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Bryophyte diversity across volcanic microhabitats in the Khaybar White Volcano Geopark (Saudi Arabia)

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CITATION

Alsahli W, Alhazzaa A, Alotaibi R, Alotaibi D, Aldosari R, Al-Megrin W A I. Prevalence of different gastrointestinal parasite horse infections in Riyadh, Saudi Arabia. **Biodiversity research journal**, 2025. 2, (**1**); 209-228.

ABSTRACT

Bryophytes are generally rare in arid environments, where the availability of suitable microhabitats significantly influences their occurrence. Volcanic landscapes may offer a variety of microsites that moderate extreme climatic conditions; however, bryophyte communities in these environments are poorly documented, particularly in the Arabian Peninsula. This study aimed to investigate bryophyte diversity and the role of volcanic microhabitats in structuring bryophyte assemblages within the volcanic landscapes of the Khaybar White Volcano Geopark in Saudi Arabia. Field surveys were conducted across a large volcanic area using standardized field relevés adapted from bryosociological practices. A total of 450 relevés were conducted at 551 sampling sites distributed across a 5 × 5 km grid, yielding 1,806 floristic records. Twelve bryophyte-bearing microhabitats were identified and characterized. Species presence-absence data were analyzed using Jaccard distances and Non-metric Multidimensional Scaling (NMDS) to explore floristic relationships among microhabitats. Redundancy Analysis (RDA) with forward selection was applied at the relevé level to identify abiotic predictors structuring species composition, including microhabitat slope, substrate depth, and categorical microhabitat descriptors.The results reveal a diverse bryophyte assemblage associated with distinct volcanic microhabitats, including shaded lava fissures, soil pockets, runoff channels, and geothermal fumaroles, the latter supporting several specialized taxa. The RDA explained 33.8% of total inertia, with microhabitat categories accounting for the largest fraction of explained variation. Species distribution patterns indicate that small-scale substrate heterogeneity plays a key role in maintaining bryophyte diversity in this extremely arid environment. These findings highlight the ecological importance of microhabitats created by volcanic substrates and suggest that such microsites may contribute to the persistence of bryophytes in desert landscapes.

KEYWORDS: Bryophytes, Volcanic microhabitats, Xerophytic flora, Geodiversity, Microhabitat heterogeneity, Conservation

INTRODUCTION

The Kingdom of Saudi Arabia (KSA) occupies a significant portion of the Arabian Peninsula, covering approximately 2.15 million km² (Chaudhary, 2001). Its diverse landscapes include extensive sandy deserts in the central and eastern regions, as well as mountainous areas exceeding 3,700 meters in elevation in the more humid southwest.

This geographic location, situated at the crossroads of Africa, Asia, and Europe, is reflected in its bryoflora, which comprises xerothermic, tropical, and paleotropical elements; however, true endemic species are relatively scarce (Kürschner & Ghazanfar, 1998; Kürschner, 2000). Bryophytes, which are highly dependent on local humidity, exhibit their greatest diversity in KSA primarily in the monsoon-influenced mountains of the South-Hejaz and Asir regions (Kürschner & Ghazanfar, 1998). In stark contrast, the hyper-arid areas, such as the Rub' al-Khali, support only a limited number of drought-tolerant taxa in the interior lowlands, including species like *Tortula atrovirens*, *Crossidium squamiferum*, and *Trichostomopsis australasiae*.As a result, previous surveys have predominantly focused on the humid southern mountain ranges, leaving many areas in central and northern Arabia inadequately documented.

Across Southwest Asia, bryoecological information remains fragmentary (Frey & Kürschner, 1981; Hugonnot et al., 2025a). Turkey represents an important exception, having recently benefited from a regional syntaxonomic synthesis (Alataş et al., 2023). Elsewhere in the Middle East and on the Arabian Peninsula, available studies vary in both scope and methodology (e.g., Gilli, 1941–1977; Frey & Probst, 1973; Kürschner, 1988; Kürschner & Ghazanfar, 1998). To date, only eleven bryophyte communities have been described from the Arabian Peninsula, primarily consisting of tufa-forming and epiphytic assemblages (Kürschner, 1984, 2003; Deil, 1989; Hugonnot et al., 2026a). These studies generally follow the Braun–Blanquet phytosociological tradition and place limited emphasis on quantitative analyses that link species assemblages to their abiotic context.

The Khaybar Volcanic Geopark, located within the Harrat Khaybar volcanic province in the Al Madinah region, provides an appropriate setting to investigate bryophyte–environment relationships in an otherwise hyper-arid landscape. The area features extensive lava fields, several types of volcanoes, contrasting basaltic formations, lava tubes, blowholes, and geothermal cavities. Together, these features create a wide variety of substrates, microtopographies, and local moisture conditions. Such ecological contexts are particularly relevant for bryophyte studies, as bryophytes are poikilohydric organisms that respond directly to substrate properties and ambient humidity (During, 1992; Bates, 1998; Glime, 2017). Previous studies have demonstrated that volcanic substrates may influence cryptogamic diversity through effects on water retention, reduction of extreme temperatures, shading, and mineral composition (Ah-Peng et al., 2007; Gabriel et al., 2006; Cong et al., 2023).

This study aims to document bryophyte diversity across the volcanic substrates of the Khaybar lava fields and to examine how microhabitat variability structures bryophyte assemblages in this extremely arid environment. We hypothesize that volcanic microhabitats with differing substrate structures, exposure, slope, and moisture retention support distinct bryophyte assemblages. Khaybar serves as a model system to explore the relationship between volcanic geodiversity and bryophyte communities. Rather than applying a classical phytosociological framework, we adopt a quantitative approach focusing on species–substrate relationships and the role of microhabitats in shaping bryophyte distribution patterns. More specifically, the objectives are (1) to compare bryophyte composition across the main volcanic microhabitats, (2) to identify the substrate and microtopographic variables influencing species distribution, and (3) to determine which microhabitats contribute most to floristic richness within this hyper-arid landscape. The results are discussed from a conservation perspective relevant to the Khaybar White Volcano Geopark.

