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Lixin Duan
Guizhou University
Xiurong Wang (xrwang@gzu.edu.cn)
Guizhou University

Research Article

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Species diversity and microhabitat characteristics of bryophytes on different types of walls in karst city

Lixin Duan [1], Xiurong Wang [1]*

[1]: College of forestry, Guizhou University, Guizhou 550025, China

*Corresponding author. E-mail: xrwang@gzu.edu.cn

Abstract

The correlation between bryophyte community characteristics, alterations in species diversity, and microhabitat characteristics on various types of urban walls remains ambiguous. This study investigates the distribution and habitat characteristics of bryophytes on various types of urban walls in karst areas. The α and β diversity indices were employed to examine the variation of bryophytes on these walls. Additionally, a canonical correspondence analysis was conducted to analyze the relationship between bryophyte species composition and their microhabitat. The results showed that: (1) There were 14 families, 31 genera, and 80 species of wall bryophytes (including six species of liverworts) on urban walls. Brachytheciaceae, Pottiaceae, and Hypnaceae were the dominant families. Bryophyte species were most abundant on stone retaining walls, followed by concrete revetment. The highest proportion of dominant bryophyte species were found on the concrete face, in the crevasses of stone walls, and on the tops of brick walls. (2) The species distribution across the nine types of walls was highly uneven, stone retaining walls exhibited the highest species diversity, while concrete revetment and freestanding walls demonstrated strong habitat heterogeneity. (3) The species composition of wall bryophytes was intricately linked to the properties of the wall and micro-environmental factors, with wall temperature and air humidity being the key determinants. These findings can serve as a benchmark for assessing the diversity and ecosystems of urban wall bryophytes. By enhancing the conservation and restoration of various types of wall bryophytes, we can bolster the self-sustaining mechanisms of urban ecosystems.

Keywords: City wall, Bryophytes, Species diversity, Microhabitat, Wall properties

1 Introduction

As the availability of land for urbanization diminishes, vertical spaces potentially offer the greatest scope for urban expansion. Walls, constructed from materials such as brick, stone, mortar, or concrete (Jim and Wendy, 2010), serve as distinctive habitats for human settlements and their surrounding environmental organisms and are prevalent in urban ecosystems (Zdeňka and Deana, 2010). Despite their ubiquity, wall ecosystems have not been systematically explored to the same extent as other habitats or ecosystems. Existing studies have shown that walls provide important habitats for a variety of organisms, including vascular plants, ferns, bryophytes, and lichens (Marcus, 2013). Despite the environmental stresses that plants on masonry walls inevitably face, such as dryness, insufficient water and nutrient supply, limited matrix volume, and an alkaline microenvironment caused by binding materials, a large number of plant species have successfully colonized walls globally, thereby enriching the urban biodiversity of stone retaining walls (Reis et al., 2006; Jim and Wendy, 2010; Jim., 2014).

Bryophytes, a vital element of natural plant resources and biodiversity, exhibit unique morphological structures and physiological characteristics. These traits enable them to flourish in harsh environments marked by extreme drought, nutrient scarcity, and cold temperatures(Yang et al., 2016; PereraCastro et al., 2020). Despite their small size, which often leads to their neglect in plant community studies, bryophyte communities are not only widespread but also diverse on urban walls. They perform functions such as rainwater retention, ecological restoration, and environmental monitoring (Roger, 2020; Trujillo-González et al., 2020; Ruklani et al., 2021), playing a pivotal role in extreme wall environments. Moreover, resources such as physical substrate, moisture, nutrients, and microclimate within the wall ecosystem are crucial for the growth of bryophytes (Chameera et al., 2018; Mustafa et al., 2021). These, in turn, provide habitats for small animals, insects, and microorganisms, thereby fostering the development of urban biodiversity. Furthermore, the compositional characteristics of bryophyte species are intimately linked to wall microenvironment factors. Prior research has indicated that the three distinct microenvironments created at the top, vertical plane, and base of the wall display varying plant species distribution. The top and base, which exhibit higher humidity levels, demonstrate greater plant diversity (Duchoslav, 2002). Factors such as the wall's microclimate, the extent of human interference, and the richness of plants in the surrounding habitat can all impact the growth of bryophytes (Oishi, 2019; Tumur et al., 2023). Environmental changes significantly influence the diversity and distribution of bryophyte species, and their community characteristics can serve as valuable indicators of changes in urban environmental quality (Yoshitaka and Tsutom, 2017; Fan et al., 2017). By quantitatively describing the characteristics of the bryophyte community and analyzing the effects of wall microhabitat on the distribution of the plant community, the relationship between the community and its environment can be elucidated. This has significant scientific value for the protection of plant resources and the enhancement of the self-sustaining mechanism of the wall ecosystem.

So far, there has been limited research on wall ecosystems, with the majority focusing on wall habitats and biota, particularly flora (Chen et al., 2020). However, there is a notable lack of investigative reports on bryophytes on domestic walls. Only the earth-rammed walls of the Tongwancheng Site in Shaanxi Province (Li et al., 2017) and the Zhaobi Mountain walls in Guiyang City (Wang et al., 2018) have been studied for bryophyte species. Yet, the intrinsic properties of walls, external environmental conditions, and their effects on bryophyte species composition and diversity have not been discussed. Furthermore, research exploring the relationship between bryophyte diversity and urban environmental factors is gaining momentum(Żołnierz et al., 2022; Tumur et al., 2023). It has been observed that the diversity within bryophyte communities is significantly influenced by the type of substrate(Daniel et al., 2016; Nagase et al., 2023). In fact, while there are numerous walls in karst cities, they often lack landscaping and maintenance. However, bryophytes on bare walls can create low-maintenance and sustainable green wall landscapes with important ecological functions(Jia et al., 2014). Currently, there are few reports on species diversity and microhabitats of different types of wall bryophytes in karst areas. Therefore, In this study, we use the most representative karst mountainous city in Southwest China as a case study to address the following questions: (1) How does the species composition and diversity of bryophyte communities differ on various types of wall substrates? (2) How is the distribution of bryophyte species characterized across different wall types? (3) What is the relationship between the distribution pattern of wall bryophyte communities and microhabitat characteristics? (4) What are the key factors influencing the distribution of wall bryophytes? The findings of this research can provide a foundation for understanding the ecological environment of urban walls, protecting biodiversity, and enhancing the self-sustainability of the urban ecosystem.

