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Original Paper

Variation in Species Diversity of Epilithic Bryophytes Along the Karst Rocky Desertification Gradient

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Abstract

Karst rocky desertification is a distinctive landscape formed by the exposure of rock surfaces, where epilithic bryophytes dominate the plant communities. Despite their prevalence, these mosses have received relatively little attention, and the species diversity of lithophilous mosses remains inadequately understood. In this study, we conducted field collections and laboratory identifications of epilithic bryophytes across various karst habitats exhibiting different levels of rocky desertification, aiming to elucidate the patterns of species diversity within these environments. Our findings reveal a total of 47 moss species, belonging to 11 families and 28 genera, with species distribution patterns as follows: PRD (22 species) > MRD (18 species) > SRD (14 species) > NRD (12 species) > LRD (11 species). Notably, the PRD and MRD habitats harbor the highest number of endemic species, each with 8 endemic species, while the other three habitats each contain 5 endemic species. Among these, Eurohypnum leptothallum is a common species across all habitats and represents a dominant species in the karst region. Four distinct moss growth forms were identified in the study area, with proportions as follows: Wefts (75%) > Turfs (15%) > Pentants (8%) > Cushion (2%). The Wefts growth form is ubiquitous across all habitats and is the most prevalent, whereas the proportion of Pendants increases *along the rocky desertification gradient, showing a higher degree of adaptation to more severely desertified environments. The α-diversity indices (richness index (R), Simpson index (D), Pielou index (E), and Shannon-Wiener index (H)) exhibit an "M"-shaped distribution along the desertification gradient, indicating the selective effects of desertification processes and the dynamic changes in species over time. The β-diversity index further suggests low species similarity between different habitats, with the similarity index (Cs) between NRD and SRD habitats being as low as 0.08, signifying substantial shifts in species composition. These results provide valuable insights into the changes in species diversity of lithophilous mosses along the rocky desertification gradient and enhance our understanding of the moss species diversity in karst rocky desertification areas.*

Keywords

karst rocky desertification, epilithic bryophytes, diversity index, life forms

1. Introduction

Karst rocky desertification areas represent a typical example of arid and semi-arid regions globally, widely distributed in the southwestern part of China, particularly in Guizhou, Yunnan, and Guangxi provinces. These regions, severely affected by prolonged soil erosion and land degradation, are characterized by a dominance of exposed limestone or other types of rocky surfaces, resulting in a fragile ecological environment (Xu & Zhang, 2022; van der Meer, 2017; Gutiérrez, Parise, De Waele, et al., 2014). However, despite the harsh ecological conditions, these areas have managed to preserve a certain degree of biodiversity, especially in terms of moss species. Mosses, as crucial components of many ecosystems, occupy important ecological niches, successfully colonizing various degraded environments (Bjerke, Bokhorst, Callaghan et al., 2017). They play significant ecological roles, including soil and water conservation (Hu, Gao, Li et al., 2013), nutrient accumulation (Bao, Zhao, Gao et al., 2019), facilitation of ecosystem succession (Li, Jin, Huang et al., 2024), enhancement of species diversity (Fontúrbel, Osorio, Riffo-Donoso et al., 2021), and promotion of carbon and nitrogen cycling (Slate, Sullivan, & Callaway, 2019; Alvarenga & Rousk, 2022).

Mosses, one of the oldest plant groups on Earth, are capable of thriving in a wide range of harsh environments, positioning them as pioneer species in ecological succession (Cheng, Gao, Zhang et al., 2021; Cheng, Li, Long et al., 2020). In the arid and nutrient-poor stony desertification regions, mosses serve as essential elements for maintaining ecological balance. Their ability to efficiently absorb and retain moisture, prevent soil erosion, and foster the growth of other plant species enables them to contribute to ecosystem stability. Research on moss species diversity has attracted significant attention since the 20th century (Gao, Si, Wang et al., 2024; Han, Su, Li et al., 2024; Ma, Si, Gao, 2024; Chen, Tu, Dai et al., 2023), with most studies focusing on species composition, geographic distribution, and community characteristics (Wang, Liu, JIAYINA et al., 2023; Wang, Deng, Liu et al., 2023). However, studies in Karst stony desertification areas remain relatively scarce. This paper aims to investigate the species distribution of mosses in Karst stony desertification areas, providing a theoretical foundation for understanding the geographic distribution patterns of mosses in these regions and offering insights for their conservation and utilization.

Specifically, this study involves the collection of moss samples from areas with varying degrees of stony desertification within the Karst region. It analyzes the changes in dominant moss species along the desertification gradient, the species distribution patterns, the characteristics of species diversity, and the distribution patterns of different life forms across various desertification levels. The research further explores the adaptive distribution patterns of different moss families and genera in relation to environmental conditions. Through these investigations, the study aims to provide scientific evidence for ecological restoration, plant community development, and the enhancement of ecosystem service functions in Karst stony desertification areas. Additionally, it seeks to offer a theoretical basis for the ecological restoration and conservation of desertification-prone regions.

