Ecological niche and interspecific relationship of dominant bryophyte communities in stone walls of cities at different elevations, Guizhou, China

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Abstract: To investigate the utilization characteristics and distribution patterns of major bryophyte communities on urban walls, we examined the bryophyte communities in stone walls at varying elevations. This study employed niche width and niche overlap indices, Chi-square Statistic Test, and association coefficient to analyze the species composition, niche characteristics, and interspecific associations within the bryophyte communities. The results showed that the stone walls across the four elevation gradients supported a total of 65 bryophyte species, including six liverwort species, but the dominant species varied from elevation to elevation E1~E4 (989-1398m). *Didymodon rufidulus*, *Didymodon ditrichoides*, and *Bryum argenteum* had larger niche widths and were primarily distributed in the E3 elevation. In each elevation gradient, there was low niche overlap among the dominant bryophyte species. Interspecific association analysis revealed a significant negative association among bryophytes, suggesting the early stage of community succession. Among the elevation gradients, E4 displayed the weakest degree of bryophyte association, while E3 exhibited the strongest negative association and relative stability. The 16 dominant species of stonewall bryophytes could be categorized into three groups. These findings provide insights into the competition mechanism of wall bryophyte communities at different elevations and offer guidance for ecological restoration of wall vegetation.

Niche is a fundamental concept in ecology used to analyze interspecific relationships and determine the mechanisms behind community formation. It not only elucidates the position of a population or individual within the ecological space of a community, specifically in terms of resource utilization [1] but also explains species coexistence and competition within a community [2]. The niche characteristics of community species primarily encompass niche width and niche overlap. Niche width reflects a species' capacity to utilize environmental resources effectively, while niche overlap measures the extent to which two species share and compete for specific resources [3]. Interspecific association refers to the spatial correlation between different species in a community, highlighting the interconnected relationships formed by community species within various habitats [4, 5]. Investigating the integration of niche and interspecific association provides a comprehensive understanding of species' resource utilization patterns, interspecific cooperation and antagonism, and overall community stability across spatial and temporal scales. Additionally, this research has practical implications for ecological restoration efforts [6, 7].

Bryophytes are primary colonizers during natural succession [8] and can thrive on diverse substrates, including bark and rocks [9]. They play a crucial role in urban ecosystems and contribute significantly to biodiversity [10, 11]. Extensive research has been conducted on bryophyte niches, primarily focusing on forest and urban ecosystems. For instance, two dominant matric moss communities found in nature reserves are situated in the early or middle stages of succession [12]. *Brachythecium* and *Bryum caespiticium* serve as pioneer species suitable for ecological restoration efforts in protected areas [13, 14]. The width of the urban bryophyte niche exhibits a significant correlation with habitat characteristics [15]. Urban soil bryophytes are mainly influenced by human disturbance and soil pH [16]. Bryophyte species distribution is shaped by multiple driving factors within their ecological niche [17], including factors like elevation, precipitation, and temperature gradients that influence bryophyte structure, community dynamics, and population maintenance [18, 19]. Previous studies have revealed the significant impact of ecological niches on altitude gradients on the abundance and richness of tree epiphytes [17]. Furthermore, there are distinct differences in the ecological niche of bryophytes across various altitude gradients, enabling them to survive in diverse environments [20]. Gaining insights into the ecological requirements and relationships of dominant bryophyte species along altitudinal gradients during resource utilization is crucial for the effective management and restoration of urban ecosystems. Notably, there is a lack of research on bryophyte niches and interspecific linkages at different altitudinal gradients in urban ecosystems.

Guiyang City, situated in the central part of Guizhou Province, is a representative karst mountainous city [21] characterized by significant variations in elevation and topography. Retaining walls constructed with stone matrices for slope protection are extensively found in urban areas, supporting diverse populations of plants and microorganisms [22]. Among these inhabitants, bryophytes have been observed to occupy a wide ecological niche [23]. Previous studies investigating plant niches and interspecific relationships in Guizhou have primarily concentrated on dominant communities of trees, shrubs, herbs, and phytoplankton in nature reserves [24], the Maolan karst area [25], mining areas [26], and reservoirs [27]. Nevertheless, there is a paucity of research specifically addressing wall bryophytes in urban areas. To date, investigations have solely examined the species diversity of wall bryophytes in Zhaobi Mountain, Guiyang [28], leaving the interaction and ecological relationship among moss community species at different elevations poorly understood. We speculate that the ecological niche of stone wall bryophytes in karst urban areas is greatly affected by the elevation gradient. Due to human disturbance and serious rock desertification, bryophyte communities on stone walls may demonstrate characteristics typical of early or intermediate stages of succession. These communities effectively utilize wall resources and the surrounding environment and may serve as pioneer species in restoring the karst urban ecosystem.

Given the study's objectives, the dominant species of wall bryophytes in the urban area of Guiyang City were selected as the research focus. The study aimed to quantitatively analyze the species' niche characteristics, community connectivity, and interspecific associations across different altitudinal gradients. This analysis sought to elucidate how the dominant species of wall bryophytes respond to varying altitudinal gradients in terms of their ecological niche and interspecific relationships. By understanding the impact of altitude on the structure and function of bryophyte communities in the urban environment, this research can provide a scientific foundation for effectively conserving karst urban bryophyte resources. Additionally, it can offer theoretical and practical insights into the ecological restoration and reconstruction of wall vegetation.

Results and analysis

Species composition and niche width of bryophytes at different elevations

There were a total of 65 bryophyte species belonging to 11 families and 27 genera observed in 120 stone walls located in Guiyang City. Among them, six species are liverworts. The dominant families at the four different elevations were Brachytheciaceae (20 species in 3 genera), Pottiaceae (18 species in 11 genera), and Bryaceae (7 species in 1 genus). At the E1 elevation range (989-1091m), there were 40 species of bryophytes observed, belonging to 8 families and 18 genera, with *Brachythecium buchananii* being the dominant species. Within the E2 elevation range (1092-1193m), there were 39 species of bryophytes identified, belonging to 19 genera and 8 families, with *Thuidium kanedae* as the dominant species. Similarly, the E3 elevation range (1194-1295m) contained 35 species of bryophytes across 20 genera and 11 families, with *Pseudosymblepharis angustata* being the dominant species. Finally, at the E4 elevation range (1296-1398m), a total of 34 species of bryophytes were recorded, representing 8 families and 16 genera, with *Eurhynchium laxirete* as the dominant species. In conclusion, the number of bryophyte species observed on the stone walls decreased with increasing elevation. However, the overall difference was not significant, and there was a noticeable variation in the dominant species among different elevations.

As shown in Table 1, the Levins niche widths of the 16 dominant species within the wall bryophyte community varied with increasing altitude. Among these species, *Didymodon rufidulus*, *Didymodon ditrichoides*, and *Bryum argenteum* exhibited the widest niche widths across all elevations, measuring 10.002, 11.896, and 12.546, respectively. This indicates that these species possess a broad ecological range and effectively utilize environmental resources. Conversely, there were 9 bryophyte species with a niche width of 1.000, implying that they appeared less frequently within each altitude gradient. For instance, *Thuidium kanedae* had a niche width of 1.000 at all four elevations, signifying its limited ecological adaptation range. Furthermore, it was worth noting that the same species displayed significant variations in niche width at different elevations. For example, *Weissia edentula* exhibited a higher niche width at the E1 (989-1091m) elevation but a lower niche width at other elevations.

