# Responses of bryophyte diversity, community and Chlorophyll content to rocky desertification succession

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**Research article**

**Keywords:** Rocky desertification, bryophyte, diversity, community, chlorophyll

**Posted Date:** March 16th, 2020

**DOI:** https://doi.org/10.21203/rs.3.rs-17326/v1

# Responses of bryophyte diversity, community and Chlorophyll content to rocky desertification succession

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**Abstract**

***Background***: bryophytes have great potential for the restoration of rocky desertification. At present, research on the correlation between bryophytes and the rocky desertification environment is in its infancy, and basic questions about the ecological response of bryophytes to rocky desertification, including biodiversity, community succession, interspecific relationships and photosynthetic physiology need to be answered urgently.

***Results***: results showed that significant differences in diversity, interspecific association and chlorophyll characteristics were observed among different degrees of rocky desertification. With the increase of rocky desertification degrees, the biodiversity of bryophytes decreases obviously, and the bryophytes which drought tolerance gradually dominates in communities. The interspecific association tend to be positive in rocky desertification succession, and positive association will be beneficial to the positive development of vegetation communities. Some bryophytes can adapt to the rocky desertification environment by reducing chlorophyll content and increasing chlorophyll a/b ratios that is beneficial to light trapping.

***Conclusions***: With the increase in rocky desertification, the biodiversity of bryophytes decreased obviously, and bryophytes with drought tolerance gradually dominated in the communities. The interspecific association tended to be positive in rocky desertification succession, and a positive association will be beneficial to the positive development of vegetation communities. Some bryophytes adapted to the rocky desertification environment by reducing their chlorophyll content and increasing their chlorophyll a/b ratios, which are beneficial for light trapping. The results of this study are useful for the management of desertified karst ecosystems.

**Key words**

Rocky desertification; bryophyte; diversity; community; chlorophyll

## 1 Introduction

Karst is a unique landform in which the landscape is formed mainly by the dissolution of surface water and groundwater on carbonate bedrock (usually limestone, dolomite or marble). Karst in southwestern China has the largest continuous distribution area in the world, and its carbonate rocks have exposed an area of 426,240 $km^2$, mainly concentrated in Guizhou, Yunnan and Guangxi provinces, among which Guizhou Province has the largest karst area of 130,000 $km^2$. Due to the vulnerability and sensitivity of the geological environment, as well as the double pressure of overpopulation and economic backwardness, karst areas in southwestern China are facing ecological environmental problems such as vegetation reduction, soil erosion and bedrock exposure. This phenomenon is defined as rocky desertification. Rocky desertification not only leads to the decline of soil nutrients but also greatly affected the hydrologic and eventually causes more geologic hazards, such as droughts, debris flow and even land subsidence. The increase of rocky desertification has threatening people's lives in areas where they are already living below the poverty line. The government has paid strong attention to the prevention and control of rocky desertification in southwestern China.

To date, there have been numerous studies on the causes, impacts and recovery of rocky desertification in southwestern China. Scholars have deeply analyzed the formation and evolution of rocky desertification from the perspectives of geology, agriculture, custom, and social economies (Jiang et al. 2014; Wang et al. 2004). There are also a large number of studies on karst top ecosystem properties (He et al. 2019; Lan et al. 2004), biological productivity (Bing et al. 2007), multi-layer and heterogeneous ecological space (Song et al. 2010; Zhou 2006), diversity of plant adaptation modes (Chunlei et al. 2017; Zhang et al. 2018), and the possibility and restoration process of vegetation restoration (Jing et al. 2019; Hu et al. 2017), among others. However, it is undeniable that the fundamental problem, i.e., how to effectively promote the positive succession of vegetation communities in rocky desertification areas, has not been solved. At present, the common practice is to increase vegetation coverage by planting ecological forests and to reduce economic pressure by grass planting and animal husbandry. These governance measures have achieved some results (Chen et al. 2018; Xiao et al. 2014), but such ecosystems are often degraded because they cannot form stable ecological structures and functions, and the natural environment of some areas where such measures are implemented does not have sufficient capacity to carry such vegetation levels. More significantly, the problem of bedrock exposure has not been effectively addressed because ecological forests and grasses cannot be grown on rocks. It is obvious that scholars have not performed enough research on the characteristics of the succession of plant communities in rocky desertification areas and often ignore the contributions of pioneer plants such as bryophytes and lichens in early succession.

Bryophytes, as pioneer plants, are a major group of higher plants, second only to seed plants in number of species. Bryophytes can grow in hot springs with temperatures approaching 53℃ (Glime and Iwatsuki 1994) or in polar regions with temperatures approaching 0℃ (Richardson 1984). Bryophytes are one of the main components of biological crusts, which can effectively reduce soil erosion and have a positive impact on the positive succession of plant communities in extreme environments (Vitt 1989). Numerous xerophytic bryophyte species have an involuted margin on the upper part of the leaf, forming a sacciform structure that protects the adaxial face of the leaf and reduces evaporation (Guerra et al. 1992). In addition, the leaf structure, such as hair-points and nerve enlargement, can help bryophytes effectively capture and conduct water, ensuring high efficiency of bryophytes with respect to water use (Bell 1982). Bryophytes maintain the same concentration of sugar and LEA (late embryogenesis abundant) proteins during water loss to protect the plant from damage (Oliver and M. J. 2005). In areas with strong light, bryophytes can also effectively reflect solar radiation through the papillose leaf to adapt to high temperature and high light (Wu et al. 2003). Bryophytes in drylands not only have a unique ecological adaptability but also have higher biomass than other pioneering plants, such as lichens and algae, so bryophytes have more significant ecological benefits and functions than lichens and algae. Bryophytes play an irreplaceable role in the restoration and reconstruction of degraded ecosystems. Plants in rocky desertification areas must have strong survival ability (drought resistance, high temperature resistance, stony growth); accordingly, bryophytes are considered to have great potential for the restoration of rocky desertification environments. The role of bryophytes in the restoration of rocky desertification is reflected in the following points: 1) Bryophytes grow densely, can form a capillary system (Wu 1998), which, combined with the special leaf structure for moisture conduction (Guerra et al. 1992), allow bryophytes to maximize the storage and use of dry-wet alternate environments while also providing water for other plants in the region. 2) Bryophytes can effectively reduce the erosion of the soil layer by rainfall, thus reducing the loss of nutrient elements and maintaining soil fertility (Zhang 2018; Shen et al. 2019). 3) The acid metabolites of bryophytes can dissolve the rock surface and accelerate the decomposition of minerals, which is beneficial to the primary stage of soil formation (Zhang et al. 2018). 4) Bryophytes can also gradually form a thinner soil layer by absorbing and accumulating air particles and combining with plant residues, laying a foundation for the positive succession of subsequent communities (Wang and Zhang 2014). At present, research on the correlation between bryophytes and the rocky desertification environment is in its infancy, and basic questions about the ecological response of bryophytes to rocky desertification, such as biodiversity, community succession, interspecific relationships and photosynthetic physiology need to be answered urgently.

Guizhou Province has the most serious impact of rocky desertification in China, and the control of rocky desertification has always been an important project in this region. Accordingly, Salaxi, a typical rocky desertification region in Guizhou Province was selected as the experimental site in the present work. Based on the five typical degrees of rocky desertification (nil, potential, slight, moderate, and severe), the biodiversity, community succession, interspecific relationship and characteristics of the chlorophyll content of bryophytes in the process of rock desertification succession were studied to preliminarily investigate the ecological response of bryophytes to rocky desertification. The results can provide a scientific basis for the restoration of rocky desertification ecosystems and have important significance for the protection of pioneer plant communities in karst areas.

## 2 Methods

### 2.1 *Study area*

Salaxi (105°02 '~105°08' E; 27°11 '~27°16 ' N) is located in Guizhou Province, China, and has a total area of 5633.30 $hm^2$ (Figure 1). In the study area, the karst plateau mountain is the main landform, and the altitude ranges from 1400 to 1742 m, with high altitude in the south and low altitude in the north. Limestone is the dominant rock, and the geomorphology is diverse, mainly consisting of karst peaks and mountains. In addition, there are many karst caves of different sizes and shapes, such as sinkholes, through caves, etc. The annual rainfall ranges from 574 to 1218 mm, with an average of approximately 823 mm (rainfall dates originate from the Guizhou

Meteorological Bureau, China). Rainfall is mainly distributed from April to October and accounts for 90 % of the total annual rainfall. The frequencies of drought in spring and winter are 39.5 % and 29.0 %, respectively. The total forest coverage rate in the study area is 35.62 %, and the vegetation types are subtropical evergreen broad-leaved forest and coniferous forest. The primary vegetation mainly includes *Pinus massoniana*, *Toxicodendron vernicifluum*, *Rhododendron simsii* and *Quercus* spp. Secondary vegetation mainly includes *Populus adenopoda*, *Quercus variabilis* and *Betula luminifera*. For a long time, unreasonable human activities have seriously damaged the native vegetation of the study area. Currently, *Quercus* spp., *Pyracantha fortuneana* and *Rhododendron* spp., among others, are dominant.

In 2018, the area of karst was 4,472.47 $hm^2$, and that of rocky desertification was 1986.81 $hm^2$. The light rocky desertification area covered 1360.77 $hm^2$, accounting for 68.49 %, the moderate rocky desertification area covered 546.22 $hm^2$, accounting for 27.49 %, and the severe rocky desertification area covered 79.82 $hm^2$, accounting for 4.02 %. The rocky desertification problem is prominent.

### 2.2 *Rocky desertification classification*

The karst rocky desertification (KRD) was classified into five degrees by Xiong et al. (2002) and the threshold of each degree is listed in Table 1.

1) nil rocky desertification (Nil RD); 2) potential rocky desertification (Pot RD); 3) slight rocky desertification (Sli RD); 4) moderate rocky desertification (Mod RD); and 5) severe rocky desertification (Sev RD).

### 2.3 *Sampling procedure*

The sampling was carried out in two stages: 1) Aiming at these five typical degrees of rocky desertification (Table 1), 22 sample plots (Figure 1) were set up in the study area. The grid method was used to establish multiple quadrats (1 m×1 m) in various plots to collect bryophytes. A metal frame (10 cm × 10 cm) was used to determine the coverage while sampling. The samples were carefully placed into brown paper bags and returned to the laboratory where bryophyte species were identified, with reference to Flora Bryophytarum Sinicorum Vols. 1–6 and Vol. 8 (Gao 1994, 1996; Li 2000, 2006; Wu 2011, 2002; Wu and Jia 2004); a total of 364 samples were collected in this stage. 2) According to the identified results, four species of bryophyte (*Didymodon constrictus*, *Bryum algovicum*, *Hyophila involuta* and *Trichostomum brachydontium*), widely distributed in the rocky desertification environment of all degrees, were collected from the plots. Ten samples of each type of bryophyte were collected in each degree of the plot. The samples were carefully placed into brown paper bags and quickly returned to the laboratory for the determination of the chlorophyll content. A total of 200 samples were collected in this stage.

**2.4** ***Determination of the chlorophyll content***

After the samples collected in the second stage were returned to the laboratory, the samples were cleaned with water and placed in a ventilated and dry location for 24 hours to dry naturally. To ensure that the determination results were not affected by the sample storage time as far as possible, the extraction and determination of chlorophyll were carried out following the method of Qiu et al. (2016).

**2.5** ***Data statistics***

*Diversity*

To compare the alpha diversity of bryophytes in different rocky desertification environments, the alpha index was calculated. The Shannon-Wiener (Whittaker 2002) diversity index (*H*), Patrick richness index (*R*) (Zhang 2011) and Pielou (1975) evenness index (*J*) were used to indicate the alpha diversity of rocky desertification species of different degrees. The Sorensen similarity index ($S_β$) was used to characterize beta diversity. The formulas are as follows:

$$H = -\sum_{i=1}^{s} P_i \, ln \, P_i$$

$P_i = N_i / N$, *Ni* is the coverage of the i-th species, and *N* is the total coverage of each species in the community;

$$R = S$$

$$J = H / ln \, S$$

*S* indicates the number of species;

$$S_\beta = 2c \, / \, (a + b)$$

*a* and *b* are the number of species in different succession stages (A and B); *c* is the number of species in which neither A nor B is found.