2. Materials and Methods

2.1 Study Area

The study area is located in the southwestern Karst region of China, specifically in the southwestern to central parts of Pingtang County, Qiannan Buyei and Miao Autonomous Prefecture, Guizhou Province (106°40′29″~107°26′19″ E, 25°29′55″~26°06′41″ N). This region falls within the Central Asian subtropical monsoon humid climate zone, with an average annual temperature of 16.2°C, annual precipitation averaging 1300 mm, and a relatively short frost-free period of approximately 50 days. The area experiences a cumulative temperature of 6203 ℃ annually, characterized by abundant heat and precipitation. The Karst plateau in the study area is typified by well-developed peak-clustered depressions, with an elevation range of 834 to 1229 meters. The degree of rocky desertification is predominantly mild to moderate, with significant stone exposure.

2.1 Sample Collection and Species Identification

In environments with varying degrees of stony desertification, namely, none rocky desertification (NRD), potential rocky desertification (PRD), light stony desertification (LRD), moderate stony desertification (MRD), and severe stony desertification (SRD), six 20 m × 20 m plots were established in each type of habitat. Within each plot, three rocks were selected, and at both the top and bottom of each rock, one 5 × 5 cm^2 moss sample was collected. In total, 180 samples were gathered, bagged, and transported back to the laboratory for species identification. Upon return to the laboratory, the moss samples were sorted and placed in a ventilated, dry area to air-dry. A small portion of each moss plant was then immersed in clean water for 3 to 5 minutes until the plant tissue had fully expanded, after which temporary slides were prepared for species identification. The morphological characteristics of the plants, including the plant, leaf, cell, and leaf margin features, were examined using an Olympus SZX-16 dissecting microscope (Olympus Corporation, Japan) and an Olympus BX53 optical microscope (Olympus Corporation, Japan). Identification was carried out to the species level by referencing authoritative sources such as *The Species Catalogue of China,* Volume 1: Plants, Volumes

1-8 of *Flora Bryophytorum Sinicorum*, Volumes 1-3 of *Bryophyte Flora of Guizhou* China, and *Moss Flora of China*, among others (Jin & Wang, 2023). Furthermore, the moss species were classified according to life forms based on the method proposed by Mägdefrau (1982).

2.2 Importance Value and Diversity Index

The relative cover and relative frequency were used to calculate the importance value (V) of moss species (Liu, Cao, Wang et al., 2008).

$$V = (C + F)/2 \tag{1}$$

where V is the importance value, relative cover C = (the cover of a bryophyte within sample site or sum of cover of all bryophytes in the sample site) × 100%, relative frequency F = (frequency within a bryophyte sample site or sum of frequency of all bryophytes in the sample site) × 100%.

The α diversity indices include richness (R), Simpson diversity index (D), Shannon-Wiener diversity index (H), and Pielou evenness index (E).

$$R = (S - 1)/lnN \tag{2}$$

$$D = \sum_{i=1}^{S} (Pi)^{2} \tag{3}$$

$$H = \sum_{i=1}^{S} (PilnPi) \tag{4}$$

$$E = \sum_{i=1}^{S} (PilnPi)/lnS \tag{5}$$

where S is the number of all bryophyte species within each gradient sample plot, N is the total number of individuals within each gradient sample plot, and using the cover proxy, Pi is the ratio of the cover of species i to the total cover of the sample.

β-diversity refers to the species diversity among habitats, which can more intuitively describe the differences in community species composition, and is an important index to study the mechanism of community construction (Chinese Academy of Sciences Biodiversity Committee, 1994). In this paper, the similarity index Sorenson (C_S) index and the dissimilarity index Cody (β_C) index were selected to compare the similarity and dissimilarity among bryophyte communities in different rocky desertification habitats.

$$C_S = 2C/(S1 + S2) \tag{6}$$

$$\beta_C = [g(H) + l(H)]/2 \tag{7}$$

where C is the number of species common to both habitats, S1 is the number of species in the first habitat, and S2 is the number of species in the second habitat; g(H) is the number of species common to both habitats, and l(H) is the number of species lacking in the second habitat.