2 Materials and methods

2.1 Study area

The study area for this research is the built-up region of Guiyang city center (106°07′-107°17′E, 26°11′-26°55′N), characterized by a karstic hill plain basin landform dominated by mountains and hills. The altitude ranges from 880 to 1659m, with the terrain rising towards the southwest and descending towards the northeast. The climate is subtropical, humid, and mild, with an average annual temperature of 15.3℃, relative humidity of 77%, and total precipitation of 1129.5mm. The region is rich in plant resources, boasting 128 species of bryophytes from 42 families and 80 genera, with Eurhynchium and Pottia being the most common genera (Li, 2021). As of April 2021, Guiyang City's urban area spans 1230km², with the central built-up area covering 369km². The city's terrain is undulating, with numerous remaining mountains in the urban area (Tang et al., 2022). This results in a wide variety of retaining and slope walls, whose unique characteristics provide suitable conditions for the settlement and growth of wall plants.

2.2 Research methods

Based on the Geospatial Data Cloud land use map of Guiyang City (http://www.gscloud.cn/), the research area was set up on the main built-up areas of six urban districts (Guanshanhu, Huaxi, Yunyan, Nanming, Baiyun, and Wudang districts). The elevation of the built-up area, extracted using ArcGIS 10.2, ranges from 989 to 1398m. Sampling points were established on a 1km×1km grid, with 2-10 bryophyte-bearing walls randomly selected from each point as sample sites (Chen et al., 2020). The survey was conducted from January to April 2023. After excluding inaccessible or non-conforming sample plots, a total of 327 sample plots were investigated (Fig 1). Each plot represented a type of wall, including nine types of brick, stone, and concrete structure freestanding wall, construction wall, and retaining wall (Table 1). Due to their ability to create small ecological niches, exhibit diverse ecological microhabitat characteristics even within a few meters (Emrah and Alperen, 2017). This study focuses on the wall as a sample square, so each wall is taken as a large sample square, and each large sample square is divided into four middle sample squares: the top (1m from the wall's peak), the face (excluding 1m below the wall's peak and the base), the base (1m from the ground), and the crevasses (the entire wall) (Fig 1). Within each medium sample square, five small sample plots (10cm×10cm) were demarcated using a metal frame and a five-point sampling method, based on site conditions. Information such as coverage, habitat, sampling site, and sampling time were recorded for each plot. A total of 1804 bryophyte specimens were collected from these small sample squares, identified at the species level, and cross-referenced with "Volumes 1–3 of Bryophyte Flora of Guizhou China" and "Atlas of Bryophytes of Guizhou (Xiomi Species Volume)"(Xiong, 2011; 2014a; b; Xiong and Cao, 2018). The specimens are stored in the bryophyte herbarium of the College of Forestry, Guizhou University.

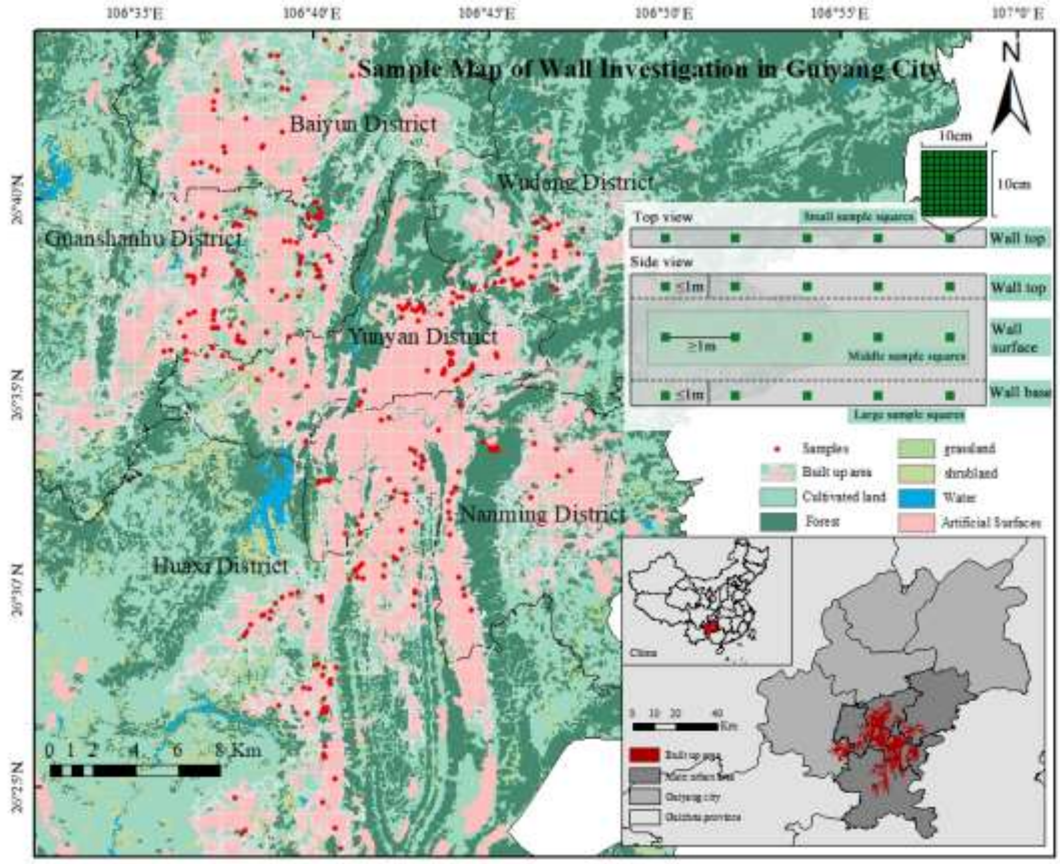

Fig. 1 Distribution of sample plots and sample setup in Guiyang urban area

Table 1 Different types of walls in the sample (The photo was taken by the author)

Concrete revetment	Concrete building wall	Concrete separate wall
		
Stone revetment	Stone building walls	Freestanding stone enclosure
		
Stone retaining wall	Brick building walls	Brick separate enclosure
		

The microhabitats measured in this study encompassed 18 wall attributes and microenvironmental factors (Table 2). The majority of these were determined through field measurements: wall height and length were gauged using a tape measure, while wall humidity and temperature were assessed with a ZTW1601A moisture tester and an AT380 medium and low temperature measuring gun, respectively. The wall's altitude and latitude/longitude were pinpointed using GPS. Light intensity, air humidity, and temperature were recorded using a DLY-1802 illuminance meter and an LM-8000A weather meter. Wall inclination and slope aspects were measured with a geological compass (Zhang et al., 2020). The shading rate and canopy density of the wall were determined following the methods of Wu Ling (Wu et al., 2015) and Smith A M (Smith and Ramsay, 2018). The remaining indicators, such as the degree of wall weathering, wall roughness, human interference, and litter, were evaluated on a scale of 1-5 degrees (Chen, 2020). To minimize errors, all degree evaluations were conducted by a single investigator.

