close to low pH. For example, the greatest abundance of these plants were found in Group A and B, which were located in sunnier and more rock outcrop habitat with higher soil pH, K, P, Ca and Mg content in plot P2 (Figure 5). However, soil pH did not play a great part in the ordination in plot P1, and this difference could be ascribed to the fact that the extensive rock outcrops with very thin soil over rock occurred in plot P1 (Figure 4).

The fact that there was more unexplained variation in plot P1 than P2, could perhaps be due to the more complicated environmental gradient observed in plot P1. The elevation range from valley-bottom to hill top was shorter in plot P2, which created smaller topographical transformation and larger variation in soil properties compared to P1. This may be responsible for the observed differences in relative explanatory contribution of the topographical and edaphic factors between the plot P1 and P2. All these results demonstrated that both topographic and edaphic factors are the important drivers of the distribution of woody plant species in karst forest. However, the topographical factors were more important than edaphic factors in the areas on steep slopes with extensive rock outcrops, while edaphic factors were more influential in the areas with gentle slope and relatively thick soil over rock in subtropical karst forest in MNNR.

Understanding the relative importance of the local environmental factors affecting plant compositions can improve the efficiency of future management and restoration measures (King et al. 2004; Lorenzoa et al. 2007). Results from this study suggested that species used in vegetation restoration should be carefully selected based on local environmental characteristics in complex karst habitat. For example, the light-demanding and drought-tolerant species *P. longipes*, *C. pubescens*, *S. austrosinensis* and *C. dunniana* should be restored mainly at the top and middle of the slopes, while *S. sumuntia*, *S. parviflora*, *V. brachybotryum* and *B. quercifolia* are the better choice for the bottom of the slopes.

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