3. Results

3.1 Species Composition and Distribution

A total of 47 bryophyte species from 28 genera and 11 families were recorded in the study area. Among these, the NRD habitat hosted 12 species from 6 families and 10 genera; the PRD habitat was home to 22 species from 9 families and 15 genera; the LRD habitat contained 11 species from 7 families and 10 genera; the MRD habitat supported 18 species from 8 families and 13 genera; and the SRD habitat harbored 14 species from 7 families and 10 genera. In terms of family richness, the sequence was PRD > MRD > LRD = SRD > NRD; for genus richness, it followed the order PRD > MRD > NRD = LRD = SRD; and for species richness, the ranking was PRD > MRD > SRD > NRD > LRD. The PRD habitat exhibited the highest bryophyte diversity, while the LRD habitat contained the fewest species. The dominant species were determined based on their importance value rankings, with the top three being designated as the dominant taxa. As shown in Table 1, the dominant species in the NRD habitat were *Eurohypnum leptothallum*, *Thuidium cymbifolium*, and *Thuidium assimile*; in the PRD habitat, they were *Eurohypnum leptothallum*, *Homalothecium leucodonticaule*, and *Anomodon rugelii*; in the LRD habitat, they were *Eurohypnum leptothallum*, *Meteorium polytrichum*, and *Erythrodontium julaceum*; in the MRD habitat, they were *Meteorium polytrichum*, *Eurohypnum leptothallum*, *Thuidium cymbifolium*, and *Erythrodontium julaceum*; and in the SRD habitat, they were *Eurohypnum leptothallum*, *Trichostomum platyphyllum*, and *Racopilum cuspidigerum*. Notably, *Eurohypnum leptothallum* was consistently identified as a dominant species across all habitats.

Table 1. Epilithic Bryophyte List and Important Values

family	genus	species	important values				
			NRD	PRD	LRD	MRD	SRD
Mniaceae	Plagiomnium	Plagiomnium cuspidatum	0.006	0.006			
		Plagiomnium japonicum			0.006		
Thuidiaceae	Thuidium	Thuidium cymbifolium	0.039	0.006		0.017	
		Thuidium assimile	0.022	0.006	0.011	0.006	
		Thuidium plumulosum				0.011	
		Thuidium kanedae				0.006	
		Thuidium glaucinoides	0.011				
	Bryonoguchia	Bryonoguchia brevifolia	0.011				
	Abietinella	Abietinella abietina				0.006	
Plagiotheciaceae	Plagiothecium	Plagiothecium laetum					0.006
Pottiaceae	Trichostomum	Trichostomum platyphyllum					0.017
		Trichostomum		0.006			0.006

		involutum					
Hedwigiaceae	Hedwigia	Hedwigia ciliata				0.006	
Hypnaceae	Eurohypnum	Eurohypnum leptothallum	0.072	0.044	0.083	0.022	0.072
	Hypnum	Hypnum hamulosum				0.006	0.006
		Hypnum callichroum	0.006				
		Hypnum plumaeforme				0.006	
	Ectropothecium	Ectropothecium zollingeri					0.011
	Taxiphyllum	Taxiphyllum giraldii				0.006	
	Gollania	Gollania ruginosa		0.006			
	Ptilium	Ptilium crista-castrensis		0.006			
	Giraldiella	Giraldiella levieri	0.006				
	Isopterygium	Isopterygium tenerum		0.006			
	Homomallium	Homomallium connexum			0.006		
Racopilaceae	Racopilum	Racopilum spectabile	0.006	0.006			
		Racopilum cuspidigerum		0.011		0.006	0.017
Entodontaceae	Erythrodontium	Erythrodontium julaceum	0.011	0.011	0.028	0.017	
	Entodon	Entodon prorepens		0.006			
		Entodon flavescens	0.006				
		Entodon plicatus		0.006			
		Entodon viridulus		0.006			
Meteoriaceae	Meteorium	Meteorium polytrichum		0.006	0.033	0.033	0.011
		Meteorium subpolytrichum					0.011
		Meteorium cucullatum				0.006	
	Aerobryidium	Aerobryidium crispifolium				0.006	
Anomodontaceae	Anomodon	Anomodon rugelii		0.017			0.017
		Anomodon viticulosus		0.006		0.022	0.006

		Anomodon minor		0.006	0.011		
		Anomodon perlingulatus			0.006		
Brachytheciaceae	Homalothecium	Homalothecium leucodonticaule		0.022	0.006	0.011	
	Brachythecium	Brachythecium viridefactum				0.011	0.011
		Brachythecium coreanum					0.006
		Brachythecium amnicolum		0.006			
	Eurhynchium	Eurhynchium coarctum	0.006	0.006			0.006
	Palamocladium	Palamocladium nilgheriense		0.006			
		Palamocladium euchloron			0.006		
	Camptothecium	Camptothecium lutescen			0.006		

Figure 1 illustrates the symbiotic species across various habitats: *Plagiomnium cuspidatum* and *Racopilum spectabile* are shared species in the NRD and PRD habitats, *Anomodon viticulosus* is a symbiont in both the PRD and LRD habitats, while *Trichostomum involutum* and *Anomodon rugelii* are symbiotic species in the SRD habitat. *Hypnum hamulosum* and *Brachythecium viridefactum* are symbionts found in both the MRD and SRD habitats. *Homalothecium leucodonticaule* occurs in PRD, LRD, and MRD, and *Eurhynchium coarctum* is a symbiotic species in NRD, PRD, and SRD. Additionally, *Thuidium cymbifolium* appears in NRD, PRD, and MRD habitats, while *Racopilum cuspidigerum* and *Anomodon viticulosus* are present in PRD, MRD, and SRD.T*huidium assimile* and *Erythrodontium julaceum* occur in the NRD, PRD, LRD, and SRD habitats, and *Meteorium polytrichum* is found in the PRD, LRD, MRD, and SRD habitats. *Eurohypnum leptothallum* is present across all five habitats.