Study area

Harrat Khaybar represents one of the most extensive lava fields in Saudi Arabia, covering more than 20,000 km². The volcanic eruptions began approximately 10 million years ago and continued through multiple eruptive phases into recent centuries (Camp & Roobol, 1989; Moufti & Németh, 2016). The harrat is characterized by a wide range of volcanic edifices, including numerous cinder cones and shield volcanoes, as well as extensive lava flows of varying ages, ranging from deeply weathered surfaces to very young flows. These features result from repeated eruptions associated with the Red Sea rifting, which induced crustal faulting and partial melting of the continental lithosphere (Camp & Roobol, 1989; Camp et al., 1991; Rasul et al., 2015).

Geothermal manifestations have also been documented in the area, and Khaybar has been recognized as a potentially promising site for geothermal energy exploration (Lashin et al., 2015). Active fumaroles emitting visible steam have been reported from several locations within the harrat (Roobol et al., 1995; Roobol et al., 2007; Chandrasekharam et al., 2015), including at least one located within a large lava tube system (Pint, 2006, 2009).

Within this volcanic province, the Royal Commission for AlUla has established the Khaybar White Volcano Geopark, which extends across approximately 600 km² (Fig. 1). Elevation in Harrat Khaybar ranges from approximately 1,800 m on the surrounding plateau to 2,093 m above sea level at Jabal Abyad, the highest point in the area. The Geopark encompasses basaltic volcanoes and extensive lava fields, but also includes rare comenditic domes and flows, derived from the re-melting of Precambrian basement material (Baker et al., 1973). The youngest eruption occurred at Jabal Qidr (often referred to as the "Black Volcano" or "Pot Mountain"), which produced its most recent lava flows only 700–1,000 years ago (Moufti & Németh, 2016). The variety of volcanic features has created a wide range of substrate types, from 'fresh' looking pahoehoe lava fields to gravelly slopes.

Figure 1: Location of Khaybar White Volcano Geopark within the Arabian Peninsula (QGIS 3.40).

Northern Arabia has an arid climate characterized by extremely hot, dry summers, while winters range from mild to relatively warm. Precipitation is primarily associated with cyclonic systems moving from the Mediterranean or Atlantic during winter and spring. Rainfall patterns are highly irregular, both spatially and temporally, often occurring as intense, short-lived storms. In many years, certain areas may experience almost no precipitation. Climatic records from the Al Madinah meteorological station illustrate these conditions well (Fig. 2), with average annual rainfall values ranging from only 36 to 44 mm and a mean annual temperature of approximately 29 °C.

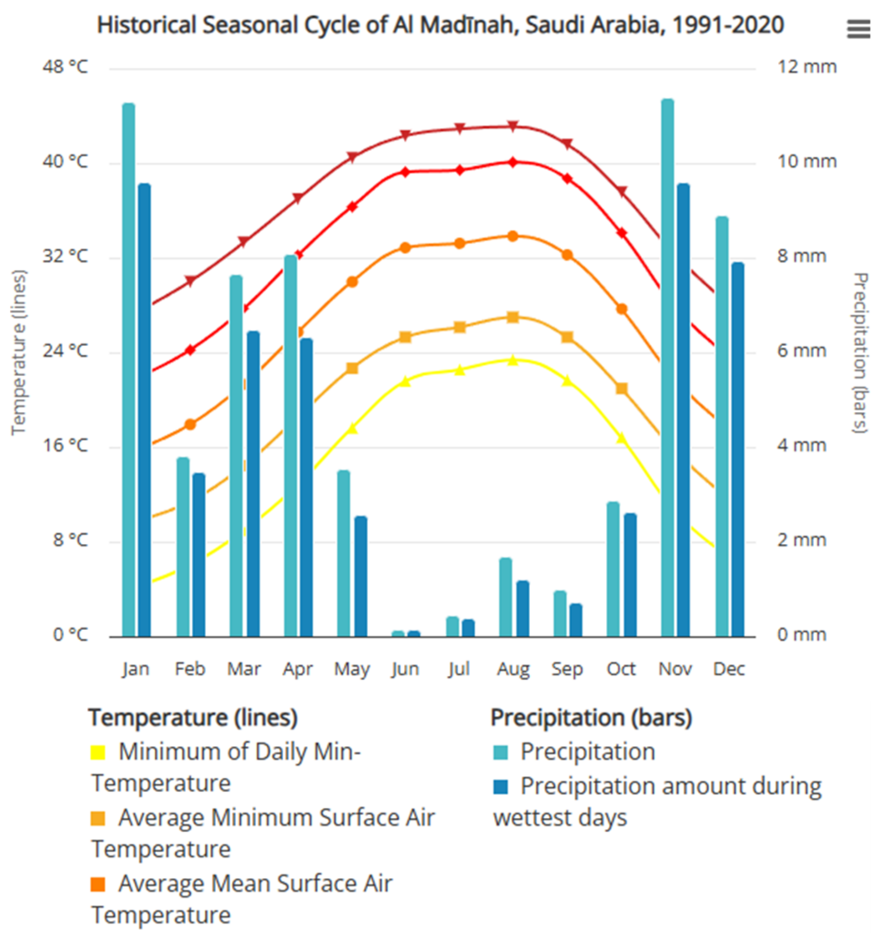

Figure 2: Climatogram for Al Madinah (26 ° 37 ′N; 37 ° 58 ′E) meteorological station (Data: 1991–2021; Climate Change Knowledge Portal)

Methods and Materials

Study Design

Fieldwork was conducted during two campaigns: from 21 to 23 February 2024 and from 15 February to 17 March 2025. A total of 551 sampling sites were visited across the study area (Fig. 3). To ensure systematic and exhaustive bryofloristic coverage, the study area was overlaid with a 5 × 5 km grid derived from high-resolution aerial imagery. This spatial framework served three purposes: guiding survey allocation, structuring sampling effort, and facilitating logistical organization.

Prior to fieldwork, high-resolution imagery was examined to identify geomorphological features likely to host bryophyte assemblages (Fig. 4). Target features included shaded north-facing slopes, block screes, wadi systems, contrasting volcanic landforms, and areas with atypical substrates or enhanced moisture availability. Accessibility was assessed using mapped 4×4 tracks, and local rangers provided additional guidance regarding site access and potentially favorable localities.