*Importance values* (*IVs*)

The importance value (IV) of bryophytes is defined as the average relative frequency (*RF*) and relative coverage (*RC*) of that species and was calculated using the following formula:

$$IV = (RF + RC) \, / \, 2$$

*Interspecific association*

A 2 × 2 species association table was listed. For each pair of species A and B, we can obtain the following as table 2.

To test for interspecific associations, a null hypothesis stating that species are independent was used.

A corrected Chi square test (Yates's correction formula) was used to test the null hypothesis of independence in the 2 × 2 contingency table (Kikvidze 1993):

$$\chi^2 = \frac{N[|ad - bc| - N/2]^2}{(a+b)(c+d)(a+c)(b+d)}$$

There is no interspecific association when $\chi^2 < 3.841$; there are associations between species when $3.841 \leq \chi^2 < 6.635$; when $\chi^2 \geq 6.635$, there are significant associations between species.

To test the strength of associations and the association coefficient (*AC*) index (Liu et al. 2019; Ofomata et al. 2010), the following measures of species association were used:

$$AC = (ad - bc)/(a+b)(b+d) \ (ad \geq bc)$$

$$AC = (ad - bc)/(b+d)(c+d) \ (bc \geq ad, d \geq a)$$

$$AC = (ad - bc)/(a+b)(a+c) \ (bc \geq ad, d < a)$$

*a*, the number of samples in which species A and B co-occurred; *b*, the number of samples in which species A occurs, but not B; *c*, the number of samples in which species B occurs, but not A; *d*, the number of samples in which neither A nor B is found; N, the total number of samples.

We used R version 3.6.0, SPSS 22 and Canoco 5.0 to statistics and analysis all data. The species association indices were conducted by the using of "spaa" package in R (Zhang and Ma 2014)

## 3 Results

### 3.1 *Species composition and diversity*

A total of 65 bryophyte species were identified belonging to 43 genera and 27 families (Table 3), of which 6 species belonging to 6 genera and 5 families are liverwort taxa; 59 species belong to 37 genera and 22 families are bryophyte taxa. The specific distribution of rocky desertification is as follows: 1) 38 species belonging to 27 genera and 19 families in Nil RD. The dominant families (genera number ≥3) are Pottiaceae and Hypnaceae; 2) 25 species belong to 19 genera and 12 families in Pot RD; the dominant family is Pottiaceae; 3) 24 species belong to 17 genera and 11 families in Sli RD; the dominant family is Pottiaceae; 4) 21 species belong to 14 genera and 9 families in Mod RD; the dominant family is Pottiaceae; 5) 16 species belong to 13 genera and 9 families in Sev RD; the dominant family is Pottiaceae. In general, Pottiaceae is dominant in the study area.

Alpha diversity represents the abundance of species. With an increased degree of rocky desertification, the alpha diversity of bryophytes is shown in Table 4. The Patrick richness index ($R$) did not show significant differences among Pot RD-Mod RD ($P > 0.05$) but did among Nil RD and Sev RD. With an increased degree of rocky desertification, there were significant differences in the Shannon-Wiener diversity index ($H$) ($P < 0.05$); after a sharp drop, there was a slight increase followed by a decline. Ranked from high to low, the values were as follows: Nil RD (19.68±1.49), > Sli RD (10.19±0.85c), > Pot RD (7.57±0.49b), > Mod RD (5.29±0.96d), > Sev RD (2.14±0.96e). With an increased degree of rocky desertification, the Pielou evenness index ($J$) exhibited significant differences ($P < 0.05$) and a coupling trend with respect to the diversity index, as follows: Nil RD (5.45±0.19a) > Sli RD (3.09±0.09c) > Pot RD (2.38±0.15b) > Mod RD (2.03±0.15d) > Sev RD (0.69±0.14e).

Beta diversity, indicating the variation of species along environmental gradients, is shown in Table 5. The Sorensen similarity index ($S_\beta$) between Pot RD and Sli RD was the highest (0.65±0.04), indicating that there were significant similarities between them. The lowest similarity index ($S_\beta$) between Nil RD and Sev RD (0.25±0.04) indicated significant differences in species composition between the two grades of RD. In general, the larger difference in $S_\beta$ appears between Nil RD and other degrees of rocky desertification (≤0.25), and a smaller difference in $S_\beta$ appears between two plots of rocky desertification.

Bryophytes do not have vascular bundles, and their branching patterns are relatively simple and they rarely appear as individuals. They usually have a fixed group structure and shape that can reflect the characteristics of the habitat. Thus, the shape and structure of the bryophyte groups are their life-form characteristics (Magdefrau 1982). Referring to Magdefrau's definition of bryophyte life forms, six life forms were found, including mats, short turfs, tall turfs, wefts, cushion and fans (Figure 2). Short turfs, tall turfs and wefts were distributed across all degrees of rocky desertification and occupied a large proportion (>12 %), which means that these three life forms of bryophytes are relatively more adaptive to rocky desertification. Mats appeared in Nil RD, Pot RD and Sli RD, cushions appeared in Nil RD, Pot RD and Sev RD and fans appeared only in Pot RD, and all accounted for a small proportion (<10 %). With an increased degree of rocky desertification, life forms, including mats and cushion, tended to disappear, and then fans appeared.

**3.2 *Community***

With the intensification of the process of rocky desertification degree, the number of bryophyte mixed-species communities showed a decreasing trend, while the single-species communities showed an increasing trend (Figure 3). The degrees Nil RD, Pot RD, Sli RD and Mod RD were principally composed of single-species communities, and the single-communities dominated in Sev RD.

To explore the evolution of the dominant species of the bryophyte community in the succession of rocky desertification, principal component analysis (PCA) was used to analyze the relationship between the importance value of bryophytes and the degree of rocky desertification. The PCA ranking was carried out by Canoco5.0 (Figure 4). The ranking results reflect the changes of species composition in the communities under the succession of rock desertification. Figure 4 shows that the succession of bryophytes in various plots did not correspond to the degree of rocky desertification but was reflected in three stages: Nil rocky desertification, potential to moderate rocky desertification, and severe rocky desertification. The specific succession was generally as follows: Nil RD (*Campylopus fragilis*, *Metzgeria consanguinea*, *Leucobryum juniperoideum*, *Plagiothecium neckeroideum*, *Hypnum oldhamii*, etc.) → Pot-Mod RD (*Didymodon constrictus*, *Hyophila involuta*, *Bryum algovicum*, *Erythrodontium julaceum*, etc.) →Sev RD (*Lindbergia sinensis*, *Didymodon ditrichoides*, *Pylaisia falcata*, *Plagiomnium cuspidatum*, etc.). In the process of rocky desertification, *Bryum dichotomum*, *Entodon concinnus*, *Trichostomum brachydontium*, among others, were the transitional species of bryophyte community succession.

Interspecific associations result from species interactions, as well as similar responses and adaptations to environmental factors (Ofomata et al. 2010; Chai et al. 2016). They are the foundation for the formation and evolution of ecological communities (Henttonen 1998). Measuring interspecific associations can aid in understanding interactions between species, ecological relationships between species, and population dynamics (Cabaret and Hoste 1998). Species with the top importance values (approximately 40 % to 50 % of the total species) were selected as the dominant species of rocky desertification (Table 6) to calculate the association coefficient (*AC*) index.

Figure 5a shows that among the total dominant bryophyte species of Nil RD, 55 pairs (46 %) showed positive associations ($0 < AC \leq 1$) and 65 pairs (54 %) showed negative associations (-1 ≤

$AC$ < 0), of which 14 pairs were significantly associated (6.635 > $\chi^2$ > 3.841, $P$ < 0.05), and 6 pairs were extremely significantly associated ($\chi^2$ > 6.635, $P$ < 0.01). The pairs of extremely significant positive associations ($\chi^2$ > 6.635, 0.5 ≤ $AC$ < 0.5) were *Lepidozia subtransveersa* with *Metzgeria consanguinea* and *Bryum algovicum*, *Brachythecium albicans* with *Brachythecium brotheri*, and *Metzgeria consanguinea* with *Heteroscyphus coalitus*. There were no species pairs with extremely significant negative associations ($\chi^2$ > 6.635, −1 ≤ $AC$ ≤ −0.5). In Pot RD (Figure 5b), 20 pairs (36 %) showed positive associations, and 35 pairs (64 %) showed negative associations, of which 12 pairs were significantly associated, and 4 pairs were extremely significantly associated. The pair with extremely significant positive associations was *Thuidium tamariscinum* with *Brachythecium albicans*. The pairs with extremely significant negative associations were *Entodon concinnus* with *Bryum algovicum* and *Hyophila involute*. In Sli RD (Figure 5c), 27 pairs (60 %) showed positive associations, and 18 pairs (40 %) showed negative associations, of which 11 pairs were significantly associated, and 4 pairs were extremely significantly associated. The pairs with extremely significant positive associations were *Erythrodontium julaceum* with *Brachythecium* albicans and *Trichostomum brachydontium*. The pair with extremely significant negative associations was *Erythrodontium julaceum* with *Hyophila involute*. In Mod RD (Figure 5d), 21 pairs (58 %) showed positive associations, and 15 pairs (42 %) showed negative associations, of which 7 pairs were significantly associated, and 4 pairs were extremely significant associated. The pairs with extremely significant positive associations were *Bryum algovicum* with *Didymodon constrictus* and *Trichostomum brachydontium* with *Campylopus fragilis*. The pairs with extremely significant negative associations were *Brachythecium albicans* with *Bryum billarderi* and *Thuidium tamariscinum* with *Didymodon fallax*. In Sev RD (Figure 5e), 26 pairs (72 %) showed positive associations, 10 pairs (28 %) showed negative associations, of which 9 pairs were significantly associated, and 3 pairs were extremely significant associated. The pairs with extremely significant positive associations were *Bryum argenteum* with *Tortula planifolia* and *Bryum algovicum*. There were no species pairs with extremely significant negative associations in Sev RD.

**3.3 *Chlorophyll content***

The chlorophyll content of four species of bryophyte (*Didymodon constrictus*, *Bryum algovicum*, *Hyophila involuta* and *Trichostomum brachydontium*) distributed across all degrees of the rocky desertification environment was measured, as shown in Figure 6. With the increase in the degree of rocky desertification, the average chlorophyll content of all bryophytes showed a significant decline ($P < 0.05$).

Changes in the chlorophyll content are one of the important indicators of plant physiological metabolism changes. Chlorophyll b can effectively capture and utilize blue-violet light for photosynthesis. Therefore, the ratio of chlorophyll a to chlorophyll b is usually lower (1.5~3.0) in shade than in sun plants. In general, low chlorophyll a/b ratios occur in leaves under low light conditions but increase under strong light conditions, which is generally considered to be a manifestation of plant adaptation to different light environments (Kitajima and Hogan 2010). The chlorophyll a/b ratios of *Bryum algovicum* and *Hyophila involuta* increased with increasing rocky desertification (Figure 7). The minimum chlorophyll a/b ratio of *Bryum algovicum* was 1.36±0.08 (Nil RD), and the maximum ratio was 2.68±0.26 (Sev RD). The minimum chlorophyll a/b ratio of *Hyophila involuta* was 1.47 ± 0.07 (Nil RD), and the maximum was 2.66 ± 0.28 (Sev RD). The chlorophyll a/b ratios of *Didymodon constrictus* showed an upward trend with a minimum of 1.31±0.05 (Nil RD) and a maximum of 1.81±0.25 (Sev RD). The chlorophyll a/b ratios of *Trichostomum brachydontium* decreased to a minimum (1.55±0.08) between Nil RD and Pot RD and then gradually increased, reaching a maximum value (2.66±0.28) in Sev RD. In general, the chlorophyll a/b ratios of the four bryophyte species reached a maximum in the Sev RD environment.

