Nova Hedwigia, Vol. 123 (2026), Issue 1-2, 85–126 **Article**
Published online January 30, 2026; published in print July 2026

Bryophyte communities from AlUla County (Saudi Arabia)

Vincent Hugonnot[1], Florine Pépin[1] and Jan Freedman[2]

[1] Impasse des Oponces, 25, 43380 Blassac, France

[2] Royal Commission for AlUla, Saudi Arabia

* Corresponding author: hugonnot.vincent@orange.fr

With 17 figures and 12 tables and 3 electronic supplements

Abstract: Bryophytes communities are poorly known in the Arabian Peninsula due to the scarcity of published works. An intensive bryosociological survey with 207 relevés carried out at the beginning of 2024 has allowed for the description of 13 distinct communities: three terricolous ones, two saxicolous, five tufa forming ones, plus three fragmentary communities of uncertain syntaxonomic significance. Many of the communities are probably original but we have refrained from describing them from a syntaxomical formal point of view in such a context of fragmentary knowledge. AlUla County, despite the hyper-arid conditions, is unexpectedly rich in remarkable bryophytic communities, some of which exhibit tropical affinities and relictual character of formerly wetter weather conditions. Many of the high heritage value communities are threatened by human activities, i.e. overgrazing by wandering herds of animals and depletion of the water resource. Finally, a case is made for the improvement of bryophytic vegetation knowledge.

Keywords: Bryosociology; synecology communities; water resource

Introduction

The Kingdom of Saudi Arabia (KSA) is the largest county in southwest Asia, covering approximately 2,150,000 km² of land and encompassing about three-quarters of the Arabian Peninsula (Chaudhary 2001). KSA is an environmentally diverse landscape. The central and eastern regions feature rocky and sandy desert environments, whereas large mountain ranges, reaching 3.700 meters above sea level, dominate the southwestern areas near the Red Sea and south to the Yemen border. The county's close proximity to Africa, Asia, and Europe significantly influences its flora and bryoflora. With few endemics, the bryoflora comprises six floristic elements (Kürschner & Ghazanfar 1998). There are few cosmopolitan or northern taxa, but many drought-adapted taxa (Xerotherm-Pangean or

 DOI: 10.1127/nova_hedwigia/1128 www.borntraeger-cramer.de 0029-5035/1128 $ 10.50

Circum-Tethyan elements). The occurrence of several interesting tropical species in KSA, which demonstrates a southeast Asian-Arabian, African-Arabian, Pantropical, or Paleotropical distribution, has been repeatedly highlighted (Kürschner 2000).

It is well-established that most of the bryological diversity in Saudi Arabia is confined to the mountainous, monsoon-influenced South-Hejaz region (Kürschner & Ghazanfar 1998), due to this group's preference for a more humid environment (Wood 2009). In contrast, only a few drought-tolerant species are recorded in other, more arid regions (*Tortula atrovirens*, *Crossidium squamiferum*, *Trichostomopsis australasiae* etc.). At the extreme, the hyper-arid Empty Quarter (Al-Rub' Al-Khali desert, located in the southeastern part of the County) presently holds no recorded bryophyte species. Subsequently, the majority of previous surveys have focused on environments more likely to support bryophyte species, such as the humid southwestern regions of the county. This has consequently resulted in large expanses of Saudi Arabia being neglected in bryophyte research.

As previously highlighted by Frey & Kürschner (1981), bryosociological studies in Southwest Asia are relatively scarce. Turkey stands out as the most intensively surveyed county in this region, having been the subject of a recent syntaxonomic synthesis (Alataş et al. 2023). Some research has been conducted in bryologically less explored countries like Afghanistan (Gilli 1969; Gilli 1971; Gilli 1975; Gilli 1977) and Iran (Frey & Probst 1973), as well as in better-known regions such as Jordan and Israel (Frey & Kürschner 1990; Frey et al. 1990; Frey & Kürschner 1992). In the mostly arid Arabian Peninsula, several bryophyte communities have been described (Kürschner 1988; Kürschner & Ghazanfar 1998) using contrasting methodological approaches, which presents an additional difficulty due to conceptual heterogeneity.

