Composition and distribution characteristics of karst epilithic moss communities

Wenping Meng
Guizhou University
Qingqing Ren
Guizhou University
Na Tu
Guizhou University
Tingjiao Leng
Guizhou University
Quanhou Dai (qhdairiver@163.com)
Guizhou University
Xingsong Yi
Guizhou University

Original Article

Keywords: Karst, karst epilithic mosses, biodiversity, community composition, distribution characteristics

DOI: https://doi.org/10.21203/rs.3.rs-57464/v1

Abstract

Background

Bryophytes have an important ecological function in maintaining ecological diversity, material transformation, and energy cycles in ecosystems. In this study, bryophytes in a typical karst area were the research objects. The coverage and abundance of rocky bryophytes in established plots were recorded. The composition and distribution characteristics of the karst epilithic mosses were analyzed by importance values, a dissimilarity index and ggplot2 in R.

Results

The karst epilithic moss communities included 207 species in 93 genera and 37 families, including 185 species in 27 families and 80 genera of mosses and 22 species in 10 families and 13 genera of liverworts. The dominant families were Pottiaceae, Brachytheciaceae, Thuidiaceae, Bryaceae, Hypnaceae, Mniaceae, Entodontaceae, and Lichenaceae. The dominant species were *Thuidium kanedae*, *Pseudosymblepharis angustata*, *Trichostomum involutum*, *Racopilum cuspidigerum*, *Brachythecium helminthocladum*, *Eurohypnum leptothallum*, *Hyophila involuta*, *Anomodon rugelii*, *Taxiphyllum taxirameum*, and *Bryohaplocladium angustifolium*. Epilithic mosses in karst habitats have five life forms: turf, weft, cushion, slanting, and pendant. The main life forms we observed were turf and weft.

Conclusions

The distribution of the epilithic moss communities is closely related to their habitats. The diversity of bryophytes in areas with high forest coverage, high humidity, and abundant water and heat conditions is higher than that of bryophytes in rocky desertification habitats.

Background

Bryophytes, as pioneer plants in the ecosystem succession process (Xue, 2013), occupy an extremely important position and have an important ecological function in maintaining the ecological diversity of ecosystems. Bryophytes, as the most primitive higher plants, have simple structures and underdeveloped pseudoroot systems and remain fixed in the ecosystem (Lou, 2013). Their special leaf surface structure and cell characteristics (Lou, 2012) make mosses resistant to high temperatures and provide them with drought resistance, a strong water storage capacity, and strong moisture retention and solidification abilities (Proctor & Pence, 2002; Krol et al., 2003; Zhang et al., 2017). Mosses play an important role in preventing soil erosion on rock surfaces (Li et al., 2013; Jia et al., 2014; Zhang et al., 2018b). Epileptic mosses grow on limestone or dolomite substrates. They are often clustered, interlaced, or creeping; they develop on the rock surface and improve the bare rock habitat through biological karstification. Mosses provide the material foundation (Harper & Belnap, 2001; Jackson, 2015) that is of great significance for the maintenance and development of karst ecosystems (Li et al., 2006; Costa et al., 2018). H_2CO_3 formed by the respiration of bryophytes and some metabolic secretions can react with minerals in rocks by acidification, alkalization, redox, chelation, etc. As the reaction process continues to advance, the composition of the rock minerals changes. Ca, Mg, Na, K, Fe, Al, Si, etc. dissolve from carbonates, silicates, aluminates, sulfides, oxides, destroying the original rock crystal structure, which dissolves the rocks and promotes weathering (Street et al., 2013; Li et al., 2015; Lammers et al., 2017). At the same time, bryophytes colonize the rock surface, and the physical and mechanical forces generated by the pseudoroot system and the dry-wet alternate freezing and thawing of the plant body act on the rock and produce rock debris. The complexation of organic matter with mineral ions often forms insoluble materials, which are bound to moss and its biological crust residues, which not only increase the amount of soil deposition but also promote the accumulation of organic matter and increase soil nutrient levels (Zhu, 1995; Liu et al., 2017).

Therefore, the study of the epilithic moss community composition, structure, and distribution characteristics and its relationship with the environment in karst ecosystems is the key to investigating ecological topics such as karst biological diversity and genetic diversity. However, the current research on bryophytes in karst mainly focuses on comprehensive research on various types of bryophytes, and there are few reports on the relationship between the composition and distribution characteristics of karst communities and the environment. Therefore, in this paper, by selecting representative karst areas for field investigations, establishing sample plots, collecting specimens, identifying specimens, and trying to explain the relationship between the composition, structure and distribution characteristics of karst communities and the environment through biometric analysis, we provide in-depth research and a scientific theoretical basis for the comprehensive management of karst biodiversity and rocky desertification areas.

Results And Analysis

Species composition of karst epilithic mosses

A total of 1,400 specimens were collected in the 2 research areas belonging to 37 families, 93 genera, and 207 species, including 27 families, 80 genera, and 185 species of mosses and 10 families, 13 genera, and 22 species of liverworts (see appendix for details). Statistics about the genera and species in the dominant families are shown in Table 1. The number of genera in the 10 most dominant families accounts for 60.22% of all genera, and the number of species in the dominant families accounts for 70.53% of the total species. Among the mosses are Pottiaceae, Brachytheciaceae, Thuidiaceae, Bryaceae, Hypnaceae, Mniaceae, Entodontaceae, Meteoriaceae, Neckeraceae, and Anomodontaceae, which were the ten most abundant families of karst epilithic mosses in this study (Table 1). These 10 families of mosses are widely distributed on the rock surface, have strong adaptability and are most common on the surface of karst rocks. The number of species of liverworts was much smaller than that of mosses. Among them, Plagiochilaceae and Porellaceae had 6 and 4 species, accounting for 2.90% and 1.93% of the total species, respectively, and are more common in humid karst rock environments.