Table 2 The wall characteristics and index types were investigated

Microhabitat	Specific indicators
Wall properties	(1)Wall height; (2)Wall length; (3)Wall inclination; (4)Wall type; (5)Weathering degree of wall; (6)Wall roughness; (7)Wall humidity; (8)Wall temperature; (9)Wall shading rate; (10)The coverage of vines
Wall microenvironment factors	(1)Canopy density; (2)Air humidity; (3)Air temperature; (4)Light intensity; (5)Litter; (6)Elevation; (7)Slope aspects; (8)Human interference

2.3 Data analysis

2.3.1 Importance value

The ecological importance value represents the importance of bryophytes in the ecological environment and shows their ecological dominance (Liu et al., 2008). The formula is as follows:

$$L=(MI+NI)/2 \tag{1}$$

Where L is the ecological importance value; MI is relative coverage; NI is the relative frequency.

2.3.2 *α* diversity index

Margalef richness index (*R*), Shannon-Wiener diversity Index (*H′*), Simpson dominance index (*D*), and Pielou evenness index (*J*) were used to analyze the α diversity index of Bryants (Zhang, 2018). The indices are as follows:

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

$$H' = -\sum_{i=1}^{s} P_i \ln P_i \tag{3}$$

$$D=1-\sum Pi^2 \tag{4}$$

$$J=H'/\ln S \tag{5}$$

Where $Pi=ni/N$, N is replaced by the total moss coverage, ni is replaced by the coverage of the i species, H' represents Shannon-Wiener diversity index, and S represents the number of plot species.

2.3.3 *β* diversity index

Jaccard index and Cody index were selected to analyze the *β* diversity index of bryophytes (Ma et al., 1995), and the indices were as follows:

$$\beta_J=c/(a+b-c) \tag{6}$$

$$\beta c=(a+b-2c)/2 \tag{7}$$

In the formula, c is the number of species shared between the two plots, and a and b are the number of species owned separately by each of the two plots. Between 0 and 1, $0<\beta_J<0.25$ indicates that the two communities are very different; $0.25\leq\beta_J<0.50$ indicates that the two communities are moderately dissimilar. $0.50\leq\beta_J<0.75$ indicates that the two communities are moderately similar.

$0.75 \leq \beta_J < 1$ indicates that the two communities are very similar.

2.4 Data processing

Based on the importance value analysis, OriginPro 9.0 was used to draw a graph to reflect the changing trend of the plant diversity index. Detrended Correspondence Analysis (DCA) was conducted on the species importance data, and the maximum gradient length of the four ranking axes was > 4. Therefore, Canonical Correspondence Analysis (CCA) was used to analyze the habitat characteristics and species composition of bryophytes. This is an eigenvalue ranking method for directly correlating multivariate ecological data matrices. For each scale, two matrices are created (Braak and Milauer, 2012): One is used for "vegetation attributes" × "plots" (response variable), the other for "habitat variables" × "plots" (explanatory variable), and the Monte-Carlo test is used to constrain the significance of the axis (F-value as a statistic). Pearson correlation analysis between wall properties and environmental factors was performed using SPSS 21.0 software. All data operations, statistics, and plots were done in Microsoft Excel 2010, Origin Pro 9.0, SPSS 21.0, and Canoco 5.0.

3 Results and analysis

3.1 Species composition of wall bryophytes

The study identified 80 species of bryophytes, spanning 31 genera and 14 families, across 327 urban wall plots. All but six of these species were mosses. The majority were from the Brachytheciaceae (3 genera, 23 species), Pottiaceae (11 genera, 19 species), and Hypnaceae (5 genera, 9 species) families, which collectively accounted for 65.5% of the total species (Supplementary Table 1). The distribution of bryophyte species varied across different types of walls, with the ranking as follows (Fig 2): stone retaining wall > concrete revetment > stone revetment > stone building walls > freestanding stone enclosure > brick building walls > brick separate enclosure > concrete building wall > concrete separate wall. The importance values of the same species also differed across various walls (Supplementary Table 2). Within the study area, 12 species, including *Brachythecium salebrosum*, *Eurhynchium savatieri*, *Brachythecium amnicola*, *Weisia controversa*, *Gollania ruginosa*, and *Didymodon ditrichoides*, were dominant (importance ≥0.40). Notably, *Weisia controversa*, *Didymodon ditrichoides*, and *Didymodon rufidulus* were found across all wall types, indicating their adaptability and wide distribution. Additionally, *Brachythecium piligerum*, *Pseudosymblepharis angustata*, *Brachythecium pulchellum*, and *Bryum argenteum* (importance value ≥0.25) were also distributed across all wall types.

The study identified 11 bryophyte species that were exclusive to a single type of wall. For instance, *Brachythecium populeum*, *Taxiphyllum aomoriense*, and *Gollania philippinensis* were solely found in concrete revetments. Similarly, *Plagiomnium maximoviczii*, *Racopilum cuspidigerum*, *Trichostomum hattorianum*, *Bryum algovicum*, *Porella obtusata*, and *Porella densifolia* were only observed in stone retaining walls. *Tortella tortuosa* and *Eurhynchium coarctum* were exclusively found in stone building walls. These species' unique physiological adaptation mechanisms suggest a preference for specific substrates as habitats.