**4 Discussion**

Only a small number of plants adapt to extreme environments, and bryophyte as a pioneer plant is no exception. As the degree of rocky desertification increases, the diversity of bryophyte species decreases, indicating that the adaptability of bryophytes to the environment differs. The life-form of Pottiaceae is turfs (short turfs and tall turfs). This type of life-form is common in the soil layer or the surface layer of the rock. The turfs grow upright, and they are able to hold water by capillary action and can also conduct it (Magdefrau 1982). Wefts are mostly blanket or mat-like, which is beneficial to the capillary system to maintain a large amount of water, and weft growth can reduce the movement of air on the surface of the leaves, thereby effectively reducing the evaporation loss of surface water. We found that *Erythrodontium julaceum*, *Thuidium tamariscinum*, *Bryum argenteum*, *Hyophila involuta*, *Trichostomum brachydontium* and *Entodon concinnus* appeared in all degrees of rocky desertification environments, and they showed good adaptability, which can be explained at the microlevel as follows. *Erythrodontium julaceum*, *Thuidium tamariscinum* and *Bryum argenteum* have hair-points that can effectively capture moisture (Bell 1982). In addition, hair-points of leaves also protect against mechanical damage caused by dryness and sunlight (Scott 1982). Both *Hyophila involuta* and *Thuidium tamariscinum* have an enlargement nerve that causes the leaves to harden significantly and provides mechanical support during the drying process, which can also be explained as a water retention mechanism in a dry environment (Bell 1982). Numerous species, such as *Erythrodontium julaceum* and *Entodon concinnus*, from dry habitats exhibit curved leaves when dry, which facilitates the rapid shrinkage of the leaves in a dry environment and can effectively reduce the loss of water from the plants (Guerra et al. 1992). In addition, *Hyophila involuta*, *Trichostomum brachydontium*, *Thuidium tamariscinum* and *Bryum argenteum* have papillose or mamillose leaves. This structure is widely considered to be one of the most common and important adaptation characteristics of bryophytes living on dry land. The papillose leaf surfaces speed up the transport of water, acting as capillary systems without interrupting gaseous exchange (Rundel & Lange 1980). This generalization has been widely recognized (Vitt 1981; Bell 1982)

The Nil RD environment has relatively more water and shading, which is suitable for mixed community growth. As the degree of rocky desertification increases, the environmental moisture content decreases, light is enhanced and the soil is reduced, which limits the survival of most bryophyte species; thus, a single community is more common. The bryophyte species in the Nil desertification environment were less similar than those under rocky desertification ($S_{\beta} \leq 0.35$) (Table 6), indicating a larger species replacement rate between these environments. In the process of rock desertification succession, the bryophyte community structure changed. The dominant plants, such as *Campylopus fragilis* and *Metzgeria consanguinea*, were gradually replaced by drought-tolerant *Lindbergia sinensis* and *Didymodon ditrichoides*. With the intensification of rocky desertification, the reduction of arbor vegetation caused the disappearance of epixylous bryophytes, such as *Metzgeria consanguinea*, *Heteroscyphus coalitus* and *Chiloscyphus minor*, and the ecological niche of epilithic bryophytes, such as *Tortula planifolia* and *Didymodon fallax*. widened. Biotic factors (vascular plant productivity, species composition, diversity, etc.) and abiotic factors (soil fertility and light transmission, etc.) impact the bryophyte community (Jonsson 2015). These factors are more turbulent in rocky desertification areas.

Negative associations among species are indicative of interspecific competition (Marcel and Lepš 1996). Negative interspecific associations dominated the overall interspecific association in the rock desertification area of Salaxi. This suggests that interspecific competition is not very intense in this area. The increasing negative associations with increasing forest stages are consistent with the harsh-benign hypothesis (Peckarsky 1983). This hypothesis predicts that competitive interactions are more likely in stable environments and that negative interspecific associations occur more often in stable sites than in unstable sites (Death and Russell 2000; Peckarsky 1983). The arbor layer in the nil rocky desertification area was highly competitive. The better shade and humidity provided a hotbed for bryophyte growth. Growth conditions were suitable for a high number of bryophyte species, so intense interspecific competition also occurred in the bryophyte layer. However, it is difficult for vascular plants to survive in rocky desertification areas, which provides sufficient survival space for some drought-tolerant bryophytes, and the competition between species is moderated, which is conducive to the formation of biological crusts in the rocky desertification environment and the positive succession of the plant community if we protected. Some scholars hold that species pairs with positive associations share similar resources and exhibit a wide niche overlap, while negative associations indicate the different habitat and resource requirements of plants (Su et al. 2015).

Due to the lack of vegetation cover, the surface layer of the rocky desertification environment had high exposure, and the illumination becomes increasingly intense with increasing rocky desertification. In addition to reducing the chlorophyll content per unit mass, the adaptation strategy of plant leaves to high intensity illumination also includes increasing the chlorophyll a/b ratio.

However, this strategy is often accompanied by a lower growth rate, which can be said to be a tolerance feature. The rate of chlorophyll a and b synthesis and decomposition affects the range of chlorophyll a/b values. Generally, in the intensity rocky desertification environment, strong light conditions lead to a decrease in chlorophyll degradation and photooxidation. However, the rate of chlorophyll b decomposition is higher than that of chlorophyll a, but under low light or in blackout environments, chlorophyll a is partially converted to chlorophyll b by hydrolysis (Kusaba, 2007). This led to the chlorophyll a/b ratios of bryophytes in Nil RD being lower than those in the rocky desertification environment. The chlorophyll a/b value of *Didymodon constrictus* fluctuated under rocky desertification (Figure 7). This reflects the better adaptability of *Didymodon constrictus* to rocky desertification environments, and this adaptability may be related to physiological processes. In addition, the chlorophyll a/b ratios of *Trichostomum brachydontium* showed a downward trend between Nil RD and Pot RD, which may indicate that this species was more suitable for the light environment of Pot RD.

## 5 Conclusions

As the degree of rocky desertification increased, the biodiversity of bryophyte species significantly decreased. In this process, the dominant species of the bryophyte community changed constantly, finally resulting in drought-tolerant bryophytes. Interspecific competition was moderate during the succession of rock desertification, which supports the harsh-benign hypothesis that interspecific competition is more common in stable sites. The positive association of bryophytes in rocky desertification areas will contribute to the positive succession of extreme environmental communities.

Reducing the chlorophyll content and increasing the chlorophyll a/b ratios are means through which bryophytes (such as *Didymodon constrictus*, *Bryum algovicum*, *Hyophila involuta* and *Trichostomum brachydontium*) adapt to rocky desertification environments. This adaptability is one of the key ways that bryophytes withstand extreme rocky desertification environments.

**Declarations**

***Compliance with ethical standards*****:** this paper compliance with ethical standards. The experimental protocol was established, we comply with the IUCN Policy Statement on Research Involving Species at Risk of Extinction and the Convention on the Trade in Endangered Species of Wild Fauna and Flora.

***Consent for publication*****:** The author confirms that the work described has not been published before (except in the form of an abstract or as part of a published lecture, review, or thesis); it is not under consideration for publication elsewhere; its publication has been approved by all co-authors, if any; and the author confirms that its publication has been approved (tacitly or explicitly) by the responsible authorities at the institution where the work is carried out; all authors agree to publication in the BMC Ecology.

***Availability of data and material***: because of the data relates to the thesis of graduate students, we can't make it public. Please contact author for data requests.

***Conflict of interest***: no conflict of interest exits in the submission of this manuscript, and manuscript is approved by all authors for publication.

***Funding information***: this work was supported by the [National Natural Science Foundation ] under Grant [number 31960262]; [Guizhou Provincial Science and Technology Foundation ] under

Grant [LH 2016 number 7199]; [Guizhou Provincial Science and Technology Foundation ] under Grant [2017 number1080] and [Guizhou Provincial Graduate Education Innovation Foundation ] under Grant [GZS 2016 number 04].

***Author contributions***: Y. L. and X. L. conceived and designed the project. Y. L., C. C., M. L., M. G. and Y. Z. conducted the field work and sample identification. Y. L., C. C., M. L. analyzed the data. Y. L. wrote the first draft of the paper. All authors contributed to the final manuscript.

***Acknowledgement***: we thank the School of Karst Science (SKS) for field-work permissions, Tang qiming for the help of identifying bryophyte species.

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**Table 1**: Classification standard of Karst rocky desertification. Xiong et al. (2002) classified the karst rocky desertification (KRD) into five degrees including: 1) nil rocky desertification (Nil RD); 2) potential rocky desertification (Pot RD); 3) slight rocky desertification (Sli RD); 4) moderate rocky desertification (Mod RD); and 5) severe rocky desertification (Sev RD).

| | **The standard of the Karst rocky desertification** | | | | |
|---|---|---|---|---|---|
| | Nil | Potential | Slight | Moderate | Severe |
| Percentage of vegetation (%) | >80 | <80 | <70 | <50 | <30 |
| Slope (°) | <15 | >15 | >15 | >20 | >25 |
| Percentage of bare rock (%) | <20 | >20 | >40 | >60 | >80 |
| Average depth of top soil (cm) | >20 | <20 | <15 | <10 | <5 |

**Table 2:** 2 × 2 contingency table or species association table. A 2 × 2 species association table was listed as table 2.

For each pair of species A and B, we can obtain the following:

| | | **Species B** | | ∑ |
|---|---|---|---|---|
| | | Present | Absent | |
| **Species A** | Present | a | b | m = a + b |
| | Absent | c | d | n = c + d |
| | ∑ | r = a + c | s = b + d | N = a + b + c + d |

**Table 3**: List of bryophytes in the study area. We have counted the families, genera, species, and important values of all bryophytes we collected.

