Response of Plant Community Species Diversity and Dominant Species Leaf Traits to Environmental Factors across Different Grades of Rocky Desertification1 Postprint

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Abstract

To investigate the variation patterns of plant community species diversity and leaf traits of dominant species across different rocky desertification grades and their responses to environmental factors, plant communities in non-, lightly, moderately, and severely rocky desertified areas were studied. The variation patterns of species diversity and leaf traits along the rocky desertification gradient were examined using diversity indices including Shannon-Wiener diversity, Margalef richness, Pielou evenness, and Simpson diversity, as well as leaf traits of dominant species such as LA, LT, LDMC, and ^{13}C. The results showed that a total of 188 vascular plant species belonging to 141 genera and 69 families were recorded in 36 quadrats. With intensifying rocky desertification, species diversity indices generally exhibited a decreasing trend; species diversity differences across different rocky desertification grades followed the order: tree layer > shrub layer > herb layer. The LA of dominant species showed a decreasing trend with intensifying rocky desertification, whereas LT, LDMC, and ^{13}C showed increasing trends, with significant differences in leaf traits among different rocky desertification grades ($P<0.05$). Combined with CCA analysis, soil thickness and soil water content were identified as the most important factors influencing plant spatial distribution in rocky desertification areas. RDA analysis revealed a significant correlation between species diversity indices and environmental factors, among which available potassium, soil water content, alkali-hydrolyzable nitrogen, soil thickness, and organic matter were the dominant factors affecting species diversity and plant leaf traits. The research results hold certain theoretical significance and guiding value for vegetation ecological conservation and vegetation restoration in rocky desertification ecosystems in southwestern Karst regions.

Full Text

Response of Plant Community Species Diversity and Leaf Traits of Dominant Species to Environmental Factors Across Different Rocky Desertification Gradients

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Abstract

To elucidate the patterns of plant community species diversity and leaf traits of dominant species across different rocky desertification (RD) gradients and their responses to environmental factors, we investigated plant communities in non-, slight, moderate, and intense RD areas. Using diversity indices (Shannon-Wiener, Margalef richness, Pielou evenness, and Simpson diversity) and leaf traits of dominant species (leaf area [LA], leaf thickness [LT], leaf dry matter content [LDMC], and 13C), we examined variation in species diversity and leaf traits along the RD gradient. Results showed that 36 sample plots contained 188 vascular plant species belonging to 69 families and 141 genera. Overall, species diversity indices decreased with intensifying RD, with diversity ranking as: arbor layer > shrub layer > herb layer across different RD grades. Dominant species LA decreased with RD intensity, while LT, LDMC, and 13C increased, showing significant differences among RD grades ($P<0.05$). Canonical correspondence analysis (CCA) revealed that soil thickness (ST) and soil water content (SWC) were the primary factors influencing plant spatial distribution in RD areas. Redundancy analysis (RDA) demonstrated significant correlations between diversity indices and environmental factors, with available potassium (AK), SWC, available nitrogen (AN), ST, and soil organic matter (SOM) emerging as dominant drivers of species diversity and leaf traits. These findings provide theoretical insights and practical guidance for ecological conservation and vegetation restoration in southwestern China’ s karst regions.

Keywords: rocky desertification degree, community dynamics, plant ordination, redundancy analysis, Guizhou Province

Introduction

Species diversity serves as a crucial indicator for characterizing plant communities, reflecting habitat differentiation, community structure, and stability. Plant functional traits—structural and physiological characteristics that respond to environmental changes and influence ecosystem functions—exhibit specific responses to ecosystem structural features (Cavender-Bares et al., 2004). Investigating the variation patterns of plant community species diversity and leaf traits and their influencing factors is therefore essential for understanding and predicting community resource utilization and structural dynamics (Sanchez-Gonzalez & Lopez-Mata, 2005; Wang, 2001).

In karst regions, fragile ecological conditions coupled with unsustainable human activities have led to severe environmental degradation and rocky desertification (Xiong et al., 2011). The tectonic compression of the Tibetan Plateau has further shaped ancient carbonate rocks into undulating highland landscapes characterized by mountains, hill-depressions, peak forests, peak clusters, and basins, creating substantial topographic relief and steep surface and subsurface gradients that facilitate soil erosion (Wang et al., 2003; Su, 2008). Compared to non-desertified areas, rocky desertification zones exhibit limited environmental capacity, poor soil fertility, severe soil erosion, and low soil volume, with intensifying RD creating distinct differences in soil physicochemical properties (Sheng et al., 2013; Wang et al., 2018). These habitat variations significantly affect plant establishment and growth (Li et al., 2013). Consequently, examining how species diversity and leaf traits of dominant species vary across different plant community layers along RD gradients is critical for revealing relationships between environmental factors and vegetation characteristics, thereby informing effective RD control strategies.