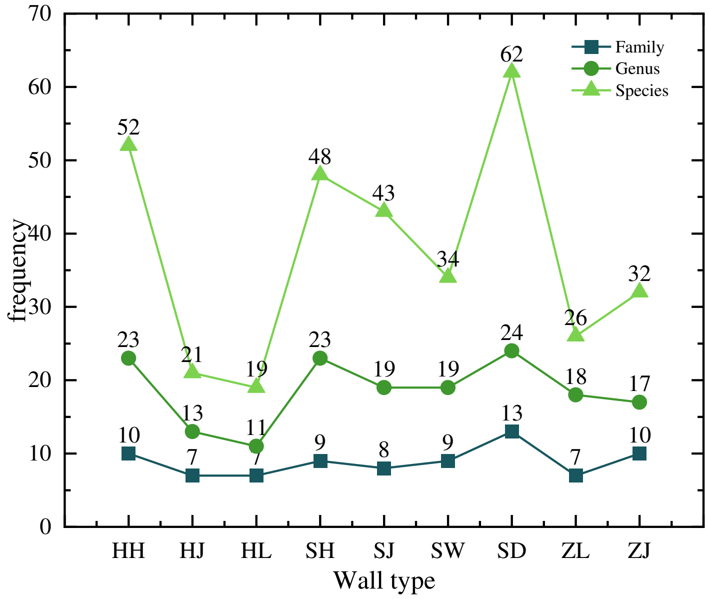

Fig. 2 The dominant families, genera and species of bryophytes on different types of urban walls

Note: HH: Concrete revetment; HJ: Concrete building wall; HL: Concrete separate wall; SH: Stone revetment; SJ: Stone building walls; SW: Freestanding stone enclosure; SD: Stone retaining wall; ZJ: Brick building walls; ZL: Brick separate enclosure.

3.2 Distribution characteristics of bryophytes in different parts of wall

Upon analyzing the nine types of walls (Fig 3), it was observed that the stone retaining wall had the highest number of bryophyte species at the top, base, and gaps. Conversely, the surface of the concrete revetment had the highest number of species. Bryophytes on the concrete and brick separate walls were only found at the top, surface, base, and gaps, with minimal quantities. The analysis of dominant species (Supplement Table 3) revealed that among the three types of concrete walls, the surface had the most abundant dominant species. For instance, *Bryum argenteum* and *Bryum dichotomum* were distributed across two types of walls, followed by dominant species at the base, including *Weisia controversa*, *Didymodon ditrichoides*, and *Bryum argenteum*. Meanwhile, in the stone revetment, the surface had the highest number of dominant species, primarily consisting of *Brachythecium salebrosum*, *Weisia controversa*, and *Rhynchostegium pallidifolium*. In the stone building walls, the dominant species, such as *Brachythecium salebrosum* and *Didymodon rufidulus*, were primarily distributed on the surface and base. In the freestanding stone enclosure, the most dominant species, including *Claopodium aciculum*, *Brachythecium fasciculirameum*, and *Gymnostomum calcareum*, were found at the top. Interestingly, there was no significant difference in the distribution of dominant species across the four parts of the stone retaining wall, which had the highest total number of species. *Brachythecium buchananii* was distributed across all four parts, followed by *Brachythecium fasciculirameum*, *Brachythecium rutabulum*, *Didymodon rufidulus*, and *Racomitrium canescens*. Lastly, the dominant species in brick walls were primarily found at the top, mainly consisting of *Brachythecium piligerum* and *Eurhynchium kirishimense*.

In conclusion, the most dominant bryophyte species were observed on the surface, gaps, and tops of concrete, stone, and brick walls. This suggests that the distribution of bryophyte communities is influenced by the growth substrate and various sections of the walls.

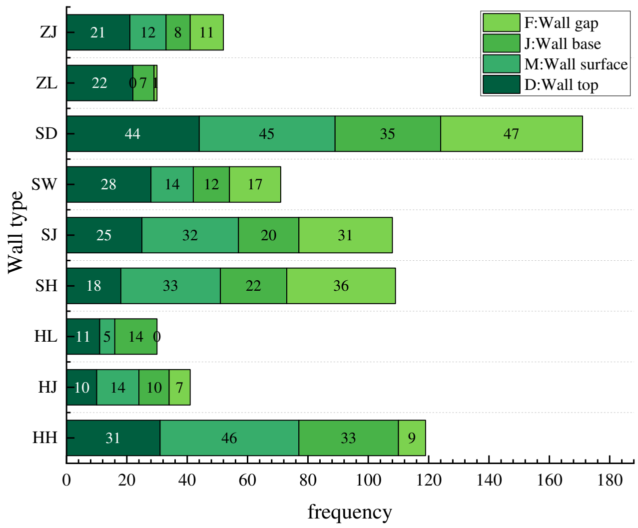

Fig. 3 The dominant species of D, M, J and F bryophytes on different types of urban walls

Note: HH: Concrete revetment; HJ: Concrete building wall; HL: Concrete separate wall; SH: Stone revetment; SJ: Stone building walls; SW: Freestanding stone enclosure; SD: Stone retaining wall; ZJ: Brick building walls; ZL: Brick separate enclosure.

3.3 Changes in wall bryophyte community α diversity along wall types

Figure 4 illustrates significant variations in the alpha diversity index among different wall bryophyte communities. The Margalef abundance index exhibited the most substantial fluctuation, ranging from 6.05 to 14.95, while other indices showed less variation. Generally, the stone retaining wall demonstrated the highest Margalef richness, Shannon-Wiener diversity, Simpson dominance index, and species diversity. The indices for concrete building walls and separate concrete walls were significantly lower than those of other wall types. The freestanding stone enclosure had the highest Pielou uniformity index, followed by the concrete building wall and separate concrete wall, with the stone revetment index being the lowest. This suggests that the distribution of bryophyte individuals on the wall is highly uneven, and the greater the abundance of bryophyte species on the wall, the lower the evenness.

