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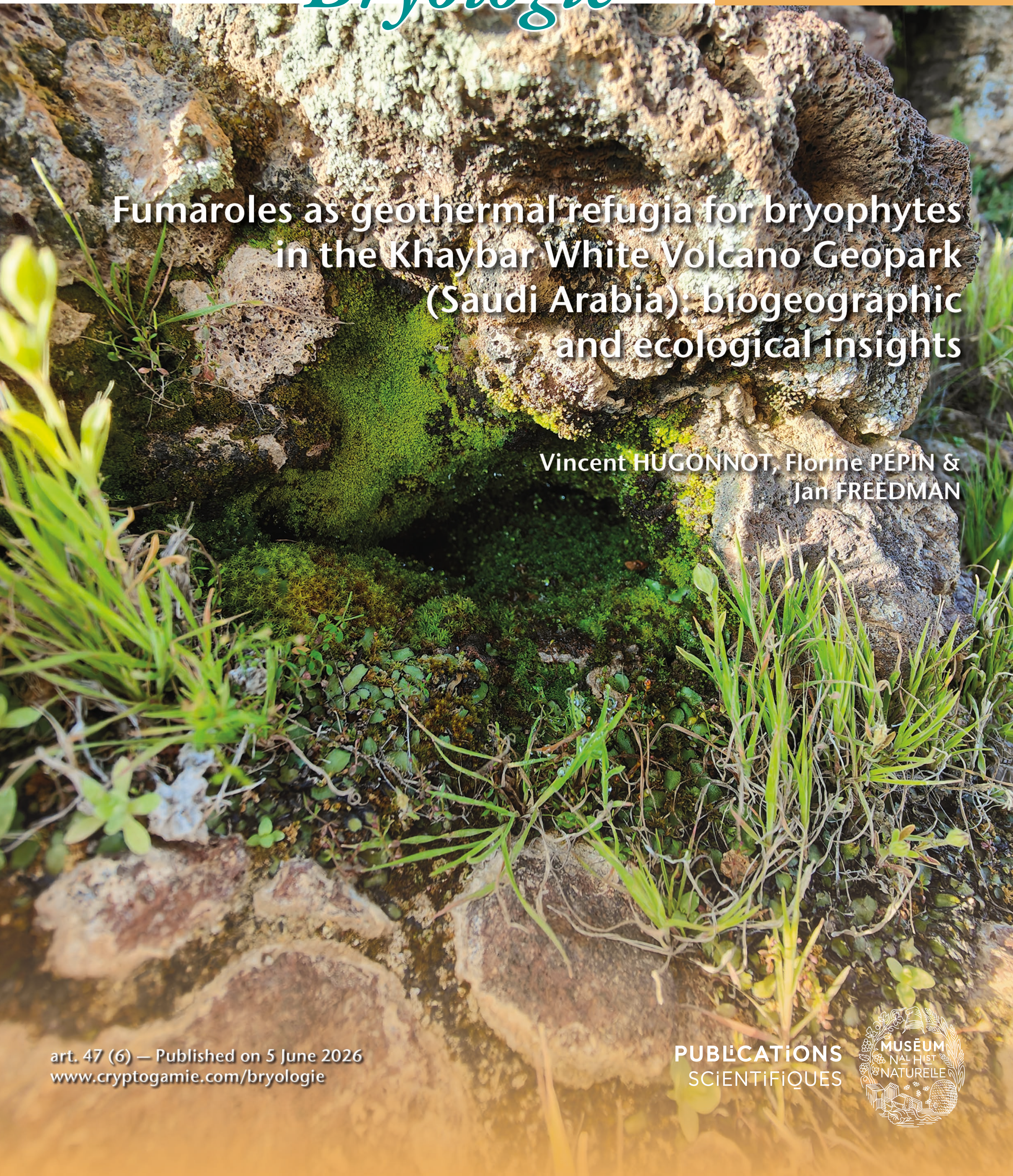

Fumaroles as geothermal refugia for bryophytes in the Khaybar White Volcano Geopark (Saudi Arabia): biogeographic and ecological insights

Vincent HUGONNOT, Florine PÉPIN &
Jan FREEDMAN

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Fumaroles as geothermal refugia for bryophytes in the Khaybar White Volcano Geopark (Saudi Arabia): biogeographic and ecological insights

Vincent HUGONNOT
Florine PÉPIN
25 impasse des Oponces, 43380 Blassac (France)
vincent.hugonnot@wanadoo.fr (corresponding author)

Jan FREEDMAN
Royal Commission for AlUla, Riyadh 12512 (Saudi Arabia)
j.freedman@rcu.gov.sa

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ABSTRACT

Fumaroles generate steep microclimatic and edaphic gradients that allow bryophyte communities to persist where the surrounding landscape is too dry or extreme. To explore this phenomenon, we surveyed bryophytes across the Khaybar White Volcano Geopark (north-western Saudi Arabia) during two field campaigns in 2024 and 2025, using a systematic 5 × 5 km grid to reduce spatial bias. Within fumarolic habitats, we counted vents by diameter class (0-2, 2-10, 10-50, >50 cm) in GPS-referenced plots and recorded bryophyte presence and abundance following the Braun-Blanquet scale. Across 188 relevés distributed among 11 fumarolic sites, we collected 1806 records representing 37 bryophyte taxa – about 72% of the 51 species known from the entire Geopark. Thirteen species were found exclusively in fumarolic microhabitats, and seven showed tropical or paleotropical affinities. Statistical analyses (Spearman correlations, n = 188) revealed that both species richness and cumulative abundance were highest in plots containing more medium-sized vents. These values declined near larger vents (>50 cm) and showed no clear relationship for smaller ones (≤10 cm). The association between medium vent abundance and bryophyte richness remained consistent across sites. Tropical species richness did not vary systematically with vent size but was clearly structured by orientation, with northerly and north-easterly slopes hosting most tropical taxa. Even so, the results suggest that clusters of medium-sized fumaroles create locally buffered conditions that support bryophyte establishment in this hyper-arid volcanic setting. We propose a preliminary Bryothermal Index (BTI) that integrates community-level indicators – species richness, abundance, and the proportion and fertility of hygrophilous or tropical-affinity taxa – to estimate geothermal influence. Future research should include high-frequency temperature and humidity logging, gas and substrate analyses, and replicated transects around vents to clarify mechanisms and validate the BTI. Despite their small extent (<1 ha), the Khaybar fumaroles stand out as microrefugia and should be considered for targeted micro-reserve protection and long-term ecological monitoring.

KEY WORDS
Fumaroles,
geothermal microrefugia,
bryophyte diversity,
tropical-affinity taxa,
hygrometric buffering,
Arabia,
orientation effects,
ecology,
steam vents,
bryothermal Index (BTI).