Recent studies have explored the coupling relationships between species diversity, functional traits, and environmental factors in karst regions. Yu et al. (2018) investigated vegetation communities in Dahua County, Guangxi, finding significant compositional and diversity differences along degradation gradients, with diversity indices declining with degradation. Wen et al. (2015) examined plant community succession patterns along latitudinal gradients in southwestern China' s karst areas, demonstrating interactions between biotic and environmental factors. Qin et al. (2018) studied forest community structure and species diversity in Maolan, Guizhou, identifying light, water, and soil conditions as primary determinants of community distribution. Pan et al. (2018) investigated relationships between shrub traits and soil on different slopes in Guilin' s karst hills, revealing that leaf thickness was significantly affected by SWC and soil nitrogen and phosphorus, leaf area by available nitrogen, and dry matter content by soil temperature and organic carbon. Song et al. (2018) examined traits of *Viburnum chinshanense* under varying RD intensities, showing significant reductions in leaf number, leaf area, specific leaf area, stem ratio, and stem diameter with increasing RD stress. While progress has been made in karst region research, integrated studies on how species diversity and plant traits respond to habitat gradients in RD areas remain relatively limited.

Accordingly, this study selected the Salaxi RD demonstration area in Guizhou, examining plant communities and dominant species across non-, slight, moderate, and intense RD areas. Using plant ordination and redundancy analysis, we address two primary objectives: (1) to characterize patterns of species diversity and leaf trait variation along RD gradients, and (2) to analyze relationships between environmental factors and both community diversity and leaf traits, identifying the key environmental drivers influencing these vegetation characteristics.

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1. Materials and Methods

1.1 Study Area The study area is located in the Salaxi RD control demonstration zone in Bijie City, Guizhou Province, within the Liuchong River watershed of Qixingguan District (105°02' 01 -105°08' 09 E, 27°11 36 -27°16 51 N). The region encompasses RD plots ranging from potential to intense, predominantly slight RD. Elevation ranges from 1,600 to 2,000 m, with annual accumulated temperature above 10°C of 3,717°C, mean annual temperature of approximately 13°C, and annual precipitation of 900–1,000 mm concentrated in July–September. The climate features warm, humid summers and cold, dry winters. The area represents a karst plateau-mountain ecosystem with fragmented peak-cluster depression landforms. Soils are primarily yellow soil, with some yellow-brown soil. Zonal vegetation consists mainly of broadleaf forest, coniferous forest, and shrubland, with varying degrees of degradation due to long-term human disturbance.

1.2 Field Sampling and Measurements

1.2.1 Plot Establishment and Vegetation Survey During June–July 2018, following extensive reconnaissance of RD distribution, we established 36 plots (20 m × 20 m) in areas with minimal human disturbance, representing non-, slight, moderate, and intense RD types according to Xiong et al.' s (2001) RD intensity classification: 8 non-RD (NRD), 8 slight RD (SRD), 10 moderate RD (MRD), and 10 intense RD (IRD) plots (Table 1). Each plot was divided into 16 subplots (5 m × 5 m) for arbor surveys, with five 5 m × 5 m shrub subplots and 1 m × 1 m herb subplots established along diagonals and at the center. We recorded species, diameter at breast height, ground diameter, height, crown width, coverage, and growth condition.

1.2.2 Leaf Sampling and Trait Measurement For 14 dominant species (*Pinus armandii, Betula luminifera, Populus alba, Pinus yunnanensis, Juglans regia, Rosa roxburghii, Corylus heterophylla, Pyracantha fortuneana, Coriaria nepalensis, Hypericum monogynum, Castanea seguinii, Rhododendron simsii, Quercus fabri, Quercus variabilis*), we selected five mature individuals per species and collected 10 healthy, mature leaves from different orientations per plant. Leaf area (LA) was measured using a portable leaf area meter (YMJ-D). Leaf thickness (LT) was measured with a digital vernier caliper. Leaf dry mass was determined using constant-temperature drying (105°C for 20 min, then

60°C to constant mass). Leaf dry matter content (LDMC) was calculated as dry mass/fresh mass (Cornelissen et al., 2003). Leaf stable carbon isotope (13C) values were measured using stable isotope mass spectrometry.