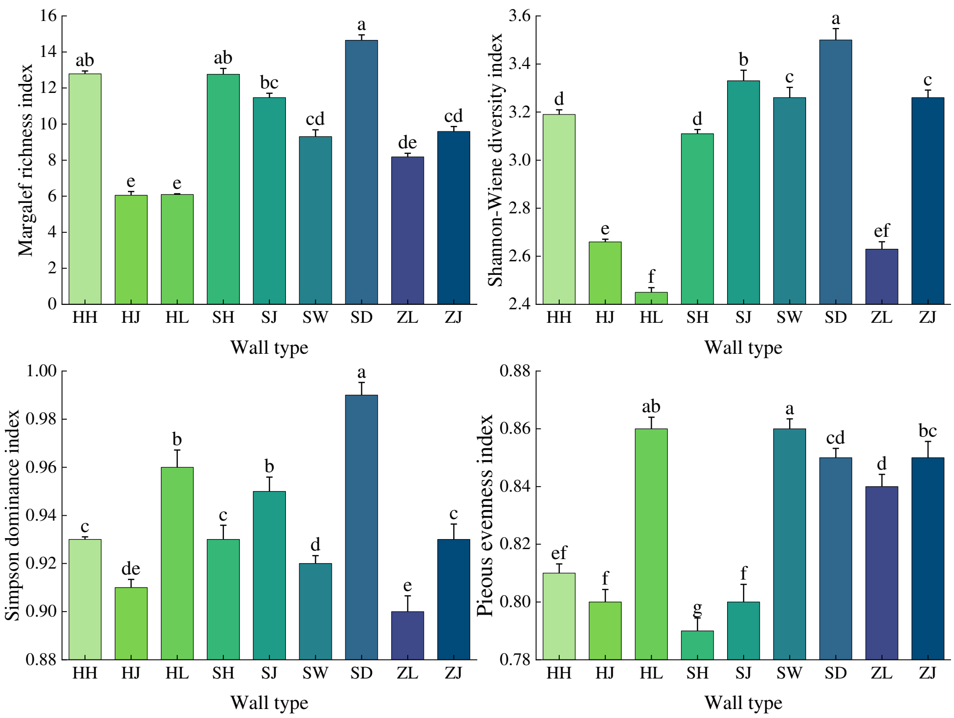

Fig. 4 Analysis of α diversity index of different types of wall bryophytes

Note: HH: Concrete revetment; HJ: Concrete building wall; HL: Concrete separate wall; SH: Stone revetment; SJ: Stone building walls; SW: Freestanding stone enclosure; SD: Stone retaining wall; ZJ: Brick building walls; ZL: Brick separate enclosure.

3.4 Changes in wall bryophyte community β diversity along wall types

The Jaccard similarity coefficient is indicative of the similarity in species composition between communities or samples, while the Cody heterogeneity index represents the rate of species composition replacement along an environmental gradient (Fang et al., 2004). As depicted in Figure 5, beta diversity varies across all wall types, and the overall trend of the Cody index across wall types is inversely related to the Jaccard similarity index. Among the nine wall types, the concrete type (HH+HJ, HH+HL, HJ+HL) exhibited the highest Jaccard similarity coefficient of 0.70 and the lowest of 0.18 across all wall types, demonstrating a trend of initial decrease followed by an increase. This suggests a high dissimilarity and medium similarity in the concrete substrate. Furthermore, among the masonry wall types (SH+SJ, SH+SW, SH+SD, SJ+SW, SJ+SD, SW+SD), the Jaccard similarity coefficients display a slight overall decreasing trend. The Cody index showed significant fluctuations, reflecting the complexity of the habitat. The HH+HL concrete walls had the largest index, indicating a significant difference in the bryophyte community structure and composition compared to other wall types. In conclusion, the habitats of bryophyte communities on different wall types exhibit spatial heterogeneity.

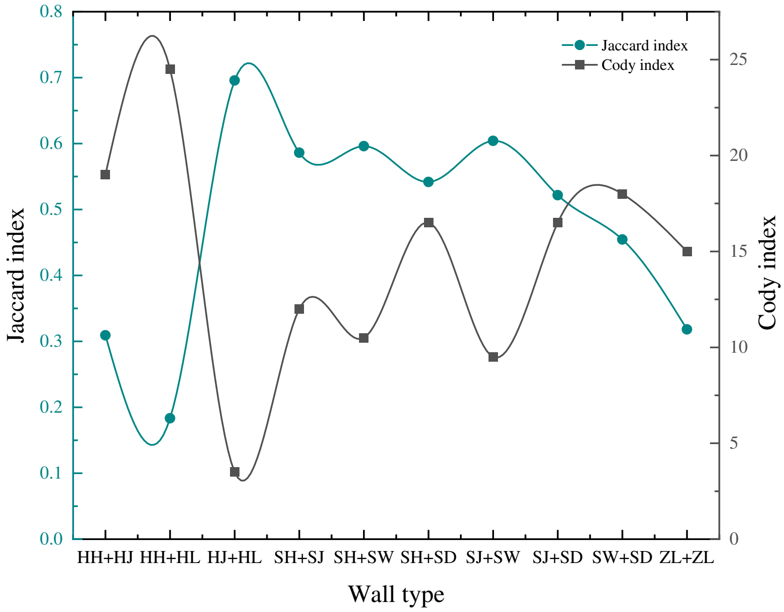

Fig. 5 Analysis of β diversity index of different wall bryophytes

Note: HH: Concrete revetment; HJ: Concrete building wall; HL: Concrete separate wall; SH: Stone revetment; SJ: Stone building walls; SW: Freestanding stone enclosure; SD: Stone retaining wall; ZJ: Brick building walls; ZL: Brick separate enclosure.

3.5 Characteristics of walling bryophyte communities and microhabitats

3.5.1 The relationship between wall attributes and wall microenvironment factors

As depicted in Figure 6 and Supplementary Table 4, the majority of wall properties exhibit significant correlations with wall types. Moreover, the wall's microenvironmental factors were found to have a strong association with air humidity. Both canopy density and human disturbance showed significant positive correlations with wall type (p<0.01), with correlation coefficients of 0.143 and 0.284, respectively. Air humidity also demonstrated a significant positive correlation with wall type (p<0.05), with a correlation coefficient of 0.139. Conversely, wall length, wall temperature, and air humidity displayed significant positive and negative correlations ($p<0.01$), with correlation coefficients of 0.220 and -0.182, respectively. Additionally, the correlation coefficients between the degree of wall weathering and wall roughness, canopy density and wall inclination, and air temperature and wall temperature were substantial, at 0.886, 0.748, and 0.764, respectively. In conclusion, the primary microenvironmental factors influencing wall properties include canopy density, air humidity, litter, and human interference, although other factors also exert varying degrees of influence.