Tufa-forming communities are considered to include both tracheophytes and bryophytes (Deil 1989), with the latter being regarded as a synusia (Kürschner & Ghazanfar 1998). Although the tufa-forming communities (*Adiantetea*) have been considered as rock types, they are highly original since they require permanent flowing water. This Class is the only one described pertaining to the hygrophytic pole, even though amphibious undescribed communities exist in the Asir Mountains (pers. obs.). Epiphytic communities have been studied quantitatively (Kürschner 1984a) and bryosociologically (Kürschner 2003a), following the traditional Braun-Blanquet school approach (1964). Complexes of bryophyte synusia, spatially or dynamically linked, have also been examined in detail (Kürschner 1984b; Frey & Kürschner 1987). Analyses of life forms and life strategies have been repeatedly employed, showing strong correlations with ecological parameters and common adaptive traits co-evolved under similar environmental constraints (Kürschner 2003b, 2004a). Despite the diversity of vegetation concepts and methods, we have compiled all available publications describing bryophyte communities from the Arabian Peninsula (Table 1). Consequently, only 11 communities are currently recorded and described from the Arabian Peninsula.

The description of bryophytic communities holds particular interest in a hyper-arid region like AlUla because it provides more information about the richness of biodiversity on our planet. This paper highlights the unexpectedly large and surprising diversity of bryophyte

communities in a hyper-arid environment. Typically, bryosociological studies are limited to a single community or a geographically small area; here, however, all communities are addressed across a vast territory. The data collected also has quantitative value in terms of the surface area covered by bryological populations. While previous studies have logically focused on areas presumed to be the richest, this study demonstrates that exploring areas that are not typical environments for bryophytes, provides a greater understanding of bryophyte communities, adaptation, and diversity.

Study area

AlUla County is located in the northwestern part of Saudi Arabia, south of Tabuk, approximately 200 km east of the Red Sea (Fig. 1), and belongs to the Saharo-Sindian regional zone (Zohary 1973; Kürschner 1998), which is generally characterised by an arid to hyper-arid climate. This county, covering an area of 22,561 km², has not previously been the subject of any bryological surveys or research. During the late winter of 2024, the authors (VH, FP) had the opportunity to conduct intensive field trips throughout the entire region, focusing on the five Nature Reserves within the county. Here, we present the sociological description of bryophyte communities observed in this area.

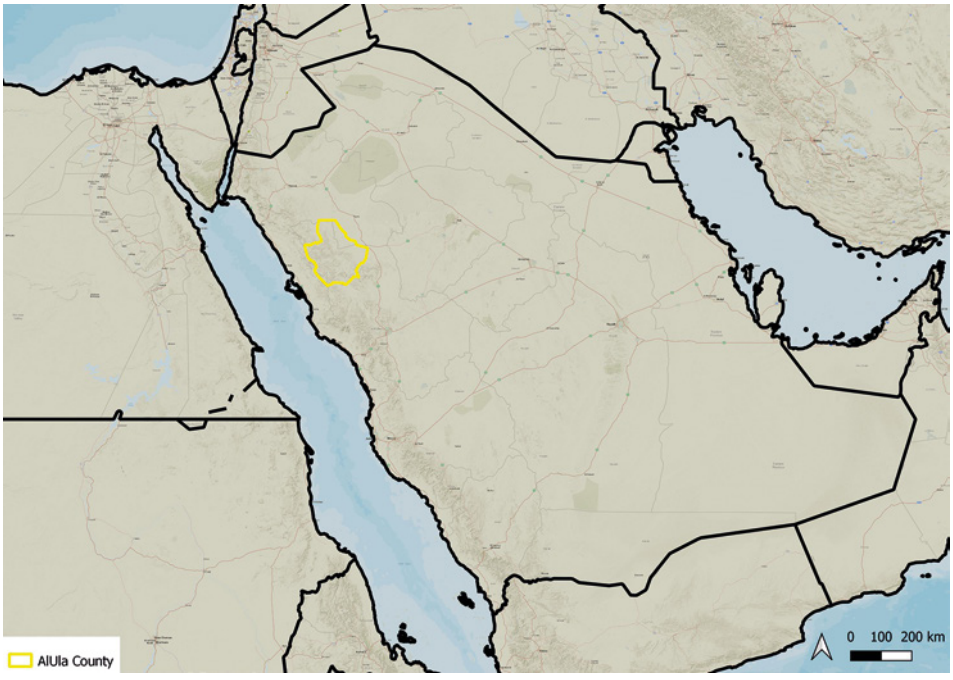

Fig. 1. Location of AlUla County within the Arabian Peninsula.