Table 1 Genera and species statistics for the dominant families of karst epilithic mosses

Family	Number of Genera	Percentage of total genera (%)	Number of Species	Percentage of total species (%)
Pottiaceae	16	17.20	35	16.91
Brachytheciaceae	4	4.30	21	10.14
Thuidiaceae	7	7.53	16	7.73
Bryaceae	3	3.23	15	7.25
Hypnaceae	7	7.53	12	5.80
Mniaceae	4	4.30	13	6.28
Entodontaceae	2	2.15	10	4.83
Meteoriaceae	6	6.45	10	4.83
Neckeraceae	5	5.38	7	3.38
Anomodontaceae	2	2.15	7	3.38
Total	57	60.22	146	70.53

Diversity of moss life forms

The life form is the external growth form used by plants to adapt to the environment. Life forms determine the most basic functional traits of plants and are an important parameter for describing the appearance characteristics of communities (Ordoñez et al., 2010). Bryophytes of the same life form generally have similar ecological habits and competitive strategies, so species with similar environmental requirements are classified as having the same life form. In this paper, according to the definition and division of bryophyte life forms by Magdefrau (1982) and other scholars, combined with field observations, karst epilithic moss lifeforms are divided into five life forms: turf, weft, cushion, slanting and pendant (Table 2). The cluster and weft life forms were observed in 82.52% of the total bryophytes and are the main life forms of karst epilithic mosses. (1) the Clustered mosses were mainly Pottiaceae and Bryaceae, with 79 species, accounting for 38.16% of the total species. Plants of this type of life form grow tightly together in a cluster, which has a great effect on water conservation and soil retention. In the stony karst environment, the light is strong, and the moss plants are more distributed in habitats with low air humidity. (2) Weft mosses are mainly Thuidiaceae, Hypnaceae, Brachytheciaceae, Anomodontaceae, Mniaceae, Entodontaceae, Plagiotheciaceae, Racopilaceae, and Leskeaceae, with 92 species, accounting for 44.44% of the total species identified in this study. This type of bryophyte interweaves and grows on the surface of the rock, which greatly enhances the water storage capacity of the cluster type and increases the water content of the rock surface. This life form is typically distributed in the wet karst habitat. (3) Cushion mosses are mainly found in Porellaceae, Aytoniaceae, Frullaniaceae, Pelliaceae, and Makinoaceae; 15 species were found in this study, accounting for 7.25% of the total species. Bryophytes of this life form often grow in pieces, making it difficult to distinguish the plants, and are mainly distributed in moist habitats. (4) Pendant mosses are mainly members of the Meteoriaceae family, and 11 species were identified in this study, accounting for 5.31% of the total species. These mosses are mainly distributed on rocky surfaces with high humidity. (5) Slanting mosses are typically in the Hypopterygiaceae and Neckeraceae families. A total of 10 species were found in this study, accounting for

4.83% of the total species. This bryophyte life form is mainly distributed on the surface of wet rock walls that are not exposed to direct sunlight and have water dripping down their surfaces.

Table 2 Statistics on the life forms of karst epilithic mosses

Life form	Number of Species	Percentage of total species (%)	Ecological characteristics
Turf	79	38.16	The main branches are erect and parallel, loosely or tightly arranged, with few branches and many bases with false roots.
Weft	92	44.44	The plants are intertwined with each other, forming loosely stacked clusters, usually branched, with few false roots attached to the substrate.
Cushion	15	7.25	The dome-shaped community grows from the initial center point, the branches and main branches have the same growth direction, and it is difficult to distinguish the plants from the outside.
Pendant	11	5.31	The plant grows into a creeping shape, and its main branches hang on the trunk, branches and other objects like hairs.
Slanting	10	4.83	The plant grows creeping or "inverted" and is slanted, but the plant is short and not overhanging, the stem is single or branched; the leaves are flat and often bilaterally symmetrical.

Analysis of dominant karst epilithic moss species

The importance values of epilithic mosses at the Maolan Nature Reserve and the Puding Karst Ecological Research Station were calculated separately. The dominant species of epilithic mosses in karst obtained by sorting are shown in Table (3).

Table (3) Comparison of dominant species of karst epilithic mosses in different habitats

Dominant species of karst epilithic mosses	Ranking of importance values	Maolan National Nature Reserve	Puding Karst Ecological Research Station
		Species	Species
	1	*Thuidium kanedae*	*Eurohypnum leptothallum*
	2	*Pseudosymblepharis angustata*	*Hyophila involuta*
	3	*Trichostomum involutum*	*Racopilum cuspidigerum*
	4	*Racopilum cuspidigerum*	*Anomodon rugelii*
	5	*Brachythecium helminthocladum*	*Taxiphyllum taxirameum*
	6	*Thuidium cymbifolium*	*Bryohaplocladium angustifolium*
	7	*Herpetineuron toccoae*	*Didymodon constrictus.var.constrictus*
	8	*Racopilum orthocarpum*	*Eurhynchium longirameum*

The dominant species of epilithic mosses in karst are mainly mosses, including plants in the dominant families such as Pottiaceae, Thuidiaceae, Racopilaceae, Brachytheciaceae, and Anomodontaceae. The dominant species of bryophytes at the Maolan National Nature Reserve are *Thuidium kanedae*, *Pseudosymblepharis angustata*, *Trichostomum involutum*, *Racopilum cuspidigerum*, *Brachythecium helminthocladum*, *Thuidium cymbifolium*, *Herpetineuron toccoae* and *Racopilum orthocarpum*. Among them, Thuidiaceae accounted for 37.5%, Pottiaceae accounted for 25%, Racopilaceae accounted for 25%, and Brachytheciaceae accounted for 12.5% of the total species. The dominant species of epilithic mosses at the Puding Karst Ecological Research Station are *Eurohypnum leptothallum*, *Hyophila involuta*, *Racopilum cuspidigerum*, *Anomodon rugelii*, *Taxiphyllum taxirameum*, *Bryohaplocladium angustifolium*, *Prototheca acuminata*, *Didymodon constrictus.var.constrictus* and *Eurynchium longirameum*; among them, Hypnaceae accounted for 37.5%, Pottiacea accounted for 25%, Thuidiaceae, Racopilaceae, and Anomodontaceae each accounted for 12.5% of the total species.

There are differences in the dominant species between the two research areas. The Maolan Nature Reserve is dominated by moist epilithic mosses of the family Bryaceae and Lichenaceae, while the drought-tolerant types of Hypnacea and Pottiacea dominated at the Puding Research Station. In short, habitat has an important influence on the population distribution of epilithic mosses in karst ecosystems.

The relationship between the distribution of bryophyte communities and the environment

Comparison of bryophyte richness between the different habitat types

The richness of karst epilithic mosses varied greatly between the different regions (Fig.1). The genera and species richness of bryophytes at the Maolan National Nature Reserve are greater than those at the Puding Karst Rocky Desertification Ecological Observation and Research Station. There are 37 families of bryophytes (27 families of mosses and 10 families of liverworts), 89 genera (76 genera of mosses and 13 genera of liverworts), and 200 species (180 species of mosses and 20 species of liverworts) at the Maolan Nature Reserve. At Puding Station, there are 14 families of bryophytes (11 families of mosses, 3 families of liverworts), 28 genera (25 genera of mosses, 3 genera of liverworts), and 63 species (59 species of mosses, 4 species of liverworts). The difference in species richness between mosses and liverworts is consistent with the difference in total species number. In short, the richness of bryophytes in karst forests in the Maolan National Nature Reserve is higher than that in karst rocky desertification areas, indicating that the health of the ecosystem is directly proportional to the biodiversity of bryophytes. The better the ecological environment, the greater the biodiversity of bryophytes.