Table1 Levins niche widths of dominant bryophyte species in stone walls at different elevations in urban areas

Number	Family	Genus	Species	elevations			
				E1	E2	E3	E4
S1	Pottiaceae	*Pseudosymblepharis* Broth	*Pseudosymblepharis angustata* (Mitt.) Hilp	1.000	1.693	1.000	2.817
S2	Pottiaceae	*Weissia* Hedw	*Weisia controversa* Hedw	4.918	2.420	5.140	7.018
S3	Brachytheciaceae	*Brachythecium* Bruch & Schimp	*Brachythecium fasciculirameum* Müll. Hal	1.000	2.907	1.000	1.828
S4	Pottiaceae	*Didymodon* Hedw	*Didymodon rufidulus* (Müll. Hal.) Broth	7.445	5.787	10.002	8.536
S5	Pottiaceae	*Didymodon* Hedw	*Didymodon ditrichoides* (Broth.) X. J. Li & S. He	3.079	7.282	11.896	3.474
S6	Thuidiaceae	*Haplocladium* Müll. Hal	*Haplocladium microphyllum* (Hedw.) Broth	3.621	5.190	1.000	3.383
S7	Pottiaceae	*Barbula* Hedw	*Barbula unguiculata* Hedw	1.000	1.000	1.000	1.694
S8	Bryaceae	*Bryum* Hedw	*Bryum dichotomum* Hedw	4.413	2.866	6.777	1.000
S9	Brachytheciaceae	*Eurhynchium* Bruch & Schimp	*Eurhynchium laxirete* Broth	3.011	1.000	1.000	1.000
S10	Brachytheciaceae	*Brachythecium* Bruch & Schimp	*Brachythecium piligerum* Cardot	4.584	2.586	4.612	7.488
S11	Pottiaceae	*Weissia* Hedw	*Weissia edentula* Mitt	6.689	2.019	2.917	1.342
S12	Thuidiaceae	*Thuidium* Bruch & Schimp	*Thuidium kanedae* Sakurai	1.000	1.000	1.000	1.000
S13	Brachytheciaceae	*Brachythecium* Bruch & Schimp	*Brachythecium brotheri* Paris	4.469	1.475	2.971	3.485
S14	Pottiaceae	*Hyophila* Brid	*Hyophila nymaniana* (M. Fleisch.) Menzel	4.449	2.968	1.000	3.578

S15	Pottiaceae	*Didymodon* Hedw	*Didymodon constrictus* (Mitt.) Saito. var. constrictus	1.000	1.768	6.000	1.000
S16	Bryaceae	*Bryum* Hedw	*Bryum argenteum* Hedw	3.662	2.682	12.546	6.703

Niche overlap of dominant bryophyte species at different elevations

The table below shows the niche overlap values of dominant species at different altitude gradients (Table 2). When the overlap value exceeds 0.5, the number of species pairs at altitudes E1 (989-1091m), E2 (1092-1193m), and E3 (1194-1295m) are the same, with 5 pairs (4%) at each altitude, while at altitude E4 (1296-1398m) there are 2 pairs (2%). For the remaining species pairs, the overlap value was below 0.5. These results suggest that the niche overlap values in this area's different altitudinal gradients are low. This may be due to resource niche differentiation caused by the similar adaptability of moss species within the same genus. Among these species, *Didymodon rufidulus*, *Didymodon ditrichoides*, and *Bryum argenteum* have the widest niches. Their average niche overlap values with other bryophytes are 0.187, 0.210, and 0.214, respectively. The niche overlap between the narrowest *Thuidium kanedae* and most bryophytes was either low or non-existent, but some exceptions have high overlap, such as *Brachythecium brotheri*. This indicates that there is no linear relationship between niche width and niche overlap. Additionally, the logarithmic ranges of each ecological overlap are 49, 40, 49, and 44, respectively. This suggests that E1 (989-1091m) and E3 (1194-1295m) have the greatest distribution dispersity, while E2 (1092-1193m) has the smallest. Overall, the niche overlap of dominant bryophyte species at each elevation gradient is low, indicating minimal species competition and a tendency to coexist, with similar resource utilization.

Table2 Niche overlap of dominant bryophyte species in stone walls at different elevations in urban areas

Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16
S1		0.23	0.00	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19
S2	0.00		0.00	0.28	0.00	0.00	0.35	0.00	0.05	0.23	0.16	0.00	0.26	0.00	0.00	0.06
S3	0.00	0.00		0.00	0.37	0.00	0.00	0.00	0.00	0.60	0.28	0.00	0.00	0.29	0.00	0.28
S4	0.10	0.59	0.00		0.00	0.06	0.00	0.00	0.05	0.34	0.65	0.35	0.51	0.00	0.00	0.16
S5	0.00	0.14	0.14	0.01		0.00	0.00	0.02	0.00	0.35	0.15	0.00	0.00	0.75	0.00	0.33
S6	0.00	0.00	0.07	0.01	0.14		0.00	0.18	0.28	0.00	0.05	0.00	0.00	0.15	0.16	0.00
S7	0.00	0.00	0.00	0.00	0.00	0.48		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S8	0.16	0.00	0.00	0.12	0.10	0.03	0.00		0.00	0.03	0.00	0.00	0.00	0.00	0.17	0.12
S9	0.00	0.00	0.00	0.00	0.07	0.16	0.00	0.00		0.05	0.11	0.00	0.00	0.16	0.00	0.00
S10	0.00	0.52	0.00	0.36	0.20	0.00	0.00	0.00	0.00		0.54	0.00	0.09	0.17	0.00	0.24
S11	0.00	0.28	0.00	0.19	0.00	0.00	0.76	0.00	0.00	0.28		0.00	0.20	0.13	0.00	0.27
S12	0.00	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.46	0.00	0.00	0.17
S13	0.00	0.00	0.00	0.13	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.10
S14	0.00	0.00	0.14	0.00	0.12	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.34
S15	0.00	0.40	0.00	0.30	0.11	0.00	0.00	0.16	0.00	0.65	0.30	0.00	0.00	0.00		0.00
S16	0.04	0.07	0.00	0.18	0.00	0.00	0.00	0.05	0.00	0.02	0.01	0.00	0.00	0.00	0.00	

Note: The species numbers are the same as in Table 1. The upper triangle of the table is the E1 niche overlap, and the lower triangle is the E2 niche overlap

Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16
S1		0.00	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S2	0.32		0.00	0.53	0.03	0.00	0.33	0.37	0.00	0.33	0.08	0.00	0.39	0.00	0.14	0.24
S3	0.00	0.00		0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00

S4	0.28	0.35	0.13		0.13	0.00	0.00	0.23	0.05	0.21	0.04	0.05	0.32	0.22	0.03	0.35
S5	0.00	0.05	0.00	0.02		0.17	0.00	0.32	0.21	0.03	0.13	0.21	0.29	0.00	0.10	0.53
S6	0.00	0.00	0.00	0.02	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.26
S7	0.00	0.34	0.00	0.00	0.00	0.06		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00
S8	0.00	0.15	0.00	0.00	0.00	0.00	0.00		0.00	0.13	0.08	0.00	0.33	0.00	0.16	0.43
S9	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.65	0.00	0.00	0.00
S10	0.24	0.10	0.12	0.40	0.21	0.06	0.14	0.00	0.00		0.10	0.00	0.00	0.17	0.00	0.28
S11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02		0.00	0.00	0.00	0.24	0.09
S12	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.65	0.00	0.00	0.00
S13	0.00	0.29	0.00	0.06	0.07	0.03	0.07	0.00	0.00	0.14	0.00	0.00		0.00	0.00	0.10
S14	0.30	0.17	0.00	0.08	0.32	0.00	0.00	0.00	0.00	0.36	0.57	0.00	0.09		0.00	0.00
S15	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.14
S16	0.12	0.35	0.00	0.25	0.25	0.20	0.00	0.00	0.00	0.12	0.19	0.24	0.03	0.28	0.00	

Note: The species numbers are the same as in Table 1. The upper triangle of the table is E3 niche overlap, and the lower triangle is E4 niche overlap

The relationship between the advantages of bryophytes at different elevations

Overall Connectedness

The calculated results of the population association for the dominant species of wall bryophytes are presented in Table 3. The variance ratio (VR) value indicates an overall negative association among the major species, as VR < 1 for all elevations. Additionally, none of the test statistics fall within the limit $\chi^2_{0.95,30} < W < \chi^2_{0.05,30}$, signifying a significant deviation of VR from 1 and thus indicating a substantial association between species (P < 0.05). Consequently, there is a significant negative correlation observed in the overall relationship between bryophyte dominance at different elevations within urban areas.