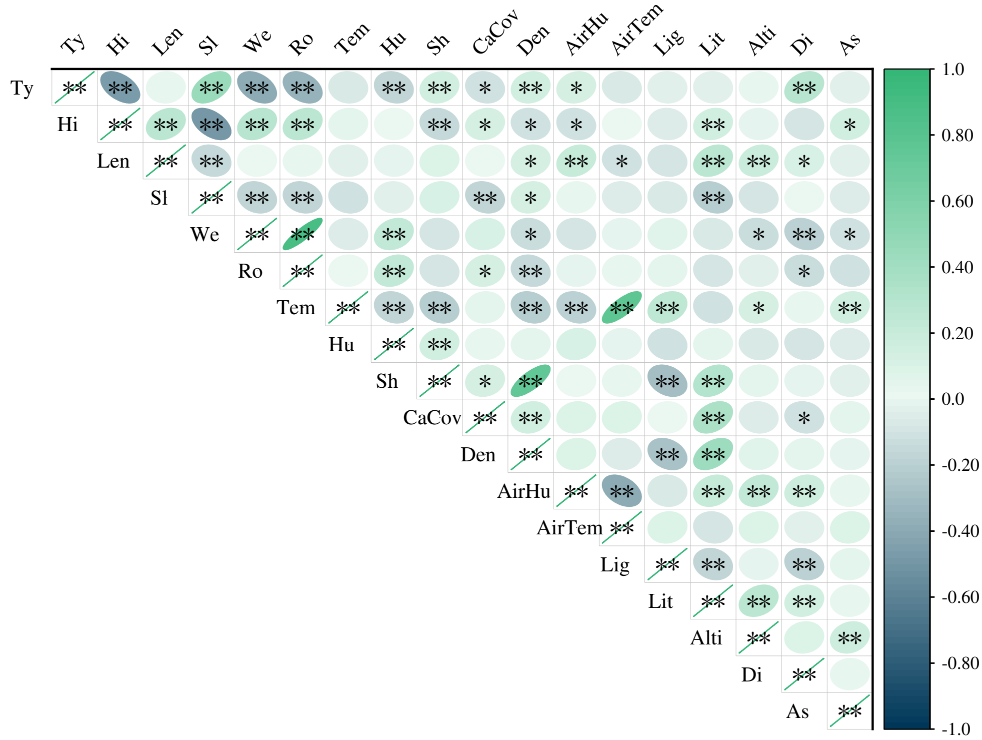

Fig. 6 Analysis of correlation coefficient between 10 wall attributes and 8 wall microenvironment factors

Note:* means significant ($P<0.05$); ** means very significant ($P<0.01$); Ty: Wall type; Hi: Wall height; Len: Wall length; Sl: Wall inclination; We: Weathering degree of wall; Ro: Wall roughness; Tem: Wall temperature; Hu: Wall humidity; Sh: Wall shading rate; CaCov: The coverage of vines; Den: Canopy density; AirHu: Air humidity; AirTem: Air temperature; Lig: Light intensity; Lit: Litter; Alti: Elevation; Di: Human interference; As: Slope aspects

3.5.2 Relationship between bryophyte communities and microhabitats

Through forward selection, nine non-significant factors were eliminated, leaving wall temperature, air humidity, wall shade rate, altitude, wall humidity, litter, wall inclination, and slope aspects as significant contributors (Supplementary Table 5). These eight factors contributed to the plant differentiation pattern at rates of 10.9%, 10.4%, 9.2%, 7.4%, 7.3%, 5.4%, 5.3%, and 5.1% respectively. Their significant correlation effectively explains the environmental variables of wall bryophytes.

As per the CCA ranking chart (Fig. 7), the eigenvalues of the first and second axes were 28.44% and 18.83% respectively, together accounting for 44.13% of the total variation. The cumulative variance of the species-habitat relationship was 72.84% (Table 3). The first axis was associated with four microenvironmental factors. Notably, air humidity was significantly negatively correlated with altitude. The species distribution along the first axis was as follows: *Didymodon ditrichoides*, *Brachythecium perscabrum*, *Didymodon constrictus*, and *Thuidium cymbifolium*, all of which exhibit drought tolerance characteristics, were primarily located in the positive direction of this axis. This suggests that these bryophyte species were predominantly found in wall environments with low air humidity and higher elevation. Conversely, hygrophilic bryophytes such as *Brachythecium piligerum*, *Brachythecium kuroishicum*, *Barbula unguiculata*, and *Hyophila involuta* were distributed in the negative direction. This distribution further confirms that the axis is associated with microenvironmental factors like air humidity and altitude, and that these factors are interrelated. The second axis was associated with wall humidity, wall shade rate, wall inclination, and wall temperature, suggesting that wall properties significantly influence the spatial distribution of wall bryophytes. In line with this, certain plants such as Brachytheciaceae (*Brachythecium buchananii*, *Eurhynchium laxirete*), Mniaceae (*Plagiomnium acutum*, *Plagiomnium vesicatum*), and liverworts (*Marchantia emarginata*, *Porella densifolia*) tend to be found on walls with higher humidity. This indicates that moisture is a key determinant of the composition and distribution of bryophytes on walls.

In addition, the similarity of community species composition across nine wall types (sample plots) was notably high, with a significant correlation observed between them and both wall attributes and micro environmental factors. Concrete revetment and stone retaining walls hosted the most species, with wall humidity and temperature, exemplified by *Claopodium aciculum* and *Gollania varians*, exerting the most influence on species diversity in concrete revetments. Air humidity, elevation, and slope aspects significantly influenced the species on the stone retaining wall and showed a strong positive correlation with the brick separate enclosure. Wall shading rate and litter exhibited a significant negative correlation with species distribution on stone revetments, stone building walls, and brick building walls, as demonstrated by *Brachythecium fasciculirameum*, *Tortella tortuosa*, and *Taxiphyllum cuspidifolium*. The inclination of the building wall, including species such as *Plagiomnium acutum* and *Taxiphyllum cuspidifolium*, was also a determining factor.