1.2.3 Environmental Factor Measurement Given the shallow and discontinuous soil in RD mountains, we collected 0–15 cm surface soil samples using diagonal five-point sampling within subplots, mixing the five samples for laboratory analysis. Soil parameters included soil water content (SWC), pH, organic matter (SOM), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), and available potassium (AK). Analytical methods followed Bao (2013): SWC by ring knife method; pH by potentiometry; TN by Kjeldahl digestion; TP and TK by sulfuric acid digestion (TP by molybdenum-antimony colorimetry, TK by flame photometry); AN by alkali-hydrolysis diffusion; AK by neutral ammonium acetate extraction-flame photometry; AP by sodium bicarbonate extraction-molybdenum-antimony colorimetry; SOM by concentrated sulfuric acid-dichromate external heating. GPS recorded geographic coordinates and altitude at plot centers, with aspect, position, and slope also recorded. Percentage of exposed rock was measured using grid methods (Song et al., 2010), and soil thickness (ST) was measured using soil auger and tape.

1.3 Data Processing

1.3.1 Plant Community Diversity Measurement Important value (IV) indicated species dominance, calculated using four diversity indices (Hui et al., 2010):

Arbor layer:

$$IV = \frac{\text{relative abundance} + \text{relative dominance} + \text{relative frequency}}{3} \times 100$$

Shrub and herb layers:

$$IV = \frac{\text{relative abundance} + \text{relative coverage} + \text{relative frequency}}{3} \times 100$$

Diversity indices:
(1) Shannon-Wiener index: $H' = -\sum_{i=1}^{n} p_i \ln p_i$
(2) Margalef richness index: $R = \frac{S-1}{\ln N}$
(3) Pielou evenness index: $E = \frac{H'}{\ln S}$
(4) Simpson diversity index: $\lambda = 1 - \sum_{i=1}^{n} p_i^2$

where p_i is the proportion of individuals of species i, S is the number of species, and N is the total number of individuals.

1.3.2 Environmental Data Processing Slope position was coded numerically: upper slope = 1, middle slope = 2, lower slope = 3 (Qiu & Zhang, 2000). Slope gradients were classified as: 0°–0.5° (level), 0.5°–2° (gentle), 2°–5° (moderate), 5°–15° (slope), 15°–35° (steep), 35°–55° (very steep), 55°–75° (vertical) (Yang et al., 2018). Aspect was converted from 0°–360° azimuth to 0–1 TRASP index (Liu et al., 2006), where higher values indicate sunnier aspects:

$$TRASP = \frac{1 - \cos[(\text{aspect} - 30)\pi/180]}{2}$$

where TRASP is the aspect index and aspect is the azimuth angle.

1.4 Statistical Analysis Excel 2016 was used for data compilation, IV calculation, and diversity index computation. One-way ANOVA and LSD multiple comparisons for diversity indices and leaf traits across RD grades were performed using SPSS 22.0, with figures generated in Sigma Plot 14.0. CCA and RDA ordinations were conducted using the Vegan package in R, with two-dimensional ordination plots created using ggplot2.

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2. Results

2.1 Species Composition, Diversity, and Leaf Trait Characteristics The 36 plots contained 188 vascular plant species (69 families, 141 genera), including 18 fern species (14 families, 17 genera; 9.57% of families, 12.06% of genera, 20.29% of species), 4 gymnosperm species (2 families, 2 genera), and 166 angiosperm species (56 families, 122 genera; 81.16% of families, 86.52% of genera, 88.30% of species).

Shannon-Wiener, Margalef richness, Pielou evenness, and Simpson diversity indices showed consistent patterns along the RD gradient, with higher values in non-RD areas and lower values in intense RD areas. Shannon-Wiener and Margalef indices followed the pattern: herb layer > shrub layer > arbor layer (Figure 1 [Figure 1: see original paper]A, B), with significant differences among RD grades across all three layers. Pielou evenness and Simpson indices were more balanced across layers (Figure 1 [Figure 1: see original paper]C, D). In slight RD areas, all indices except Margalef richness were higher in herb and shrub layers compared to moderate RD ($P<0.05$).

Leaf trait analysis of 14 dominant species revealed LT ranging from 0.12–0.66 mm, increasing overall with RD intensity, with significant differences between non-RD and moderate/intense RD ($P<0.05$). LA ranged from 0.60–44.62 cm^2, decreasing with RD intensity. LDMC ranged from 0.27–0.53 $g \cdot g^{1}$, peaking in intense RD and differing significantly from other grades ($P<0.05$). 13C correlated positively with RD grade, reaching maximum values in intense RD areas (Figure 2 [Figure 2: see original paper]).