Table3 Overall association of dominant bryophyte species in stone walls at different elevations in urban areas

Elevation	Variance ratio (VR)	Statistic (W)	χ^2 ($\chi^2_{0.95,30}$, $\chi^2_{0.05,30}$)	Results
E1	0.25	7.37	[18.49,43.77]	Significant negative correlation
E2	0.40	12.04	[18.49,43.77]	Significant negative correlation
E3	0.19	5.81	[18.49,43.77]	Significant negative correlation
E4	0.20	5.57	[18.49,43.77]	Significant negative correlation

Correlation of bryophyte dominance

A chi-square statistic test was conducted on 120 pairs of dominant lichen species found on walls at various elevations, and the results are presented in Table 4 and Supplementary Table 1. The logarithms of positive associations in the four elevation gradients were smaller than those of negative associations, representing 24.17%, 18.33%, 20.83%, and 20.83% of the total species logarithms, respectively. The logarithms of negative associations were significantly higher than those of positive associations. The significant association ratio of bryophyte pairs in the four altitude gradients was low, suggesting a weak degree of interdependence among bryophytes. The bryophyte community as a whole exhibited independent distribution rather than association distribution, indicating an early stage of succession.

Table 4 χ^2 test table of species pairs of dominant bryophyte species in stone walls at different elevations in urban areas

Elevation	Positive correlation (Proportion of total species pairs)				Negative correlation (Proportion of total species pairs)			
	Distinctly significant (P≤0.01)	Significant (P≤0.05)	Not significant (P >0.05)	Sum	Distinctly significant (P≤0.01)	Significant (P≤0.05)	Not significant (P >0.05)	Sum

E1	2（1.67%）	1（0.83%）	26（21.67%）	29（24.17%）	2（1.67%）	2（1.67%）	87（72.50%）	91（75.83%）
E2	6（5.00%）	2（1.67%）	14（11.67%）	22（18.33%）	2（1.67%）	3（2.50%）	93（77.50%）	98（81.67%）
E3	2（1.67%）	3（2.50%）	20（16.67%）	25（20.83%）	6（5.00%）	3（2.50%）	86（71.67%）	95（79.17%）
E4	2（1.67%）	5（4.17%）	18（15.00%）	25（20.83%）	4（3.33%）	3（2.50%）	88（73.33%）	95（79.17%）

The division range of interspecific association coefficients (*AC*) varied among each altitude gradient (Fig. 1). The *AC* value of E3 (1194-1295m) ranged from 0.06 to -0.79, with the maximum value of 0.06 being the lowest among all altitudinal gradients. This suggests that the negative association between bryophyte species was strongest at this altitude and remained relatively stable. At elevations E1-E4 (989-1398m), there were 36, 15, 30, and 2 pairs of bryophyte species that showed positive connections, while 84, 105, 90, and 118 pairs showed negative connections. The highest number of positively connected dominant species pairs was observed at E1 (989-1091m) elevation, while the highest number of negatively connected dominant species pairs was observed at E4 (1296-1398m) elevation. This indicates that the degree of bryophyte connection was weakest and the number of independently distributed species pairs was largest at E4 (1296-1398m) elevation.

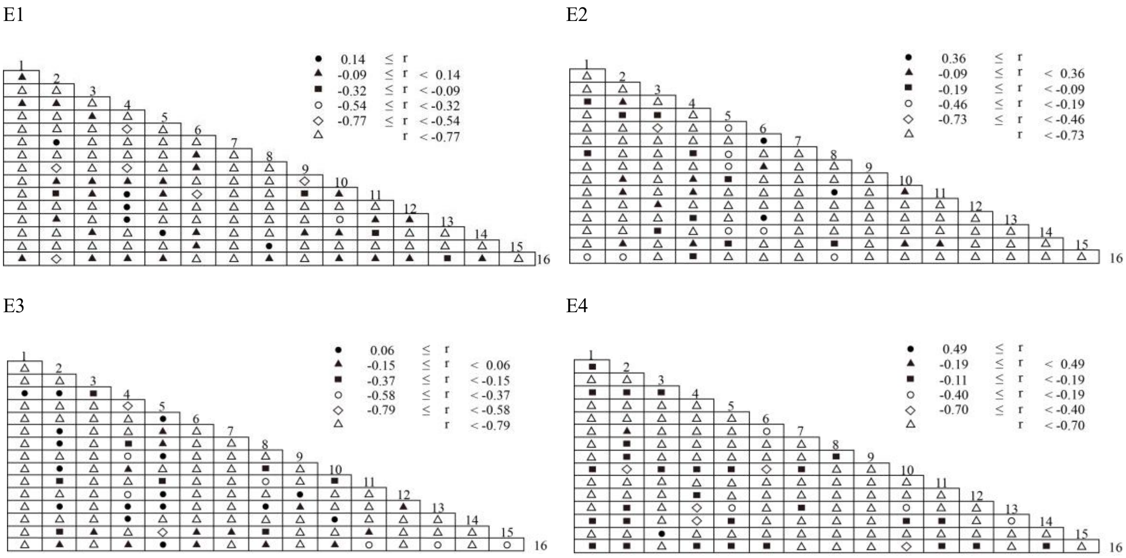

Fig.1 Half-matrix of *AC* values of correlation between the advantages of bryophytes in stone walls at different elevations

Correlation degree of bryophyte dominance

The Pearson correlation coefficient can be further validated using the χ^2 test to assess the potential degree of co-occurrence between two species [29]. The results of the test (Fig. 2) indicate that the number of species positively associated with E1-E4 (989-1398m) was 26 (21.67%), 24 (20.00%), 22 (18.33%), and 32 (26.67%) respectively. There were 8, 10, 6, and 2 species pairs that showed extremely significant and significant positive associations, respectively. The number of species with negative associations were 94 (78.33%), 96 (80.00%), 98 (81.67%), and 88 (73.33%), while the species pairs with significant negative associations were 1, 0, 2, and 0, respectively. Most of the species pairs were not significantly correlated and the correlation was weak. In summary, the number of species with negative associations was significantly higher than the number of species with positive associations, indicating that most species are not closely related to each other and the interspecific connection is weak. The influence between species in the growth process is minimal, indicating strong interspecific independence and susceptibility to external disturbances.

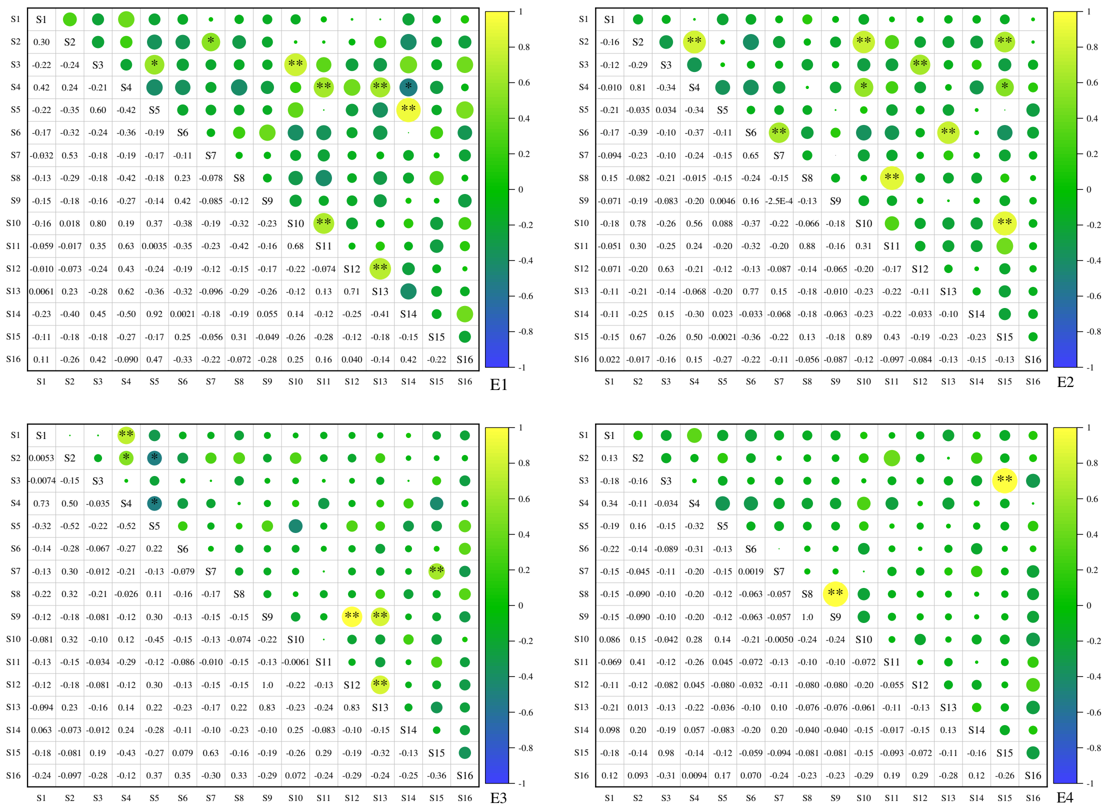

Fig.2 Half-matrix of Pearson correlation coefficient between bryophyte dominance pairs at different elevations. (*:p≤0.05, **:p≤0.01)

Ecological species group

Species with similar ecological niches and habits within a community can be categorized as an ecological species group [30]. In this study, 16 dominant bryophytes were grouped into three ecological species groups based on cluster analysis (Fig. 3) and principal component analysis (Fig. 4) sequencing, taking into account the correlation of species' ecological habits, interspecific associations, and habitat characteristics.