Sampling Strategy

The sampling design was stratified and targeted rather than random. Survey effort was distributed across grid cells and focused on geomorphological situations considered potentially favorable to bryophytes. This strategy aimed to maximize species detection in an otherwise extremely species-poor environment.

This approach was deemed appropriate given the study's primary objective: to document bryophyte diversity and characterize species–microhabitat relationships rather than to produce unbiased estimates of species frequencies or occupancy rates at the landscape scale. In a hyper-arid environment where bryophytes are extremely sparse and patchily distributed, a random sampling design would have yielded predominantly empty relevés and severely underestimated local diversity. It should be noted that targeting a priori favorable sites introduces a positive detection bias; occurrence frequencies reported here reflect the proportion of bryophyte-bearing relevés in which each taxon was recorded and should not be interpreted as landscape-level occupancy estimates.

Within each 25 km^2 grid cell, surveys followed a consistent structure that combined four complementary approaches: vehicle-based reconnaissance to access remote sectors and optimize spatial coverage across the large volcanic area; pedestrian prospection at selected sites, where all bryological observations were made on foot; targeted inspection of sites identified a priori as favorable based on imagery analysis; and opportunistic searches of additional microhabitats encountered in the field.

Not all visited sites yielded bryophyte records; in a hyper-arid environment, a proportion of surveyed localities proved devoid of bryophytes, and relevés were only established where at least one bryophyte taxon was detected.

Data Collection

Data were collected using a standardized protocol derived from bryosociological practice, without applying a formal phytosociological framework. Relevés were not based on fixed-area plots; instead, each relevé corresponded to a homogeneous bryophyte-bearing microhabitat patch surveyed exhaustively. For each relevé, species abundance and dominance were recorded using adapted scales. Key environmental variables recorded included slope, substrate depth, aspect, and vegetation cover.

Two slope measurements were distinguished: overall slope, which corresponds to the inclination of the surrounding geomorphological unit (such as a lava slope or a wadi flank), and microhabitat slope, which refers to the local inclination of the bryophyte-bearing surface (such as vertical block faces or inclined sediment pockets). This distinction allows for separating landscape-scale topographic context from the fine-scale conditions directly experienced by bryophytes.

Nearly all 41 grid cells were surveyed, although four remote units were inaccessible and excluded. Survey intensity varied among cells due to local differences in richness and logistical constraints, but a consistent study design was maintained throughout. In total, 450 relevés yielded 1,806 floristic records. Species occurrence frequencies were calculated at both habitat and microhabitat levels as the proportion of relevés in which each taxon was recorded. All sites were photographed to document habitat structure and microhabitat conditions. No physical or chemical soil analyses were conducted, as the study primarily aimed to assess floristic patterns in relation to field-observable microhabitat and substrate features at the landscape scale.

Species assemblages were summarized for each of the twelve microhabitats using lists of frequent taxa, exclusive or quasi-exclusive taxa, and shared background flora. A binary presence–absence matrix (species × microhabitats) was constructed to analyze distribution patterns, with species ranked by frequency across microhabitats. A heatmap was employed to visualize shared versus restricted occurrences.

Microhabitat Classification

Microhabitats were treated as operational, fine-scale ecological units defined a priori in the field. They correspond to recurrent ecological situations characterized by consistent combinations of substrate structure, microtopography, and contrasting shelter-versus-exposure conditions relevant to bryophyte establishment and persistence. They do not represent formal geomorphological or phytosociological entities, and no attempt was made to describe new bryophyte associations. Although not strictly bounded, these categories are associated with underlying geological factors such as rock type, volcanic formation, and erosion mechanisms. They were not treated as independent sampling units but as operational, integrative descriptors capturing sets of ecological constraints that were only partly represented by measured continuous variables.

On this basis, twelve bryophyte-bearing microhabitats were identified through expert field assessment (Table I; Figs. 5–6). The focus was on identifying environmental constraints and habitat types of potential conservation relevance within a hyper-arid volcanic landscape.

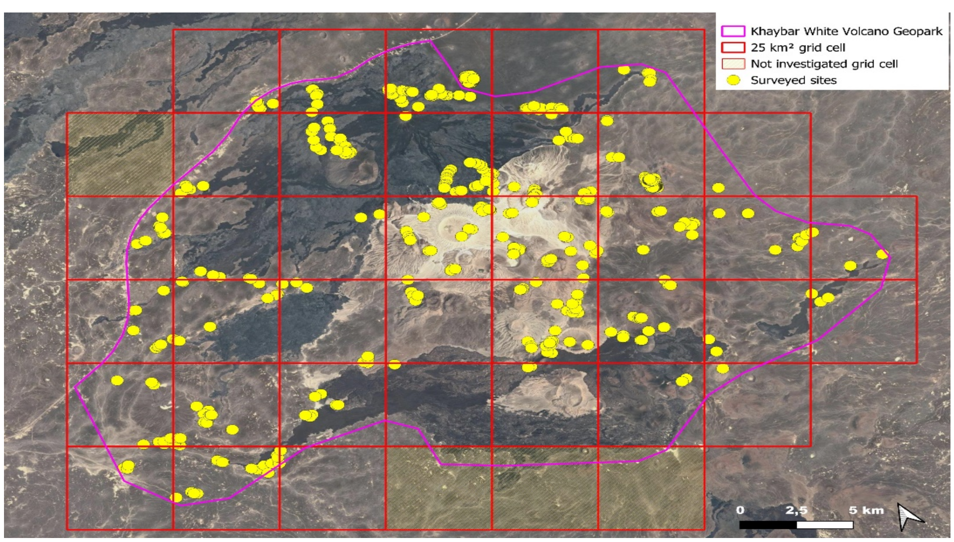

Figure 3. Distribution of the 551 surveyed sites across the Khaybar White Volcano Geopark, superimposed on the 5 × 5 km sampling grid (QGIS 3.40).

Figure 4. Representative view of volcanic landforms in the Khaybar White Volcano Geopark.