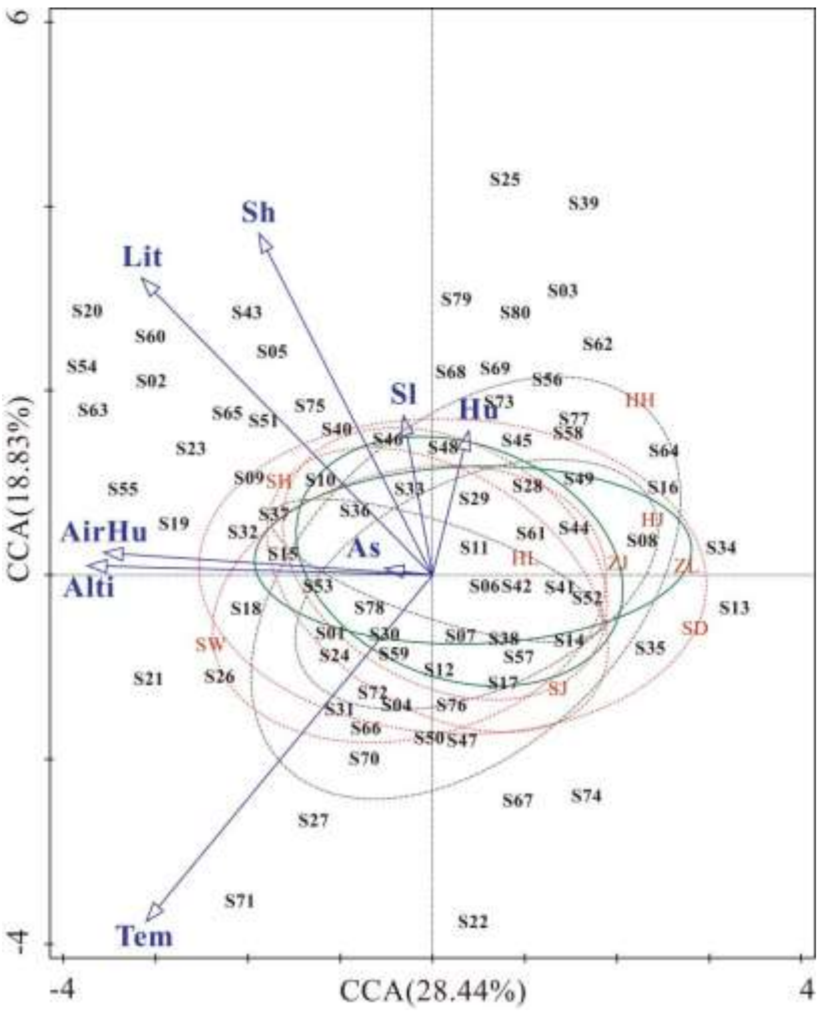

Fig. 7 CCA ranking of the relationship between bryophyte species, wall types (plots) and wall microenvironment factors

Note: Hu: Wall humidity; AirHu: Air humidity; Sh: Wall shading rate; Alti: Elevation; Tem: Wall temperature; Lit: Litter; Sl: Wall inclination; As: Slope aspects; The bryophytes represented by Si are shown in Supplementary Table 2

Table 3 CCA Analysis Results

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.2844	0.1883	0.1636	0.1439
Explained variation (accumulation)	1.30	2.16	2.90	3.56
Pseudo-canonical correlation	0.7011	0.604	0.5685	0.5699
Explained fitted variation (accumulation)	26.55	44.13	59.4	72.84

4 Discussion

4.1 Species composition characteristics of wall bryophytes

Walls are often considered potential habitats in urban landscapes, with bryophytes frequently pioneering the wall substrate due to their extensive species variety and broad habitat adaptability. This study reveals that the species composition of bryophyte communities varies significantly across different wall habitats in Guiyang City. Generally, Brachytheciaceae, Pottiaceae, and Hypnaceae, which are the dominant bryophyte families in Guiyang city, have the highest species count and exhibit strong adaptability to the urban environment. Species such as *Weisia controversa*, *Didymodon ditrichoides*, and *Didymodon rufidulus* are found across all wall types. The species composition characteristics align with the research findings from the Zhaobi Mountain wall in Guiyang (Wang et al., 2018), suggesting that this plant group has a broad ecological range and is well-adapted to various wall environments. In addition, this study found a particularly rich variety of bryophyte species on stone retaining walls and concrete revetments. In terms of dominant species composition, the wall bryophytes were primarily composed of Pottiaceae species, known for their drought tolerance. This supports Li Yang's (Li et al., 2017) perspective that Pottiaceae can serve as an indicator species for wall microhabitat changes. However, 13.8% of rare species and liverworts were only found in specific walls, tending towards more extreme drought or humidity conditions (Zhang et al., 2002). Their limited distribution range may contribute to the differences in species composition among bryophyte communities. In conclusion, the species composition of bryophyte communities is closely tied to the diversity of urban wall plant communities or habitats.

This study reveals variations in species composition and distribution across different sections of the wall. Bryophyte species such as *Bryum argenteum*, *Weisia controversa*, and *Didymodon ditrichoides* are most prevalent on the concrete face. Research indicates that drought-tolerant bryophyte turfs can establish themselves in large numbers on the surface of rough concrete substrates, adapting to extreme drought conditions (Zhang et al., 2002). Additionally, the study found that Brachytheciaceae wefts were widely distributed on the tops of brick walls. This is likely because, in urban brick enclosures, the top and bottom of the walls often serve as micro-stations where species are more likely to colonize (Emrah and Alperen, 2017). Furthermore, Brachytheciaceae and Pottiaceae species were predominantly found in the crevices of stone walls. This is likely due to the narrow gaps between the joints and cracks in the retaining walls constructed from stacked stones, which promote sediment and seed deposition, plant establishment, and moisture accumulation (Jim, 1998). The distribution of bryophyte communities across various sections of the wall effectively mirrors the heterogeneity of the wall's physical environmental characteristics. Enhancing the protection and restoration of diverse bryophyte species on the wall can bolster the self-sustaining capacity of the urban ecosystem.