RÉSUMÉ
Refuges géothermiques bryophytiques dans le Khaybar White Volcano Geopark : perspectives biogéographiques et écologiques.
Les fumerolles génèrent de forts gradients microclimatiques et édaphiques qui permettent à des communautés bryophytiques de se développer dans des paysages environnants trop secs ou extrêmes. Afin d'explorer ce phénomène, nous avons inventorié les bryophytes dans le Khaybar White Volcano Geopark (nord-ouest de l'Arabie Saoudite) lors de deux campagnes de terrain menées en 2024 et 2025, selon une maille systématique de 5 × 5 km destinée à réduire les biais spatiaux. Dans les fumerolles, les évents ont été comptés par classes de diamètre (0-2, 2-10, 10-50, > 50 cm) au sein de placettes géoréférencées, et la présence ainsi que l'abondance des bryophytes ont été relevées selon l'échelle de Braun-Blanquet. Au total, 188 relevés répartis sur 11 sites ont fourni 1 806 enregistrements correspondant à 37 taxons bryophytiques, soit environ 72 % des 51 espèces connues dans l'ensemble du Géoparc. Treize espèces ont été observées exclusivement dans les fumerolles, et sept présentent des affinités tropicales ou paléotropicales. Les analyses statistiques (corrélations de Spearman, n = 188) ont montré que la richesse spécifique et l'abondance cumulée étaient maximales dans les placettes comportant un plus grand nombre de fumerolles de taille moyenne. Ces valeurs diminuaient à proximité des grands évents (> 50 cm) et ne montraient pas de relation claire pour les petits (≤ 10 cm). Comme les fumerolles moyennes sont également les plus fréquentes, une partie de ce signal peut refléter leur représentation dans le jeu de données ; néanmoins, l'association entre leur abondance et la richesse bryophytique demeurait constante entre les sites. La richesse en espèces tropicales ne variait pas systhématiquement avec la taille des évents, mais se trouvait nettement structurée par l'exposition : les pentes orientées au nord et au nord-est concentraient la majorité des taxons tropicaux. Néanmoins, les résultats suggèrent que les groupements de fumerolles de taille moyenne créent des conditions localement tamponnées favorables à l'installation des bryophytes dans ce contexte volcanique hyperaride. Sur cette base, nous proposons un indice préliminaire, le Bryothermal Index (BTI), intégrant plusieurs indicateurs à l'échelle des communautés – richesse spécifique, abondance, proportion et fertilité des taxons hygrophiles ou à affinité tropicale – pour estimer l'influence géothermale. Les recherches futures devraient inclure des enregistrements microclimatiques à haute fréquence (température et humidité), des analyses de gaz et de substrat, ainsi que des transects répétés autour des évents pour préciser les mécanismes et valider le BTI. Malgré leur faible superficie (< 1 ha), les fumerolles de Khaybar se distinguent comme d'excellents micro-refuges et méritent d'être considérées pour une protection ciblée sous forme de micro-réserves et pour un suivi écologique à long terme.

MOTS CLÉS
Fumerolles,
micro-refuges géothermiques,
diversité bryophytique,
taxons à affinité tropicale,
tamponnement hygrométrique,
Arabie,
effet d'exposition,
Bryothermal Index (BTI)

INTRODUCTION

Fumaroles are geothermal vents where steam and volcanic gases escape through openings in the ground. They occur in tectonically and volcanically active regions (Waring 1965), including oceanic islands (e.g., Pantelleria, Ischia, Tenerife, Hawaii), high-altitude volcanoes (e.g., Teide in the Canary Islands, Toussidé in the Tibesti; De Miré & Quézel 1959), and polar volcanic zones such as Deception Island in the South Shetland Islands (Lewis Smith 2005). Although scattered worldwide, fumaroles often show similar ecological patterns, which makes them useful for comparative work.

Close to fumarole vents, the ground can get extremely hot – sometimes above 80°C – and becomes more acidic, while organic matter and available nutrients drop sharply (Andersson 1988; Burns 1997). The gases released, mostly steam, carbon dioxide, and sulfur compounds, make the air humid but chemically harsh, and vegetation can change completely within just a few meters. Similar situations are seen in geothermal areas of Iceland, Japan, and New Zealand (Glime & Iwatsuki 1997; Elmarsdóttir *et al.* 2003; Glime *et al.* 2023). Temperatures vary widely between sites – from more than 100°C at Yellowstone (Hurwitz *et al.* 2020) to milder geothermal gradients in cooling volcanic fields (Hildreth & Fierstein 2012) – yet it is the temperature and moisture at the soil surface that ultimately determine which plants can colonize and survive (Harris *et al.* 2012).

Bryophyte assemblages at fumaroles are highly specialized. They occupy narrow thermal and moisture niches and can remain metabolically active under conditions lethal to most vascular plants (Longton & Holdgate 1979; Glime & Iwatsuki 1997; Convey *et al.* 2008). Some species, such as *Campylopus introflexus* (Hedw.) Brid. and *C. pilifer* Brid. subsp. *vaporarius* (De Not.) Brullo, tolerate surface temperatures up to 47°C and subsurface values near 75°C (Convey & Lewis Smith 2006). Others – *Calymperes erosum* Müll. Hal., *Isopterygium tenerum* (Sw.) Mitt., *Trematodon longicollis* Michx. – show tropical affinities and are restricted to fumarolic microhabitats in the Mediterranean and Macaronesian islands (Brullo *et al.* 2001, 2004; Puglisi *et al.* 2006).

In polar regions, geothermal fields such as Deception Island and the South Sandwich Islands also support bryophyte-

Fig. 1. — Location of Khaybar White Volcano Geopark (**yellow star**) within the Arabian Peninsula.

dominated vegetation absent from surrounding polar deserts (Bargagli *et al.* 1996; Lewis Smith 2005; Convey & Lewis Smith 2006). Temperature and humidity gradients produce sharp community zonation, with turnover linked to centimeter-scale soil-temperature differences (Pearman *et al.* 2024). Plant associations such as *Campylopodetum vaporarii* and *Calymperetum erosi* have been described from Mediterranean and Macaronesian fumarolic sites characterized by microclimatic conditions of a tropical hot-moist type (Brullo *et al.* 2004). These communities are often phytogeographically distinctive, mixing Oceanic, Mediterranean, and Tropical elements. Some thermophilous lineages are even postulated to be Tertiary tropical relicts that persisted locally in fumarolic sites (Brullo *et al.* 2001; García *et al.* 2016).

On the Arabian Peninsula, fumaroles remain little studied, but several volcanic fields – including Harrat Khaybar, Rahat, Lunayyir, and Hutaymah – show localized geothermal activity related to Holocene-Quaternary basaltic volcanism along the Red Sea rift (Waring 1965; Roobol *et al.* 2007; Lashin *et al.* 2015; Rasul *et al.* 2015). At Harrat Khaybar, faint steam vents reaching about 25°C have been observed during winter (Roobol *et al.* 1994), while nearby areas display gas-emitting springs and slightly elevated geothermal gradients (Lashin *et al.* 2015; Aboud *et al.* 2022). Together, these mild geothermal features suggest that residual magmatic heat still lingers beneath the Arabian volcanic plateaus (Moufti & Németh 2016).

Despite these indications, no bryophyte survey has targeted Arabian fumarolic systems. Yet the combination of residual heat, high humidity, and sheltered microtopography could allow thermophilous – or even tropical – bryophytes to persist where the hyper-arid ambient would otherwise exclude them. Building on a comprehensive floristic survey of the Khaybar White Volcano Geopark (Hugonnot *et al.* 2025), this study aims to: 1) document the diversity and structure of bryophyte assemblages in fumarolic habitats; 2) test how fumarole size and vent number relate to bryophyte occurrence; and 3) evaluate the ecological and biogeographic significance of these geothermal microrefugia within western Arabia's volcanic landscapes.

MATERIAL AND METHODS

Study site

Harrat Khaybar is one of the largest lava fields in Saudi Arabia, covering more than 20 000 km^2 (Camp & Roobol 1989; Moufti & Németh 2016). Volcanism began about ten million years ago and continued intermittently until very recent times (Camp & Roobol 1989). The harrats include a wide range of volcanic types and lava flows, from ancient, eroded deposits to sub-recent formations. This volcanic landscape developed through several eruptive phases associated with Red Sea rifting, which caused faulting and partial melting of the Arabian Plate crust (Rasul *et al.* 2015). The earliest eruptions date to around 10 Ma, while the most recent occurred in the late Holocene, about 700-1 000 years ago, when Jabal Qidr – also known as Pot Mountain or the Black Volcano – erupted (Camp & Roobol 1989; Camp *et al.* 1991; Moufti & Németh 2016).

Geothermal activity is still detectable, showing that the magmatic system beneath Khaybar remains warm. Several fumaroles and small steam vents have been reported in different parts of the harrat (Roobol *et al.* 1994; Chandrasekharam *et al.* 2015), including one inside a large lava tube (Pint 2006, 2009). Because of these features, Harrat Khaybar has been identified as a potential site for geothermal-energy exploration (Lashin *et al.* 2015).