Furthermore, certain species are endemic to specific habitats: *Giraldiella levieri*, *Thuidium glaucinoides*, *Bryonoguchia brevifolia*, *Entodon flavescens*, and *Hypnum callichroum* are exclusive to the NRD habitat. *Gollania ruginosa*, *Brachythecium amnicolum*, *Ptilium crista-castrensis*, *Palamocladium nilgheriense*, *Isopterygium tenerum*, *Entodon prorepens*, *Entodon plicatus*, and *Entodon viridulus* are endemic to the PRD habitat. *Plagiomnium japonicum*, *Homomallium connexum*, *Anomodon perlingulatus*, *Palamocladium euchloron*, and *Camptothecium lutescens* are exclusive to the

LRD habitat. *Thuidium plumulosum*, *Thuidium kanedae*, *Abietinella abietina*, *Hedwigia ciliata*, *Hypnum plumaeforme*, *Taxiphyllum giraldii*, *Meteorium cucullatum*, and *Aerobryidium crispifolium* are restricted to the MRD habitat. Finally, *Plagiothecium laetum*, *Trichostomum platyphyllum*, *Ectropothecium zollingeri*, *Meteorium subpolytrichum*, and *Brachythecium coreanum* are exclusive to the SRD habitat.Among these, the PRD and MRD habitats each host the highest number of endemic species, with eight species unique to each. The remaining three habitats each harbor five endemic species.

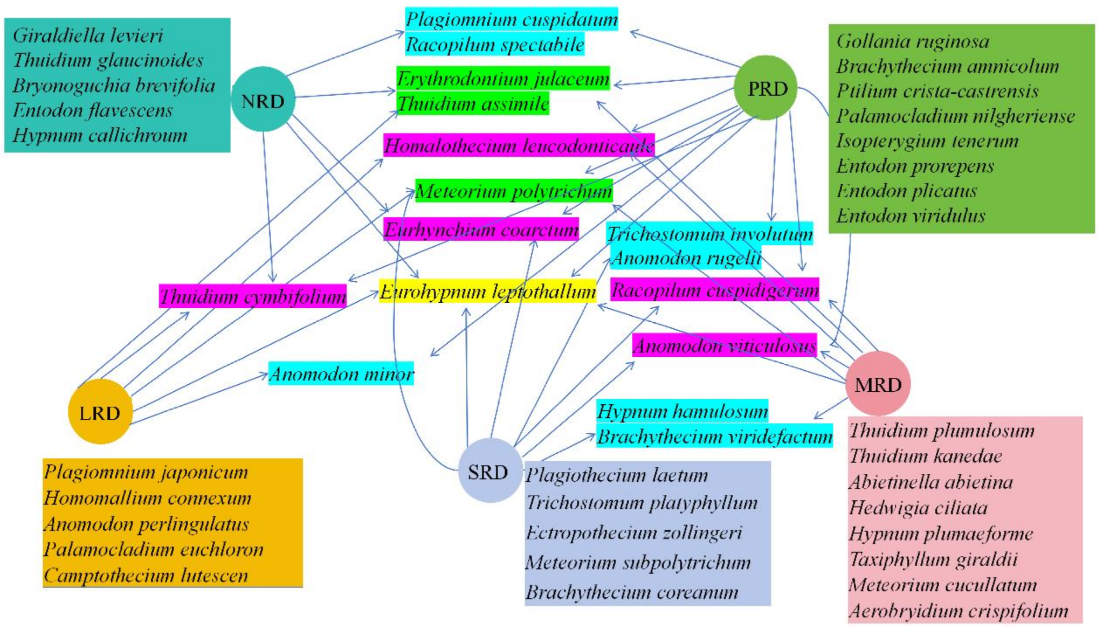

Figure 1. Species Distribution Network Diagram. Cyan Is a Sympatric Species in Two Habitats, Purple is a Sympatric Species in Three Habitats, Green Is a Sympatric Species in Four Habitats, and Yellow Is a Sympatric Species in Five Habitats

3.2 Epilithic Bryophyte Life Form

The proportion of life forms exhibits significant variation across different habitats. In the NRD habitat, only two life forms of mosses are present: Wefts, which dominate at 83%, followed by Turfs, which account for 17%. The PRD, LRD, and MRD habitats are home to three distinct life forms of mosses: Wefts, Turfs, and Pentants. As the degree of rocky desertification intensifies, the proportion of Pentants gradually increases. In the SRD habitat, an additional life form, Cushion, is observed, although it constitutes only 2% of the total. Overall, within the entire study area, the proportions of the four life forms are as follows: Wefts (75%) > Turfs (15%) > Pentants (8%) > Cushion (2%).