4.2 Species diversity characteristics of wall bryophytes

Species diversity is pivotal in maintaining the functionality and stability of community ecosystems

(González-Hernández. et al., 2020), serving as an indicator of habitat conditions, community composition, individual distribution patterns, and other community characteristics (Ren et al., 2021). This study revealed that the alpha species diversity index of bryophyte communities in stone retaining walls surpassed that in other types of walls. This suggests a richer species composition, a more complex community structure, and higher stability within these bryophyte communities. However, the species distribution across the nine wall types is highly uneven, particularly in the wall substrates of slope protection and separate enclosure walls. This unevenness may be attributed to variations in the physical structure of the walls, construction methods, slope, and substrates, leading to spatial heterogeneity in the diversity distribution of bryophytes (Jim, 1998). Beta diversity serves as a measure of the differences between vegetation communities and the rate of species change along environmental gradients (Hu et al., 2022). This study found significant variations in the beta diversity of bryophyte communities across different wall types. The Jaccard similarity coefficients reached their highest and lowest values on concrete substrates, indicating a high degree of dissimilarity in bryophyte species and a rapid community turnover rate on concrete revetment and freestanding enclosures. In contrast, the turnover rates were slower on the remaining concrete substrates. The trend of the Cody index contradicts that of the Jaccard similarity coefficient, with three low values of the Cody index appearing in the three gradient ranges of stone walls. This suggests that the beta diversity of these walls is minimal, with less obvious vegetation type transitions and relatively slow species turnover. These findings serve as a reference for studying the spatial heterogeneity of plant communities in wall ecosystems. The similarity across the nine types of wall habitats was high, yet the species diversity within each community and the similarity between communities showed significant differences. This indicates that the distribution of urban wall bryophytes exhibits spatial heterogeneity, which can effectively supplement urban ecological space and enhance urban biodiversity.

4.3 Relationship between wall bryophyte communities and microhabitat characteristics

The potential of walls as habitats is contingent on the environmental characteristics of the urban wall itself and its surroundings. This study found that most wall attributes significantly correlate with wall types. Existing research indicates that the physical characteristics of various wall types differ, influencing numerous other attributes, including moisture retention, microclimate, and decomposition rate (Darlington, 1981). Common cracks and accumulated sediment in brick and stone enhance water storage (Della, 2004), whereas concrete walls lack inherent water storage potential, relying solely on environmental precipitation for moisture (Robert and Simon, 2009). Therefore, the wall microenvironmental factors in this study were strongly associated with air humidity. Canopy density, litter, and human interference also significantly affect wall properties. This could be because that urban walls are predominantly located in areas with height differences, such as mountains, roads, and parks (Chen, 2020), characterized by a rich diversity of trees and plants, and high canopy density. Concurrently, human disturbance is inevitable in urban habitats, which further impacts the habitat potential of wall plants.

This study reveals that Canonical Correspondence Analysis ranking can elucidate the relationship between the distribution of bryophyte communities and microhabitats in urban walls. Wall humidity and temperature are the most influential factors affecting species on concrete slope protection. This may be because concrete revetments are predominantly located in karst geological areas, where some walls are exposed to intense sunlight, resulting in wall temperatures as high as 30.1°C. However, the growth of bryophytes on the substrate surface of the wall can enhance the hydrothermal conditions of the underlying surface and absorb the wall's "moisture" (Patiño and Vanderpoorten, 2018; Cheng et al., 2019), thereby influencing the species composition of bryophytes. Additionally, this study found that air humidity, elevation, and slope aspects significantly influence species on stone retaining walls. Prior research has suggested that slope aspects and elevation directly impact the spatial redistribution of solar radiation and precipitation (Pan et al., 2021). This is the primary reason for changes in species composition and diversity of bryophyte communities (Wang et al., 2023). Thirdly, this study discovered a significant negative correlation between wall shading rate and litter species distribution on stone revetments, stone building walls, and brick building walls. This can be attributed to the fact that slope protection walls are primarily located along urban roads with significant height differences while building walls are situated in residential areas rich in trees. These areas exhibit a high wall shading rate, and litter tends to accumulate more on the steeper slopes of walls and the tops of building walls (Ilić et al., 2023). Lastly, this study also found that wall inclination influences the species of building walls, with certain bryophytes more likely to colonize at the top and base of the vertical wall space. This colonization promotes bryophyte growth by absorbing more water (Katia et al., 2020). In conclusion, the primary factors affecting the distribution of wall bryophytes are wall temperature and air humidity. However, as the types of walls vary, significant differences are observed in the species composition and microhabitat characteristics of the wall bryophytes.

The diversity of bryophyte species in wall ecosystems is intricately linked to habitat heterogeneity, wall characteristics, and microenvironmental factors of the wall. Future studies should consider long-term, seasonal follow-ups, in conjunction with the role of other vascular plants. This approach will provide a clearer understanding of the changes in urban wall bryophyte community diversity and its environmental driving mechanisms, thereby enhancing the biodiversity and ecological resilience of urban ecosystems.

5 Conclusion

(1) There were 14 families, 31 genera, and 80 species of wall bryophytes (including six species of liverworts) in Guiyang city. Brachytheciaceae, Pottiaceae, and Hypnaceae were the dominant families. Bryophyte species were most abundant on stone retaining walls, followed by concrete revetment. The highest proportion of dominant bryophyte species were found on the concrete face, in the crevasses of stone walls, and on the tops of brick walls.

(2) Alpha species diversity indicates that the walling bryophyte community has a rich species composition, relatively complex community structure, and high stability, but the species distribution was very uneven. The beta diversity fluctuated in the whole range of wall types, and bryophyte species were very different on concrete revetment and freestanding enclosures, and community turnover rates were rapid. The type transition of moss vegetation in stone walls was not obvious, and the species turnover rate was relatively slow. The distribution of species across the 9 types of walls was highly uneven, with the construction method, slope, and substrate of the walls significantly influencing the diversity distribution of bryophytes. For instance, stone retaining walls exhibited the highest species diversity, while concrete revetment and freestanding walls demonstrated strong habitat heterogeneity.

(3) The Pearson and Canonical Correspondence Analysis results indicate a significant correlation between most wall attributes and wall types, while wall microenvironment factors closely align with air humidity. The species composition of wall bryophytes was intricately associated with wall properties and microenvironmental factors, with wall temperature and air humidity serving as key determinants. As wall types vary, significant differences emerge in the species composition of wall bryophytes and

their microhabitat characteristics. Specifically, wall humidity and temperature significantly impact the species found on concrete revetments, while air humidity, elevation, and slope aspects greatly influence the species present on stone retaining walls. The species distribution of wall shade and litter on stone revetments, stone building walls, and brick building walls show a negative correlation. The inclination of the wall significantly influences the species found on building walls.

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