Table 1. Main data relating to previously described bryophytic communities in Arabian Peninsula.

	Higher syntaxon	Name of community	Synonym	Ecology	Known distribution	Reference
Epiphytic	Indeterminate	Lejeuneo rhodesiae-Semathophylletum socotrensis Kürschner 2004 (Subass. hyophyletosum involutae Kürschner 2004; Subass. papillarietosum croceae Kürschner 2004)		On trunks, branches and twigs in Afromontane evergreen forests	Haghier mountains (Socotra)	Kürschner, 2004
	Frullanio dilatatae-Leucodontetea sciuroidis Mohan 1978; Syntrichion laevipilae Ochsn. 1928	Leptodonto-Leucodontetum schweinfurthii Kürschner 2003	Hypno-Leucodontetum dracaenae nom nud. in Kürschner & Ghazanfar 1998; Hypnum vaucheri association Kürschner 1984	On shaded Juniperus procera branches and trunks in Afromontane Juniperus woodlands	Asir mountains (Saudi Arabia, Yemen)	Kürschner, 2003
	Frullanio dilatatae-Leucodontetea sciuroidis Mohan 1978; Syntrichion laevipilae Ochsn. 1928	Orthotricho-Fabronietum socotranae Kürschner 2003	Fabronietum socotranae nom. nud. in Kürschner & Ghazanfar 1998; Orthotrichum diaphanum association Kürschner 1984	On exposed branches and trunks in Acacia origena woodlands	Asir mountains (Saudi Arabia, Yemen)	Kürschner, 2003
Terricolous (saxicolous)	Psoretea decipientis Matt. ex Follm. 1974; Mannion androgynae Ros & Guerra 1987	Riccietum jovet-astii-argenteolimbatae Kürschner 2003		Shallow soils in temporarily moist depressions on volcanic rocks	Jabal Arays (Yemen)	Kürschner, 2003
	Indeterminate	Not described yet: Barbula consanguinea/Hyophila involuta community		soil on xerotropical Anogeissus dhofarica forests	al-Mahra, Yemen and Dhofar, Oman	Kürschner, 2008
	Psoretea decipientis Matt. ex Follm. 1974; Aloino bifrontis-Crossidion crassinervis Ros & Guerra ex Marst. in Marst. 2006	Tortula atrovirens-Crossidium squamiferum synusia		Limestone rocks and boulders	Jebel Tuwayq (Saudi Arabia)	Frey & Kürschner, 1987

Table 1. cont.

	Higher syntaxon	Name of community	Synonym	Ecology	Known distribution	Reference
Terricolous (saxicolous)	Indeterminate	Grimmia trichophylla-Pseudoleskeopsis leikipiae complex		Granite rocks and steep walls in deep gorges	Asir mountains (Saudi Arabia)	Kürschner, 1984
	Indeterminate	Crossidium squamiferum-Grimmia div. sp. community		Dry rocks and boulders	Central and Southern parts of the Arabian Peninsula	Kürchner & Ghazanfar, 1998
Saxicolous	Grimmietea alpestris Had. & Vondr. in Jež. & Vondr. 1962; Grimmion commutatae v. Krus. 1945	Grimmietum commutato-campestris V.Krus. 1945 grimmietosum affinis Marst. 1996, geographical race of Schlotheimia balfourii		Acidic, dry and sun-exposed rocks	Haghier mountains (Socotra)	Kürschner, 2006
Hygrophilic	Adiantetea capilli-veneris Braun-Blanq. ex Braun-Blanq., Roussine & Nègre 1952	Adianto-Primuletum verticillatae Deil 1989		Dripping calcareous rocks	Haraz and Asir mountains	Deil, 1989
	Adiantetea capilli-veneris Braun-Blanq. ex Braun-Blanq., Roussine & Nègre 1952	Adianto-Epipactidetum veratrifoliae Deil 1989		Dripping calcareous rocks	UAE, North Yemen, Oman, Israel	Deil, 1989; Baierle, 1993