Comparison of the similarity of bryophytes between different habitat types

There are 55 species in common between the two research areas, including 53 species of mosses and 2 species of liverworts. The species composition similarity coefficient is 41.83%. The species in common are mainly dominant species of the dominant genera in the Brachytheciaceae, Bryaceae, Mniaceae, and Anomodontaceae families, including *Hygrophilus involuta*, *Hyophila javanica*, *Trichostomum involutum*, *Eurohypnum leptothallum*, *Brachythecium pulchellum*, *Brachythecium viridefactum*, *Anonydon abbrevia*, *Anomodon minor*, *Bryum argenteum*, *Bryum algovicum*, *Racopilum cuspidigerum*, *Racopilum orthocarpum*, *Thuidium plumulosum*, *Thuidium kanedae*, etc. The common species of liverworts are *Porella japonica var. Japonica* and *Plagiochasma rupestre,* which belong to Porellaceae and Aytoniaceae, respectively. These bryophytes have strong environmental adaptability, a wide distribution range, and a wide niche and are among the widespread species of karst epilithic mosses.

Analysis of differences in bryophytes between different habitat types

The difference coefficient for the epilithic moss species in the two study areas is 0.58, which is between 0.50 and 0.75, indicating that the epilithic moss communities of the Maolan Reserve and Puding Ecological Station are moderately dissimilar. There are large differences in richness (Figure 2). There are 200 species of bryophytes in 37 families and 89 genera at Maolan Nature Reserve, 63 species in 28 genera in 14 families of bryophytes at Puding Station. A total of 87.30% of the bryophyte species in the Puding Ecological Research Station are also distributed in the Maolan Nature Reserve, and the species in the Bryaceae family at Puding Ecological Station re exactly the same as the species of the Bryophyta family in the Maolan Nature Reserve. The diversity of the bryophytes, genera and species at the Maolan Nature Reserve is much higher than that at the Puding Ecological Station. For example, there are 15 genera and 34 species, 7 genera and 16 species, and 7 genera and 12 species of Pottiaceae, Thuidiaceae, and Hypnaceae at the Maolan Nature Reserve, respectively, while there are only 5 genera and 9 species, 2 genera and 4 species, and 3 genera and 4 species of these families at the Puding Ecological Station. Hypopterygiaceae, Bartramiaceae, Amblystegiaceae, Cryphaeaceae, Grimmiaceae, Calliergonaceae, Habrodontaceae, Metzgeriaceae, Pallaviciniaceae, Plagiochilaceae, Pelliaceae, and Makinoaceae only live in moist habitats and were only found in the Maolan Reserve in this study.

Distribution characteristics of karst epilithic mosses

Among the bryophytes in the Puding Ecological Station area, 58 species are found in dry habitats, and only 5 species are found in humid habitats. The 52 common species between the two areas are distributed in dry habitats (Figure 3A). This shows that the epilithic mosses in the Puding Ecological Station are mainly dry stony plants. These bryophytes have strong drought tolerance and are able to survive in arid and water-deficient environments. The species of stony bryophytes distributed in the moist habitats in the Maolan Nature Reserve are much larger than those distributed in dry habitats. Among them, the 35 common species between the two areas are distributed in both dry and moist habitats (Figure 3B). This shows that such plants have a wide niche, low requirements for environmental conditions, and strong adaptability and can be considered broad-spectrum species. The epilithic moss species that are unique to the Maolan Nature Reserve are mainly distributed in humid habitats, and the types distributed in dry habitats are different from those in the dry Puding area. This result shows that environmental factors such as rainfall, air humidity, light intensity, and forest canopy density in the region have a decisive effect on the species diversity and distribution of karst bryophytes.

Discussion

Composition and characteristics of karst epilithic moss communities

There were 207 species of epilithic mosses in 37 families and 93 genera, including 185 species in 27 families and 80 genera of mosses and 22 species in 13 genera and 10 families of liverworts, in this study. According to previous studies, there are 1643 species of 366 genera in 94 families of bryophytes in Guizhou (Xiong&Cao, 2017), and the families, genera and species of stony karst mosses account for 39.36% of the total families, 25.41% of the total genera, and 12.54% of the total species of bryophytes in Guizhou. Among the bryophytes in Guizhou, 1/3 of the families and 1/4 of the genera are distributed on rock surfaces. This shows that epilithic mosses form an important part of the total bryophytes in Guizhou. At the same time, plants of different genera in the same family of bryophytes have different habitat requirements. Therefore, although the total number of epilithic mosses accounted for 39.36% of Guizhou bryophytes, the total number of species only accounted for 12.66% of the total species. The investigation found 200 species of stony bryophytes in 37 families and 89 genera, among which 27 families, 76 genera and 180 species are mosses and 10 families, 13 genera and 20 species are liverworts. Compared with the findings of Zhang (1993), who identified 186 species, 93 genera, and 28 families of mosses (including soil, tree, rotwood and other types), our study found more families and species, which may be due to the greater sampling scope in this survey; our survey results showed a higher number of moss families, genera and species. However, compared with the 144 species, 94 genera and 45 families surveyed by Lin (1989) (including 49 species, 27 genera, and 21 families of liverworts as well as 95 species, 67 genera, and 24 families of moss), the total number of families was lower, especially for the liverworts. The Blepharostomataceae found in the 1989 investigation was not included in the Bryophyte Flora of Guizhou, and it may be that the editor did not collect this family after 1989. In the Bryophyte Flora of Guizhou, there is no description of the distribution of Aneuraceae, Jungermanniaceae, etc., in Libo. This may be due to the overexploitation and intense human activities in the Maolan Nature Reserve in recent years, resulting in a decline in the biodiversity of bryophytes. The characteristics of the unique bryophyte community are no longer obvious. There is a trend of gradual assimilation with other karst areas in Guizhou. It is recommended that the Maolan National Nature Reserve management pay attention to the coordination of ecological development and protection as well as the protection of habitat diversity and biodiversity.