Table I: Recognized microhabitats within Khaybar White Volcano Geopark

Microhabitat	Explanation	Geological formation	Structure	Wadi	Texture
Volcanic cliff face	Smooth basalt rock wall forming a vertical volcanic cliff face	Strato volcano	Scarp	no	Rock surface
Rock block face	Exposed basaltic surface, often with high microtopographic heterogeneity	Strato volcano	Inclined slope	no	Rock surface
Consolidated pozzolanic deposit	Indurated pyroclastic substrate of pozzolanic composition, likely altered tuff	Strato volcano	Inclined slope	no	Compact gravel
Earthy patch beneath boulders	Fine-textured soil accumulation in a sheltered microsite beneath large volcanic blocks	Strato volcano	Inclined slope	no	Boulder
Fumarole	Active or relict geothermal vent, often with elevated temperatures and mineral-enriched substrate	Strato volcano	Crater	no	Boulder
Cemented detrital fill in erosional runnels	Cemented detrital fill within erosional runnels, reflecting the induration of coarse comendite sediments accumulated in small incised channels.	Shield Volcano	Crater	no	Compact gravel
Aeolian dust deposits	Localized accumulation of fine particles forming a stable soil pocket	Lava field (Harrat)	Fresh lava flow	no	Sand grey, less than 4 mm
Rock fissures beneath lava slab	Narrow crevices in basaltic rock, offering sheltered microsites with increased moisture retention	Lava field (Harrat)	Crevice	no	Sand grey, less than 4 mm
Earthy patch at the burrow entrance	Soil accumulation enriched by bioturbation at the entrance of a burrowing animal	Volcanic fissure	Fresh lava flow	no	Sand grey, less than 4 mm
fuge beneath a lava slab, subject to episodic wadi inun	Protected soil pocket under a lava slab, flood-prone during wadi discharge events	Volcanic fissure	Cave	yes	Sand grey, less than 4 mm
Earthy banks	Slightly inclined accumulations of loose volcanic soil		Valley	yes	Sand grey, less than 4 mm
Exposed mudflat	Temporarily desiccated sedimentary surface, usually fine-textured and subject to periodic waterlogging		Valley	yes	Mud flats

1: Volcanic cliff face

2: Rock block face

3: Consolidated pozzolanic deposit

4: Earthy patch beneath boulders

5: Fumarole

6: Cemented detrital fill in erosional runnels

Figure 5: Diversity of bryophyte-bearing microhabitats associated with volcanic landforms in the Khaybar White Volcano Geopark (see Table I and Fig. 7).

7: Aeolian dust deposits

8: Rock fissures beneath lava slab

9: Earthy patch at burrow entrance

10: Soil refuge beneath a lava slab, subject to episodic wadi inundation

11: Earthy banks

12: Exposed mudflat

Figure 6: Diversity of bryophyte-bearing microhabitats associated with volcanic landforms in the Khaybar White Volcano Geopark (see Table I and Fig. 7).

Data Analysis

All statistical analyses were performed in R, utilizing the vegan package for ordination analyses and associated routines. Pairwise Jaccard distances were calculated from the presence-absence matrix, which were then used to perform a two-dimensional Non-metric Multidimensional Scaling (NMDS) ordination, providing a synthetic visualization of floristic affinities among microhabitats.

To investigate relationships between bryophyte assemblages and abiotic conditions, abundance–dominance data recorded in each relevé were Hellinger-transformed prior to analysis (Legendre & Gallagher, 2001). Environmental predictors included continuous variables (slope, microhabitat slope, and substrate depth) and categorical microhabitat descriptors coded as dummy variables.

Exploratory detrended correspondence analyses (DCA; not shown) indicated short compositional gradients (< 3 standard deviation units), supporting the use of linear ordination methods. Redundancy Analysis (RDA) with forward selection was applied to identify significant predictors (Blanchet et al., 2008). Adjusted R^2 was used as the selection criterion, and model significance was assessed using Monte Carlo permutation tests (n = 999).

Predictor collinearity was examined prior to model selection, revealing that several categorical and continuous descriptors were partially redundant. Forward selection and variance partitioning were employed to retain only the most informative predictors. Variance partitioning quantified the unique and shared contributions of topographic, edaphic, and microhabitat variables to the total explained variation.

Analyses were conducted at two complementary levels. At the relevé level, constrained ordination (RDA) related fine-scale variation in species composition to measured environmental gradients. At the microhabitat level, descriptive and exploratory approaches-including heatmaps, NMDS, and core/exclusive species assignments-were used to summarize floristic affinities across recurrent ecological situations.

The distinction between core, shared, and exclusive species serves as an analytical heuristic to highlight contrasting ecological functions rather than as a formal classification. For each microhabitat, species were assigned to three groups:

- **Core species**: occurring in at least two-thirds of the microhabitats (≥ 8/12);
- **Exclusive species**: restricted to a single microhabitat;
- **Other shared species**: occurring in more than one microhabitat but not frequent enough to qualify as core taxa.

A stacked bar plot was utilized to compare the relative proportions of these three groups across microhabitats. Analyses based on microhabitat-level aggregation-including presence–absence matrices, heatmaps, NMDS, and core/exclusive species assignments-are intended as descriptive and exploratory syntheses. In contrast, constrained ordination analyses (RDA) were conducted at the relevé level to relate species composition to measured environmental gradients.

Taxonomy and Voucher Specimens

Taxonomy follows Kürschner & Frey (2020), with the exception of the eleven cases listed in Hugonnot et al. (2025b). Some taxa present unresolved taxonomic issues and are reported provisionally, including

Didymodon cf. rigidulus, Fissidens cf. arnoldii, and Entosthodon cf. commutatus. Voucher specimens are held in the private herbarium of V. Hugonnot and F. Pépin. Specimens were identified using standard floras and taxonomic treatments for Southwest Asian bryophytes, with microscopic examination when necessary. Problematic material was retained under open nomenclature.

Results

Microhabitat Diversity

The survey of volcanic formations at Khaybar revealed a wide range of bryophyte-bearing microhabitats closely linked to geological structure and local erosional dynamics (Fig. 5, 6, 7). In stratovolcanoes, bryophytes and other cryptogams were primarily associated with vertical cliff faces (1), exposed block faces (2), and consolidated pozzolanic deposits (3). Additional microhabitats were identified beneath boulder accumulations (4) and around active or fossil fumaroles (5). The shield volcano exhibited more limited bryophyte development, primarily within cemented detrital fills of erosional runnels (6). Lava fields displayed a distinct suite of microhabitats, including aeolian dust deposits (7), fissures beneath lava slabs (8), and sheltered soil pockets occasionally influenced by episodic wadi flooding (10). Adjacent wadis provided further suitable situations, such as earthy patches around burrow entrances (9), loose earthy banks (11), and exposed mudflats (12).