As part of the Arabian Shield, AlUla has a rich geodiversity, covering all three main rock types in a relatively small area. Precambrian igneous and metamorphic rocks, as well as Cambrian and Early Ordovician sandstones (Hadley 1987), are exposed across the landscape. The sandstones that dominate the central and northern parts of AlUla are the older Siq and younger Quweira and Saq Formations, all composed of fine to medium-grained quartz (Hadley 1987). The rifting and opening of the Red Sea created several extensive basaltic lava fields (locally known as harrats) during the Tertiary dating from around 10 million years ago until around 500,000 years ago (Hadley 1987; Rasul et al. 2015; Altherr et al. 2019). More recent alluvium deposits can be found across the region, especially in valleys (wadis), ranging from large water-travelled boulders to fine-grained wind-blown sand (Al-Bassam et al. 2014).

A rich and varied geodiversity in an area will result in a range of habitats, and subsequently, increased biodiversity (Comer et al. 2015; Lawler et al. 2015; Alahuhta et al. 2018). The erosion of different rock types, particularly in the absence of vegetation cover and low annual rainfall, has created a wide range of habitats across AlUla. The crystalline igneous and metamorphic rocks in the south erode very differently than the sandstones in the north, creating different landscapes and different types of soils. The geodiversity of AlUla is a contributing factor to the establishment of five Nature Reserves, which aim to protect over 50% of the county. Harrat Uwayrid, Harrat AlZabin, Wadi Nakhlah, Sharaan and AlGharameel Nature Reserves, are different from each other based on the ecology and the underlying geology.

The climate of most parts of North Arabia is characterised by very hot, dry summers and cool to warm winters. Rain-bearing cyclonic depressions during winter and spring that originate in the Atlantic or Mediterranean are the main source of precipitation. Throughout the area, rainfall is erratic and unpredictable in time, quantity, and space and often falls as heavy local showers. In some years, certain areas may receive almost no rain. The data obtained for the AlUla meteorological station illustrate the mean annual regional climate (Fig. 2). The mean annual rainfall is 61 mm and the mean annual temperature is 24.6 °C.

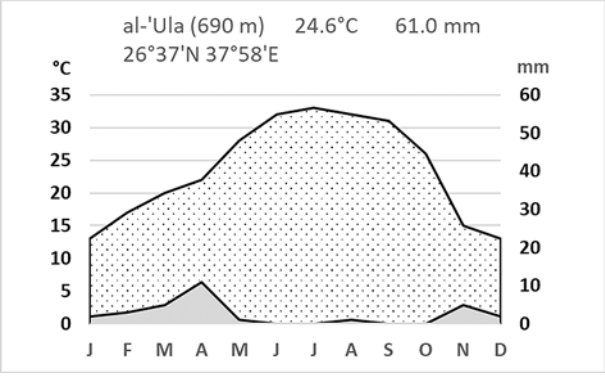

Fig. 2. Climatogram for AlUla meteorological station (Data: 1991–2021).

Materials and methods

The surveys were conducted from January 13 to February 27, 2024, with 488 selected sites surveyed (Fig. 3). The selection of sites was informed by the examination of geological and topographical maps to identify potential sources of moisture, such as wadis, springs, and wetlands. An additional site selection criterion was accessibility based on the presence of trails within a clear and safe walking distance of less than five kilometres from a road or track. Local ranger's information regarding safe access for prospecting and the presence of potential habitats for bryophytes was included in site selection. All sites meeting the aforementioned selection criteria were visited during the field session.

A total of 207 bryosociological relevés were systematically surveyed using the traditional the traditional Braun-Blanquet (1964) appraoch and the adapted abundance-dominance scale of Frey & Kürschner (1995). The species cited in this paper are those sharing the same microhabitat, not species growing nearby within distinct communities. Additionally, classic ecological parameters were recorded (e.g., exposure, inclination, bryophyte cover, soil depth where relevant, etc.). We have refrained from describing any new association or community of lower rank (i.e. sub association or races) because the surveys were carried out in a restricted geographical framework and in particularly harsh ecological conditions.