| Family | Genus | No. | Species | Importance value | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Nil | Potential | Slight | Moderate | Severe |
| Leucobryaceae | *Leucobryum* | 1 | *Leucobryum glaucum* (Hedw.) Angstr. | 1.45 | — | — | — | — |
| | | 2 | *Leucobryum juniperoideum* (Brid.) Müll. Hal. | 2.69 | — | — | 3.95 | — |
| | *Campylopus* | 3 | *Campylopus fragilis* (Brid.) Bruch & Schimp. | 9.26 | — | — | 3.95 | — |
| | | 4 | *Campylopus ericoides* (Griff.) A. Jaeger | 1.50 | — | — | — | — |
| Leskeaceae | *Claopodium* | 5 | *Claopodium gracillimum* (Cardot & Thér.) Nog. | 0.81 | — | 1.91 | — | — |
| | *Lindbergia* | 6 | *Lindbergia sinensis* (Müll. Hal.) Broth. | — | — | — | — | 4.41 |
| Metzgeriaceae | *Metzgeria* | 7 | *Metzgeria consanguinea* Schiffn. | 7.00 | — | — | — | — |
| Lophocoleaceae | *Chiloscyphus* | 8 | *Chiloscyphus minor* (Nees) J.J. Engel & R.M. Schust. | 1.45 | — | — | — | — |
| | *Heteroscyphus* | 9 | *Heteroscyphus coalitus* (Hook.) Schiffn. | 3.21 | — | — | — | — |
| Pottiaceae | *Didymodon* | 10 | *Didymodon fallax* (Hedw.) R.H. Zander | — | 1.82 | — | 3.95 | 4.52 |
| | | 11 | *Didymodon ditrichoides* (Broth.) X.J. Li & S. He | — | 5.72 | 2.93 | — | 5.22 |
| | | 12 | *Didymodon constrictus* (Mitt.) Saito | 1.71 | 2.60 | 5.99 | 11.44 | 6.18 |
| | *Bryoerythrophyllum* | 13 | *Bryoerythrophyllum inaequalifolium* (Taylor) R.H. Zander | — | — | 2.27 | — | — |
| | | 14 | *Bryoerythrophyllum alpigenum* (Vent.) P.C. Chen | 1.07 | — | — | — | — |
| | *Gymnostomum* | 15 | *Gymnostomum aeruginosum* Smith | — | 2.34 | — | — | — |
| | *Trichostomum* | 16 | *Trichostomum brachydontium* Bruch | 1.45 | 5.20 | 3.15 | 4.70 | 5.05 |
| | *Barbula* | 17 | *Barbula unguiculata* Hedw. | 1.32 | — | — | 2.84 | — |
| | *Tortula* | 18 | *Tortula planifolia* X.J. Li | — | — | 2.70 | — | 10.11 |
| | *Hyophila* | 19 | *Hyophila involuta* (Hook.) A. Jaeger | 1.60 | 9.63 | 8.22 | 3.68 | 4.68 |
| | | 20 | *Hyophila setschwanica* (Broth.) Hilp. Ex P.C. Chen | — | 4.06 | — | 3.06 | — |
| | | 21 | *Hyophila javanica* (Nees & Blume) Brid. | 0.94 | — | 2.93 | 2.61 | — |
| | *Weissia* | 22 | *Weissia controversa* Hedw. | — | 4.16 | — | — | — |
| Diphysciaceae | *Diphyscium* | 23 | *Diphyscium foliosum* (Hedw.) D. Mohr | 2.75 | — | — | 4.21 | — |
| Frullaniaceae | *Frullania* | 24 | *Frullania chenii* S. Hatt. & P.J. Lin | — | — | 2.09 | — | — |
| Hypnaceae | *Hypnum* | 25 | *Hypnum sakuraii* (Sakurai) Ando | 0.94 | — | — | — | — |
| | | 26 | *Hypnum oldhamii* (Mitt.) A. Jaeger | 2.85 | — | — | — | — |
| | | 27 | *Hypnum submolluscum* Besch. | — | — | 2.39 | — | — |
| | *Taxiphyllum* | 28 | *Taxiphyllum taxirameum* (Mitt.) M. Fleisch. | 0.94 | — | — | — | — |
| | *Pseudotaxiphyllum* | 29 | *Pseudotaxiphyllum pohliaecarpum* (Sull. & Lesq.) Z. Iwats. | 3.84 | — | — | — | — |
| Pylaisiaceae | *Pylaisia* | 30 | *Pylaisia falcata* Schimp. | 0.94 | — | 3.46 | — | 3.71 |
| Sematophyllaceae | *Sematophyllum* | 31 | *Sematophyllum subpinnatum* (Brid.) E. Britton | 3.05 | — | — | — | — |
| | | 32 | *Sematophyllum phoeniceum* (Müll. Hal.) M. Fleisch. | — | 5.37 | — | — | — |
| Entodontaceae | *Erythrodontium* | 33 | *Erythrodontium julaceum* (Schwaegr.) Paris | — | 4.94 | 14.64 | 3.72 | 5.86 |
| | *Entodon* | 34 | *Entodon concinnus* (De Not.) Paris | — | 6.51 | 4.13 | 3.19 | 3.17 |
| Pterobryaceae | *Pterobryopsis* | 35 | *Pterobryopsis crassicaulis* (Müll. Hal.) M. Fleisch. | — | 2.08 | — | — | — |
| Pylaisiadelphaceae | *Brotherella* | 36 | *Brotherella henonii var. henonii* | 1.07 | — | — | — | — |
| Plagiotheciaceae | *Plagiothecium* | 37 | *Plagiothecium cavifolium* (Brid.) Z. Iwats. | — | 5.10 | — | — | 10.65 |
| | | 38 | *Plagiothecium laetum* Bruch & Schimp. | 1.32 | — | — | — | — |
| | | 39 | *Plagiothecium neckeroideum* Buch & Schimp. | 4.84 | — | — | — | — |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Anomodontaceae | *Anomodon* | 40 | *Anomodon minor* (Hedw.) Lindb. | — | 2.86 | — | — | — |
| Brachytheciaceae | *Brachythecium* | 41 | *Brachythecium brotheri* Paris | 4.05 | 2.60 | — | 3.28 | — |
| | | 42 | *Brachythecium albicans* (Hedw.) Bruch & Schimp. | 5.01 | 5.20 | 7.63 | 12.72 | — |
| | | 43 | *Brachythecium pulchellum* Broth. & Paris | — | 3.64 | 2.13 | — | — |
| | | 44 | *Brachythecium formosanum* Takaki | — | — | 2.27 | — | — |
| | | 45 | *Brachythecium amnicolum* Müll. Hal. | — | — | 2.44 | — | — |
| | | 46 | *Brachythecium populeum* (Hedw.) Bruch & Schimp. | 1.32 | — | — | — | — |
| | *Okamuraea* | 47 | *Okamuraea brachydictyon* (Cardot) Nog. | — | — | 2.13 | — | — |
| | *Palamocladium* | 48 | *Palamocladium euchloron* (Müll. Hal.) Wijk & Margad. | — | 2.60 | — | — | — |
| Dicranaceae | *Dicranum* | 49 | *Dicranum scoparium* Hedw. | 2.24 | — | — | — | — |
| Fabroniaceae | *Fabronia* | 50 | *Fabronia papillidens* C. Gao | — | — | 2.18 | — | — |
| Ptychomitriaceae | *Ptychomitrium* | 51 | *Ptychomitrium gardneri* Lesq. | — | 2.19 | 2.36 | — | — |
| Mniaceae | *Plagiomnium* | 52 | *Plagiomnium cuspidatum* (Hedw.) T.J. Kop. | — | — | 2.13 | — | 6.40 |
| | | 53 | *Plagiomnium rostratum* (Schrad.) T.J. Kop. | 0.99 | — | — | — | — |
| Lejeuneaceae | *Lejeunea* | 54 | *Lejeunea curviloba* Steph. | — | 3.28 | — | — | — |
| Dicranellaceae | *Dicranella* | 55 | *Dicranella heteromalla* (Hedw.) Schimp. | — | 4.16 | — | — | — |
| | | 56 | *Dicranella coarctata* (Müll. Hal.) Bosch & Sande Lac. | 1.07 | 2.79 | — | — | — |
| Thuidiaceae | *Pelekium* | 57 | *Pelekium versicolour* (Hornsch. Ex Müll. Hal.)A. touw | — | 2.08 | — | — | — |
| | *Thuidium* | 58 | *Thuidium tamariscinum* (Hedw.) Schimp. | 7.15 | 12.44 | 3.02 | 9.04 | 5.00 |
| Bryaceae | *Bryum* | 59 | *Bryum argenteum* Hedw. | 0.94 | 3.18 | 3.15 | 2.30 | 11.02 |
| | | 60 | *Bryum algovicum* Sendt. Ex Müll. Hal. | 3.08 | 10.10 | 5.95 | 12.32 | 7.48 |
| | | 61 | *Bryum dichotomum* Hedw. | 1.07 | — | 10.16 | 3.72 | — |
| | | 62 | *Bryum billarderi* Schwägr. | 1.07 | — | — | — | — |
| Lepidoziaceae | *Lepidozia* | 63 | *Lepidozia subtransveersa* Steph. | 4.48 | — | — | — | — |
| Bartramiaceae | *Philonotis* | 64 | *Philonotis mollis* (Dozy & Molk.) Mitt. | — | 3.38 | — | — | — |
| Grimmiaceae | *Grimmia* | 65 | *Grimmia incurva* Schwaegr. | 1.07 | — | — | — | — |

**Table 4**: Diversity of bryophytes under different rocky desertification degrees. There is no significant difference ($P$>0.05) between degrees with the same letter, and there are significant differences ($P$<0.05) between degrees with different letters.

| Index | Nil | Potential | Slight | Moderate | Severe |
|---|---|---|---|---|---|
| *R* | 24.75±1.50a | 13.6±1.81b | 12.75±1.51b | 11.20±0.84b | 7.75±1.71c |
| *H* | 19.68±1.49a | 7.57±0.49b | 10.19±0.85c | 5.29±0.96d | 2.14±0.96e |
| *J* | 5.45±0.19a | 2.38±0.15b | 3.09±0.09c | 2.03±0.15d | 0.69±0.14e |

**Table 5**: Similarity index of bryophytes between different degrees of rocky desertification. There is no significant difference ($P$>0.05) between degrees with the same letter, and there are significant differences ($P$<0.05) between degrees with different letters.

| **Degrees** | **Potential** | **Slight** | **Moderate** | **Severe** |
|---|---|---|---|---|
| Nil | 0.27±0.04a | 0.35±0.02b | 0.31±0.05c | 0.25±0.05a |
| Potential | —— | 0.65±0.06d | 0.52±0.06e | 0.58±0.12f |
| Slight | —— | —— | 0.49±0.03g | 0.49±0.04g |
| Moderate | —— | —— | —— | 0.54±0.09e |

**Table 6**: Dominant species of bryophytes under different degrees of rocky desertification. Species with the top importance values (approximately 40 % to 50 % of the total species) were selected as the dominant species of rocky desertification to calculate the association coefficient (AC) index.

| NO. | Nil RD | Pot RD | Sli RD | Mod RD | Sev RD |
|---|---|---|---|---|---|
| 1 | *Campylopus fragilis* | *Thuidium tamariscinum* | *Erythrodontium julaceum* | *Bryum algovicum* | *Bryum argenteum* |
| 2 | *Thuidium tamariscinum* | *Bryum algovicum* | *Bryum dichotomum* | *Didymodon constrictus* | *Plagiothecium cavifolium* |
| 3 | *Metzgeria consanguinea* | *Hyophila involuta* | *Hyophila involuta* | *Brachythecium albicans* | *Tortula planifolia* |
| 4 | *Sematophyllum phoeniceum* | *Entodon concinnus* | *Brachythecium albicans* | *Thuidium tamariscinum* | *Bryum algovicum* |
| 5 | *Brachythecium albicans* | *Didymodon ditrichoides* | *Didymodon constrictus* | *Trichostomum brachydontium* | *Brachythecium albicans* |
| 6 | *Plagiothecium neckeroideum* | *Brachythecium albicans* | *Bryum algovicum* | *Bryum billarderi* | *Plagiomnium cuspidatum* |
| 7 | *Lepidozia subtransveersa* | *Trichostomum brachydontium* | *Entodon concinnus* | *Diphyscium foliosum* | *Didymodon constrictus* |
| 8 | *Brachythecium brotheri* | *Plagiothecium cavifolium* | *Pylaisia falcata* | *Didymodon fallax* | *Erythrodontium julaceum* |
| 9 | *Pseudotaxiphyllum pohliaecarpum* | *Erythrodontium julaceum* | *Trichostomum brachydontium* | *Campylopus fragilis* | *Didymodon ditrichoides* |
| 10 | *Heteroscyphus coalitus* | *Dicranella heteromalla* | *Bryum argenteum* | —— | —— |
| 11 | *Bryum algovicum* | *Weissia controversa* | —— | —— | —— |
| 12 | *Sematophyllum subpinnatum* | —— | —— | —— | —— |
| 13 | *Hypnum oldhamii* | —— | —— | —— | —— |
| 14 | *Diphyscium foliosum* | —— | —— | —— | —— |
| 15 | *Leucobryum juniperoideum* | —— | —— | —— | —— |
| 16 | *Dicranum scoparium* | —— | —— | —— | —— |