The relationship between the distribution of stony moss communities and the environment

Bryophytes are simple in structure, without vascular tissue or a true root system, and almost all of their nutrients are derived from the external natural environment. Therefore, habitat conditions, especially the canopy density and humidity, are of great importance to the growth and development of bryophytes and their distribution and reproduction. However, different types of bryophytes have different environmental requirements. The investigation found that the richness of bryophytes in the Maolan National Nature Reserve is significantly higher than that of the Puding rocky desertification area, and the dominant species in the two areas are also completely different. The dominant species of bryophytes in the Maolan National Nature Reserve are *Thuidium kanedae*, *Pseudosymblepharis angustata*, *Trichostomum involutum*, and *Racopilum cuspidigerum;* however, the dominant species in the rocky desertification area are *Eurohypnum leptothallum*, *Hyophila involuta*, and *Anomodon rugelii*. This is consistent with the findings of Yin et al. (2016) on the interspecific association of dominant species of bryophytes in karst areas with severe rocky desertification. The Maolan National Nature Reserve is a typical mixed karst evergreen broad-leaved forest and evergreen broad-leaved deciduous forest. The forest has high canopy density, low solar radiation received by the rock surface, low altitude, a warm and humid climate, and high habitat heterogeneity. However, the Puding Karst Ecosystem Observation and Research Station has low vegetation coverage, exposed rock, strong solar radiation received on the rock surface, severe rocky desertification, and low habitat heterogeneity. There are large differences in environmental factors such as air temperature, humidity, and light intensity between the two study areas, leading to large differences in the composition, distribution, and diversity of families, genera, and species of bryophytes in the two study areas.

Conclusion

Karst epilithic mosses are rich in biodiversity, with a total of 37 families, 93 genera and 207 species, including 27 families, 80 genera and 185 species of mosses and 10 families, 13 genera and 22 species of liverworts. The dominant families are Pottiaceae, Brachytheciaceae, Thuidiaceae, Bryaceae, Hypnaceae, Mniaceae, Entodontaceae, Neckeraceae, and Anomodontaceae. The dominant species are *Thuidium kanedae*, *Pseudosymblepharis angustata*, *Trichostomum involutum*, *Racopilum cuspidigerum*, *Brachythecium helminthocladum*, *Eurohypnum leptothallum*, *Hyophila involuta*, *Anomodon rugelii*, *Taxiphyllum taxirameum*, and *Bryohaplocladium angustifolium*. There are five life forms of karst bryophytes: turfs, wefts, cushions, slanting, and pendants. However, the main life forms in the study area were turf and weft. The species richness of karst bryophytes in moist habitats is significantly higher than that in dry habitats. This shows that the distribution of karst epilithic moss communities is closely related to their habitats. The richness of epilithic mosses in areas with high forest coverage, high humidity and abundant water and heat conditions is higher than that in stony desertification habitats. This shows that the biodiversity of bryophytes can be used as an evaluation index for the regional ecological environment. At the same time, drought-tolerant plants such as *Eurohypnum leptothallum*, *Hyophila involuta*, and *Anomodon rugelii*, the dominant species in rocky desertification areas, can provide new ideas for the future comprehensive management of rocky desertification areas.

Materials And Methods

Study area

We selected typical karst areas at the Libo Maolan National Nature Reserve and the Puding Karst Ecosystem Observation and Research Station of the Chinese Academy of Sciences as the research areas(Fig.4). The Maolan National Nature Reserve is located in southeastern Guizhou, E107°52'10"~108°45'40", N25°09'20"~25°20'50" (Zhu, 1997), and is in the subtropical monsoon humid climate zone. The annual precipitation is 1752.5 mm, the average annual relative humidity is 83%, the average annual temperature is 15.3 °C, the average temperature of the coldest month (January) is 5.2°C, the average temperature of the hottest month (July) is 23.5°C, and the total annual solar radiation is 63289.80 Kw/m^2. The karst peak forests and peak-cluster depressions in the area are composed of pure limestone and dolomite, forming a typical karst landform. The forest coverage rate is 87.4%, and the main vegetation type is a karst native mixed evergreen-deciduous broad-leaved forest. Rich in biodiversity and with a healthy ecosystem, it is unique for being the most stable karst forest ecosystem in the same latitude zone, known as “the emerald on the belt of the earth”. It was included in the Karst World Natural and Cultural Heritage program in 2007, which mainly protects subtropical karst forest ecosystems and rare and endangered wildlife (Wu et al., 2020).

The Puding Karst Ecosystem Observation and Research Station of the Chinese Academy of Sciences is located in Puding County, Anshun city, Central Guizhou Province. The average annual precipitation is 1300 mm, the average annual temperature is 15.1 °C, the average temperature in the coldest month (January) is 5.2 °C, and the average temperature in the hottest month (July) is 23 °C. The area is dominated by karst landforms of dolomite and limestone, with an exposure rate of 85% and a vegetation coverage rate of 10-20% (Peng et al., 2009). The main vegetation is secondary vegetation, such as *Broussonetia papyrifera*, *Alangium chinense*, *Caesalpinia crista*, *Akebia trifoliata*, *Celtis sinensis*, *Rhus chinensis*, *Pyracantha fortuneana*, *Castanea mollissima*, *Rubus corchorifolius*, *Ageratina adenophora* and *Phytolacca americana*, which are typical in rocky desertification areas in Guizhou Province.

Field research methods

Samples were collected at the Puding Karst Ecosystem Observation and Research Station of the Chinese Academy of Sciences from May 10 to May 20, 2019, and samples were collected at 14 points in the Libo Maolan National Nature Reserve from June to July. Four 20 m´20 m plots were set up at Puding Station, and a 2 m´2 m plot every 4 m was sampled according to the system sampling method. Five 20 cm ´20 cm small plots were established in the 2 m´2 m plots. Each plot contained a total of 65 small plots, for a total of 260 surveyed small plots in Puding. In the inner area of the Maolan National Nature Reserve, Yaogu, Yaolan, Shishang Forest, Dongduo, Sanchahe, Jiayi, Banzhai, Yaosuo, Wuyanqiao, Xiaoqikong, Wengang, Dongtang, and Laqiao were selected as the 14 sampling points. Ten 2 m´2 m samples were established randomly along a line at each sampling point, and five 20 cm´20 cm small plots were established in each 2 m´2 m sample. There was a total of 50 small samples per sample point, for a total of 700 small samples. The moss on the ground in the sample area was divided into 100 2 cm × 2 cm sampling areas with iron mesh screens, and the number of occurrences of each moss at the intersections of the iron mesh were calculated and recorded as the coverage. At the same time, we investigated the types of all trees and shrubs in the sample area, calculated the number of communities of each moss, recorded their abundance, and recorded the associated tree species. The species of the bryophytes collected from the ≤0.5 cm surface soil layer in the sample plot were identified (Gao, 1994, 1996; Wu, 2002; Wu & Jia , 2004, 2011; Gao & Wu , 2010).