Within this vast volcanic field, the Royal Commission for AlUla manages a 600 km^2 area known as the Khaybar White Volcano Geopark (Fig. 1). The geopark includes basaltic cones and lava flows situated next to silicic, comenditic domes formed by remelting of the Precambrian basement (Baker *et al.* 1973). The coexistence of mafic and felsic volcanic rocks makes Khaybar one of the most geologically diverse volcanic systems on the Arabian Peninsula.

The regional climate is typical of northern Arabia, with very hot, dry summers and cool to warm winters. Most precipitation comes from winter and spring cyclonic systems originating in the Atlantic or the Mediterranean. Rainfall is highly variable, often falling as short, localized showers, and some years bring no rain at all to parts of the region. Meteorological data from the Al Madinah station reflect these conditions (Fig. 2), showing a mean annual rainfall of 36-44 mm and a mean annual temperature of 29°C.

Sampling design and survey effort

As the Al Madinah station lies at low elevation (*c.* 620 m a.s.l.) some 60 km from the study area, it is used here only as the nearest regional reference; conditions at the Khaybar White Volcano site (*c.* 1900 m a.s.l.) are likely somewhat cooler, the actual mean annual temperature probably being several degrees lower owing to the altitudinal difference.

Bryological surveys were carried out during two field campaigns (21-23 February 2024 and 15 February-17 March 2025) across the 600 km^2 Khaybar White Volcano Geopark in northwestern Saudi Arabia. A 5 × 5 km grid, based on high-resolution aerial imagery, guided the sampling to maintain even spatial coverage and limit geographic bias. Within each

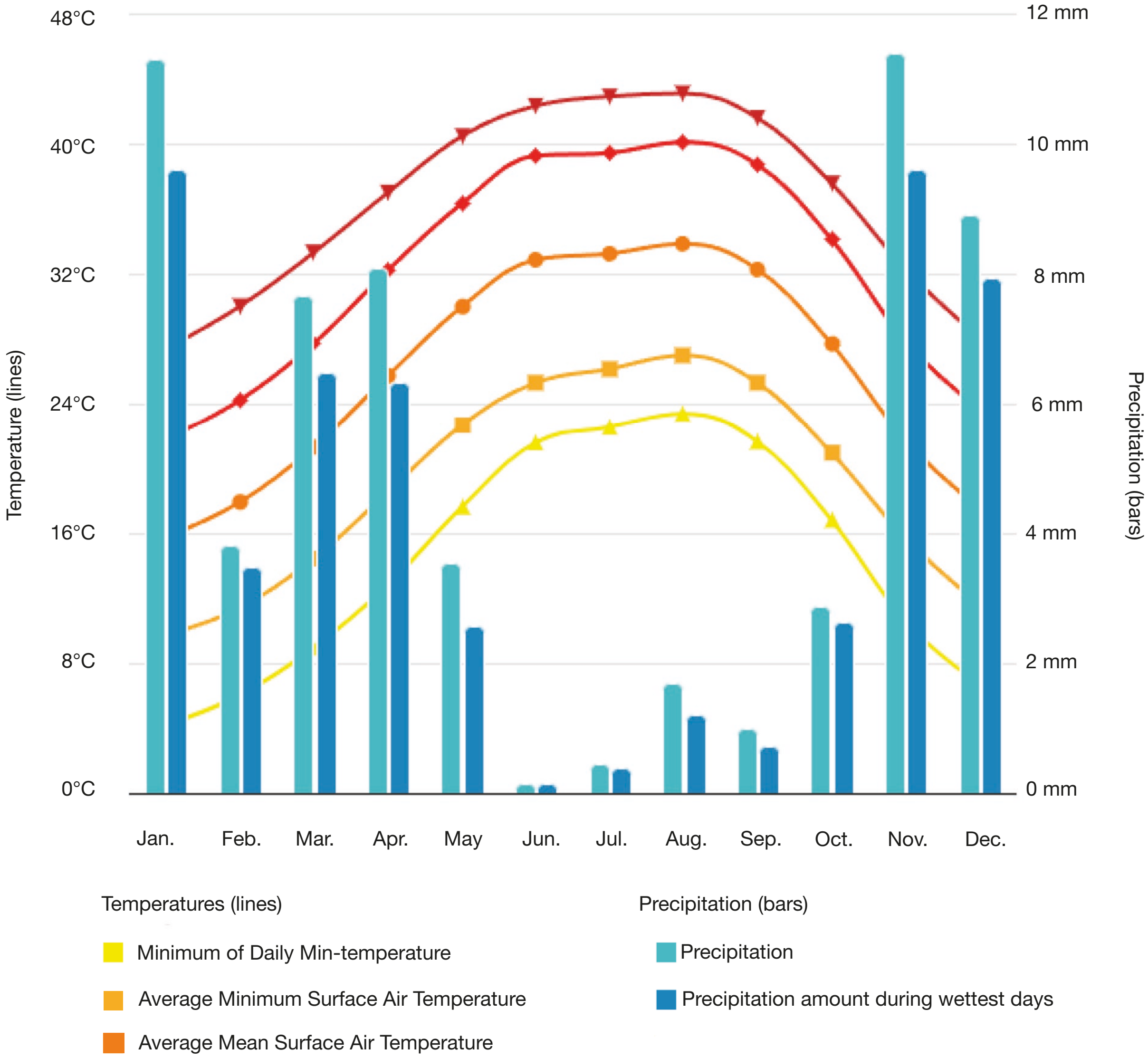

Fig. 2. — Climatogram for Al Madinah (24°28'N, 39°36'E; *c.* 620 m a.s.l.), the nearest regional reference station to the Khaybar White Volcano site, based on monthly data for 1991-2021 (World Bank Group, Climate Change Knowledge Portal: Observed Climate Data, ERA5 0.25°; Hersbach *et al.* 2020).

grid cell (*c.* 25 km^2), survey intensity was adjusted to terrain complexity and observed bryophyte richness, and searches continued until few or no new taxa appeared.

Fieldwork combined 4×4 vehicle access along existing tracks with foot surveys covering 5-10 km per day on foot and 20-40 km by vehicle. Steep or remote zones were sometimes less accessible, but overall sampling effort remained evenly distributed across the grid. Local rangers helped identify accessible fumarole areas and moist microhabitats, which were prioritized for detailed exploration.

In total, 551 sites were surveyed (Hugonnot *et al.* 2025), covering the full range of volcanic substrates – basalt flows, pyroclastic deposits, and silicic domes. Key bryophyte-rich habitats were identified through photo-interpretation before fieldwork and included north-facing slopes, shaded wadis (temporary watercourses), coarse screes, seepage zones, and especially fumarolic vents.

TAXONOMY AND DATA STANDARDIZATION

Taxonomy mainly follows Kürschner & Frey (2020), with adjustments for certain genera (*Didymodon*, *Bryum*) based on recent revisions. Synonyms and nomenclatural variants were harmonized to ensure consistency across records. The delimitation of the Arabian Peninsula follows Kürschner (2000), excluding Iraq and Jordan.