**Fig. 1**: Location and basic information of the experimental site.

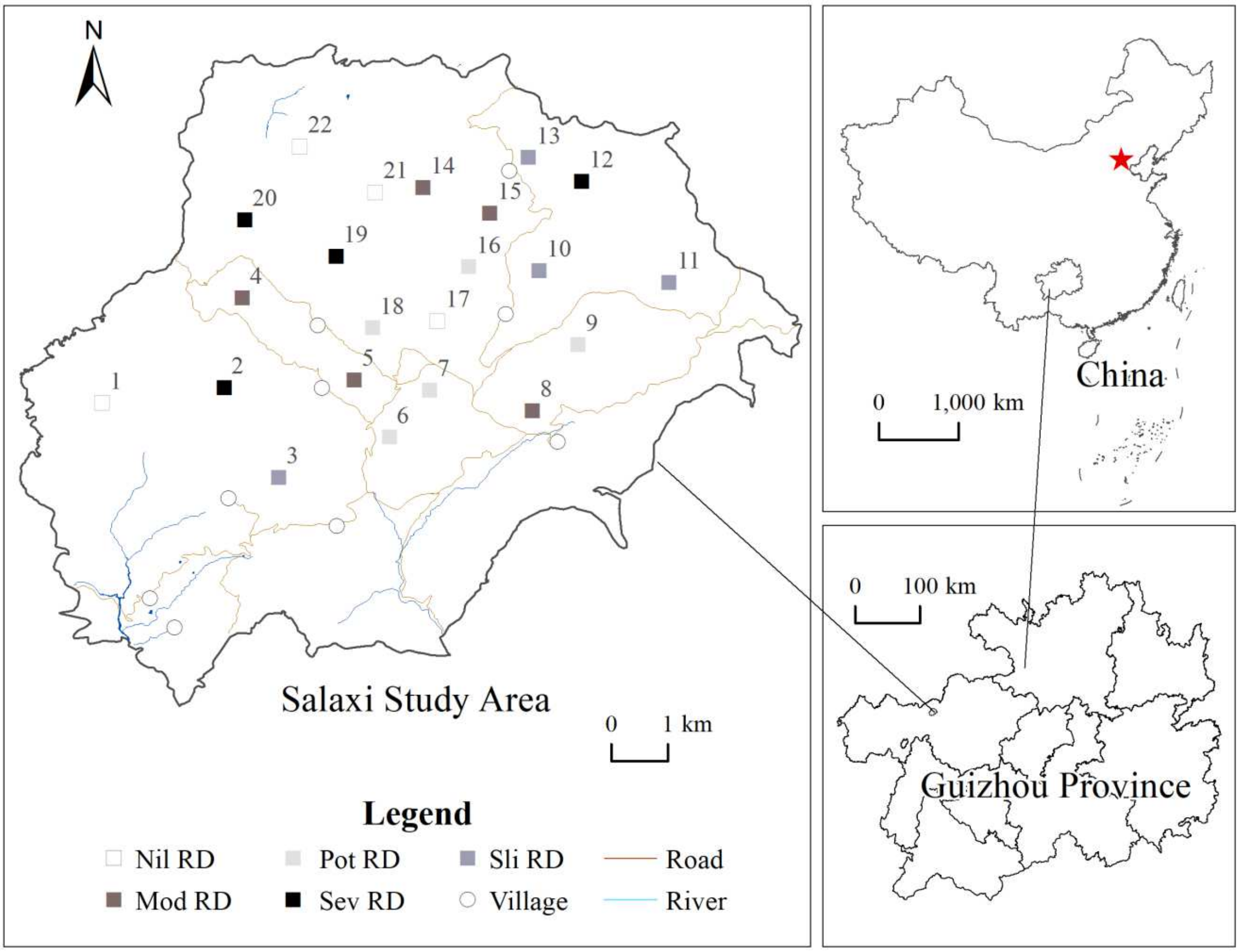


**Fig. 2**: Life-forms of bryophytes under different degrees of rocky desertification.

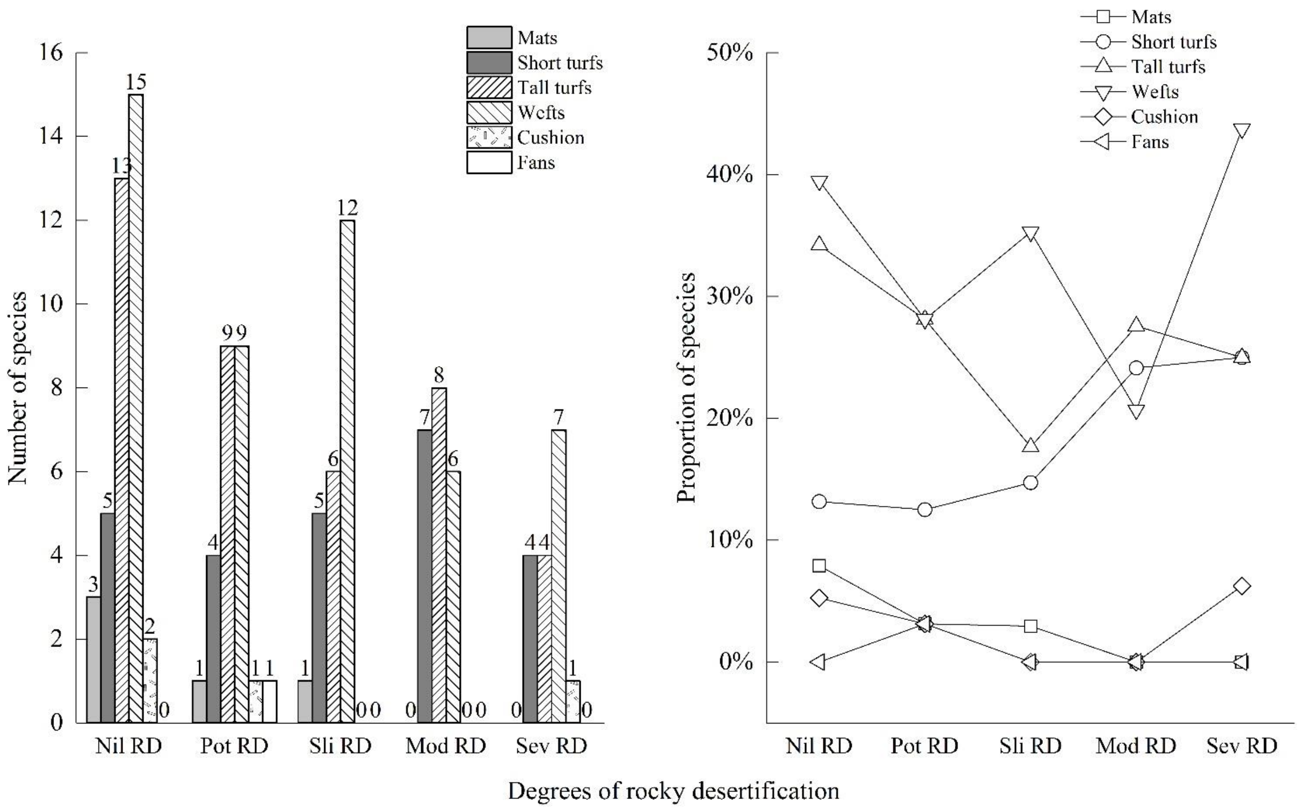


**Fig. 3**: Distribution characteristics of bryophyte communities.

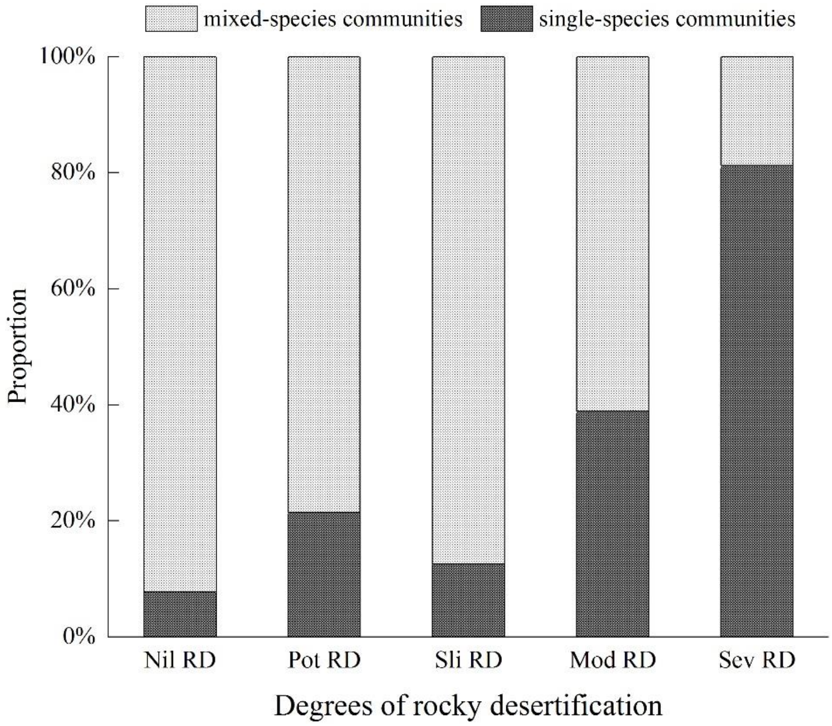


**Fig.4**: Principal component analysis of bryophyte community data with the projection of species' importance values. The arrows represent the degree of rock desertification; the circle represents species; the numbers of bryophytes are listed in Table 4.

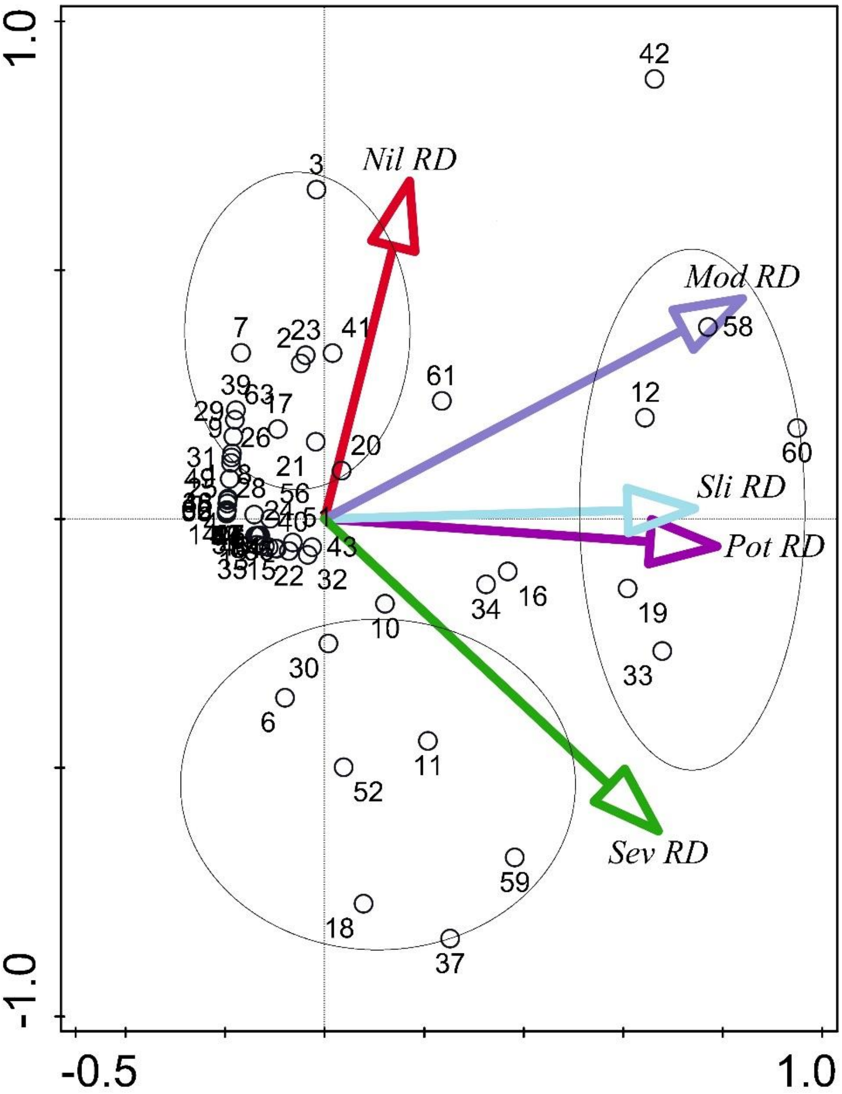


**Fig. 5**: Semi-matrix graph of AC interspecific coefficient (upward-pointing triangle) and Chi square test ($\chi^2$, downward-pointing triangle) of dominant bryophyte species in different rocky desertification degrees. a, Nil RD; b, Pot RD; c, Sli RD; d, Mod RD; e, Sev RD.