2.2 Relationships Among Community Distribution, Diversity, and Environmental Factors CCA ordination of 188 plant species and 15 environmental factors across 36 plots explained 75.26% of variance, with the first four axes having eigenvalues of 0.8331, 0.6390, 0.6034, and 0.5353, indicating effective representation of plant-environment relationships (Zhong et al., 2019). pH and rock exposure rate showed the strongest positive correlations with axis 1 ($P<0.01$), while ST, SWC, and SOM showed the strongest negative correlations (Table 2 , Figure 3 [Figure 3: see original paper]), suggesting axis 1 represents a habitat gradient from thick, moist, organic-rich soils (left) to high rock exposure and pH (right). Axis 2 correlated positively with slope, AP, and altitude (significantly with AP and altitude) and negatively with TP and TK, reflecting topographic and partial soil nutrient gradients. SWC and ST emerged as key factors influencing community distribution.

Community ordination showed that *Pinus yunnanensis*, *Betula luminifera*, and *Populus alba*-dominated communities occupied areas with greater ST, SWC, and nutrients. *P. yunnanensis*, *Juglans regia*, *Castanea seguinii*, and *Rosa roxburghii* communities occurred on sunny slopes with moderate habitat quality. *Corylus heterophylla*, *Pyracantha fortuneana*, *Cotoneaster franchetii*, and *Quercus variabilis* communities were found at lower altitudes but higher slope positions. *Artemisia lavandulaefolia*, *Trifolium repens*, and *Conyza canadensis* communities occupied high-RD, low-nutrient areas.

DCA analysis of diversity indices for arbor, shrub, and herb layers yielded maximum axis lengths of 1.6699 (<4), justifying RDA. The first four RDA axes had eigenvalues of 2.9556, 1.3327, 0.3467, and 0.0657, cumulatively explaining 92.30% of variance with a diversity-environment explanation of 92.84%. Axis 1 correlated positively with SOM and AK and negatively with AP and rock exposure rate (Table 3 , Figure 4 [Figure 4: see original paper]), reflecting gradients in rock exposure and soil nutrient availability. Axis 2 correlated positively with TK and negatively with slope and pH, representing topographic and TK gradients. Arbor layer diversity correlated positively with ST and SWC, shrub layer diversity with SOM and AK, and herb layer diversity with slope and pH, while rock exposure rate correlated negatively with diversity across all layers (Figure 4 [Figure 4: see original paper]).

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3. Discussion

3.1 Species Diversity Response to Rocky Desertification Gradients The 36 plots contained 188 vascular species across 69 families and 141 genera, dominated by herbs and shrubs, particularly from Poaceae, Asteraceae, Fabaceae, and Rosaceae. Compared to karst plateau-mountain sites in Qianxi County (Li et al., 2016) and peak-cluster depressions in Ziyun County (Zhang et al., 2015), our study area showed higher taxonomic richness despite similar latitudes and habitats, suggesting that RD control measures in Salaxi have effectively promoted vegetation recovery. However, compared to non-desertified karst forests in Maolan, Guizhou (Qin et al., 2018), Mulun, Guangxi (Lan et al., 2016), and Nonggang, Guangxi (Huang et al., 2016), our study area exhibited substantially lower species richness and abundance, indicating that degraded RD ecosystems feature slower growth rates, greater interspecific and intraspecific growth variation, and reduced biodiversity (Hou et al., 2016).

Karst RD' s unique binary structure causes severe soil and water loss, substantially limiting plant growth (Wang & Li, 2007). Our results show declining species diversity with intensifying RD, with drought-tolerant, infertile-resistant shrubs and herbs (*Pyracantha fortuneana*, *Cotoneaster franchetii*, *Conyza canadensis*, *Artemisia lavandulaefolia*) becoming dominant in moderate and intense RD areas where arboreal layers were absent. This demonstrates that harsh RD habitats impose significant stress on plant establishment and growth, consistent with Sheng et al. (2015). RDA ordination revealed higher arbor layer diversity significantly associated with ST and SWC, supporting Bello et al. (2006) who found diversity and richness increasing from arid to humid gradients. Soil organic matter, AK, and AN significantly affected shrub layer diversity, while herb layer diversity in intense RD areas was constrained by slope. Studies indicate that slope correlates positively with RD (Li et al., 2009; Yan & Yang, 2010), and their combined effects enhance water infiltration, reducing SWC in intense RD areas and favoring species less responsive to water availability, consistent with our findings.