Data analysis

Importance value (IV)=[relative frequency + relative coverage (relative abundance)]/2

Sørensen (1948) similarity coefficient Cs=2C/(A+B)×100%

In the formula, A is the total number of species of vegetation type A, B is the total number of species of vegetation type B, and C is the total number of species of vegetation types A and B.

Sørensen difference coefficient βsor=(b□c)/(2a□b□c) where a is the number of common species between two communities, b and c are the numbers of unique species in the two communities, the β value is between 0 and 1. A β value between 0 and 0.25 indicates that the two communities are very similar; between 0.25 and 0.50 indicates that the two communities are moderately similar; between 0.50 and 0.75 indicates that the two communities are moderately dissimilar; and between 0.75 and 1.00 indicates that the two communities are extremely dissimilar.

Microsoft Excel 2010, Arc GIS10.2 and R language and ggplot2 were used for statistical data analysis and figure drawing.

Declarations

Acknowledgments:

We thank Jia Chen from the Puding Karst Ecosystem Observation and Research Station of the Chinese Academy of Sciences and Luyan Tang, Xingxing Liu, and Tingting Li from the Guizhou Normal University School of Life Sciences.

Conflicts of interest/Competing interests

Not applicable

Availability of data and material (data transparency)

Not applicable

Code availability (software application or custom code)

Not applicable

Ethics approval (include appropriate approvals or waivers)

Not applicable

Consent for publication (include appropriate statements)

If the article is accepted, I agree to publish it in this journal.

Funding

This work was supported by National Natural Science Foundation of China (41671275), National Nature Science Foundation of China and the Karst Science Research Center of Guizhou Province (U1812401), Science and Technology Fund of Guizhou ([2020]1Y074), Youth Key Fund of Sciences Academy of Guizhou([2020]03), Forestry Research of Guizhou Province ([2019]06).

References

1. Costa DP, Amado-Filho GM, Pereira RC, Paradas WC, Miyataka H, Okamoto Y, Asakawa Y (2018) Diversity of secondary metabolites in the liverwort Syzygiella rubricaulis (Nees) Stephani (Jamesoniellaceae, Marchantiophyta) from neotropical high mountains. Chem Biodivers 15:e1800239. DOI:10.1002/cbdv.201800239
2. Gao Q (1994) Flora Bryophytarum Sinicorum, vol 1. Science Press, Beijing
3. Gao Q (1996) Flora Bryophytarum Sinicorum, vol 2. Science Press, Beijing
4. Gao Q, Wu YH (2010) Genera Hepaticopsida et Anthocerotopsida Sinicorum. Science Press, Beijing
5. Harper KT, Belnap J (2001) The influence of biological soil crusts on mineral uptake by associated vascular plants. J Arid Environ 47:347–357
6. Jackson TA (2015) Weathering, secondary mineral genesis, and soil formation caused by lichens and mosses growing on granitic gneiss in a boreal forest environment. Geoderma 251:78–91
7. Jia SH, Li JF, Wang ZH, Zhang ZH (2014) Ecological function of bryophyte on karst rocky desertification slopes along mountainous roads. Chin J Ecol 33:1928–1934
8. Krol E, Dziubinska H, Trebacz K (2003) Low-temperature induced transmembrane potential changes in the liverwort Conocephalum conicum. Plant Cell Physiology 44:527–533

9. Li JF, Wang ZH, Zhang ZH (2013) Bryophyte diversity and the effect of soil formation along with water conservation in karst rocky desertification region. Res Environ Sci 26:759–764
10. Li W, Yu LT, Wu Y, Jia LP, Yuan DX (2006) Enhancement of Ca2 + release from limestone by microbical extracelluar carbonic anhydrase. Biores Technol 98:950–953
11. Li T, Wang HY, Zhou ZJ, Chen XQ, Zhou JM (2015) A nano-scale study of the mechanisms of non-exchangeable potassium release from micas. Appl Clay Sci 118:131–137
12. Liu TL, Cong CL, Hu D, Wang SJ, Zhang XQ (2017) Carbonic anhydrase activity of six epilithic mosses and their underlying soil in the Puding karst area, Guizhou Province. Carsologica Sinica 36:187–192
13. Lin QW(1989). Maolan Karst Forest Science Survey—Preliminary Investigation Report on Bryophytes in Maolan Karst Forest Region[M]. Guizhou People's Publishing House,Guiyang
14. Lammers K, Smith MM, Carroll SA (2017) Muscovite dissolution kinetics as a function of pH at elevated temperature. Chem Geol 466:149–158
15. Lou HX (2012) Bryophyte Chemistry and Biology. Science Press, Beijing
16. Lou YX (2013) Study on Response Mechanism and Biological Indicators of Bryophytes to Heavy Metal Pollution. PhD dissertation, Shanghai Normal University, Shanghai
17. Ordoñez JC, Bodegom PM van, Witte JPM et al (2010) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility[J]. Glob Ecol Biogeogr 18(2):137–149
18. Peng X, Huang Y, Che JX,et al (2009) Study on the Changing Law of Soil Properties under Different Rocky Desertification Grades—Taking Guiding Karst Central Puding Station as an Example[J]. Carsologica Sinica 28(4):402–405
19. Proctor MCF, Pence VC (2002) Vegetative tissues: Bryophytes vascular “resurrection plants” and vegetative propagules. In: Pritchard H, Back M (eds) Desiccation and Plant Survival. CABI Publishing, Wallingford, pp 207–237
20. Sørensen T (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. Biologiske Skrifter 5:1–34
21. Simpson EH (1949) Measurement of diversity. Nature 163:688
22. Street LE, Subke J-A, Sommerkorn M, Sloan V, Ducrotoy H, Phoenix GK, Williams M (2013) The role of mosses in carbon uptake and partitioning in arctic vegetation. New Phytol 199:163–175
23. Smith AJ (1982) Magdefrau K. Life-forms of bryophytes[M]. Bryophyte ecology. Chapman & Hall, New York, pp 45–59
24. Wu P, Cui YC, Zhao WJ, Ding FJ, Yang WB(2020).The stoichiometric characteristics of 68 typical plant leaves in Maolan Karst area[J]. Journal of Ecology,,2020(14):1–18[2020 – 0502].http://kns.cnki.net/kcms/detail/11.2031.q
25. 0935.003.html
26. Wu PC (2002) Flora Bryophytarum Sinicorum, vol 6. Science Press, Beijing
27. Wu PC, Jia Y (2004) Flora Bryophytarum Sinicorum,vol.8. Science Press, Beijing
28. Wu PC, Jia Y (2011) Flora Bryophytarum Sinicorum, vol 5. Science Press, Beijing
29. Xue JH (2013) Forest Ecology. China Forestry Publishing House, Beijing
30. Xiong YX, Cao W (2017) Review of researches on planttaxonomy in Guizhou. Journal of Mountain Agriculture Biology 36(1):001ï½011
31. Zhang ZH (1993) A catalogue on music of Maolan karst forest area Libo county Guizhou. Journal of Guizhou normal university(natural science) 11(1):33–42
32. Yin SF, Wang ZH, Zhang ZH (2016) Interspecific association among dominant species of bryophytes in karst severe rocky desertification area[J]. Ecological Science 35(5):90–95
33. Zhu XM (1995) The process of the original soil formation. Research of Water Soil Conservation 4:83–89
34. Zhou SQ(1997). Karst Forest Ecology Research[M]. Guizhou Science and Technology Press,Guiyang
35. Zhang XQ, ZhaoYZ, Wang SJ (2017) Responses of antioxidant defense system of epilithic mosses to drought stress in karst rock desertified areas. Acta Geochimica 36:205–212
36. Zhang XQ, Long HY, Liu TL, Cong CL (2018b) Comparison of water absorption characteristic and water retention capacity of five epilithic mosses in the karst areas of Guizhou Province. Carsologica Sinica 37:835–841