Species Richness and Floristic Backbone

Across the twelve microhabitats, species richness was relatively homogeneous, with most microhabitats sharing a recurrent assemblage of bryophytes (Fig. 8; Table II). This widespread background flora—dominated by taxa such as *Trichostomopsis australasiae*, *Crossidium squamiferum*, *Didymodon cf. rigidulus*, *Entosthodon cf. commutatus*, and *Grimmia orbicularis*—occurred across both exposed and sheltered volcanic settings, accounting for the limited floristic originality observed among microhabitats.

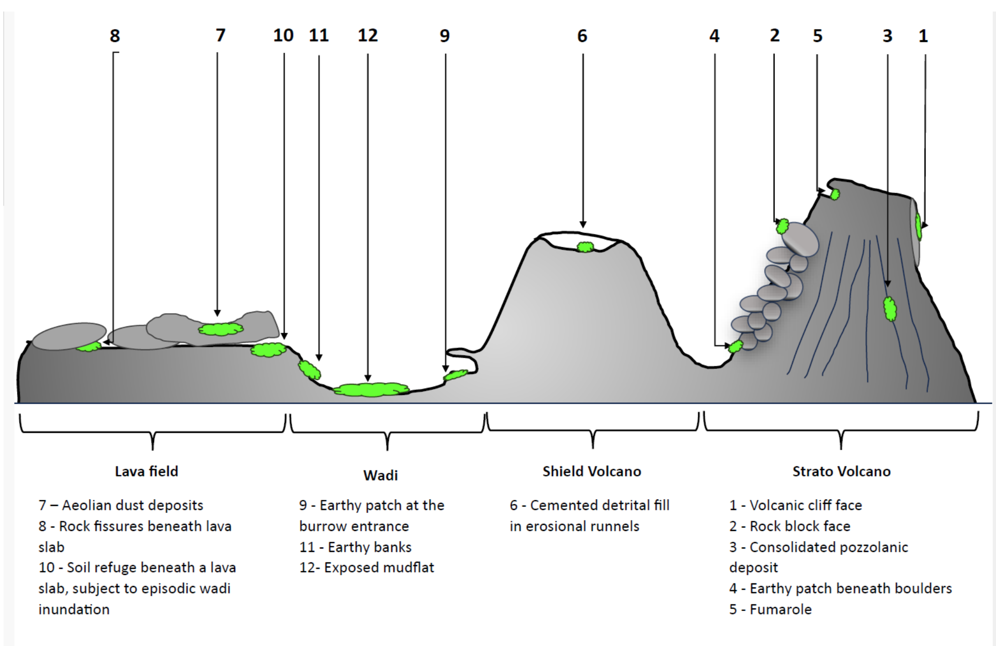

Figure 7: Toposequence of bryophyte microhabitats within Khaybar White Volcano Geopark.

Table II: Bryophyte assemblages of each microhabitat.

	Microhabitat	Number of relevés	Species richness	Top 5 most abundant species	Exclusive or quasi-exclusive species	Shared background flora
1	Volcanic cliff face	4	9	Grimmia orbicularis, Syntrichia caninervis var. caninervis, Tortula atrovirens, Bryum dichotomum, Trichostomopsis australasiae	-	Trichostomopsis australasiae, Didymodon desertorum, Grimmia orbicularis, Bryum dichotomum, Tortula atrovirens
2	Rock block face	14	22	Grimmia orbicularis, Tortula atrovirens, Crossidium crassinervium, Crossidium squamiferum, Trichostomopsis australasiae	Grimmia capillata	Trichostomopsis australasiae, Entosthodon cf. commutatus, Didymodon desertorum, Grimmia orbicularis, Tortula muralis var. muralis, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens, Crossidium crassinervium
3	Consolidated pozzolanic deposit	50	31	Grimmia orbicularis, Tortula atrovirens, Trichostomopsis australasiae, Crossidium crassinervium, Crossidium squamiferum	-	Trichostomopsis australasiae, Entosthodon cf. commutatus, Didymodon desertorum, Grimmia orbicularis, Tortula muralis var. muralis, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens, Crossidium crassinervium
4	Earthy patch beneath boulders	39	23	Tortula atrovirens, Trichostomopsis australasiae, Crossidium crassinervium, Grimmia orbicularis, Tortula mucronifera	Plagiochasma rupestre	Trichostomopsis australasiae, Entosthodon cf. commutatus, Didymodon desertorum, Grimmia orbicularis, Tortula muralis var. muralis, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens, Crossidium crassinervium
5	Fumarole	188	37	Vinealobryum vineale, Tuerckheimia svihlae, Ptychostomum torquescens, Tortella nitida, Entosthodon cf. commutatus	Fossombronia caespitiformis subsp. caespitiformis, Scorpiurium circinatum, Fissidens sp., Fissidens sciophyllus, Anoectangium aestivum, Plagiochasma eximium, Molendoa sendtneriana, Syntrichia fragilis	Trichostomopsis australasiae, Entosthodon cf. commutatus, Didymodon desertorum, Grimmia orbicularis, Tortula muralis var. muralis, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens
6	Cemented detrital fill in erosional runnels	12	14	Grimmia orbicularis, Tortula atrovirens, Tortula inermis, Crossidium squamiferum, Microbryum starckeanum	-	Trichostomopsis australasiae, Didymodon desertorum, Grimmia orbicularis, Tortula muralis var. muralis, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens, Crossidium crassinervium
7	Aeolian dust deposits	93	25	Bryum dichotomum, Microbryum starckeanum, Trichostomopsis australasiae, Tortula inermis, Tortula mucronifera	Pterygoneurum subsessile	Trichostomopsis australasiae, Entosthodon cf. commutatus, Didymodon desertorum, Grimmia orbicularis, Tortula muralis var. muralis, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens, Crossidium crassinervium
8	Rock fissures beneath lava slab	26	15	Bryum dichotomum, Trichostomopsis australasiae, Tortula atrovirens, Grimmia orbicularis, Microbryum starckeanum	-	Trichostomopsis australasiae, Grimmia orbicularis, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens, Crossidium crassinervium
9	Earthy patch at the burrow entrance	1	3	Bryum dichotomum, Tortula muralis var. muralis, Funaria hygrometrica, Trichostomopsis australasiae, Tortula inermis	-	Tortula muralis var. muralis, Bryum dichotomum
10	Soil refuge beneath a lava slab, subject to episodic wadi inundation	12	10	Bryum dichotomum, Microbryum starckeanum, Tortula lindbergii, Entosthodon cf. commutatus, Tortula atrovirens	-	Trichostomopsis australasiae, Entosthodon cf. commutatus, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens, Crossidium crassinervium
11	Earthy banks	24	19	Bryum dichotomum, Entosthodon cf. commutatus, Microbryum starckeanum, Crossidium crassinervium, Aloina rigida	Geheebia erosa	Trichostomopsis australasiae, Entosthodon cf. commutatus, Didymodon desertorum, Grimmia orbicularis, Tortula muralis var. muralis, Bryum dichotomum, Microbryum starckeanum, Tortula atrovirens, Crossidium crassinervium
12	Exposed mudflat	10	5	Riccia cavernosa, Bryum dichotomum, Entosthodon cf. commutatus, Geheebia siccula, Fissidens cf. arnoldii	Geheebia siccula	Entosthodon cf. commutatus, Bryum dichotomum