Group I, consisting of six species, includes *Pseudosymblepharis angustata* (S1), *Brachythecium fasciculirameum* (S3), *Barbula unguiculata* (S7), *Eurhynchium laxirete* (S9), *Thuidium kanedae* (S12), and *Didymodon constrictus* (S15). This group exhibits the smallest ecological adaptation range, strong species independence, loose distribution, and weak interspecific associations. Most of these dominant species prefer shade and moisture, primarily distributed in wet rocks, rock surface soil, and wet forest land at elevations E1 (989-1091m) and E3 (1194-1295m).

Group II comprises five species: *Haplocladium microphyllum* (S6), *Bryum dichotomum* (S8), *Weissia edentula* (S11), *Brachythecium brotheri* (S13), and *Hyophila nymaniana* (S14). These bryophytes exhibit a wider niche width at E1 elevation (989-1091m), but their occurrence frequency was low at other altitudes. The interspecific association among them was weak, and they were primarily found on the soil and rocks surrounding roadsides and buildings.

Group III consists of five species: *Weisia controversa* (S2), *Didymodon rufidulus* (S4), *Didymodon ditrichoides* (S5), *Brachythecium piligerum* (S10), and *Bryum argenteum* (S16). Among these, the dominant bryophyte species at E3 elevation (1194-1295m) exhibit the widest niche width and a strong positive interspecific association, indicating their similar ecological characteristics. Most of these dominant species belong to the light-tolerant, drought-tolerant, barren-tolerant, and ecologically adaptable species of Brachybryaceae, which were widely distributed in the initial stages of stone wall plant community succession. Hence, they can serve as preferred pioneer species for ecological restoration in artificial vegetation within this region.

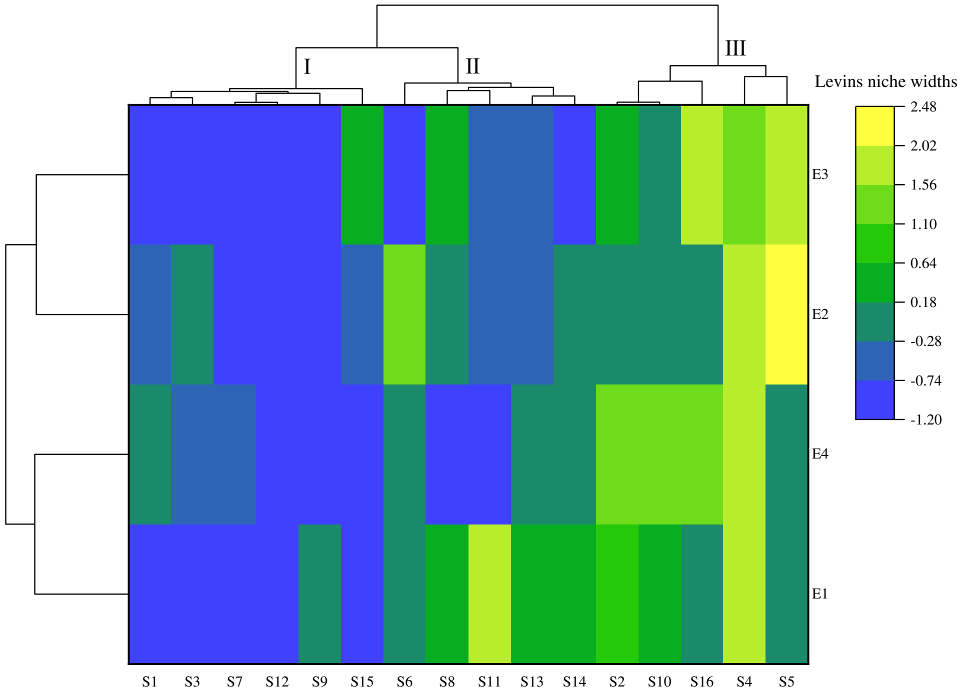

Fig. 3 Cluster analysis of dominant bryophyte species in stone wall at different elevations

Note:The species numbers are the same as in Table 1

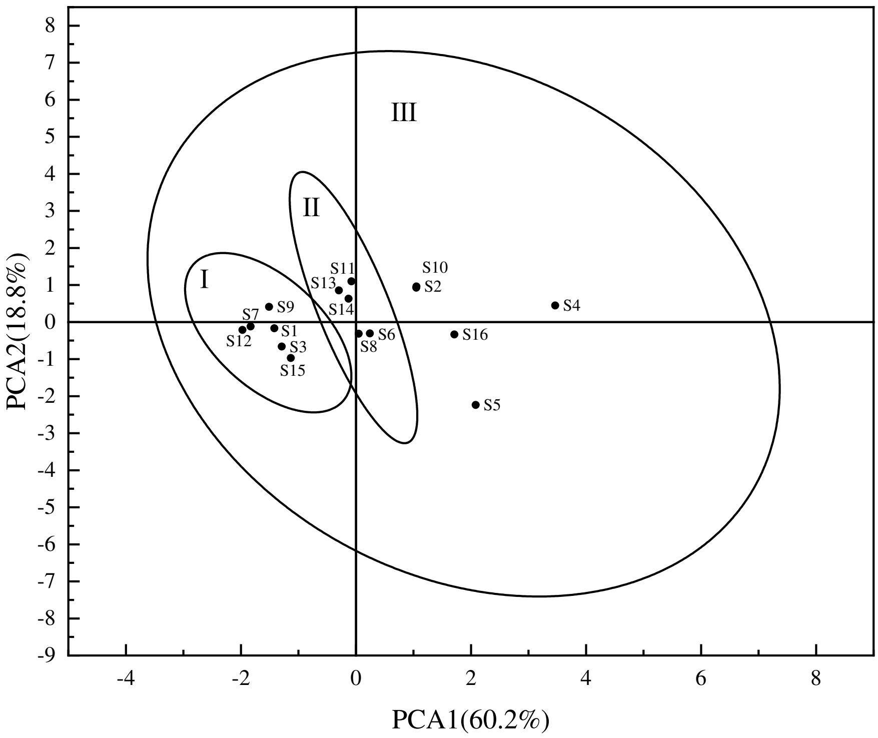

Fig. 4 PCA 2D ranking map of 16 bryophyte species based on niche width values

Note:The species numbers are the same as in Table 1

Discussion

A total of 65 species, including six species of liverworts, belonging to 27 genera and 11 families were found in the stone wall bryophytes of Guiyang City. The average annual relative humidity in this study area is 77%, which classifies it as a high-humidity area in China. This high humidity enables the wall bryophytes to obtain sufficient water from the air, thus creating highly favorable environmental conditions for their growth. Brachytheciaceae, Pottiaceae, and Bryaceae were widely distributed on stone walls. These mosses are capable of thriving in extreme environments characterized by drought, nutrient deprivation, and cold [31]. Moreover, elevation can serve as a strong predictor for the species composition and abundance of stone wall bryophytes [23]. In this study, it was observed that the number of bryophyte species decreases with increasing altitude, although the overall difference is small. Additionally, the dominant species vary across different altitude gradients, which aligns with the findings of Jin Yalin's research [32].