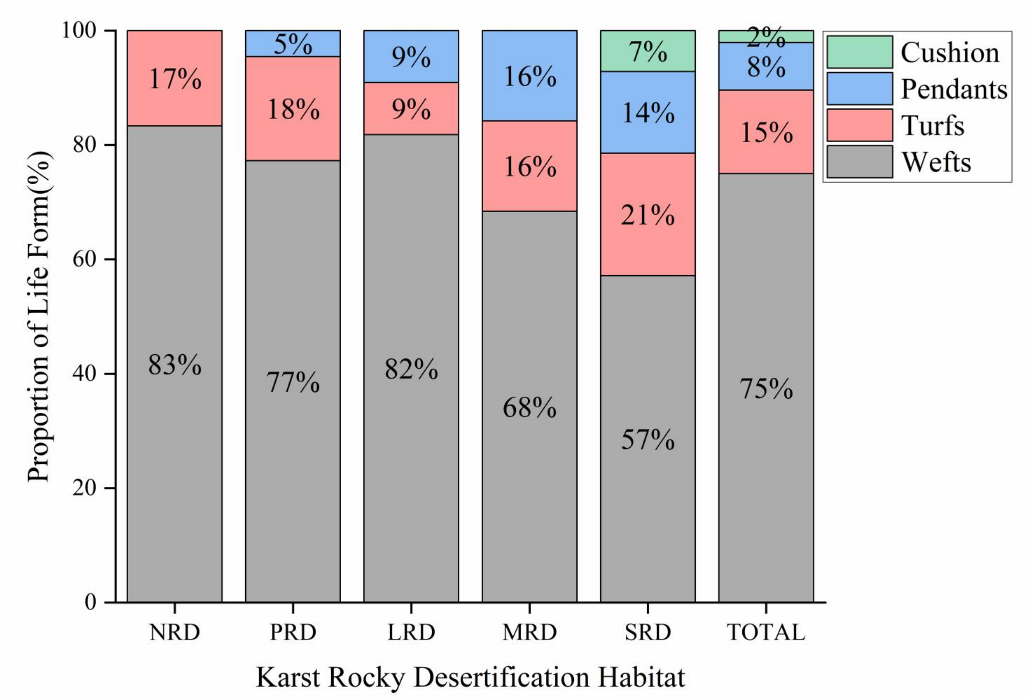

Figure 2. Life Forms of Epilithic Bryophytes in Different Rocky Desertification Degrees

3.3 Epilithic Bryophyte Species Diversity Content

3.3.1 α Diversity

The species richness index (R) exhibits an "M"-shaped distribution across various habitats, fluctuating first by increasing, then decreasing, followed by another increase and decrease, from the NRD habitat to the SRD habitat. The PRD habitat shows the highest species richness index (5.86), while the NRD habitat displays the lowest (3.07). The Simpson index (D) remains relatively high, with values exceeding 0.7, and shows little variation across the different rocky desertification habitats. The Shannon-Wiener index (H) is generally above 2, with the exception of the LRD habitat, where it is notably lower at 1.86. The Pielou index (E) closely mirrors the pattern observed in the Simpson index (D). Both the species richness index (R), the Simpson index (D), and the Shannon-Wiener index (H) display an "M"-shaped distribution along the rocky desertification gradient (Table 2).

Table 2. α diversity Indices of Epilithic Bryophytes in Different Rocky Desertification Habitats

diversity index	NRD	PRD	LRD	MRD	SRD
R	3.07	5.86	2.79	4.74	3.63
D	0.81	0.91	0.77	0.92	0.83
H	2.01	2.80	1.86	2.68	2.23
E	0.81	0.91	0.77	0.93	0.84

3.3.2 β Diversity

The Cs index is lowest in the NRD and SRD habitats, with a value of only 0.08, and it exceeds 0.26 in the other three habitats. The Cs index in the PRD, LRD, MRD, and SRD habitats is all above 0.3. The Cs index in the LRD and SRD habitats is relatively low (0.16), while it reaches 0.34 in the MRD habitat. Both the MRD and SRD habitats exhibit a Cs index of 0.38 (Table 3). The Cs index is generally higher between two adjacent habitats, with the lowest values observed between the NRD and SRD habitats, which span the greatest gradient. Similarly, the βc index is higher between adjacent habitats; however, in contrast to the Cs index, the βc index reaches its peak in the PRD and MRD habitats, separated by one gradient.