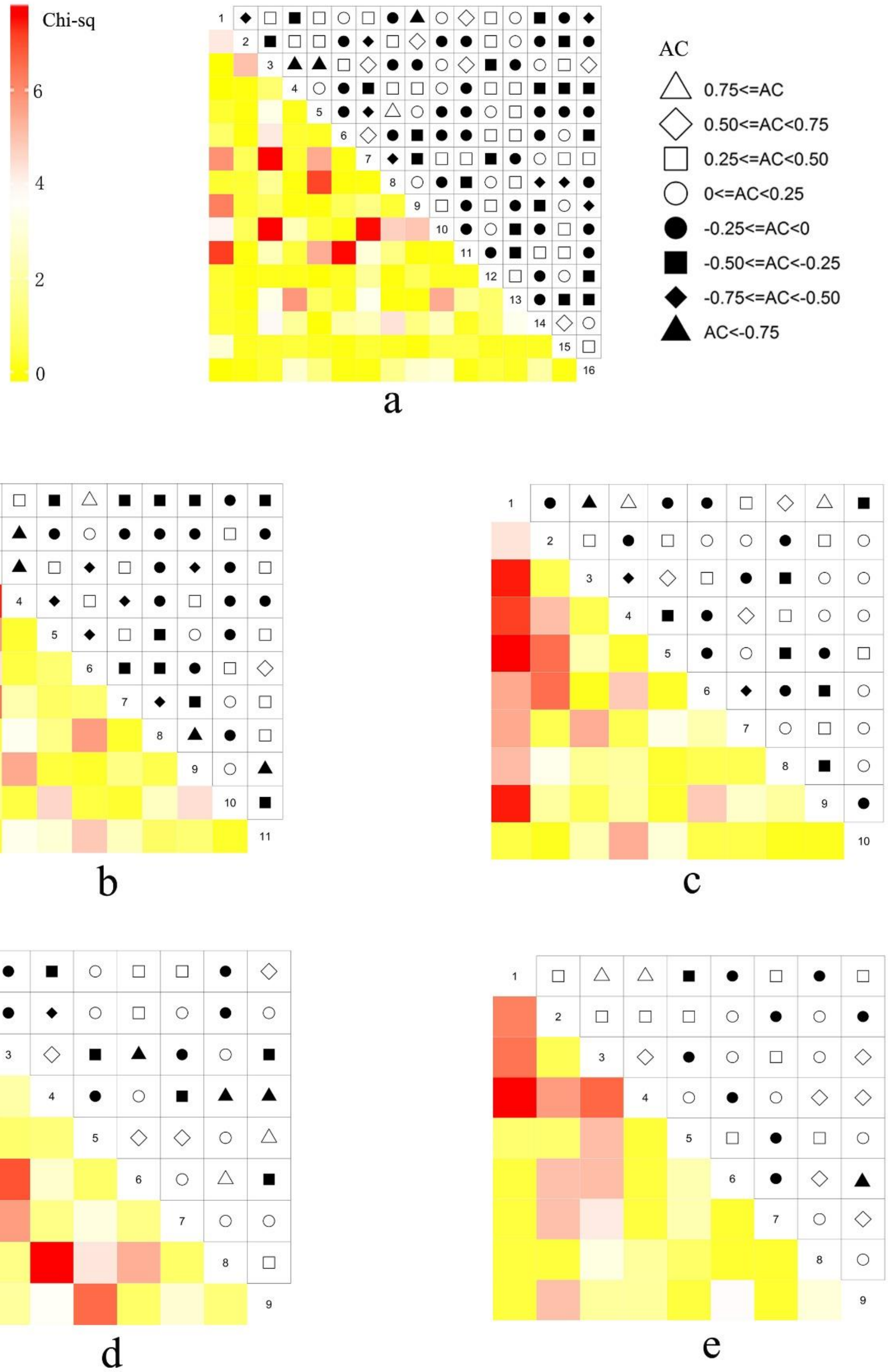


**Fig. 6**: Chlorophyll contents of four bryophyte species under different degrees of rocky desertification.

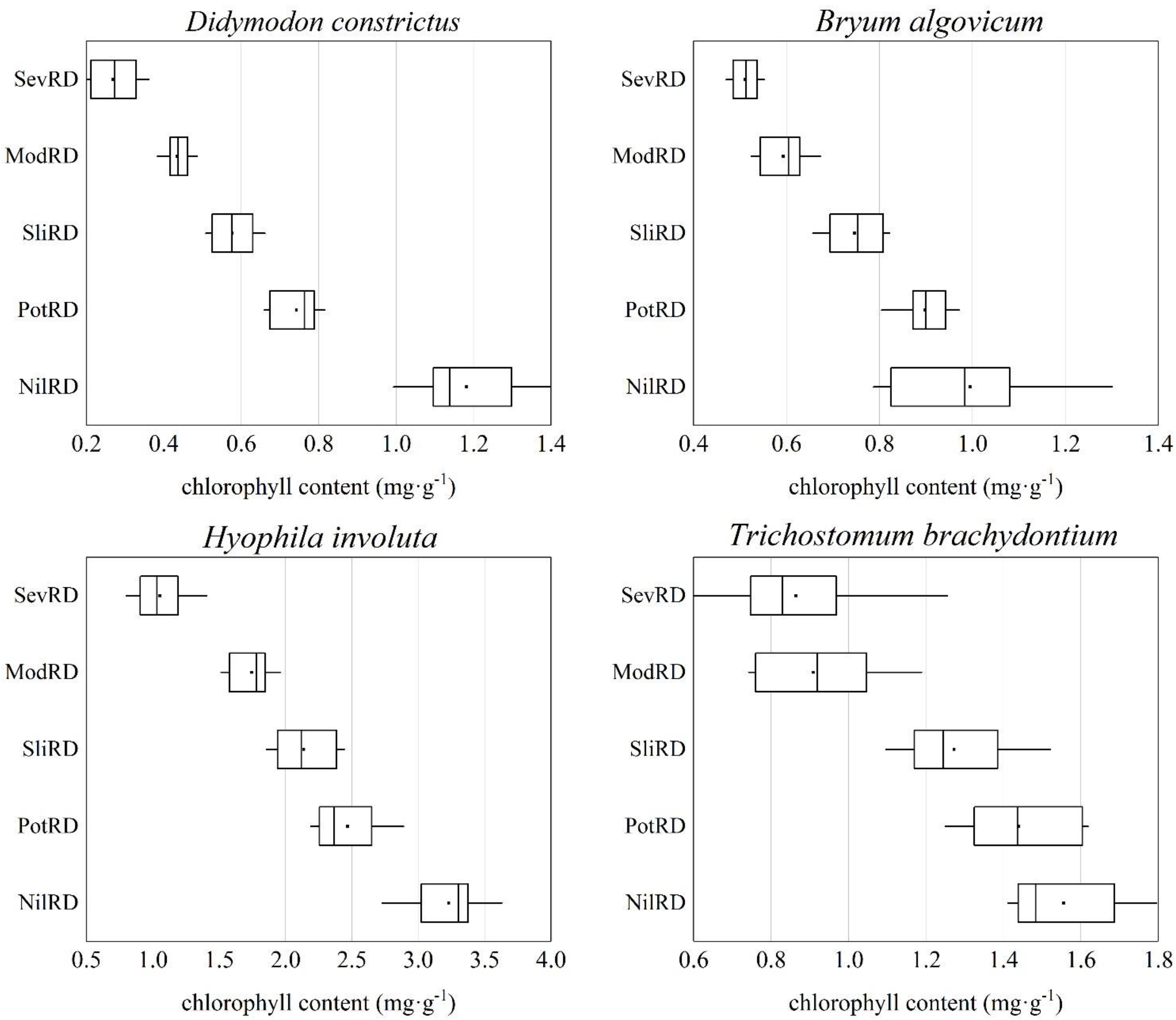
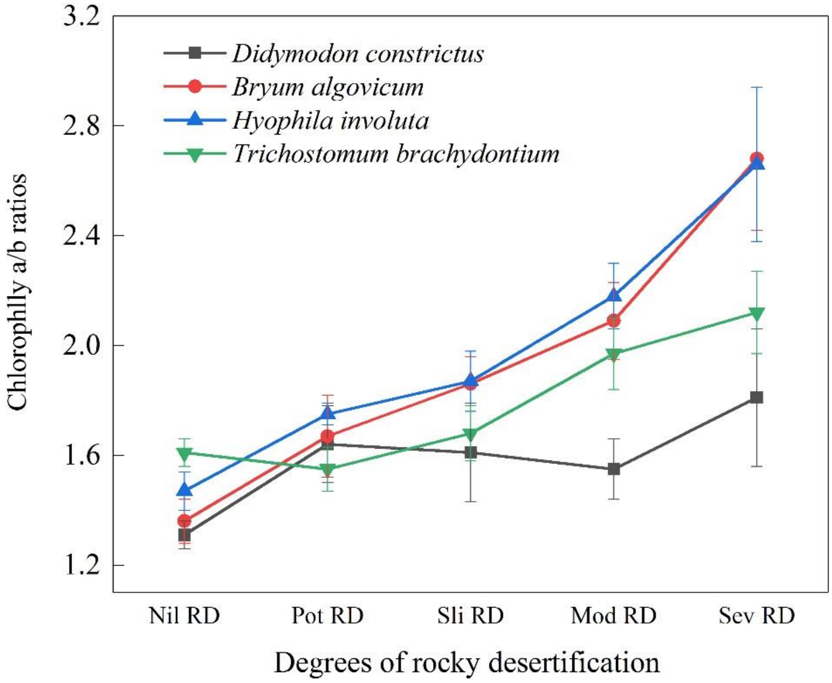


**Fig. 7**: Chlorophyll a/b ratios of four bryophyte species under different degrees of rocky desertification.



# Figures

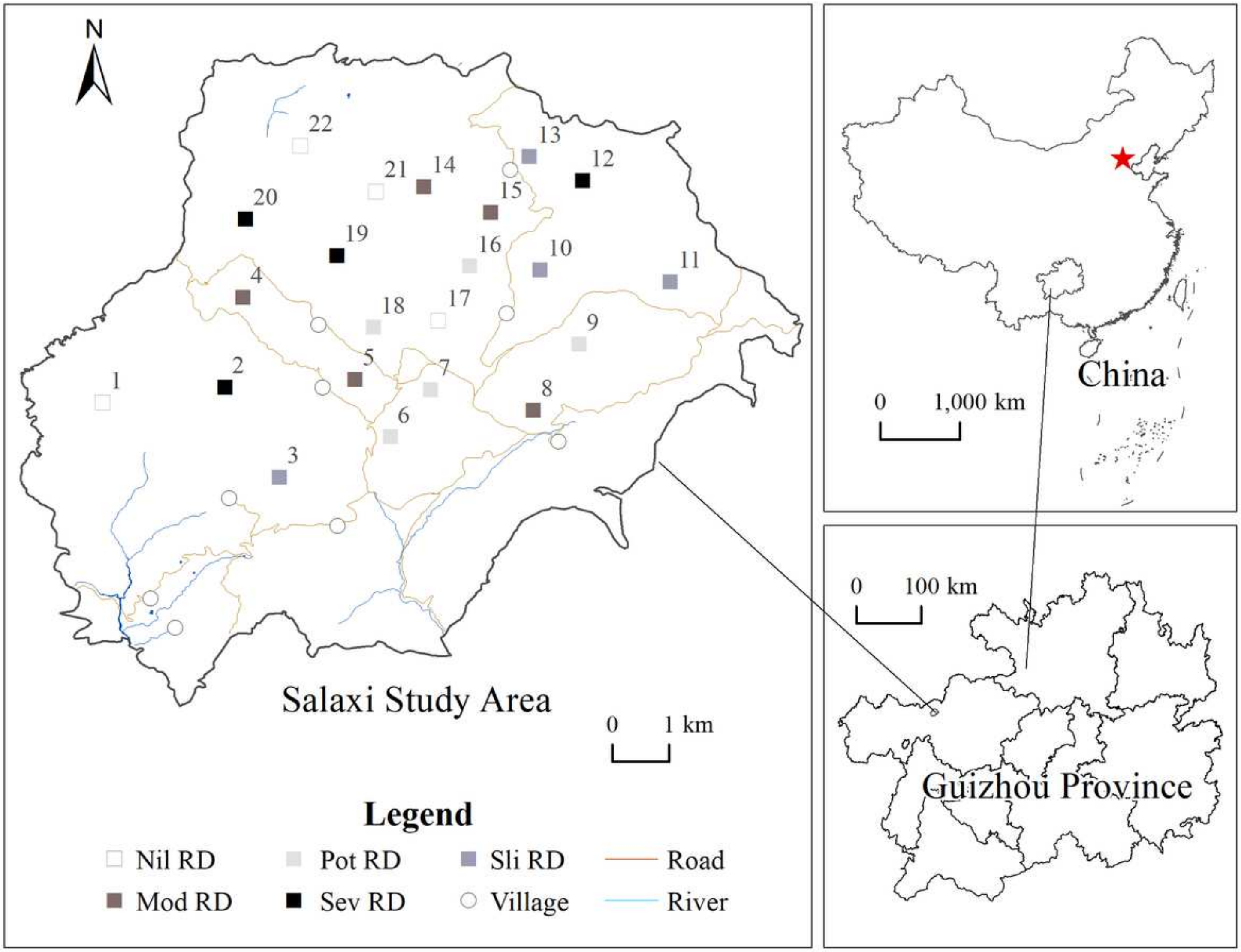



**Figure 1**

Location and basic information of the experimental site. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