Niche width is an indicator of a species' status and role within a community [33]. The study results revealed that *Didymodon rufidulus*, *Didymodon ditrichoides*, and *Bryum argenteum* exhibited the widest niche widths across all elevations. These species were found in the E3 (1194-1295m) elevation range. Previous research has indicated that as altitude increases, temperature variability also increases, resulting in greater niche width plasticity for genetic species. Furthermore, species at middle and high altitudes are more likely to occupy larger ranges [34].

Additionally, *Didymodon* can serve as a climate change indicator in the Tibetan Plateau [35], while the three bryophytes mentioned demonstrate better adaptability and drought tolerance in the challenging stone wall environment [31, 36]. Consequently, these moss species can effectively utilize the resources available within the stone wall habitat, enabling them to establish stable populations at this specific altitude. However, the nine bryophyte species with a niche width of 1.000 displayed relatively weak utilization and adaptation to environmental resources. This indicates that differences in resource utilization capacity and niche width among species are not solely determined by habitat selection but also by long-term species adaptation to their environment [37, 38]. Furthermore, the same species may exhibit significant variations in niche width across different altitudinal gradients. This could be attributed to the direct influence of altitude on solar radiation and precipitation redistribution, which subsequently affects bryophyte growth at varying altitudinal gradients [39]. Therefore, greater attention should be given to variations in plant niches and species characteristics in communities at different elevations when formulating plant restoration strategies.

Niche overlap values are indicative of the competition among populations sharing the same resources [40]. The findings of this study reveal a low niche overlap among 16 species of stone wall moss in Guiyang City. This could be attributed to most species coexisting through niche differentiation at their resource sites, thus minimizing inter-specific resource competition and resulting in a low level of niche overlap [41]. For instance, the ample availability of water in the stone wall habitat satisfies the needs of individuals within the community, allowing for the coexistence of moss species with similar resource utilization patterns [37]. Furthermore, the relationship between niche width and niche overlap value in this study is complex and does not follow a simple linear pattern. Previous research has demonstrated that species with smaller niche widths may exhibit larger niche overlaps due to similar or complementary resource requirements stemming from shared biological characteristics [42, 43]. Additionally, this study observed a higher distribution dispersity of niche overlap values in the E1 (989-1091m) and E3 (1194-1295m) altitudes, indicating relatively intense competition. Relevant studies have shown that plants along vertical gradients exhibit distinct population distribution patterns and separated ecological niches as a result of long-term interaction and habitat adaptation, particularly light factors [44].

Interspecific associations reflect the stability of plant communities and serve as a crucial parameter for vegetation succession [45]. In general, the dominant species of stone wall bryophytes in the four elevations in an urban area exhibited significant negative correlations, indicating the community structure and species composition are in the early stage of unstable succession. This phenomenon may be attributed to the influence of environmental stress from the walls, the necessity for plant species to possess adequate environmental tolerance for survival, the insignificant impact of interspecific cooperation and coexistence [46-48], and the greater influence of external factors. Concurrently, the bryophyte species in E4 (1296-1398m) displayed the highest levels of independent distribution among species pairs. Previous studies have demonstrated that altitude can affect niche selection, with certain species exhibiting pronounced growth advantages in high-altitude areas [49]. The strong negative correlation observed in the elevation gradient of E3 (1194-1295m) suggests that the bryophyte community at E3 (1194-1295m) elevation is relatively stable, with most stone walls in this altitude area located in parks with diverse vegetation, similar stone wall types, and minimal environmental impact differences. In addition, the classification of ecological species groups enables a thorough analysis of the structure and function of plant communities. In this study, 16 dominant bryophyte species were categorized into three groups. Group III exhibited the widest ecological adaptation range at E3 elevation (1194-1295m). Furthermore, the prevalence of Sphagnaceae reaffirms the superior ecological adaptability of drought-tolerant sphagnaceae in arid and resource-poor wall environments [50]. These species can serve as pioneer species for the ecological restoration of stone walls in the area.

The examination of the ecological niche and interspecific association characteristics of stone wall moss species in Guiyang City enhances comprehension of bryophyte distribution patterns across varied elevation gradients. In addition, it offers significant scientific knowledge to support the preservation of biodiversity and ecological reconstruction in karst territories. It should be noted that altitude is merely one among numerous environmental factors that impact the distribution of wall bryophytes. Future studies should incorporate environmental data from the area to comprehensively analyze other factors affecting the distribution of bryophyte species and their interspecific relationships. Future research should include environmental data from the region to provide a thorough analysis of additional factors impacting the distribution of bryophyte species and their inter-species relationships.

Conclusion

(1)The findings revealed that the stone walls across four elevation gradients supported a total of 65 bryophyte species, including six liverwort species, but the dominant species varies from elevation to elevation. Brachythecium buchananii was the dominant species in E1 (989-1091m), *Thuidium* in E2 (1092-1193m), *Pseudosymblepharis angustata* in E3 (1194-1295m), and *Eurhynchium laxirete* in E4 (1296-1398m).

(2)The niche analysis showed that *Didymodon rufidulus*, *Didymodon ditrichoides*, and *Bryum argenteum* had larger niche widths and were primarily distributed in the E3 elevation. In each elevation gradient, there was low niche overlap among the dominant bryophyte, indicating minimal species competition and a tendency for coexistence.

(3)Interspecific association analysis revealed a significant negative association among the moss species, suggesting a weak interdependence and independent distribution of each species, and the early stage of community succession. Among the elevation gradients, E4 displayed the weakest degree of bryophyte association and the largest number of independently distributed species pairs, while E3 exhibited the strongest negative association and relative stability.

(4)Cluster analysis and principal component analysis demonstrated that the 16 dominant species of stonewall bryophytes could be categorized into three groups, with group III exhibiting the widest niche width. Species within this group can be considered pioneer species for ecological restoration efforts on stonewalls.

Materials and methods

Study area

Guiyang City (106°07 '-107° 17'E, 26°11' -26° 55'N) is a significant central city in southwestern China, situated amidst mountains and hills, making it a prime example of a karst region. The terrain varies greatly, with higher elevations in the southwest and lower elevations in the northeast, resulting in a substantial elevation range (880-1659m) [51]. The climate is characterized as subtropical humid, with an average annual temperature of 15.3°C, an average annual relative humidity of 77%, and an annual precipitation of 1129.5mm. Due to the karst topography and the presence of residual mountains within the urban area, there are numerous retaining walls and slope protection walls. Stone walls are widespread throughout the urban area of Guiyang City, providing an environment for the settlement and growth of urban plants.

Research methods

The geographical elevation data (DEM) for the built-up area of Guiyang City was obtained from the geospatial data cloud at http://www.gscloud.cn/. Subsequently, the elevation of the study area was extracted using ArcGIS 10.2. The elevation of Guiyang City's built-up area ranges from 989m to 1398m and was categorized into four altitude gradients based on equal height difference intervals in ArcGIS 10.2: E1 (989-1091m), E2 (1092-1193m), E3 (1194-1295m), and E4 (1296-1398m). To establish a sample size of 30 representative community areas per altitude gradient, a total of 120 plots were selected and numbered according to the respective altitude gradient (Fig. 5). Each plot represents a stone wall. The stone walls are divided into large squares, with each square being further divided into three mesoid squares (2m x 2m) to collect wall bryophytes. Using the community minimum area method, within each medium quadrate, five small quadrants (10cm×10cm) were identified using metal frames for sampling and recording coverage, habitat, elevation, and other relevant information. A total of 1804 bryophyte specimens were collected and subsequently identified to species level using the reference texts "Volumes 1–3 of Bryophyte Flora of Guizhou China" and "Atlas of Bryophytes of Guizhou (Xiomi Species Volume)" [52-55]. The bryophyte specimens are currently housed in the bryophyte herbarium of the College of Forestry at Guizhou University .