Table 3. β Diversity Indices of Epilithic Bryophytes in Different Rocky Desertification Habitats

diversity index		PRD	LRD	MRD	SRD
Cs	NRD	0.29	0.26	0.27	0.08
	PRD		0.36	0.30	0.33
	LRD			0.34	0.16
	MRD				0.38
βc	NRD	9.50	8.00	9.00	9.50
	PRD		8.50	11.00	8.00
	LRD			7.50	6.50
	MRD				7.50

4. Discussion

4.1 Species Distribution Characteristics

The species richness being highest in the PRD habitat and lowest in the LRD habitat. Specifically, the pattern of species richness is as follows: PRD > MRD > SRD > NRD > LRD. The PRD habitat represents the onset of stony desertification, where moss species richness significantly increases, suggesting that moss species in karst regions exhibit greater adaptability to rocky environments, thereby proliferating extensively across various moss species in this habitat. While the NRD habitat provides the most favorable conditions, with lower exposure to intense sunlight and radiation, moss survival may be hindered by the superior growth of vascular plants, which could result in a competitive disadvantage for mosses, leading to lower species richness.

Moreover, our results demonstrate a trend contrary to classical ecological theories (Intermediate-Disturbance Hypothesis). Connell (1978) proposed that moderate disturbances within ecosystems yield the highest plant biodiversity. Among the five levels of rocky desertification, LRD represents a medium disturbance state, yet moss species diversity is lowest under this intermediate disturbance, which underscores the distinct ecological dynamics between mosses and vascular plants.

The NRD habitat hosts a total of 6 families, 10 genera, and 12 species of epilithic bryophytes, with dominant species found only in the Bryaceae and Pottiaceae families. This suggests that Bryaceae and Pottiaceae may possess stronger competitive abilities compared to other families, enabling them to thrive more effectively in competition with vascular plants.As the habitat transitions into more advanced stages of rocky desertification, Pottiaceae continues to maintain its dominant ecological role, indicating that epilithic bryophytes in karst regions, particularly *Eurohypnum leptothallum* (Hypnaceae) (Cong, Liu, Kong et al., 2017; Tu, Yan, Dai et al., 2021), have fully adapted to rocky environments. Similarly, species such as *Thuidium assimile* (Thuidiaceae), *Meteorium polytrichum* (Meteoriaceae), and *Erythrodontium julaceum* (Entodontaceae) are capable of thriving in most stages of rocky desertification, and in some cases, they dominate certain stages of rocky desertification, demonstrating their robust adaptability to these habitats (Table 1). Figure 1 shows that the PRD and MRD habitats harbor the highest number of endemic species, each with 8 species. The PRD habitat, marking the transition from none rocky desertification to rocky desertified terrain, likely fosters endemic species with strong adaptations to rocky environments, distinguishing them from those in the NRD habitat. The higher number of endemic species in the MRD habitat may be attributed to the harsher conditions of this habitat, which exerts a selective pressure on moss species, filtering out other species that cannot survive or reproduce there (Wang, Wei, Chen et al., 2023). The remaining three habitats each support five endemic species, suggesting that the selective pressure on moss species may be relatively similar across these environments.

4.2 Adaptation of Life Forms of Epilithic Bryophytes to Rocky Desertification Habitats

Life forms represent the classification types of external morphology, structure, and traits that plants exhibit as a result of long-term environmental adaptation. Different life forms are associated with their biological characteristics and ecological adaptation abilities (Xia, Ye, Yang et al., 2024; Zhan, Feng, Mei et al., 2024). Wefts mosses intertwine and form loose, layered clusters that adhere to the substrate, making them easy to peel off. This life form of moss grows by intertwining and creeping across rock surfaces. Its water retention capacity is significantly enhanced compared to tufted types, which increases the moisture content of the rock surface, and consequently, it is more common in humid habitats (Sillett, Gradstein, & Griffin, 1995). The predominant families include Thuidiaceae, Hypnaceae, Brachytheciaceae, and Entodontaceae. These life forms occupy more than 50% of various rocky desertification habitats and are the primary life form of epilithic bryophytes in Karst rocky desertification environments. Turfs mosses have upright main stems that grow in clusters, either loosely or tightly arranged, with few branches and often with rhizoid at the base. This life form of moss grows densely together in clumps, which enhances water retention, reduces air flow between the surface and leaf gaps, and consequently minimizes transpiration. This allows them to adapt to habitats characterized by high temperatures, drought, and strong ultraviolet radiation (Wang, Liu, & Bao, 2016; Sand-Jensen & Hammer, 2012). The predominant families in this life form include Pottiaceae and Racopilaceae. Pendants mosses grow in a creeping form, with major branches resembling root-like structures that hang suspended on rock faces, demanding high atmospheric humidity [34]. The dominant family here is Meteoriaceae, with five species accounting for 7.14% of the total species. This life form of epilithic bryophytes is primarily found on rock surfaces in the shaded, more humid areas beneath forests. In contrast, the cushion life form is only found in SRD habitats, represented solely by *Plagiothecium laetum*. The proportion of Turfs increases along the desertification gradient, indicating that Turfs exhibit stronger adaptability in more extreme environments.