Appendix

The list of epilithic mosses in Karst area						
Family	**Genera**	**Species**	**Number of Genera**	**Percentage of total genera (%)**	**Number of Species**	**Percentage of total species (%)**
Pottiaceae	*Trichostomum*	*Trichostomum involutum*	16	17.20	35	16.91
		Trichostomum crispulum				
		Trichostomum brachydontium				
	Pseudosymblepharis	*Pseudosymblepharis angustata*				
		Pseudosymblepharis subduriuscula				
		Pseudosymblepharis papillosula				
	Hydrogonium	*Hydrogonium sordidum*				
		Hydrogonium williamsii				
		Hydrogonium javanicum				
		Hydrogonium amplexifolium				
	Hyophila	*Hyophila spathulata*				
		Hyophila rosea				
		Hyophila javanica				
		Hyophila involuta				
		Hyophila setschwanica				
	Tortella	*Tortella humilis*				
		Tortella tortuosa				
	Timmiella	*Timmiella diminuta*				
	Barbula	*Barbula unguiculata*				
	Weissia	*Weissia edentula*				
		Weissia microstoma				
	Tortula	*Tortula muralis var. aestiva*				
	Anoectangium	*Anoectangium aestivum*				
		Anoectangium stracheyanum				
		Molendoa sendtneriana var.yunnanica				
		Anoectangium clarum				
	Vesicularia	*Vesicularia montagnei*				
	Scopelophila	*Scopelophila cataractae*				
	Pleurochaete	*Pleurochaete squarrosa*				
	Gymnostomum	*Gymnostomum aurantiacum*				
		Gymnostomum subrigidulum				
		Gymnostomum calcareum				

	Didymodon	*Didymodon constrictus.var.constrictus*				
		Didymodon ditrichoides				
	Syntrichia	*Syntrichia longimucronata*				
Racopilaceae	*Racopilum*	*Racopilum cuspidigerum*	1	1.08	3	1.45
		Racopilum orthocarpum				
		Racopilum aristatum				
Leskeaceae	*Leskeella*	*Leskeella nervosa*	5	5.38	5	2.42
	Pseudoleskeopsis	*Pseudoleskeopsis zippelii*				
	Duthiella	*Duthiella flaccida*				
	Schwetschkea	*Schwetschkea gymnostoma*				
	Lindbergia	*Lindbergia brachyptera*				
Neckeraceae	*Neckeropsis*	*Neckeropsis lepineana*	5	5.38	7	3.38
	Homaliodendron	*Homaliodendron flabellatum*				
		Homaliodendron exiguum				
	Homaliadelphus	*Homaliadelphus targionianus*				
	Thamnobryum	*Thamnobryum alopecurum*				
		Thamnobryum sandei				
	Pinnatella	*Pinnatella makinoi*				
Meteoriaceae	*Meteoriopsis*	*Meteoriopsis reclinata*	6	6.45	10	4.83
	Meteorium	*Meteorium miquelianum*				
		Meteorium subpolytrichum				
		Meteorium cucullatum				
		Meteorium papillarioides				
	Chrysocladium	*Chrysocladium retrorsum*				
	Trachypus	*Trachypus bicolor*				
		Trachypus humilis				
	Aerobryopsis *Aerobryopsis*	*Aerobryopsis subdivergens*				
	Toloxis	*Toloxis semitorta*				
Entodontaceae	*Entodon*	*Entodon luridus*	2	2.15	10	4.83
		Entodon flavescens				
		Entodon longifolius				
		Entodon compressus				

		Entodon yunnanensis				
		Entodon viridulus				
		Entodon pylaisioides				
		Entodon mderopod				
		Entodon cladorrhizans				
	Erythrodontium	Erythrodontium julaceum				
Thuidiaceae	Bryonoguchia	Bryonoguchia molkenboeri	7	7.53	16	7.73
	Thuidium	Thuidium subglaucinum				
		Thuidium kanedae				
		Thuidium cymbifolium				
		Thuidium pristocalyx				
		Thuidium plumulosum				
	Haplocladium	Haplocladium strictulum				
		Haplocladium microphyllum				
		Haplocladium angustifolium Broth.				
	Claopodium	Plagiothecium cavifolium				
		Claopodium prionophyllum				
		Claopodium pellucinervis				
	Cyrto-hypnum	Cyrto-hypnum pygmaeum				
		Cyrto-hypnum contortulum				
	Herpetineuron	Herpetineuron toccoae				
	Leptopterigynandrum	Leptopterigynandrum austro-alpinum				
Hypnaceae	Taxiphyllum	Taxiphyllum aomoriense	7	7.53	12	5.80
		Taxiphyllum taxirameum				
	Pseudotaxiphyllum	Pseudotaxiphyllum arquifolium				
	Isopterygium	Isopterygium tenerum				
		Isopterygium courtoisii				
		Isopterygiopsis pulchella				
	Hypnum	Hypnum subimponens subsp. ulophyllum				
		Hypnum densirameum				
		Hypnum leptothallum				
	Herzogiella	Herzogiella striatella				
	Vesicularia	Vesicularia hainanensis				
	Ectropothecium	Ectropothecium penzigianum				
Brachytheciaceae	Eurhynchium	Eurhynchium laxirete	4	4.30	21	10.14
		Eurhynchium longirameum				