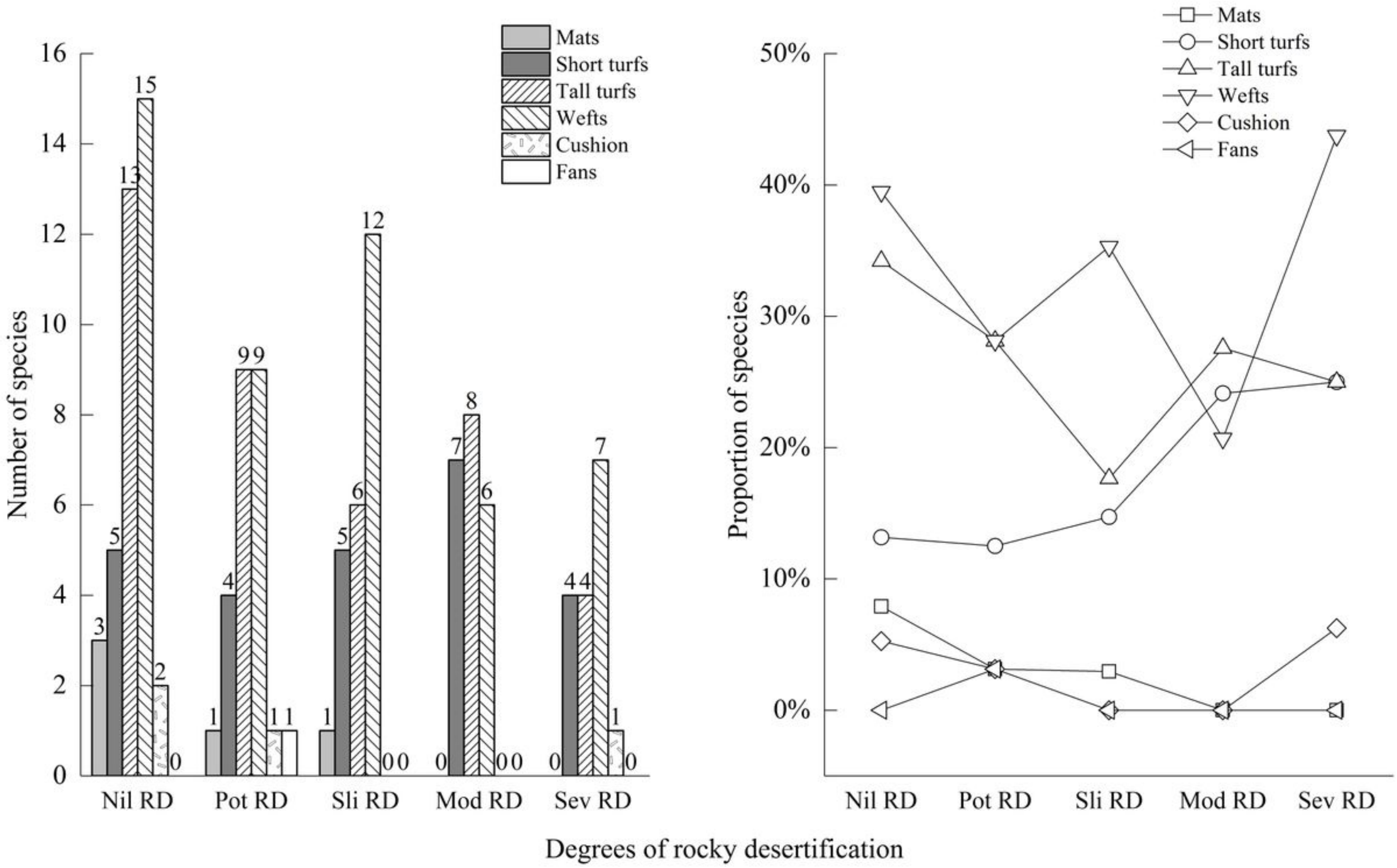



**Figure 2**

Life-forms of bryophytes under different degrees of rocky desertification.

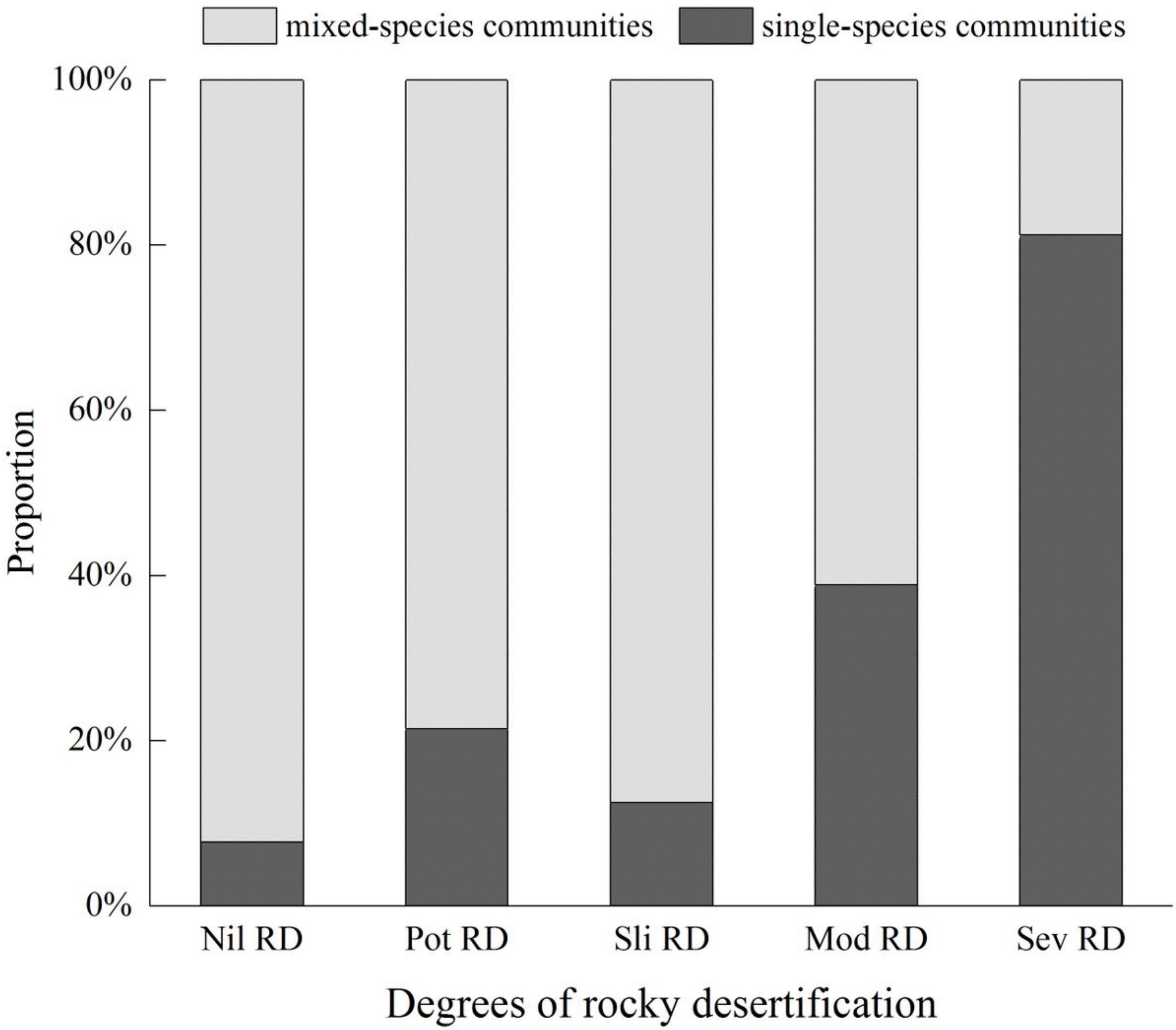



**Figure 3**

Distribution characteristics of bryophyte communities.

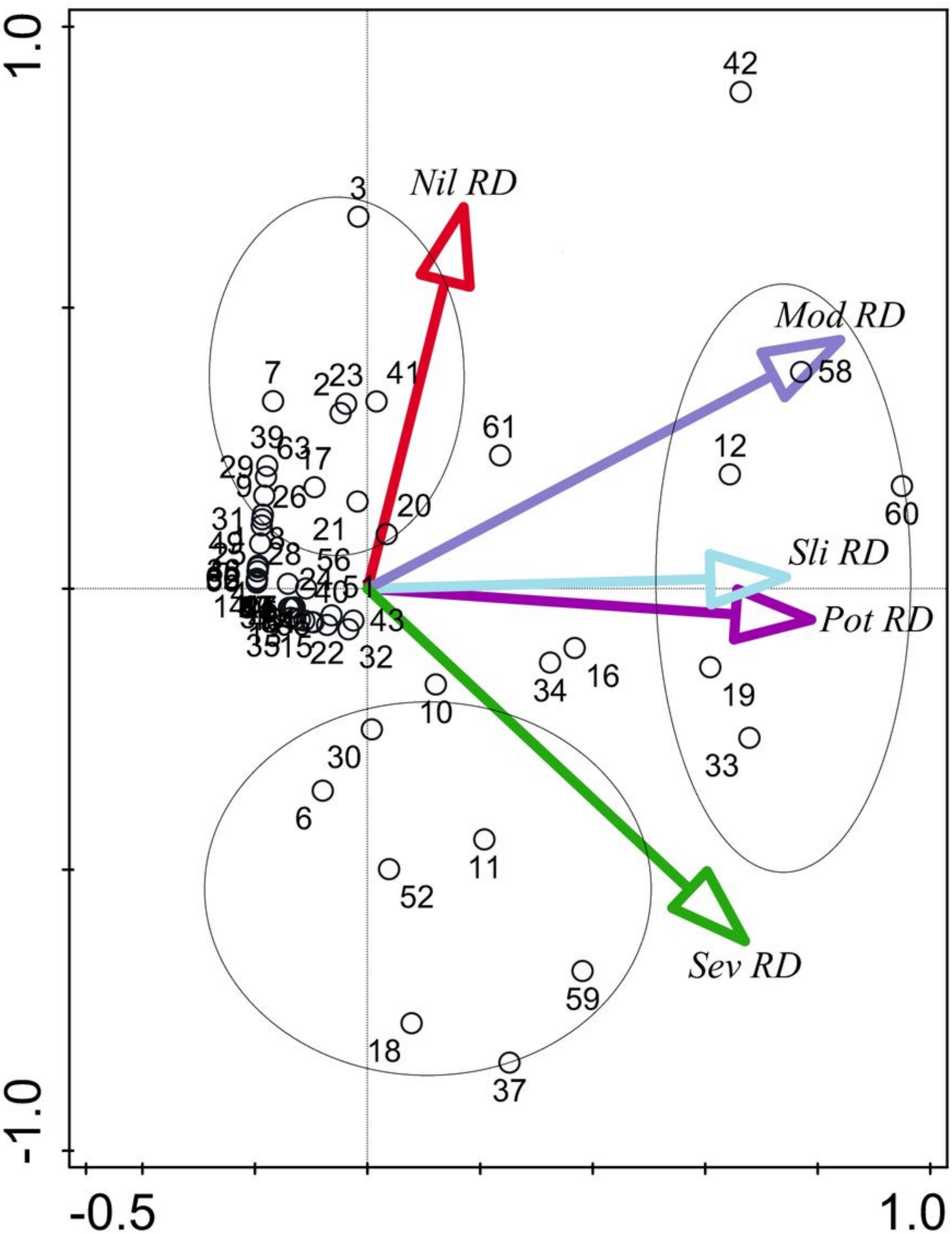
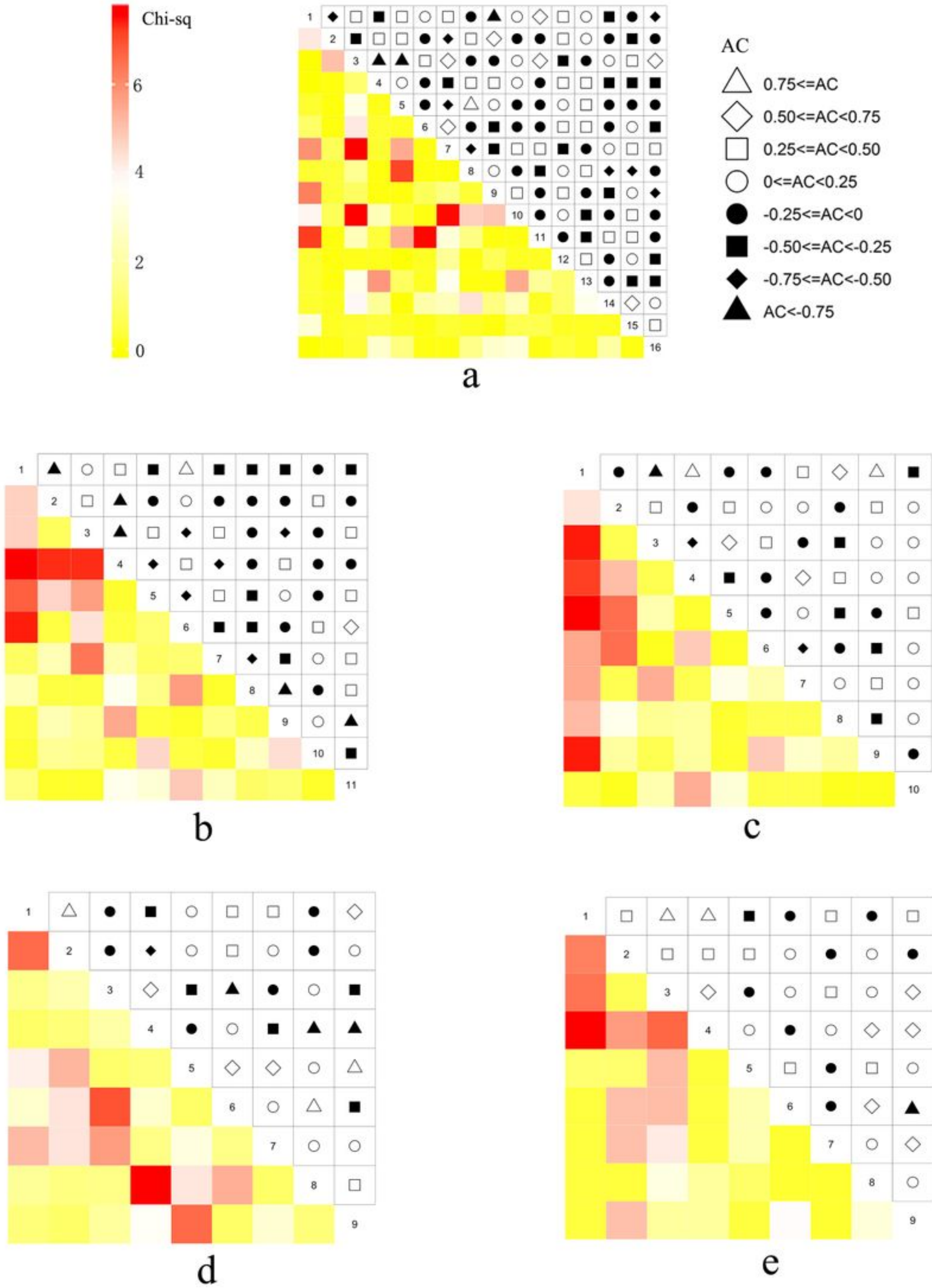