4.3 Adaptation of Species Diversity of Epilithic Bryophytes to Rocky Desertification Habitats

4.3.1 Adaptation of α Diversity of Epilithic Bryophytes to Rocky Desertification Habitats

The richness index (R) is primarily used to measure the number of species in a community (Cong, Xu, & Tang, 2020). The richness index for the NRD habitat is 3.07, indicating that in areas free from rocky desertification, the species count remains relatively stable. This stability could be attributed to the absence of desertification disturbances, leading to a relatively intact ecosystem capable of sustaining a consistent number of species. The richness index for the PRD habitat is the highest, reaching 5.86. Despite the presence of a desertification trend in the PRD stage, the ecosystem still provides relatively rich habitats, supporting a diverse range of species. In contrast, the richness index for the LRD habitat is the lowest among all stages, indicating that desertification negatively impacts species numbers. This reduction may be due to factors such as soil erosion and decreased vegetation cover, which prevent some species from adapting to environmental changes, leading to their decline or disappearance. The richness indices for the MRD and SRD habitats show an increase compared to LRD, possibly due to the presence of species that are adapted to the rocky desertification environment, thereby maintaining species numbers at a certain level.

The Simpson index (D) primarily measures the dominance of species within a community. A higher value indicates that the dominant species occupy a larger proportion of the community, while a lower value suggests a more even distribution of individual species (Song, Li, Chen et al., 2021). The Simpson index for the NRD habitat is 0.81, reflecting a relatively even distribution of species individuals, with no single species dominating the community. This indicates a balanced ecosystem. The Simpson index for the PRD habitat is relatively high, primarily due to the presence of the dominant species *Eurohypnum leptothallum*, which possesses a strong competitive ability for resources. As desertification progresses, these species may exert increased competitive pressure on other species. The Simpson index for the LRD habitat is the lowest, suggesting that the distribution of species individuals is more even, potentially due to desertification leading to the reduction of some species and a narrowing of the population disparity among the remaining species. The Simpson index for the MRD habitat is the highest, with dominant species such as *Eurohypnum leptothallum*, *Meteorium polytrichum*, and *Anomodon viticulosus* all exhibiting high importance values. This indicates that in moderately rocky desertified habitats, dominant species prevail. The Simpson index for the SRD habitat is 0.83, suggesting that although desertification is more severe, the distribution of species individuals remains relatively even. However, compared to the NRD habitat, there is a tendency for dominant species to emerge.

The Shannon-Wiener index (H) provides a comprehensive reflection of both specie richness and evenness within a community. A higher index value indicates greater community diversity (Jawuoro, Koech, Karuku et al., 2017). The Shannon-Wiener index for the NRD habitat is 2.01, indicating high species richness and evenness, reflecting a stable ecosystem with balanced interspecies relationships. The Shannon-Wiener index for the PRD habitat is the highest, suggesting that despite the potential threat of desertification, the species diversity within the ecosystem remains relatively high. In contrast, the Shannon-Wiener index for the LRD habitat is lower, indicating that desertification has negatively impacted species diversity, leading to a reduction in both richness and evenness. The Shannon-Wiener index for the MRD habitat is 2.68, showing a slight increase, which may be due to the adaptation of moss species and other flora to the desertified environment, partially restoring species richness and evenness. The Shannon-Wiener index for the SRD habitat is moderate, indicating that despite severe desertification, the ecosystem still maintains a certain level of diversity, with species adapted to desertification playing a key role.

The Pielou evenness index (E) measures the distribution of species individuals within a community, with higher values indicating more uniform distribution of individuals across species (Guo & Cao, 2000). The Pielou index for the NRD habitat is 0.81, suggesting that the distribution of species individuals is even, and resource use is relatively balanced. The Pielou index for the PRD habitat is also relatively high, indicating a fairly uniform distribution of species individuals. The Pielou index for the LRD habitat is the lowest, indicating that desertification has led to the rapid decline of some species, while others remain relatively unchanged, thereby disrupting the original evenness of the community. The Pielou index for the MRD habitat is the highest, suggesting that despite increased desertification, species individuals are most evenly distributed. This may reflect the formation of a new balance within the ecosystem as it adapts to the desertified environment. The Pielou index for the SRD habitat has increased, potentially due to the survival of species that are adapted to harsh environments, leading to a more even distribution of species numbers.