Microhabitat-restricted taxa

Ecological differentiation was instead driven by a small number of taxa (Tab. II). *Plagiochasma rupestre* was confined to shaded soil crevices beneath boulders; *Fossombronia caespitiformis*, *Tuerckheimia svihlae*, *Anoectangium euchloron* and *Husnotiella revoluta* were characteristic of fumaroles; *Pterygoneurum subsessile* occurred mainly in aeolian dust deposits; and *220eheebias pp*. Were associated with earthy banks and mudflats.

Ordination analyses

The heatmap (Fig. 9) illustrates the prevalence of shared taxa across multiple microhabitats, with only a small subset being restricted to specific ecological situations. Consistently, the NMDS ordination (Fig. 10) demonstrates a tight clustering of most microhabitats based on shared species composition. However, fumaroles and mudflats are slightly displaced due to the presence of specialized taxa. These analyses suggest that differentiation among microhabitats primarily arises from rare, habitat-restricted species rather than from significant differences in overall species composition.

The global RDA model explained 33.8% of total inertia (adjusted $R^2 = 0.30$, $p = 0.005$). Forward selection retained four predictors: microhabitat slope, substrate depth, and the categorical variables 'fumarole' and 'aeolian dust deposits'. In the RDA biplot (Fig. 11), microhabitat slope and overall slope are strongly aligned with RDA1, indicating a shared topographic gradient, while substrate depth mainly contributes to variation along RDA2. The categorical predictors capture additional microhabitat-specific variation not explained by continuous gradients. Variance partitioning (Fig. 12) indicates that microhabitat categories account for the largest fraction of explained variation, followed by topographic and edaphic variables, with all predictor blocks being significant ($p < 0.05$).

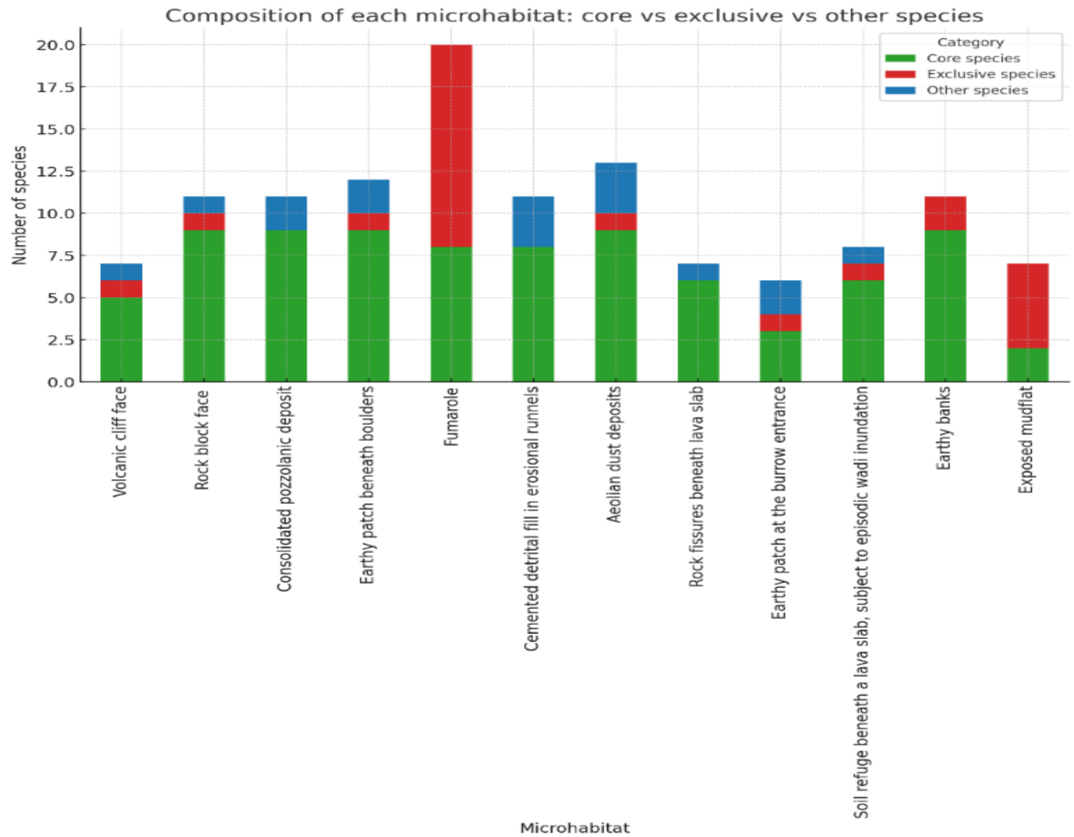

Figure 8: Composition of each microhabitat.