		Eurhynchium savatieri				
		Eurhynchium filiforme				
	Brachythecium	*Brachythecium piligerum*				
		Brachythecium helminthocladum				
		Brachythecium viridefactum				
		Brachythecium glaciale				
		Brachythecium starkei				
		Brachythecium coreanum				
		Brachythecium dicranoides				
		Brachythecium plumosum				
		Brachythecium pulchellum				
		Brachythecium kuroishicum Besch.				
		Brachythecium brotheri				
		Brachythecium moriense				
		Brachythecium buchananii				
		Brachythecium fasciculirameum				
	Homalothecium	*Homalothecium laevisetum*				
		Homalothecium leucodonticaule				
	Okamuraea	*Okamuraea brachydictyon*				
Regmatodontaceae	*Regmatodon*	*Regmatodon longinervis*	1	1.08	2	0.97
		Regmatodon serrulatus				
Mniaceae	*Plagiomnium*	*Plagiomnium succulentum*	4	4.30	13	6.28
		Plagiomnium rostratum				
		Plagiomnium plagiomnium				
		Plagiomnium vesicatum				
		Plagiomnium acutum				
		Plagiomnium rhynchophorum				
		Plagiomnium maximoviczii var.emarqinatum				
		Plagiomnium maximoviczii				
	Mnium	*Mnium spinulosum*				
		Mnium laevinerve				
		Mnium thomsonii				
	Rhizomnium	*Rhizomnium punctatum*				
	Trachycystis	*Trachycystis flagellaris*				

Plagiotheciaceae	*Plagiothecium*	*Plagiothecium euryphyllum var. brevirameum*	2	2.15	5	2.42
		Plagiothecium cavifolium				
		Plagiothecium piliferum				
		Plagiothecium neckeroideum				
	Struckia	*Struckia argentata*				
Bryaceae	*Pohlia*	*Pohlia gedeana*	3	3.23	15	7.25
		Pohlia macrocarpa				
	Bryum	*Bryum argenteum*				
		Bryum argenteum				
		Bryum funkii .				
		Bryum algovicum				
		Bryum capillare				
		Bryum truncorum				
		Bryum caespiticium				
		Bryum yuennanense				
	Brachymenium	*Brachymenium pendulum*				
		Brachymenium exile				
		Brachymenium leptophyllum				
		Brachymenium nepolens				
		Brachymenium capitulatum				
Fissidentaceae	*Fissidens*	*Fissidens crenulatus*	1	1.08	5	2.42
		Fissidens ganguleei				
		Fissidens dubius				
		Fissidens grandifrons				
		Fissidens adelphinus				
Anomodontaceae	*Haplohymenium*	*Haplohymenium flagelliforme*	2	2.15	7	3.38
		Haplohymenium triste				
		Haplohymenium pseudo-triste				
	Anomodon	*Anomodon viticulosus*				
		Anomodon minor				
		Anomodon perlingulatus				
		Anomodon rugelii				
Bartramiaceae	*Philonotis*	*Philonotis lancifolia*	1	1.08	2	0.97
		Philonotis capiformis				
Hookeriaceae	*Hypopterygium*	*Hypopterygium flavo-limbatum*	1	1.08	2	0.97
		Hypopterygium japonicum				

Orthotrichaceae	*Orthotrichum*	*Orthotrichum anomalum*	1	1.08	1	0.48
Amblystegiaceae	*Amblystegium*	*Amblystegium serpens*	1	1.08	1	0.48
Scorpidiaceae	*Hygrohypnum*	*Hygrohypnum luridum*	1	1.08	1	0.48
Cryphaeaceae	*Pilotrichopsis*	*Pilotrichopsis dentata*	1	1.08	1	0.48
Ptychomitriaceae	*Ptychomitrium*	*Ptychomitrium linearifolium*	1	1.08	3	1.45
		Ptychomitrium wilsonii				
		Ptychomitrium formosicum				
Dicranaceae	*Dicranum*	*Dicranum scoparium*	1	1.08	1	0.48
Grimmiaceae	*Racomitrium*	*Racomitrium fasciculare var. atroviride*	1	1.08	2	0.97
		Racomitrium canescens				
Calliergonaceae	*Calliergon*	*Calliergon cordifolium*	1	1.08	1	0.48
	Calliergonella	*Calliergonella cuspidata*	1	1.08	1	0.48
Fabroniaceae	*Fabronia*	*Fabronia matsumurae*	2	2.15	2	0.97
	Juratzkaea	*Juratzkaea sinensis*				
Habrodontaceae	*Habrodon*	*Habrodon perpusillus*	1	1.08	1	0.48
Frullaniaceae	*Frullania*	*Frullania apiculata*	1	1.08	2	0.97
		Frullania gaudichaudii				
Porellaceae	*Porella*	*Porella japonica var. japonica*	1	1.08	4	1.93
		Porella caespitans				
		Porella densifolia subsp. densifolia				
		Porella densifolia var.paraphyllina				
Plagiochilaceae	*Plagiochila*	*Plagiochila shangaica*	2	2.15	6	2.90
		Plagiochila trabeculata				
		Plagiochila durelii subsp. durelii				
		Plagiochila elegans				
		Plagiochila duthiana				
	Pedinophyllum	*Pedinophyllum interruptum*				
Marchantiaceae	*Marchantia*	*Marchantia emarginata subsp. emarginata*	1	1.08	1	0.48
Pelliaceae	*Pellia*	*Pellia endiviifolia*	1	1.08	1	0.48
Aytoniaceae	*Plagiochasma*	*Plagiochasma rupestre*	3	3.23	3	1.45
	Plagiochasma					
	Asterella	*Asterella mussuriensis*				
	Reboulia	*Reboulia hemisphaerica*				
Metzgeriaceae	*Metzgeria*	*Metzgeria conjugata*	1	1.08	1	0.48

Pallaviciniaceae	*Pallavicinia*	*Pallavicinia lyellii* *Pallavicinia ambigua*	1	1.08	2	0.97
Makinoaceae	*Makinoa*	*Makinoa crispata*	1	1.08	1	0.48
Wiesnerellaceae ▯ Dumortieraceae	*Dumortiera*	*Dumortiera hirsuta*	1	1.08	1	0.48
total						
37			93		207	