BRYOLOGICAL RELEVÉS

At each site, standardized in situ relevés recorded species presence and absence, and abundance was visually estimated using the Braun-Blanquet cover scale ("+" to 5; Braun-Blanquet 1964). These data were later converted into frequency values across plots for comparison. Environmental variables – slope, exposure, vegetation type, and substrate – were noted systematically. Specimens were collected with minimal disturbance, air-dried in the field, and stored in V. Hugonnot's private

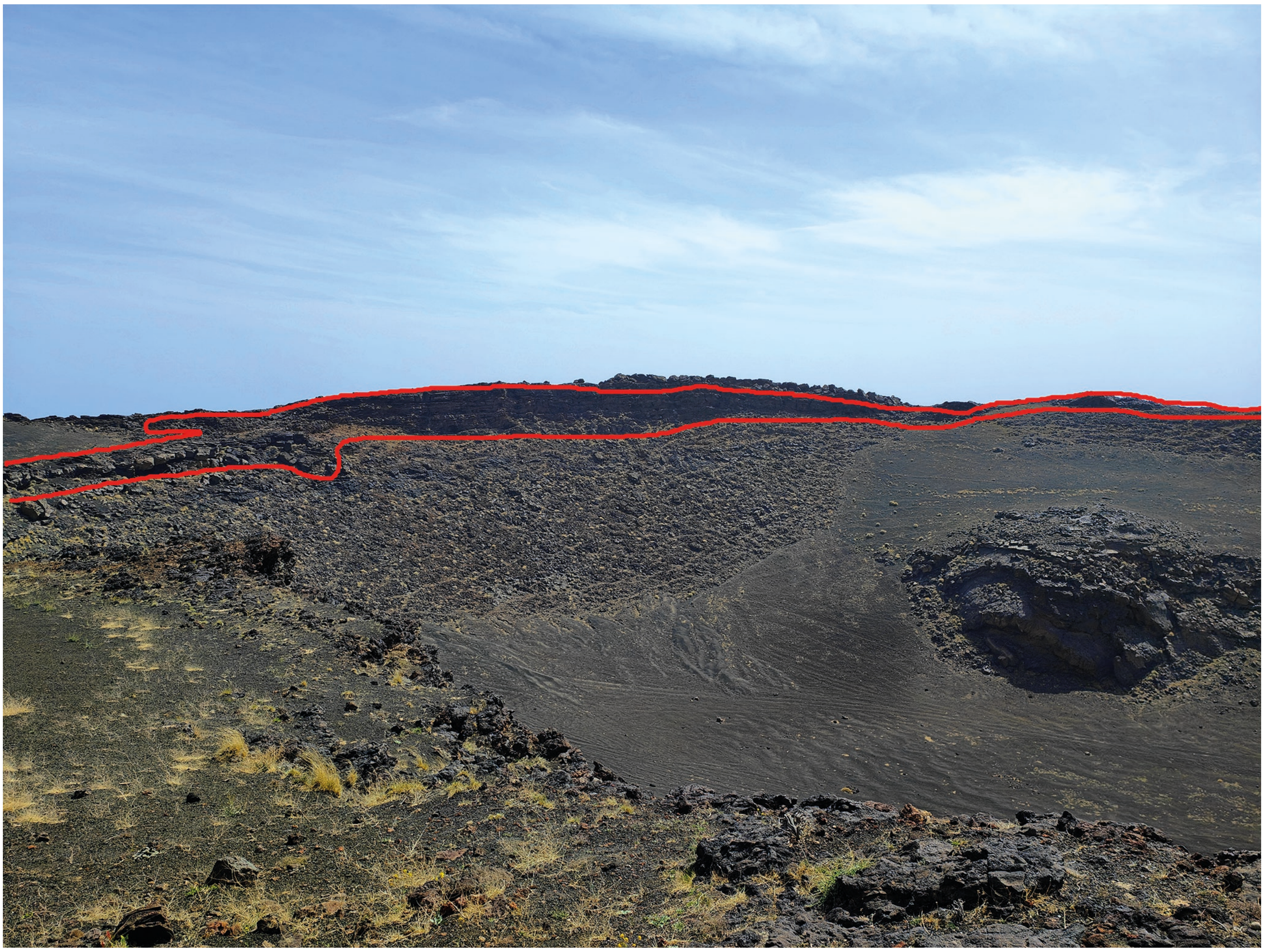

FIG. 3. — Northeast slope of the Jabal Al-Mashawiya with the fumarole zone outlined in **red**.

herbarium. Duplicate samples will be deposited at the Royal Commission for AlUla (RCU) in 2026. Several specimens remain taxonomically uncertain (*Didymodon* cf. *rigidulus*, *Fissidens* cf. *arnoldii*, *Entosthodon* cf. *commutatus*).

FUMAROLE DETECTION AND DEFINITION

Particular attention was given to fumaroles, which were systematically searched during all traverses (Fig. 3). For each fumarolic site, a GPS point was recorded with an estimated horizontal accuracy of about 3 m. Within this radius, all visible vents were counted and measured, so each point represents a fumarolic cluster covering a circular area of roughly 28 m².

In the fumarole zones of the Khaybar White Volcano Geopark, primary vent openings cannot be delimited as discrete point sources, as present-day geothermal activity is diffuse and low-intensity. Radial gradients comparable to those described at Mount Toussidé (De Miré & Quézel 1959) are therefore not spatially identifiable, and distances to vents were not recorded. Sampling was instead structured around microtopographic units and the main types of volcanic deposits, which represent the ecologically relevant microhabitats in this system.

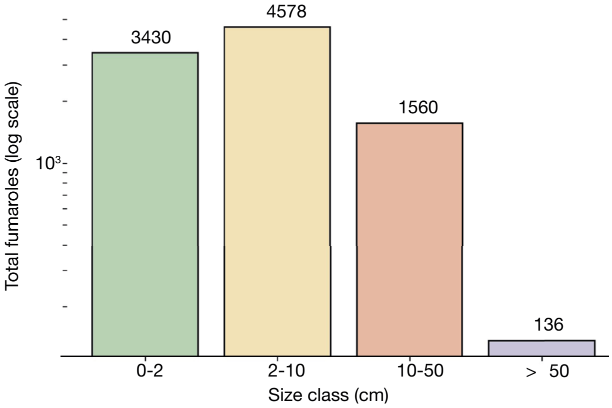

FIG. 4. — Total number of fumaroles grouped by size class (in cm). A logarithmic scale is used to better reflect the wide range in values.

Vent diameter (cm) was measured to the nearest centimetre with a ruler or tape and grouped into four size classes (0-2, 2-10, 10-50, >50 cm). These categories capture the broad range of vent sizes observed in the field while keeping enough contrast for ecological interpretation. The thresholds

TABLE 1. — List of fumarole bryophyte taxa of the Khaybar White Volcano site, their frequency and chorology (fertility means sporophyte occurrence).