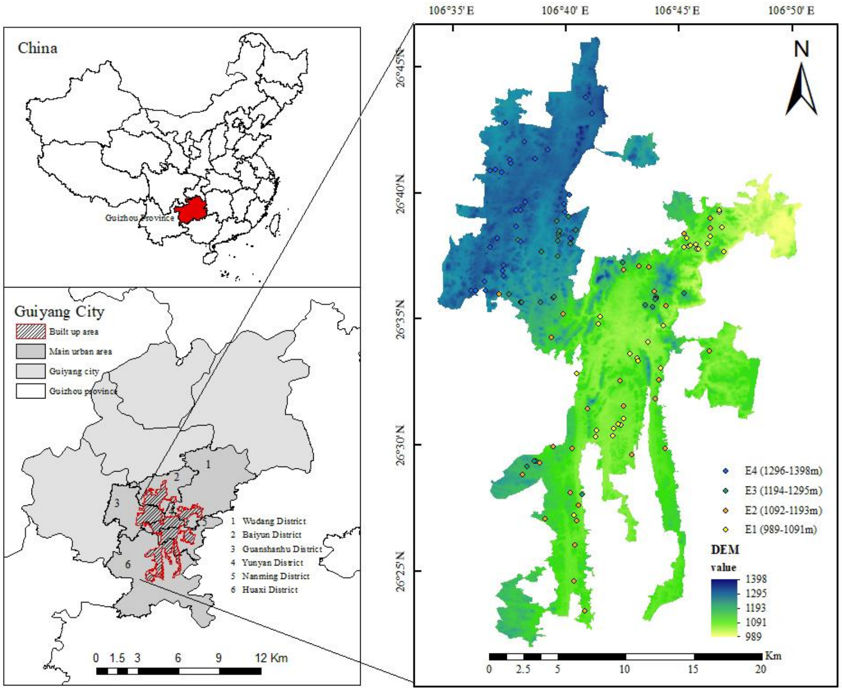

Fig. 5 Map of bryophytes at different elevations of stone walls in Guiyang City

Statistical analysis

The bryophyte species that dominate the analysis must be present simultaneously in each elevation gradient [56] and have a total importance value exceeding 0.50. The Levins niche width, Pianka niche overlap value, overall connectivity, χ^2 statistic, and degree of connectivity were calculated using the functions niche width(), niche.overlap(), sp. assoc(), and sp. pair() in the spa package of R3.5.1 software, based on their respective importance values. Pearson correlation analysis, cluster analysis, and principal component analysis were conducted using OriginPro9.0 to examine the relationships among plant pairs.

Data processing and analysis

Importance value

The relative coverage and relative frequency of bryophytes are used to calculate the ecological importance value of bryophytes [16]. The calculation formula is as follows:

$$L=(MI+NI)/2 \quad (1)$$

Where L is the ecological importance value; MI is relative coverage; and NI is the relative frequency. Relative coverage = average coverage of one bryophyte/sum of average coverage of all bryophyte species, relative frequency = frequency of one bryophyte/sum of frequency of all bryophyte species.

Niche width

The Levins niche width [29] is as follows:

$$BL = 1/\sum_{j=1}^{r} P_{ij}^{2}$$

(2)

Where, P_{ij} is the ratio of the importance value of species i on resource bit j to the sum of the importance value of species i on all resource bits, and r is the total number of resource bits.

Niche overlap

The Pianka index calculates the niche overlap between species pairs [29] as follows:

$$O_{ik} = \sum_{j=1}^{r} P_{ij} P_{kj} / \sqrt{(\sum_{j=1}^{r} P_{ij}^2)(\sum_{j=1}^{r} P_{kj}^2)} \quad (3)$$

Where, O_{ik} is the niche overlap index of species *i* and k; P_{ij} And P_{kj} are the important values of species *i* and species *k* on resource *j*, respectively.

Overall Connectedness

Schluter's [57] variance ratio (*VR*) test method was employed to assess the overall correlation level within plant communities and determine the significance of correlation coefficients.

$$\delta_T^2 = \sum_{i=1}^{S} P_i(1 - P_i) \quad (4)$$

$$S_T^2 = (\frac{1}{N}) \sum_{j=1}^{N} (T_j - t) \quad (5)$$

$$VR = S_T^2 / \delta_T^2 \quad (6)$$

$$p_i = n_i / N \quad (7)$$

$$W = N \times VR \quad (8)$$

Where *S* is the total number of species, *N* is the total number of quadrats, T_j is the number of species in the *j* quadrat, n_i is the number of species in the *i* quadrat, and *t* is the average number of species in the quadrat.

Under the independence hypothesis, *VR*=1, when *VR* > 1, the plant community is positively connected, and when *VR* < 1, the plant community is negatively connected. There are positive associations, negative associations, and non-association among plant communities [58]. In addition, since positive and negative associations between species can cancel each other out, statistical *W* is used to further examine the degree to which *VR* values deviate from 1. When $\chi_{0.95,N}^2 < W < \chi_{0.05,N}^2$, there was no significant correlation between species; On the contrary, there is a significant correlation between species.

Interspecies pair association

Chi-square test (χ^2), association coefficient (*AC*), and Pearson correlation were employed to quantify the interspecific association among dominant species in the community. A 2×2 contingency table was constructed for each pair of species, and the counts for variables *a*, *b*, *c*, and *d* were recorded. Here, *a* represents the number of quadrats where both species A and B coexist, *b* represents the number of quadrats where species B exists but A doesn't, *c* represents the number of quadrats where species A exists but B doesn't, and *d* represents the number of quadrats where neither species A nor B exists.

(1)Chi-Square Statistic Test(χ^2)

The Chi-Square Statistic Test (χ^2) with Yates's correction formula is a qualitative measure used to determine the presence of correlation between two species at a specified confidence level. The formula is as follows [59, 60]:

$$\chi^2 = \frac{N[(|ad-bc|)-(1/2)N]^2}{(a+b)(c+d)(a+c)(b+d)} \quad (9)$$

N is the quadrat number. When *ad* > *bc*, the interspecies pairs are positive, and when *ad* < *bc*, the interspecies pairs are negative. When $\chi^2 < 3.841$, the species pairs were not connected. When $3.841 < \chi^2 < 6.635$, there was a correlation between species pairs. When $\chi^2 > 6.635$, there was a significant association between species pairs.

(2)Association Coefficient AC [7]:

$$ad \geqslant bc \text{ 时}, AC = \frac{ad-bc}{[(a+b)(b+d)]} \tag{10}$$

$$ad < bc \text{ 且 } d \geqslant a \text{ 时}, AC = \frac{ad-bc}{[(a+b)(a+c)]} \tag{11}$$

$$ad < bc \text{ 且 } d < a \text{ 时}, AC = \frac{ad-bc}{[(b+d)(d+c)]}$$

(12)

The AC value further verified the chi-square test results, and the association coefficient (AC) range was [-1, 1]. The closer AC was to 1, the stronger the positive association between species pairs was. On the contrary, the closer the AC value is to -1, the stronger the negative association between species pairs is. If the AC value is 0, the species pairs are completely independent.

(3)Pearson correlation

Pearson correlation coefficient is used to measure the degree of correlation between two species and is a quantitative index of interspecific correlation. The formula is as follows [61]:

$$r_{s(i,k)} = [\sum_{j=1}^{N}(x_{ij} - \overline{x_i})(x_{kj} - \overline{x_k})] / \sqrt{\sum_{j=1}^{N}(x_{ij} - \overline{x_i})^2 (x_{kj} - \overline{x_k})^2}$$

(13)

The $r_{s(i,k)}$ is the Pearson correlation coefficient between species i and species k in the quadrat, N is the total number of quadrats, x_{ij} and x_{kj} are the important value of species i and species k, respectively. They form vector sums $\overline{x_i}$ and $\overline{x_k}$. The $\overline{x_i}$ and $\overline{x_k}$ are the average values of the importance of species i and i in the j-quadrat, respectively. The value of (0,1) $r_{s(i,k)}$ is positively correlated, the value of (-1, 0) $r_{s(i,k)}$ is negatively correlated, and the value of (0) $r_{s(i,k)}$ is not correlated.

Division of ecological species groups

The ecological species group represents the association of species sharing similar ecological habits within a community, providing a more accurate reflection of the relationship between the community and population and the population's adaptation to the environment and dominant ecological factors [62]. In this study, based on the results of the species χ^2 test, AC association coefficient, and Pearson correlation coefficient test, cluster Analysis and Principal Component Analysis (PCA) [63] were used to classify the dominant bryophyte species of stone wall by using niche width matrix as the index.

Data availability

The datasets generated during or analysed during the current study are available from the corresponding author on reasonable request.

References

[1] Joseph, G. The Niche-Relationships of the California Thrasher. *The Auk.* (4), 4. doi:10.2307/4072271 (1917).