Figures

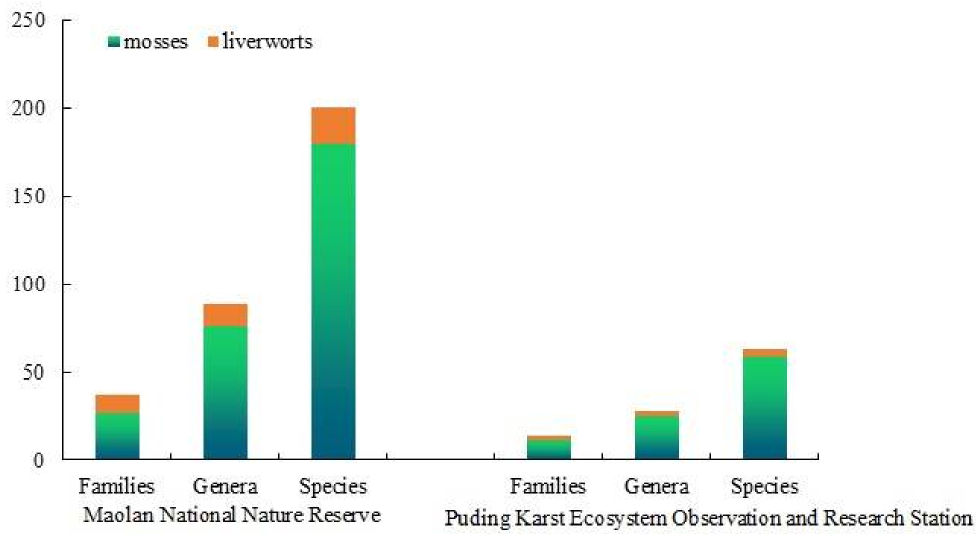

Figure 1

Comparison of the richness of bryophytes between different habitat types

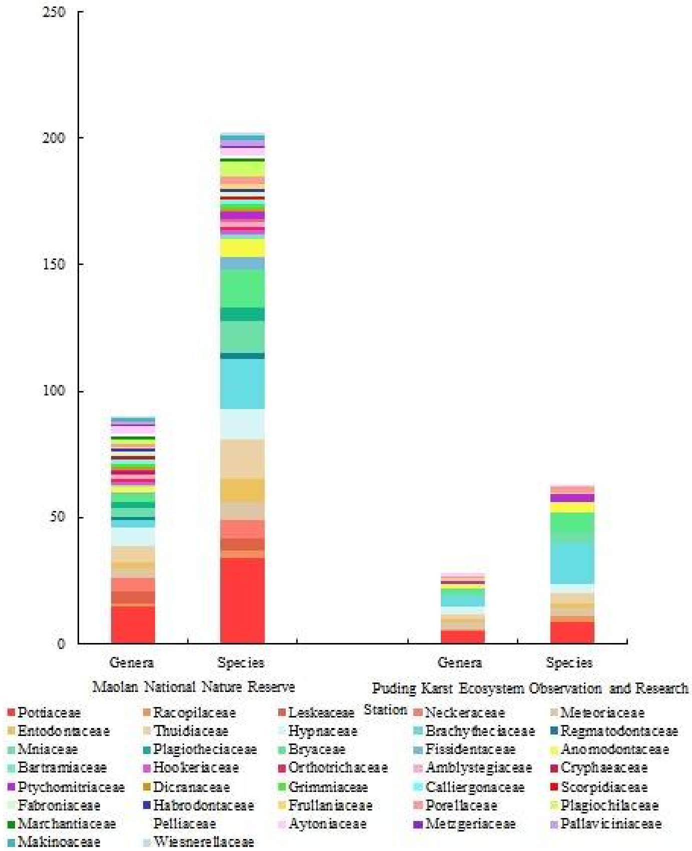

Figure 2

Differences in genera and species richness of karst epilithic mosses in different regions

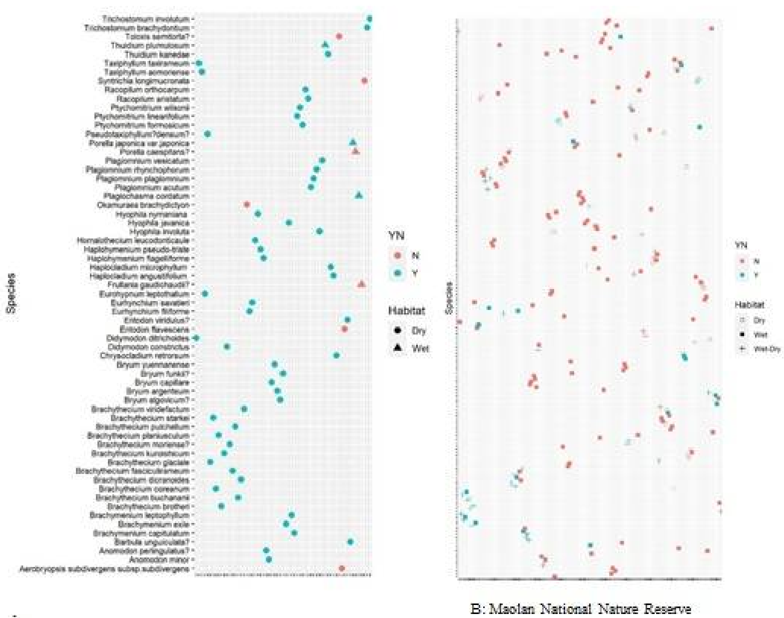

Figure 3

Distribution characteristics of karst bryophytes and their relationship with the environment

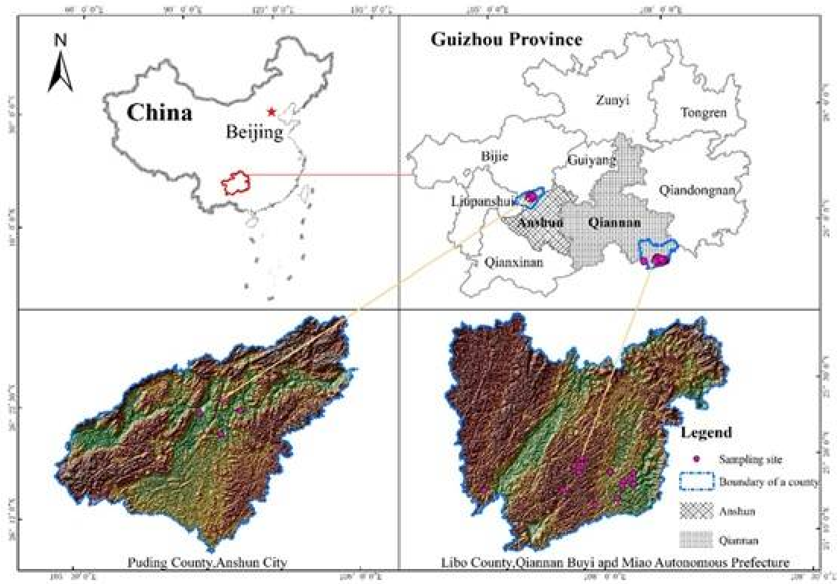

Figure 4

Geographical location of the study area and distribution of sampling points