Figure 9: Heatmap of the species presence across the 12 microhabitats (generated in R).

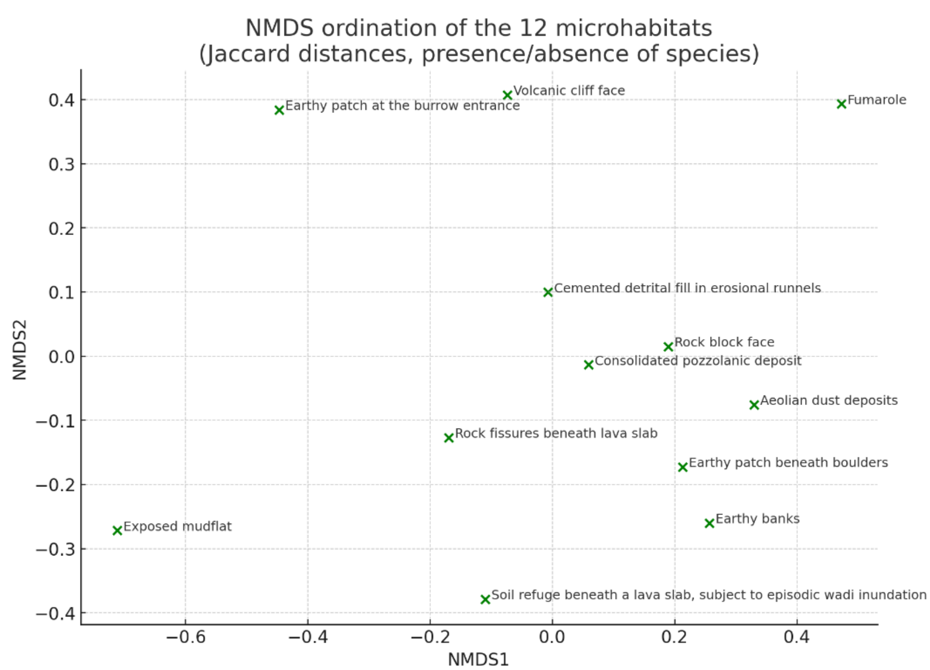

Figure 10: NMDS ordination of the 12 microhabitats (generated in R).

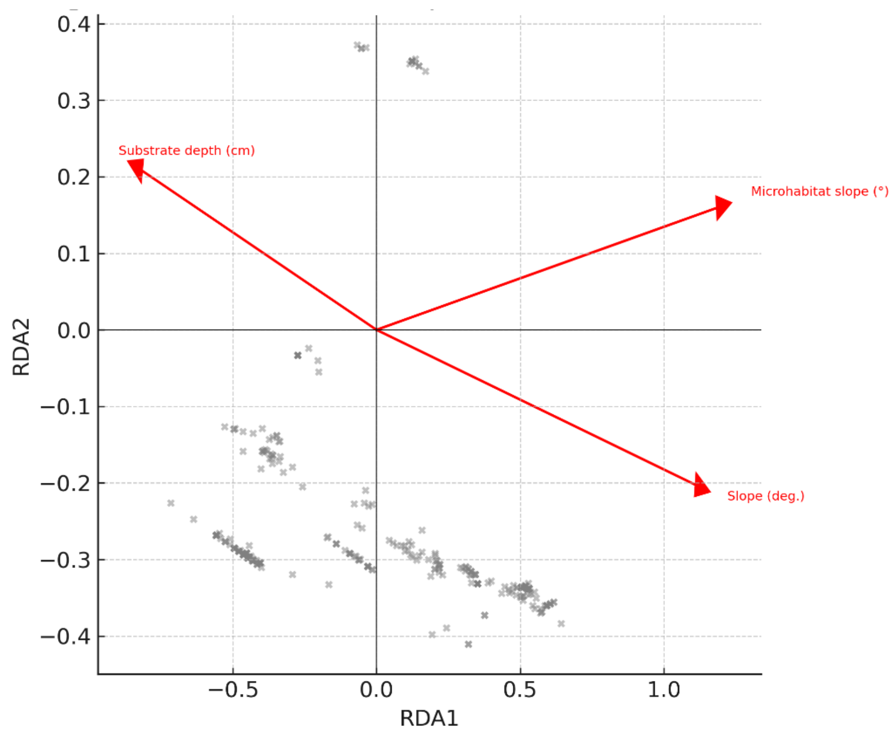

Figure 11: Canonical biplot (RDA1 × RDA2) showing site scores, species scores and environmental vectors. Microhabitat slope and overall slope are the dominant gradients along RDA1, while substrate depth contributes mainly to variation along RDA2. Categorical microhabitat descriptors (fumarole, aeolian dust deposits) capture additional microhabitat-specific variation (generated in R).

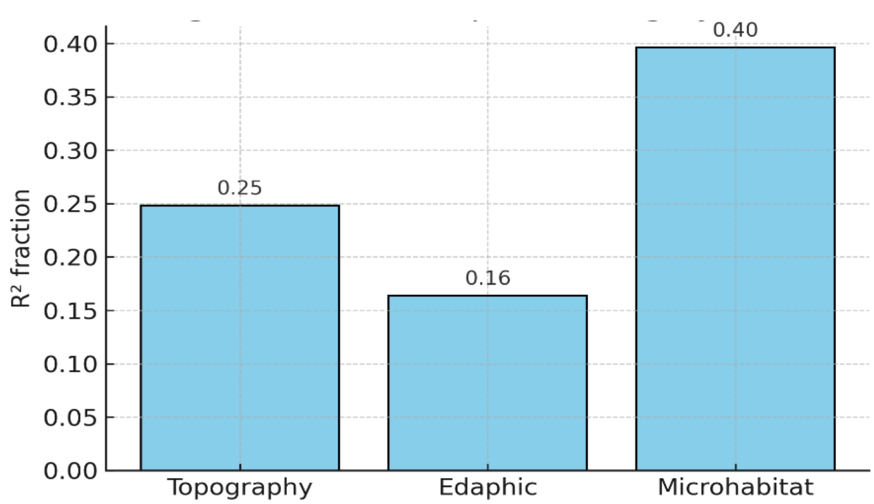

Figure 12. Variance partitioning of bryophyte assemblages into unique fractions attributable to topography, edaphic factors, and microhabitat categories (generated in R).