Taxa	Fertility	Frequency	Chorology
Anoectangium aestivum (Hedw.) Spruce	–	0.23	Subcosmopolitan
Anoectangium euchloron (Schwägr.) Spruce	–	5.85	Pantropical
Bryum dichotomum Hedw.	+	0.94	Cosmopolitan
Didymodon cf. *rigidulus* Hedw.	–	5.38	Xerothermic Pangean
Didymodon desertorum (J.Froehl.) J. A. Jiménez & M. J. Cano	–	1.29	Circum–Tethyan
Entosthodon cf. *commutatus* Durieu & Mont.	+	6.55	Circum–Tethyan
Entosthodon muhlenbergii (Turner) Fife	–	0.12	Circum–Tethyan
Fissidens cf. *arnoldii* R.Ruthe	–	0.12	Circum–Tethyan
Fissidens sciophyllus Mitt.	–	2.81	Paleotropical
Fissidens crispus Mont.	+	0.35	Circum–Tethyan
Fossombronia caespitiformis (Raddi) De Not. ex Rabenh. subsp. *caespitiformis*	+	1.99	Circum–Tethyan
Funaria hygrometrica Hedw.	+	0.12	Subcosmopolitan
Grimmia orbicularis Bruch ex Wilson	+	0.94	Northern
Gymnostomum calcareum Nees & Hornsch. var. *calcareum*	–	1.64	Cosmopolitan
Gymnostomum mosis (Lorentz) Jur. & Milde	–	4.33	Circum–Tethyan
Husnotiella revoluta Cardot	–	1.05	Pantropical
Hymenostylium hildebrandtii (Müll. Hal.) R. H. Zander	–	0.12	Paleotropical
Microbryum davallianum (Sm.) R. H. Zander	+	0.12	Circum–Tethyan
Microbryum starckeanum (Hedw.) R. H. Zander	+	0.58	Cosmopolitan
Molendoa sendtneriana (Bruch & Schimp.) Limpr.	–	0.35	Subcosmopolitan
Plagiochasma eximium (Schiffn. ex Steph.) Steph.	–	0.12	Paleotropical
Ptychostomum pseudotriquetrum (Hedw.) J. R. Spence & H. P. Ramsay	–	0.35	Subcosmopolitan
Ptychostomum torquescens (Bruch & Schimp.) Ros & Mazimpaka	+	9.59	Subcosmopolitan
Scorpiurium circinatum (Brid.) M. Fleisch. & Loeske	–	3.74	Circum–Tethyan
Syntrichia fragilis (Taylor) Ochyra	–	0.12	Pantropical
Syntrichia laevipila Brid.	–	0.23	Circum–Tethyan
Syntrichia rigescens (Broth. & Geh.) Ochyra	–	0.47	Circum–Tethyan
Targionia hypophylla L.	+	0.82	Xerothermic Pangean
Timmiella barbuloides (Brid.) Mönk.	+	5.50	Circum–Tethyan
Tortella nitida (Lindb.) Broth.	–	8.07	Circum–Tethyan
Tortula atrovirens (Sm.) Lindb.	+	0.23	Xerothermic Pangean
Tortula mucronifera W.Frey, Kürschner & Ros	+	0.12	Arabian endemic
Tortula muralis Hedw. var. *muralis*	+	1.52	Cosmopolitan
Trichostomopsis australasiae (Hook. & Grev.) H. Rob.	–	4.56	Xerothermic Pangean
Tuerckheimia svihlae (E. B. Bartram) R. H. Zander	–	13.10	American and Asian tropical
Vinealobryum vineale (Brid.) R. H. Zander	–	13.92	Circum–Tethyan
Weissia condensa (Voit) Lindb.	+	2.69	Circum–Tethyan

were defined empirically after inspecting the strongly right-skewed size distribution, with many small vents and only a few large openings.

Because the sampling area (radius = 3 m) was constant across plots, the number of vents per class is directly comparable between sites and does not require area standardization. No direct measurements of gas flux or temperature were possible for logistical reasons, but qualitative indicators of activity – such as condensation, surface humidity, and soil discoloration – were noted. The lack of microclimate loggers (soil and air temperature, relative humidity, vapor flux) is recognized as a limitation; future surveys should include autonomous sensors to record diurnal and seasonal variation.

DATA ANALYSIS

To examine how fumarole features affected bryophyte diversity, we combined two complementary datasets. The first was the fumarole survey, which recorded for each GPS-referenced plot the number of vents in four diameter classes (0-2, 2-10, 10-50, and >50 cm). The second described bryophyte assemblages at the same plots, with species presence and abundance estimated using the Braun-Blanquet scale. Abundance scores were converted to ordinal values ("+" = 0.1, "1" = 1, "2" = 2, etc.) and summed per site to obtain total abundance.

Species richness (number of taxa per plot) and total abundance were used as response variables. Fumarole size and total vent count were treated as independent variables – the first reflecting vent morphology, the second indicating overall activity. Vent size classes were handled as quantitative variables corresponding to the number of fumaroles per class in each plot. Relationships were assessed using non-parametric Spearman correlations, as data departed from normality. Each correlation used 188 plots (n = 188). Because multiple tests were performed, only strong associations ($\rho > 0.3$, $p < 0.001$) were retained for interpretation. No formal false discovery rate (FDR) correction was applied, consistent with the exploratory nature of the study. These correlations describe associations rather than mechanisms but offer an initial quantitative view of how fumarole morphology may shape bryophyte assemblages.

Biogeographical data for each element were compiled from the main regional syntheses available for the Arabian and adjacent floras. These include Frey & Kürschner (1988), Kürschner (1998), Kürschner & Sollman (2004), Jiménez *et al.* (2003), and Cano & Jiménez (2013). Records of tropical bryophytes were extracted from the field dataset and grouped

Fig. 5. — A large fumarole (approximately 2 m wide) on the Northeast slope of the Jabal Al-Mashawiya.

by exposure. Sixteen cardinal and intercardinal directions were first used, then aggregated into eight main classes (N, NE, E, SE, S, SW, W, NW) for clarity. Their frequency distribution was compared with a uniform null model using a chi-square goodness-of-fit test. The directional pattern of tropical taxa was visualized as a polar bar chart, with the eight exposure classes arranged clockwise from true north.

RESULTS

Across the 11 fumarolic sites identified within and near the Khaybar White Volcano Geopark, we conducted 188 bryological relevés, yielding a total of 1806 floristic records. These relevés documented 37 bryophyte taxa occurring in fumarolic habitats, including seven tropical or paleotropical species (Tables 1; 2).

Fumarole sizes and distribution

Fumarolic vents showed a strongly right-skewed size distribution (Fig. 4). The 2-10 cm diameter class was the most frequent (4578 vents, 47% of the total) (Fig. 5). Vent frequency peaked in the 2-10 cm class and declined steeply toward larger sizes, the > 50 cm class being marginal (136 vents).

The 11 fumarolic sites were not evenly distributed: two clusters of high density occurred in the northeastern part of the volcanic complex, whereas isolated fumaroles (fewer than ten vents) were scattered across the eastern and southwestern margins (Fig. 6).

Most fumaroles occurred between 1850 and 1900 m a.s.l., with a median altitude of 1869 m and a mean of 1858.5 m (IQR = 1859-1885 m; $\sigma = 80.5$ m) (Fig. 7).

Bryophyte diversity

Out of the 51 bryophyte taxa recorded in the Geopark overall (Hugonnot *et al.* 2025), 37 species (72.5%) were found in fumarolic habitats. Among these, 13 taxa (25.5%) occurred exclusively in fumaroles, 24 taxa (47.1%) were shared between fumaroles and other volcanic substrates, and 14 taxa (27.5%) were confined to non-fumarolic sites (Fig. 8; Table 1).

A subset of species – including *Tuerckheimia svihlae* (E. B. Bartram) R. H. Zander, *Tortella nitida* (Lindb.) Broth., and *Vinealobryum vineale* (Brid.) R. H. Zander – showed strong fidelity to fumarolic conditions, accounting for much of the