[2] Chen, Y., Yuan, Z. L., Bi, S. et al. Macrofungal species distributions depend on habitat partitioning of topography, light, and vegetation in a temperate mountain forest. *Scientific Reports*. **8**(1). https://doi.org/10.1038/s41598-018-31795-7 (2018).

[3] Zhu, G. P., Liu, G. Q., Bu, W. J., Gao. Y. B. Ecological niche modeling and its applications in biodiversity

conservation. *Biodiversity Science*. **21**(01), 90-98. doi: 10.3724/SP.J.1003.2013.09106 (2013).

[4] Gleason, H. A. The individualistic concep of the plant association. *Springer Japan*. (1926).

[5] Legendre, P. L., Legendre, L. F. J. Numerical Ecology. *Ecology*. **63**(2), 853. doi:10.2307/1938982 (1983).

[6] Liu, R. H., Chen, L., Tu, H. R. et al. Niche and interspecific association of main species in shrub layer of Cyclobalanopsis glauca community in karst hills of Guilin, southwest China. *Acta Ecologica Sinica*. **40**(06), 2057-2071. doi:10.5846/stxb201904090689 (2020).

[7] Zhang, L. M., Lan, B., Zhang, D. S. et al. Niche and interspecific association of dominant herbaceous plants in the water-level-fluctuating zone of Fuling—Fengjie section of the Three Gorges Reservoir. *Acta Ecologica Sinica*. **42**(08), 3228-3240. doi:10.5846/stxb202011162953 (2022).

[8] Wang, S. Q., Zhang, Z.H., Wang, Z. H. Bryophyte communities as biomonitors of environmental factors in the Goujiang karst bauxite, southwestern China. *Science of The Total Environment*. 538, 270-278. https://doi.org/10.1016/j.scitotenv.2015.08.049.2015.08.049 (2015).

[9] Baker, T. P., Jordan, G. J., Fountain Jones, N. M. et al. Distance, environmental and substrate factors impacting recovery of bryophyte communities after harvesting. *Applied Vegetation Science.* **21**(1), 64-75. https://doi.org/10.1111/avsc.12343 (2018).

[10] Ruklani, S., Rubasinghe, S. C. K., Jayasuriya, G. A review of frameworks for using bryophytes as indicators of climate change with special emphasis on Sri Lankan bryoflora[J]. *Environmental Science and Pollution Research*. **28**(43), 60425-60437. https://doi.org/10.1007/s11356-021-16588-2 (2021).

[11] Rosentreter, R. Biocrust lichen and moss species most suitable for restoration projects. *Restoration Ecology*. **28**(S2), S67-S74. https://doi.org/10.1111/rec.13082 (2020).

[12] Liu, Y., Zheng, Y. Y., Ao, Y. Y. Niche and interspecific association of dominant bryophytes on different substrates. *Acta Ecologica Sinica*. **39**(01), 286-293. doi:10.5846/stxb201711162042 (2019).

[13] Guo, L., Wei, B. L., Hu, J. T. et al. Ecological niche of bryophytes based on two resource axes. *Acta Ecologica Sinica*. **37**(21), 7266-7276. doi:10.5846/stxb201608101638 (2017).

[14] Wang, J.Q., Li, S. Q. Interspecific associations and niches of dominant bryophytes under different planted forests in the North Shanxi province. *Science of Soil and Water Conservation*. **20**(02), 49-57. doi:10.16843/j.sswc.2022.02.007 (2022).

[15] Xu, S. C., Cao, T., Yu, J. et al. Niche of epiphytic bryophytes on trees in Shanghai City. *Chinese Journal of Ecology*. **25**(11),1338-1343. doi:10.13292/j.1000－4890.2006.0255 (2006).

[16] Liu, Y., Cao, T., Wang, J. Relationships between distribution of soil-born bryophytes in urban area of Hangzhou and related ecological factors. *Chinese Journal of Applied Ecology.* (04), 775-781. doi:10.13287/j .1001 -9332.2008.0192 (2008).

[17] Doležal, J., Korznikov, K., Altman, J. et al. Ecological niches of epiphyllous bryophytes along Afrotropical elevation gradient. *Oikos*. **5**, e09772. https://doi.org/10.1111/oik.09772 (2023).

[18] Farias, R. S., Pereira Silva, M. P., Maciel-Silva, A. S. et al. Influence of environmental factors on the distribution of Calymperes and Syrrhopodon (Calymperaceae, Bryophyta) in the Atlantic Forest of Northeastern Brazil. *Flora*, **234**, 158-164. https://doi.org/10.1016/j.flora.2017.07.011 (2017).

[19] Becker-Scarpitta, A., Auberson-Lavoie, D., Aussenac, R. et al. Different temporal trends in vascular plant and bryophyte communities along elevational gradients over four decades. *Ecology and Evolution*. **12**(8). https://doi.org/10.1002/ece3.9102 (2022).

[20] Mežaka, A. Epiphytic bryophyte and lichen transplant niches along an elevational gradient in Pacific Northwest coniferous forests. *American Journal of Botany*. e16215. https://doi.org/10.1002/ajb2.16215 (2023).

[21] Tang, N., Wang, Z. T., Bao, Y. et al. Exploring the relationship between the plant diversity of the urban remnant mountains and its surrounding urban matrix characteristics：A case study of Guiyang City. *Acta*

Ecologica Sinica. **42**(15), 6320-6334. doi:10.5846/stxb202101070069 (2022).

[22] Collier, M. J. Field Boundary Stone Walls as Exemplars of 'Novel' Ecosystems. *Landscape Research*. **38**(1), 141-150. https://doi.org/10.1080/01426397.2012.682567 (2013).

[23] Ruas, S., Rotchés-Ribalta, R., Ó HUallacháin, D. et al. Assessing stone walls habitat quality - Which factors affect bryophytes and macrolichens on farmland stone walls in Ireland? *Ecological Indicators*. **139**, 108948. https://doi.org/10.1016/j.ecolind.2022.108948 (2022).

[24] Yang, L., Yan, L. B., An, M. T. et al. Competition and synergistic mechanisms of species in Phyllostachys edulis-Alsophila spinulosa association based on niche theory. *Chinese Journal of Applied Ecology*. 34(08), 2065-2072. doi:10.13287/j.1001-9332.202308.002 (2023).

[25] Yu, X. Y., Yu, R., Huang, J. et al. Niche characteristics of dominant plant populations of Loropetalum subcordatum community in Maolan karst forest, Guizhou. *Chinese Journal of Ecology*. 36(12), 3470-3478. doi:10.13292/j.1000-4890.201712.017 (2017).

[26] Song, H. Y., Sun, C. L., Chai, Z. Z. Niche and Interspecific Relationships of Dominant Herbaceous Plant Populations in the Waste Slag Field of A Lead-Zinc Mine in Northwestern Guizhou. *Acta Agrestia Sinica.* **30**(10), 2764-2771. 10.11733/j.issn.1007-0435.2022.10.027 (2022).

[27] Ma, Y. M., Li, Q. H., Pan, S. P. et al. Dynamic analysis of niche and interspecific association of dominant phytoplankton species in Huaxi Reservoir of Guizhou Plateau. *Journal of Lake Sciences.* 33(03), 785-796. doi:10.18307/2021.0314 (2021).

[28] Wang, W., Wang, D.F., Wang, Z.H., Zhang, C.H. Study on Diversity of Bryophytes on the Wall in Karst Urban Guiyang City. *Journal of Tropical and Subtropical Botany*. **26**(05), 473-480. doi: 10.11926/jtsb.3890 (2018).

[29] Zhang, J.T. Quantitative ecology, The third edition. *Beijing: Science Press*. (2018).

[30] Greigsmith, P., Greig, P., Greig, P. et al. Quantitative plant ecology: Studies in ecology. (1983).

[31] Perera-Castro, A. V., Waterman, M. J., Turnbull, J. D. et al. It Is Hot in the Sun: Antarctic Mosses Have High Temperature Optima for Photosynthesis Despite Cold Climate. *Frontiers in Plant Science*. **11**, 1178. https://doi.org/10.3389/fpls.2020.01178 (2020).

[32] Jin, Y., Wang, X. Diversity of lithophytic moss species in karst regions in response to elevation gradients. PLOS ONE. **18**(6), e286722. https://doi.org/10.1371/journal.pone.0286722 (2023).