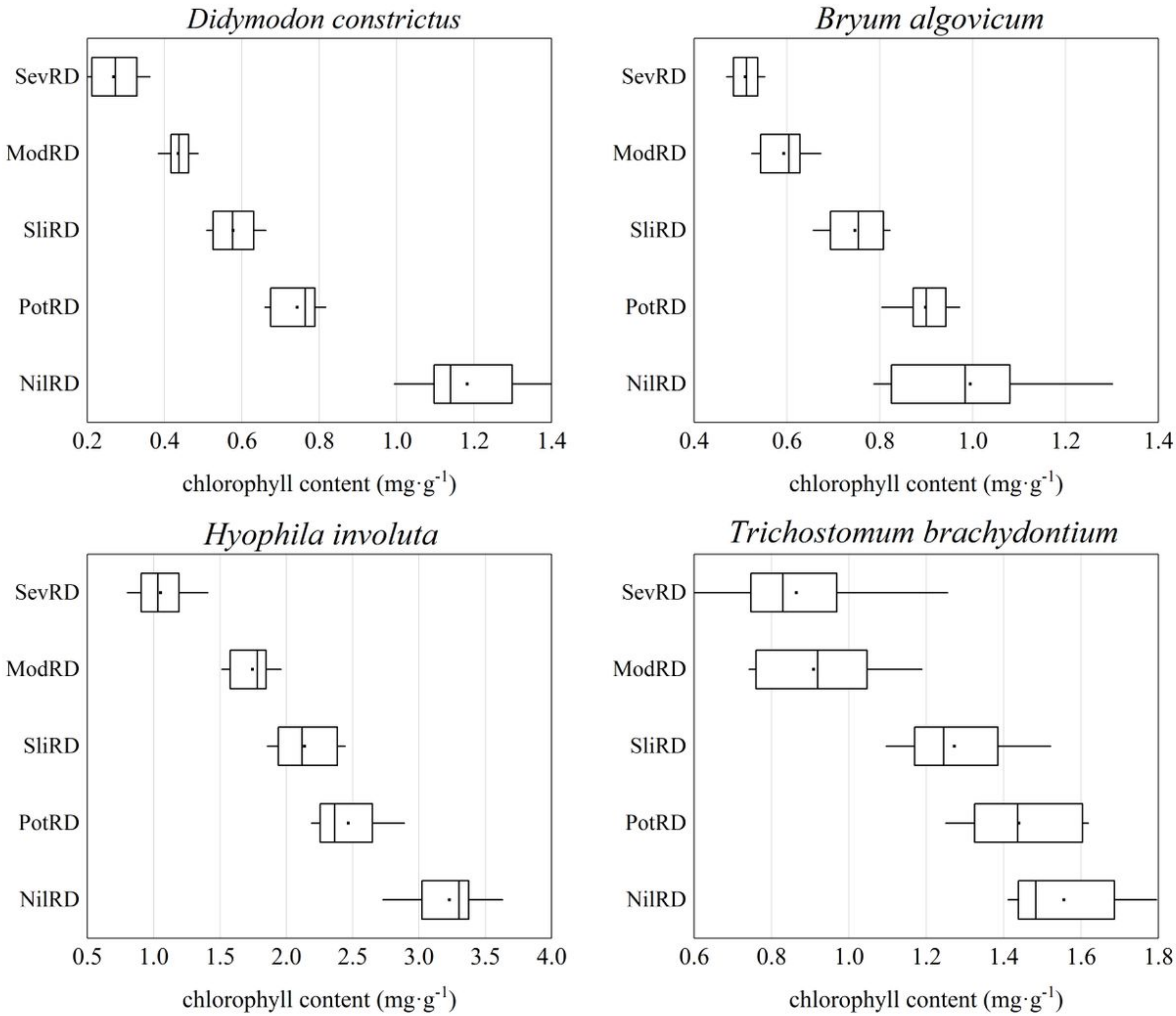

Figure 4

Principal component analysis of bryophyte community data with the projection of species' importance values. The arrows represent the degree of rock desertification; the circle represents species; the numbers of bryophytes are listed in Table 4.




## Figure 5

Semi-matrix graph of AC interspecific coefficient (upward-pointing triangle) and Chi square test (χ2, downward-pointing triangle) of dominant bryophyte species in different rocky desertification degrees. a, Nil RD; b, Pot RD; c, Sli RD; d, Mod RD; e, Sev RD.




## Figure 6

Chlorophyll contents of four bryophyte species under different degrees of rocky desertification.

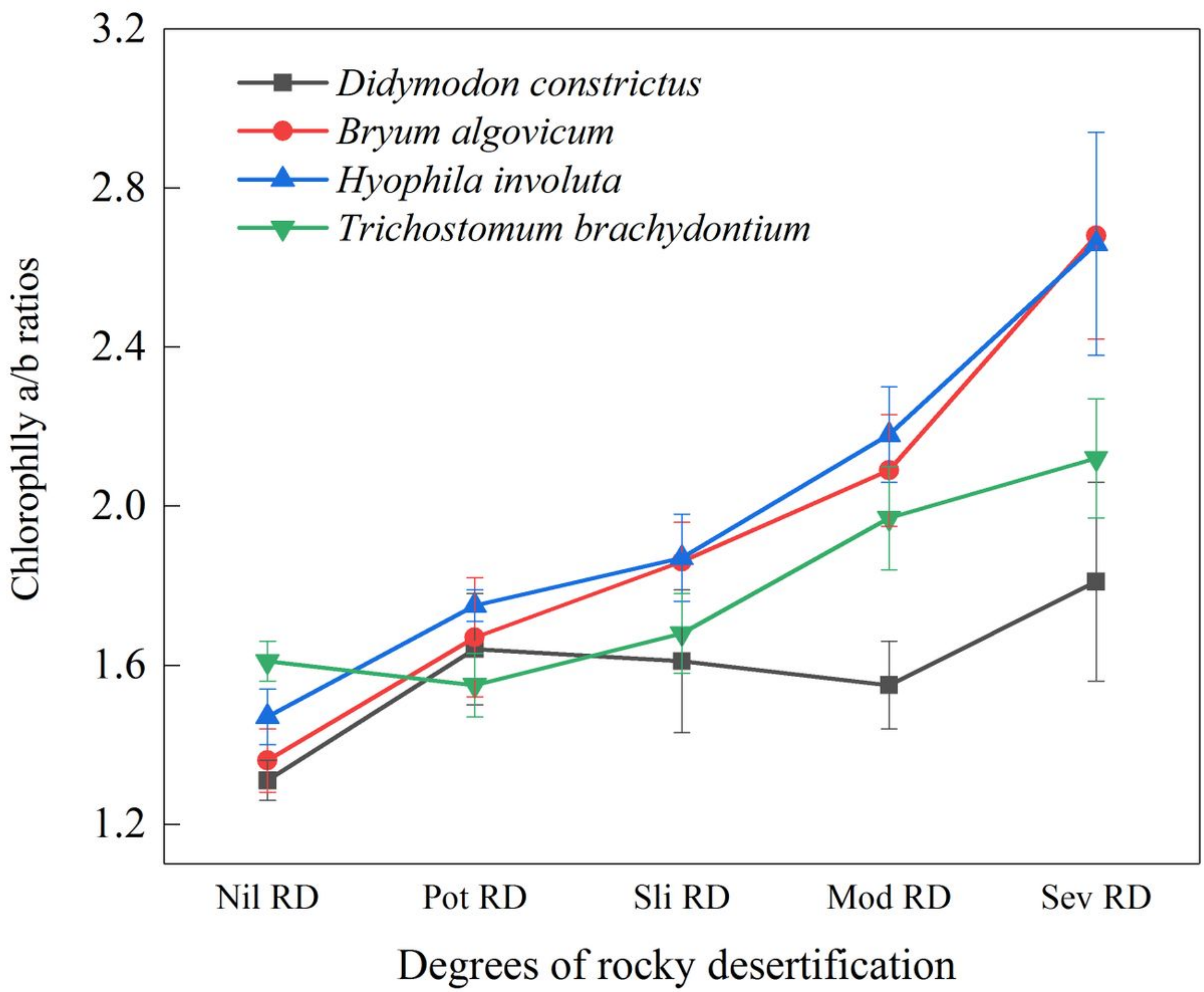



**Figure 7**

Chlorophyll a/b ratios of four bryophyte species under different degrees of rocky desertification.

## Supplementary Files

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- Graphicalabstract.jpg