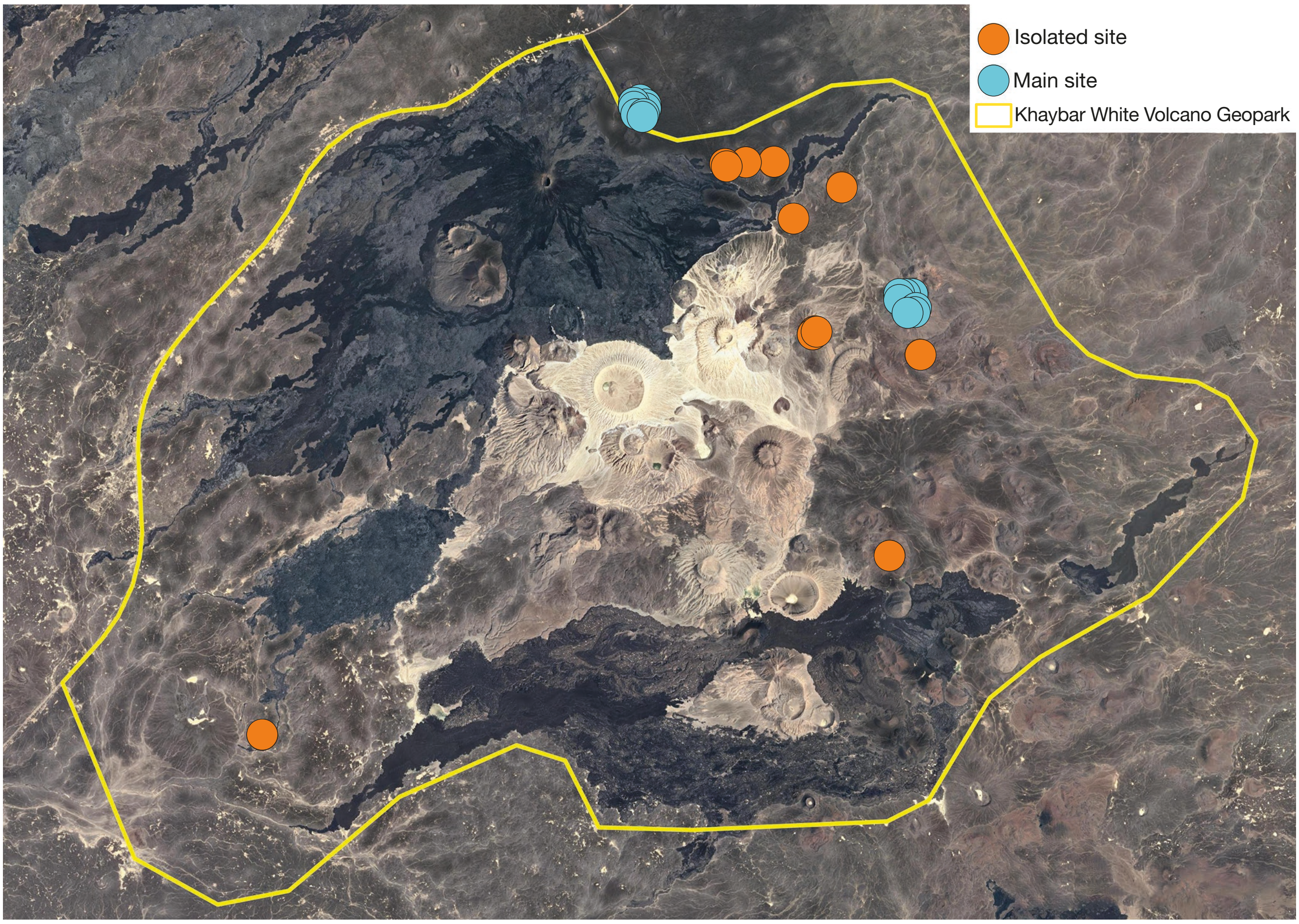

Fig. 6. — Location of all recorded fumaroles (main sites concentrate a large number of fumaroles whereas isolated sites count less than ten fumaroles).

Table 2. — Chorology and frequency of tropical taxa.

Species	Biogeography	Main center of distribution	Outliers	Frequency in Arabian Peninsula
Anoectangium euchloron (Schwägr.) Spruce	Pantropical	South, Central, North America ; Eastern, Central Asia (Cano & Jiménez 2013)	—	Unknown
Husnotiella revoluta Cardot		Central America, South, North America (Jiménez *et al.* 2003)	Asir Mountains (Yemen) (Jiménez *et al.* 2003) ; Kenya (Pócs *et al.* 2007)	One locality
Syntrichia fragilis (Taylor) Ochyra		America, Europe, Asia, Africa (Kramer 2023)	Asir Mountains (Saudi Arabia, Yemen) (Frey & Kürschner 1988)	Very common
Fissidens sciophyllus Mitt.	Paleotropical	Tropical Africa (Bruggeman-Nannenga 1997)	Asir Mountains (Saudi Arabia, Yemen) (Kürschner & Frey 2020)	Common
Hymenostylium hildebrandtii (Müll. Hal.) R. H. Zander		Tropical Africa (Somalia) (Kürschner 1998)	Asir Mountains (Saudi Arabia) (Kürschner 1998)	Common
Plagiochasma eximium (Schiffn. ex Steph.) Steph.		Tropical Africa (Bischler 1978)	Asir Mountains (Saudi Arabia, Yemen), Dhofar (Oman) (Kürschner & Frey 2020)	Common
Tuerckheimia svihlae (E. B. Bartram) R. H. Zander	American and Asian tropical	Central America, Eastern Asia (Eckel in BFNA 2007)	Yemen (Kürschner & Sollman 2004)	Very rare

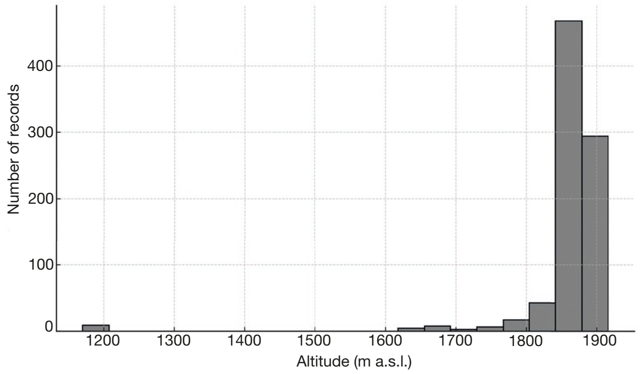

FIG. 7. — Altitude distribution of fumaroles.

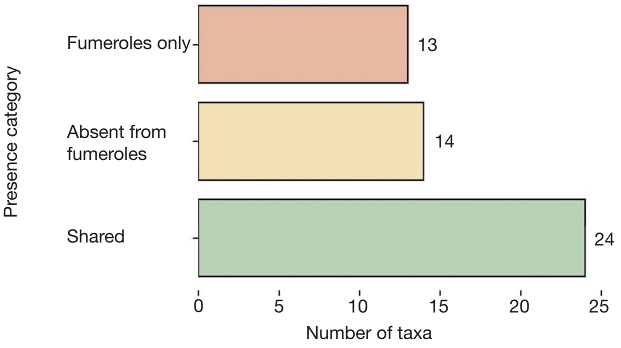

FIG. 8. — Distribution of bryophyte presence categories in the Khaybar White Volcano site.

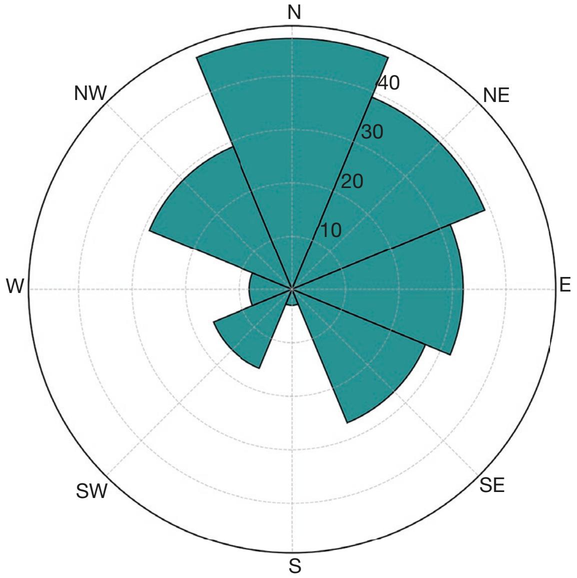

FIG. 9. — Distribution of tropical bryophyte occurrences by exposure.

local abundance. In contrast, species such as *Tortula atrovirens* (Turner ex Sm.) Lindb. and *Bryum dichotomum* Hedw. were frequent outside fumaroles but almost absent within them.

Fifteen taxa (40%) were fertile with sporophytes, whereas 22 taxa (60%) were observed only in the gametophytic stage (Table 1).

BRYOPHYTES AND FUMAROLES CHARACTERISTICS

The seven tropical or paleotropical taxa identified belong to three main distributional groups: pantropical (n = 3), paleotropical (n = 3), and American-Asian tropical (n = 1) (Table 2). With the exception of *Anoectangium euchloron* (Schwägr.) Spruce, all had been previously reported as outliers in wet montane habitats of the Arabian Peninsula (Asir, Dhofar, Yemen).