[33] Manlick, P. J., Pauli, J. N. Human disturbance increases trophic niche overlap in terrestrial carnivore communities. *Proceedings of the National Academy of Sciences.* **117**(43), 26842-26848. https://doi.org/10.1073/pnas.20127741 (2020).

[34] Maccagni, A., Willi, Y. Niche breadth and elevational range size: a comparative study on Middle-European Brassicaceae species. *Phil. Trans. R. Soc. B*. **377**:20210005. https://doi.org/10.1098/rstb.2021.0005 (2022).

[35] Kou, J., Wang, T., Yu, F. et al. The moss genus Didymodon as an indicator of climate change on the Tibetan Plateau. *Ecological Indicators*. **113**, 106204. https://doi.org/10.1016/j.ecolind.2020.106204 (2020).

[36] Yang, X. W., Zhao, Y. G., Xu, M. X. Variation of morphological structure of dominant species in moss crusts in hilly Loess Plateau region. *Chinese Journal of Ecology.* **35**(02), 370-377. doi:10.13292/j.1000-4890.201602.007 (2016).

[37] Yuan, Y. Z., Shi, Y. L., Liu, B. et al. Analysis on niche of bryophyte communities in four habitats in periglacial region of Glacier No.1 of Tianshan Mountains. *Journal of Plant Resources and Environment.* **31**(03), 26-34. doi:10.3969/j.issn.1674-7895.2022.03.04 (2022).

[38] Niu, K. C., Chu, C. J., Wang, Z. H. Dynamic niche: a new foundation for rebuilding theory of community ecology (in Chinese). *Sci Sin Vitae*. **52**(03), 403-417. doi: 10.1360/SSV-2021-0160 (2022).

[39] Rahman, I. U., Hart, R. E., Ijaz, F. et al. Environmental variables drive plant species composition and distribution in the moist temperate forests of Northwestern Himalaya, Pakistan. PLOS ONE, 17(2):e260687.

https://doi.org/10.1371/journal.pone.0260687 (2022).

[40] Pianka, R. E. Niche Overlap and Diffuse Competition. *Proc. Natl. Acad. Sci. U. S. A*. **71**(5), 2141-2145. https://doi.org/10.1073/pnas.71.5.2141 (1974).

[41] Bahtinisha, IMIN., Li, Z. S., Anwar, TUMUR. Niche characteristics of saxicolous lichens in Tianshan No. 1 Glacier, Xinjiang, China. *Journal of Arid Land Resources and Environment.* **36**(01), 159-166. doi: 10.13448 /j.cnki.jalre.2022.021 (2022).

[42] Lu, Y., Chen, W., Yao, J. et al. Multiple Spatial Scale Analysis of the Niche Characteristics of the Rhododendron dauricum Plant Communities in Northeast China. *Chinese Geographical Science*. **30**(4), 614-630. https://doi.org/10.1007/s11769-020-1138-8 (2020).

[43] Webb, C. O., Ackerly, D. D., McPeek, M. A., Donoghue, M. J. Phylogenies and Community Ecology. *Annual Review of Ecology & Systematics*. **33**, 475-505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448 (2002).

[44] Hu, X. J., Cheng, J. M., Yang, X. M. et al. Spatial Distribution Pattern and the Community Characteristic of Quercus liaotungensis Forest in the Ziwuling Region. *Journal of Northwest Forestry University.* **25**(05), 1-6. doi:CNKI:SUN:XBLX.0.2010-05-002 (2010).

[45] Liu, L. T., Wang, X. D., Wen, Q. et al. Interspecific associations of plant populations in rare earth mining wasteland in southern China. *International Biodeterioration & Biodegradation*. **118**, 82-88. https://doi.org/10.1016/j.ibiod.2017.01.011 (2017).

[46] Jim, C. Y. Ecology and conservation of strangler figs in urban wall habitats. *Urban Ecosystems*. **17**(2), 405-426. https://doi.org/10.1007/s11252-013-0322-3 (2014).

[47] Reis, V. A. d., Lombardi, J. A., de Figueiredo, R. A. Diversity of vascular plants growing on walls of a Brazilian city. *Urban Ecosystems.* **9**(1), 39-43. https://doi.org/10.1007/s11252-006-5528-1 (2006).

[48] Jim, C. Y., Chen, W. Y. Habitat effect on vegetation ecology and occurrence on urban masonry walls. *Urban Forestry & Urban Greening*. **9**(3), 169-178. https://doi.org/10.1016/j.ufug.2010.02.004 (2010).

[49] Coelho, M. C. M., Gabriel, R., Hespanhol, H. et al. Bryophyte Diversity along an Elevational Gradient on Pico Island (Azores, Portugal). *Diversity*. **13**(4):162. https://doi.org/10.3390/d13040162 (2021).

[50] Li, Y., Dong, Y. Z., Li, W. Z., Bai, Q., Xu, J. Diversity Research of the Bryophyta on the Wall of Tongwan Castle Site. Chinese Wild Plant Resources. 36(02):61-65. doi: 10.3969/j.issn.1006-9690.2017.02.015 (2017).

[51] Sun, Y. Z., Wang, Z. T., Bao, Y. et al. Response of plant community characteristics of urban remnant mountains to different ways and intensity of artificial disturbance. *Acta Ecologica Sinica*. **43**(11), 4632-4650. doi:10.5846/stxb202202200405 (2023).

[52] Xiong, Y. X. Atlas of Bryophytes of Guizhou (Xiomi Species Volume). *Guiyang: Guizhou Science and Technology Press*. (2011).

[53] Xiong, Y. X. The First Volume of Bryophytes in Guizhou. *Guiyang: Guizhou Science and Technology Press.* (2014a).

[54] Xiong, Y. X. The Second Volume of Bryophytes in Guizhou. *Guiyang: Guizhou Science and Technology Press*. (2014b).

[55] Xiong, Y. X.,Cao, W. The Third Volume of Bryophytes in Guizhou. *Guiyang: Guizhou Science and Technology Press*. (2018).

[56] Hu, Y., Wang, H. C., Jia, H. P. et al. Ecological Niche and Interspecific Association of Plant Communities in Alpine Desertification Grasslands: A Case Study of Qinghai Lake Basin. *Plants*. **11**(20), 2724. https://doi.org/10.3390/plants11202724 (2022).

[57] Schluter, D. A Variance Test for Detecting Species Associations, with Some Example Applications. *Ecology*. **65**(3), 998-1005. https://doi.org/10.2307/1938071 (1984).

[58] Gu, L., Gong, Z. W., Li, W. Z. Niches and Interspecific Associations of Dominant Populations in Three Changed Stages of Natural Secondary Forests on Loess Plateau, P.R. China. *Scientific Reports*. **7**(1):6604. https://doi.org/10.1038/s41598-017-06689-9 (2017).

[59] Song, Y. C. The second edition of Vegetation ecology. *Beijing: Higher Education Press.* (2017).

[60] Tao, M., Yue, X. J., Yue, S. et al. Phytoplankton community structure and cyanobacteria bloom risk of reservoirs in hilly regions of Sichuan Province based on dominant species niche and interspecific association. *Acta Ecologica Sinica*. **41**(23), 9457-9469. doi:10.5846/stxb202008182155 (2021).

[61] Du, Z. Y., Xing, W. L., Xu, L. et al. Niche characteristics and interspecific association of main plant species in antimony mining sites of karst rocky desertification area, Guizhou, China. *Acta Ecologica Sinica*. **43**(07), 2865-2880. doi:10.5846/stxb202203300794 (2023).

[62] Xu, M. H., Liu, M., Zai, D. T., Liu, T. A review of contents and methods used to analyze various aspects of plant interspecific associations. *Acta Ecologica Sinica*. **36**(24), 8224-8233. doi:10.5846/stxb201505311092 (2016).

[63] Tu, H. R., Li, J. F., Yang, L. T. et al. Interspecific associations of the main tree populations of the Cyclobalanopsis glauca community in Karst hills of Guilin, Southwest China. *Chinese Journal of Applied Ecology*. 30(01), 67-76. doi:10.13287/j.1001-9332.201901.018 (2019).

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Competing interests

The authors declare no competing interests.

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