3.2 Leaf Trait Response of Dominant Species to Rocky Desertification

LT indicates plant adaptation strategies, while LA represents photosynthetic capacity and growth rate (Ding et al., 2014). LDMC reflects drought adaptation (Mao et al., 2009). Zhong et al. (2018) reported mean LT, LA, and LDMC of 0.17 mm, 17.74 cm^2, and 0.40 $g \cdot g^{1}$ for woody plants in Puding, whereas our means were 0.36 mm, 12.87 cm^2, and 0.42 $g \cdot g^{1}$. Compared to Puding' s better-preserved secondary evergreen-deciduous mixed forest with higher rainfall and lower latitude, our study area features greater human disturbance, dominated by deciduous trees and evergreen shrubs in different canopy positions. Yan et al. (2016) demonstrated that microclimate regulation follows: forest > shrubland > farmland > RD bare land. Consequently, our plants increase LT and LDMC while decreasing LA to conservatively survive harsh conditions.

Leaf traits of dominant species varied significantly across RD habitats, with LT and LDMC increasing and LA decreasing along the RD gradient. Significant differences in LT and LA occurred between non-/slight RD and moderate/intense RD, indicating that plants in moderate and intense RD areas have lower growth rates and stronger drought resistance. Leaf 13C directly measures water use efficiency (WUE), influenced by plant and environmental factors, particularly SWC (Bello et al., 2006). Our results show positive correlation between 13C and RD grade, with WUE ranking: non-RD > slight RD > moderate RD > intense RD, suggesting that intense RD plants exhibit better adaptation to impoverished conditions.

3.3 Relationships Among Species Diversity, Leaf Traits, and Environmental Factors Along RD Gradients CCA ordination identified ST and SWC as key factors influencing species distribution. RDA further examined correlations between diversity and environmental factors, revealing that the top six factors affecting diversity were: rock exposure rate > AK > SWC > AN > ST > SOM. This confirms RD as the dominant factor, with SWC, ST, and nutrients changing along the RD gradient. AK, SWC, AN, ST, and SOM are primary drivers of community diversity and functional trait variation, consistent with Sheng et al. (2015). Intensifying RD reduces plant numbers, vegetation cover, and ST, increasing diurnal temperature range, weakening soil water and nutrient retention, and exacerbating aridity. Severe human disturbance and poor habitat quality inhibit soil microbial activity, slowing transformation of available nutrients (Huang et al., 2018). Studies show that soil pockets in rock crevices and concave topography in southwestern karst regions retain thicker soil layers with better water and nutrient retention, facilitating plant establishment (Wen et al., 2015).

Plant resource-use strategies are shaped by habitat quality, which influences functional trait expression across environments (Liu & Ma, 2012). Our RDA showed that axis 1 correlated negatively between rock exposure rate and SWC, ST, AK, and AN. As RD intensified, LT, LDMC, and 13C increased while LA decreased. In non- and slight RD areas with higher vegetation cover, reduced soil erosion and moderated diurnal temperature ranges enhanced soil biological activity, accelerating nutrient transformation and improving water/nutrient retention, thereby increasing available K and N. This allowed plants to allocate more photosynthate to leaf area growth. In moderate and intense RD areas, significant soil erosion forced plants to adapt to resource scarcity by investing photosynthate in leaf dry matter and cellular construction (Pan et al., 2018) to maintain water and nutrient storage, increasing leaf biomass allocation, thickness, dry matter content, and WUE. This demonstrates clear trait responses to habitat differences.

3.4 Vegetation Restoration and Reconstruction in Rocky Desertification Areas Plants surviving in RD areas have undergone strict natural selection, exhibiting rock-adapted, calciphilous, drought-tolerant, and infertile-resistant characteristics. Our study shows that Asteraceae, Poaceae, and Rosaceae are widely distributed and abundant across RD grades, indicating strong adaptability and potential as pioneer species for improving initial ecological conditions in intense RD areas. Furthermore, as RD intensifies, LDMC and 13C values increase significantly (Du et al., 2008). Among our 14 dominant species, *Corylus heterophylla*, *Pyracantha fortuneana*, *Coriaria nepalensis*, *Hypericum monogynum*, *Rosa roxburghii*, and *Quercus variabilis* exhibited favorable adaptive traits in moderate and intense RD areas, suggesting their value for optimizing plant communities and ecological restoration in RD regions.

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Note: Figure translations are in progress. See original paper for figures.