Species richness and total abundance increased significantly with the number of vents belonging to the medium-size class (10-50 cm; ρ around 0.58, $p < 0.001$). The relationship weakened for larger vents (> 50 cm) and disappeared for the smallest ones (≤2 cm). In contrast, tropical richness showed no consistent trend across size classes since plots dominated by larger vents did not support more tropical taxa than those associated with smaller ones.

SPATIAL DISTRIBUTION OF TROPICAL BRYOPHYTES

All seven tropical taxa occurred at Jabal Al-Mashawiya (Fig. 10). At Jabal Al Aklil, only *Anoectangium euchloron*, *Fissidens sciophyllus* Mitt., and *Tuerckheimia svihlae* were present (Fig. 11). Outside these two craters, tropical species were recorded only sporadically, as isolated populations. Notably, *Anoectangium euchloron*, *Fissidens sciophyllus*, and *Tuerckheimia svihlae* co-occurred in Jabal Umm Touq.

Species showed contrasting microspatial patterns at Jabal Al-Mashawiya: *Tuerckheimia svihlae* was widely distributed along the inner crater rim; *Anoectangium euchloron* and *Fissidens sciophyllus* were abundant on west- and north-facing slopes; *Husnotiella revoluta* Cardot occasionally extended into more south-exposed micro-sites; and *Plagiochasma eximium*, *Hymenostylium hildebrandtii* (Schiffn. ex Steph.) Steph., and *Syntrichia fragilis* (Taylor) Ochyra were restricted to one or a few locations.

Direction of exposure had a marked influence on the distribution of tropical taxa (Fig. 9). Occurrences were highly uneven across orientations ($\chi^2 = 63.8$, df = 7, $p < 3\times10^{-11}$, tested against a uniform null model). Northerly and north-easterly exposures (N, NE) concentrated most of the records, jointly accounting for more than half of all observations, whereas southerly and westerly orientations (S, SW, W) were strongly under-represented.

DISCUSSION

This study provides the first comprehensive inventory of bryophytes inhabiting fumarolic habitats in the Arabian Peninsula. Several of the species recorded are new to the region, confirming that these geothermal sites represent priority areas for further bryological exploration across Arabia's volcanic fields (Hugonnot *et al.* 2025).

Overall, the data indicate that fumaroles influence bryophyte assemblages in Khaybar, but in a complex way. Field observations suggest that dense fumarolic clusters help stabilize local conditions, while statistical patterns show that bryophyte richness and abundance peak where medium-sized vents are

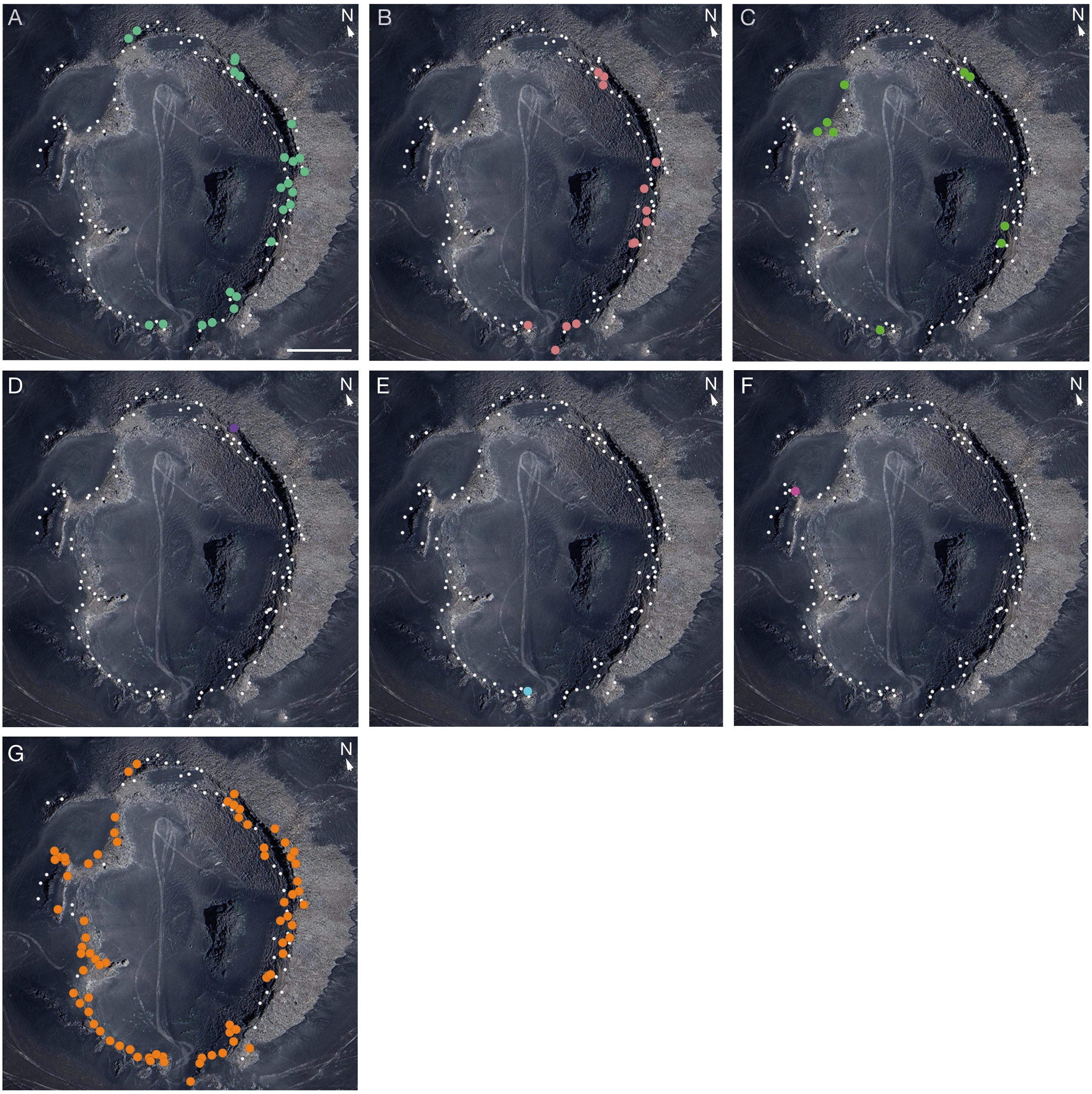

Fig. 10. — Location of tropical bryophyte species in Jabal Al-Mashawiya: **A**, *Anoectangium euchloron* (Schwägr.) Spruce; **B**, *Fissidens sciophyllus* Mitt.; **C**, *Husnotiella revoluta* Cardot; **D**, *Hymenostylium hildebrandtii* (Müll. Hal.) R. H. Zander; **E**, *Plagiochasma eximium* (Schiffn. ex Steph.) Steph.; **F**, *Syntrichia fragilis* (Taylor) Ochyra; **G**, *Tuerckheimia svihlae* (E. B. Bartram) R. H. Zander. **White dots** indicate the location of fumaroles not hosting the species in question. Scale bar: 100 m.

most common. The weaker relationship observed for larger vents (>50 cm) may reflect their greater exposure to light and temperature fluctuations, which can reduce humidity and microclimatic buffering. However, because no direct temperature or humidity measurements were taken, it cannot be ruled out that larger vents are also thermally more active. The results should therefore be interpreted as correlational, though fully consistent with ecological expectations for geothermal microhabitats.

Tropical richness showed no clear trend across size classes, implying that fumarole size alone does not determine the distribution of tropical taxa. This lack of correlation supports the idea that tropical-affinity species respond mainly to microclimatic stability rather than to vent morphology itself – a distinction developed further in the proposed Bryothermal Index framework. These relationships should be viewed as correlational rather than causal, as no direct temperature, humidity, or gas-flux data were collected. Future studies that combine microclimatic monitoring with geochemical profiling will be needed to clarify the mechanisms behind these patterns.