Discussion

Community Structuring by Abiotic Gradients

The constrained ordination analyses indicate that bryophyte assemblages in the Khaybar White Volcano Geopark are non-randomly structured and respond to a hierarchical set of ecological constraints. At the relevé level, the primary axis of variation captured by the RDA reflects a dominant topographic–edaphic gradient, mainly associated with microhabitat slope and substrate depth. Steep, compact rocky surfaces are preferentially occupied by drought-tolerant, firmly attached taxa such as *Grimmia orbicularis* and *Tortula atrovirens*. In contrast, deeper or more developed substrates support a broader spectrum of terricolous species.

Variance partitioning complements this pattern by demonstrating that, while continuous topographic and edaphic variables structure species composition along major ecological gradients, categorical microhabitat descriptors account for the largest fraction of the overall explained variation. This finding indicates that recurrent microhabitat configurations capture additional, non-redundant ecological constraints that are not fully represented by measured continuous variables alone.

These results illustrate a hierarchical structuring of bryophyte assemblages at the scale of volcanic landscapes. Broad-scale abiotic gradients delineate the primary ecological space available to bryophytes, while discrete microhabitats—such as fumaroles or aeolian dust deposits—introduce finer-scale differentiation through locally distinct combinations of substrate stability and contrasting exposure conditions. Comparable structuring of bryophyte assemblages by topographic and edaphic gradients has been documented in other regions, including lava flows in La Réunion (Ah-Peng et al., 2007) and volcanic slopes in Turkey (Kara et al., 2014). Similar patterns have also been reported in volcanic subterranean systems and lava-associated habitats, where local shelter, substrate stability, and moisture retention create ecological discontinuities that favor specialized bryophyte taxa (Gabriel et al., 2006; Cong et al., 2023).

Despite the statistical significance of the constrained models, a substantial proportion of compositional variation remains unexplained. Such patterns are likely typical of bryophyte assemblages in extreme environments, where stochastic establishment, dispersal limitation, and historical contingencies interact.

A Shared Floristic Backbone Across Habitats

The marked floristic cohesion observed across the twelve microhabitats is largely driven by a limited set of highly stress-tolerant bryophytes that form a shared xerophytic component, notably *Trichostomopsis australasiae* and *Tortula atrovirens*. These taxa are recurrent constituents of biological soil crusts in arid environments, contributing to the formation of cryptogamic surface layers alongside cyanobacteria and lichens. Their ecological success in such environments is linked to pronounced desiccation tolerance and the ability to rapidly resume metabolic activity following episodic wetting events, allowing them to persist under prolonged periods of environmental stress (Blanco-Sacristán, 2025; Hugonnot et al., 2025a, b).

Specialized Microhabitats

In contrast to this otherwise homogeneous floristic background, a limited number of microhabitats contribute disproportionately to the differentiation of bryophyte assemblages. The RDA identifies fumaroles as a key microhabitat type, hosting exclusive or near-exclusive taxa such as *Fossombronia caespitiformis*, *Tuerckheimia* *svihlae*, *Anoectangium euchloron*, and *Husnotiella revoluta*, several of which have tropical or paleotropical affinities (Hugonnot et al., 2026b). Aeolian dust deposits within lava flows also emerge as a distinct microhabitat type, primarily supporting the rare *Pterygoneurum subsessile*. These depressions, generated by the impermeability of basaltic surfaces combined with local sediment accumulation, create uncommon edaphic conditions within an otherwise inhospitable volcanic matrix.

Volcanic Geodiversity as a Driver of Cryptogamic Diversity

The patterns detected in the Khaybar White Volcano Geopark demonstrate the indirect yet fundamental role of volcanic geodiversity in hyper-arid conditions (Moufti & Németh, 2016). Geodiversity does not act as an independent ecological driver; rather, it provides the geological framework that generates a mosaic of substrates, microtopographies, and disturbance regimes, conditioning both broad abiotic gradients and discrete ecological situations relevant to bryophyte establishment.

At the landscape scale, volcanic landforms control the spatial distribution of major topographic and edaphic gradients, including slope steepness, substrate stability, and the availability of weathered material, thereby constraining the regional pool of bryophyte species that can persist under extreme climatic conditions. At finer spatial scales, specific geomorphological features modify exposure conditions and the fine-scale geomorphological context, creating ecological conditions that differ from those prevailing on surrounding volcanic surfaces.

These fine-scale situations do not give rise to fully distinct bryophyte communities but selectively accommodate a limited number of ecologically specialized taxa that remain rare or absent elsewhere in the landscape. In this sense, volcanic geodiversity contributes disproportionately to bryophyte diversity by maintaining marginal habitat niches rather than increasing overall compositional stock among habitats. Such fine-scale geological heterogeneity can be interpreted as providing microsites with locally favorable shelter conditions that support the short-range persistence of specialized taxa.

The relationship between volcanic geodiversity and bryophyte diversity was not formally quantified in this study. The interpretations presented here remain qualitative. A direct test of this relationship, for instance through correlation between a geodiversity index and species richness or beta-diversity at the grid-cell level, would be needed to substantiate this inference and is identified as a priority for future work.

Conservation Implications

This study highlights the importance of conserving fine-scale habitat heterogeneity within the Khaybar White Volcano Geopark. Although bryophyte assemblages are largely dominated by a limited suite of xerophytic taxa, a small number of microhabitats—particularly fumaroles, shaded soil pockets beneath boulders, and aeolian dust deposits—support ecologically restricted species and contribute disproportionately to overall bryophyte diversity. Owing to their limited spatial extent, these microhabitats are likely to be especially vulnerable to disturbances associated with geotourism, off-road vehicle use, trampling, and infrastructure maintenance. Their identification and integration into site-level planning and monitoring frameworks would therefore enhance the conservation of bryophyte assemblages characteristic of hyper-arid volcanic environments. Particular attention should be paid to fumaroles, sediment-filled hollows, and shaded block accumulations, which support the most distinctive elements of the local bryoflora.

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