4.3.1 Adaptation of β Diversity of Epilithic Bryophytes to Rocky Desertification Habitats

β-diversity reflects the degree of variation in species composition between habitats at different stages of rocky desertification, providing insight into the heterogeneity between habitats (Li, Zhang, & Wang, n.d.). The similarity index (Cs) ranges from 0 to 1, with higher values indicating greater similarity in species composition. Overall, the Cs of NRD habitats is low compared to other habitats, with the Cs value between NRD and SRD habitats being as low as 0.08, indicating a significant shift in species composition. The heterogeneity between PRD and LRD habitats is relatively high, whereas their similarity with MRD and SRD habitats is more stable, suggesting that the changes in species composition during the desertification process are more stable. The Cs for NRD is relatively high and similar to those of PRD, LRD, and MRD, signifying similar levels of species composition variation across these regions. From PRD to LRD, the Cs is 0.36, indicating a high similarity in species composition between these two regions. The Cs between PRD and MRD, as well as between PRD and SRD, are 0.30 and 0.33, respectively, slightly lower than the similarity observed with LRD. The Cs for LRD vs. MRD and LRD vs. SRD are 0.34 and 0.16, respectively, while the Cs value for MRD vs. SRD is 0.38, showing that species composition in LRD and MRD is more similar, and higher than that between LRD and SRD.

The dissimilarity index (βc) index reflects the dynamic changes in habitat heterogeneity, with higher values indicating greater dissimilarity between regions. The βc typically range from 6.50 to 11.00. From NRD to PRD, the βc decreases from 9.50 to 8.50, indicating a reduction in habitat dissimilarity. From NRD to LRD, the βc decreases further to 8.00, signifying continued homogenization. From NRD to MRD, the βc increases to 9.00, suggesting an increase in habitat dissimilarity. The βc from NRD to SRD returns to 9.50, indicating that the dissimilarity between NRD and SRD habitats is comparable to that within NRD itself. From PRD to LRD, the βc rises from 8.50 to 11.00, showing increased dissimilarity. Conversely, the βc from PRD to MRD and SRD decrease to 8.00, indicating reduced dissimilarity. From LRD to MRD, the βc value decreases from 11.00 to 7.50, and from LRD to SRD, it decreases to 6.50, while the βc from MRD to SRD remains at 7.50, illustrating an overall downward trend in habitat dissimilarity throughout the desertification process.

5. Conclusion

Through the identification and analysis of epilithic bryophytes specimens collected from different levels of rocky desertification in Pingtang County, it was found that a total of 47 moss species belonging to 28 genera and 11 families were present in the study area. Specifically, the NRD habitat contained 12 species from 10 genera and 6 families, the PRD habitat had 22 species from 15 genera and 9 families, the LRD habitat included 11 species from 10 genera and 7 families, the MRD habitat contained 18 species from 13 genera and 8 families, and the SRD habitat had 14 species from 10 genera and 7 families. The highest species richness was observed in the PRD habitat, with species counts following the order of PRD > MRD > SRD > NRD > LRD.The dominant species in the NRD habitat were *Eurohypnum leptothallum*, *Thuidium cymbifolium*, and *Thuidium assimile*. In the PRD habitat, the dominant species were *Eurohypnum leptothallum*, H*omalothecium leucodonticaule*, and *Anomodon rugelii*. In the LRD habitat, the dominant species were *Eurohypnum leptothallum*, *Meteorium polytrichum*, and *Erythrodontium julaceum*. The MRD habitat exhibited dominance of *Meteorium polytrichum*, *Eurohypnum leptothallum*, *Thuidium cymbifolium*, and *Erythrodontium julaceum*. In the SRD habitat, the dominant species were *Eurohypnum leptothallum*, *Trichostomum platyphyllum*, and *Racopilum cuspidigerum*. *Eurohypnum leptothallum* was the dominant species across all habitats.The wefts life form exhibited the highest proportion across all habitats, signifying its role as the primary life form of epilithic bryophytes in karst rocky desertification regions. Additionally, the proportion of pendants mosses showed a tendency to increase along the gradient of desertification, reflecting their greater adaptability to more extreme environments.The α-diversity index exhibited an

"M"-shaped distribution, initially increasing, then decreasing, followed by an increase and another decrease from the NRD habitat to the SRD habitat. This pattern suggests dynamic species turnover throughout the process of rocky desertification, with the appearance of unique and shared species across various habitats, highlighting the selective influence of desertification on moss species. The Cs index remained low across the desertification gradient, with significant species composition changes, indicating a high level of habitat heterogeneity. The βc index in the LRD, MRD, and SRD habitats was relatively stable, indicating a trend towards increasing habitat similarity.

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