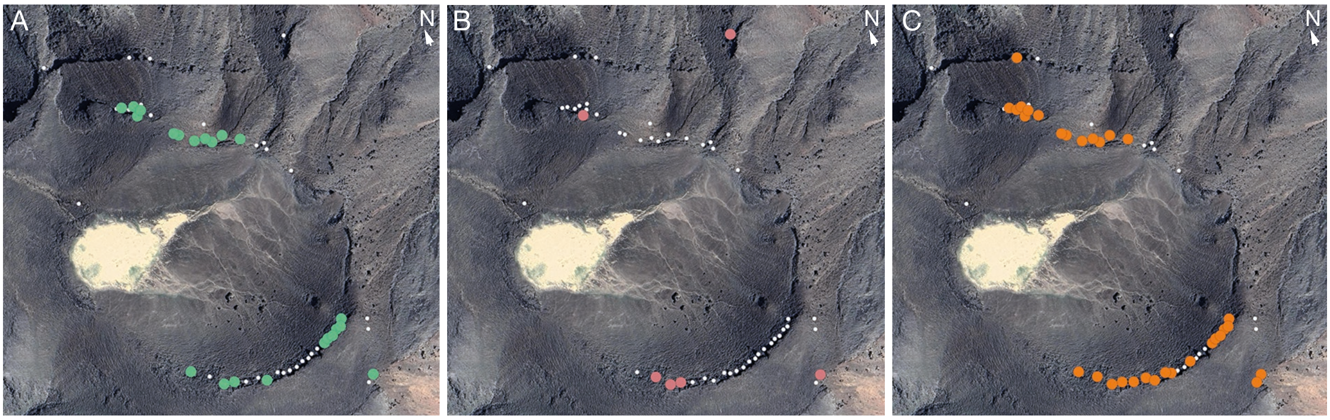

Fig. 11. — Location of tropical bryophyte species in Jabal Al Aklil Volcano: **A**, *Anoectangium euchloron* (Schwägr.) Spruce; **B**, *Fissidens sciophyllus* Mitt.; **C**, *Tuerckheimia svihlae* (E. B. Bartram) R. H. Zander. **White dots** indicate the location of fumaroles not hosting the species in question. Scale bar: 100 m.

Slope orientation clearly influenced the distribution of tropical taxa. Most records occurred on north- and north-east-facing slopes, while south- and west-facing exposures were much rarer. This likely reflects lower solar radiation and higher moisture retention on shaded slopes – conditions generally favourable to bryophytes in arid or montane settings. Fumarolic activity may also buffer the microclimate (Glime & Iwatsuki 1997; Convey *et al.* 2008), but no clear signal emerged at Khaybar: orientation appears to be the dominant factor here, shaping humidity and the persistence of hygrophilous species, with any geothermal contribution intertwined with topographic and radiative effects. Similar interactions between slope exposure, geothermal flux, and bryophyte composition are known from Mount Etna (Puglisi & Sciandrello 2023) and from Icelandic geothermal sites, where vegetation closely follows fine-scale temperature and moisture gradients (Glime *et al.* 2023). While slope orientation evidently affects tropical taxa, it remains uncertain whether the same holds true for the whole bryophyte assemblage; further analyses would be required to separate the roles of geothermal buffering, radiation, and topography.

Beyond these community-level patterns, the distribution of tropical-affinity taxa raises broader biogeographical questions. Geothermal microrefugia, though extremely localized, may play a significant role in maintaining tropical-affinity taxa beyond their present climatic envelope. In Khaybar, these refugia harbour several tropical and paleotropical species – particularly *Husnotiella revoluta*, *Fissidens sciophyllus*, and *Anoectangium euchloron* – which occur far outside the influence of monsoonal climates and are geographically isolated from their main tropical ranges in Dhofar, Asir, and Yemen. Their occurrence in these geothermal refugia can be interpreted under two working hypotheses that are not mutually exclusive. Genetic analyses will be required to discriminate between these two scenarios:

1) Relictual survival, whereby populations represent remnants of a formerly wider tropical flora that persisted locally through Holocene aridification within geothermal refugia. This scenario parallels the “oceanic-Mediterranean relict” model described for fumarolic mosses in Macaronesia and Sicily (Brullo *et al.* 2001); if the relictual hypothesis holds, we expect low intra-population genetic diversity, dominance of vegetative reproduction, and evidence of long-term occupancy (e.g., thick, stratified cushions). Conversely, the LDD hypothesis predicts higher genetic diversity and the presence of juvenile gametophytes.

2) Long-distance dispersal (LDD), whereby sporadic recruitment occurs via stochastic vectors such as high-altitude winds, migratory birds, or dust transport. In this view, Arabian volcanic highlands act as “oases” intermittently colonized by diaspores from remote tropical regions.

The fumarolic fields of Mount Toussidé in the Tibesti (Chad, Sahara) provide a classical analogue for vegetation structuring under geothermal influence. Although the geothermal flux at Khaybar appears weaker than at Toussidé, the two systems share structural parallels. In the Sahara, a concentric pattern was described with a microbial core, a belt of hygrophilous cryptogams, and an outer zone of xerophytic vascular plants (De Miré & Quézel 1959; Anthelme *et al.* 2011). A comparable organization is hypothesized for Khaybar, where tropical-affinity bryophytes are concentrated in the most humid and thermally buffered microzones around fumaroles. This pattern remains to be quantitatively verified. Future work should therefore assess lateral gradients in bryophyte composition and cover around vents, as microclimatic buffering likely decays rapidly with distance.

Bryophytes at Khaybar are both beneficiaries of geothermal buffering and potential bioindicators of low-intensity geothermal activity. In the absence of visible gas emissions, their persistence and fertility may reveal subtle thermal anomalies, as previously suggested (Burns 1997; Glime & Iwatsuki 1997). The positive association observed between bryophyte richness and the number of medium-sized fumaroles, with a weaker signal for larger vents, supports the view that the structure and density of fumaroles mediate microclimatic improvement and shape community structure. Building on this evidence, we propose a preliminary Bryothermal Index (BTI) integrating both compositional and functional attributes of bryophyte

Fig. 12. — A medium-size fumarole (approximately 15 cm wide) with visible traces of humidity on the Northeast slope of the Jabal Al-Mashawiya.

assemblages. The BTI would combine general measures of species richness or abundance – reflecting the overall strength of geothermal influence – with the relative proportion and fertility of hygrophilous or tropical-affinity taxa, which reflect the persistence of humid microclimates and the strength of geothermal buffering within fumarolic habitats. Although still conceptual, this composite index could be calibrated through long-term monitoring along measured temperature and humidity gradients, using automated loggers and repeated population assessments. Validation should include replicated microclimatic transects across active, dormant, and non-fumarolic sites to test whether BTI values reliably track the underlying geothermal intensity.

Although they cover less than one hectare in total, the fumarolic zones of Khaybar host distinct bryophyte assemblages – including relict tropical elements absent from other habitats (Brullo *et al.* 2004; Glime 2007) – that give them exceptional conservation importance. Visible disturbances include wind-blown litter and debris accumulating in vent openings, which can alter microclimate, substrate chemistry, and nutrient balance. We recommend manual removal of debris, periodic inspections, and the designation of small protective zones (50-100 m radius) around fumarolic clusters, with discreet signage and adjusted visitor pathways to limit trampling.

For long-term conservation, sites should be monitored through fixed photo-transects combined with frequent microclimate recordings (e.g., every 15 min). Key indicators to follow include the proportion of tropical taxa, site-level γ-diversity, fertility ratio, and total bryophyte cover. These parameters capture both the compositional and functional responses of bryophyte communities to geothermal stability. Together, they will provide a functional ecological framework for assessing ecological integrity and evaluating conservation effectiveness through time.

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