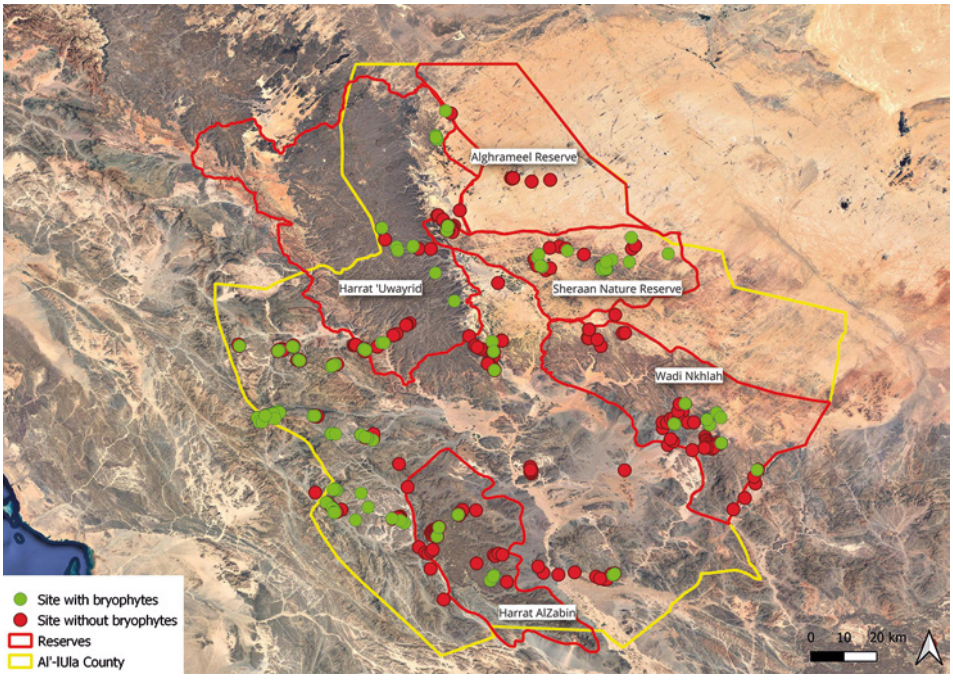

Fig. 3. Location of surveyed sites (Nature Reserve are indicated with red lines).

Table 2. Nomenclature for names deviating from Kürschner & Frey (2020).

Accepted nomenclature	Kürschner & Frey, 2020	Followed reference
Molendoa handelii (Schiffn.) Brinda & R.H. Zander	Anoectangium handelii Schiffn.	Brinda & Zander, 2020
Clevea spathysii (Lindenb.) Müll. Frib.	Athalamia spathysii (Lindenb.) S. Hatt.	Rubasinghe, 2011
Ptychostomum capillare (Hedw.) Holyoak & N. Pedersen	Bryum capillare Hedw.	Holyoak, 2021
Ptychostomum pseudotriquetrum (Hedw.) J.R. Spence & H.P. Ramsay	Bryum pseudotriquetrum (Hedw.) G. Gaertn.,	Holyoak, 2021
Ptychostomum torquescens (Bruch & Schimp.) Ros & Mazimpaka	Bryum torquescens Bruch & Schimp.	Holyoak, 2021
Trichostomopsis australasiae (Hook. & Grev.) H. Rob.	Didymodon australasiae (Hook. & Grev.) R.H. Zander	Jiménez et al., 2022a
Geheebia siccula (M.J. Cano, Ros, García-Zam. & J. Guerra) J.A. Jiménez & M.J. Cano	Didymodon sicculus M.J. Cano, Ros, García-Zam. & J. Guerra	Jiménez et al., 2022a
Geheebia tophacea (Brid.) R.H. Zander	Didymodon tophaceus (Brid.) Lisa	Jiménez et al., 2022a
Vinealobryum vineale (Brid.) R.H. Zander	Didymodon vinealis (Brid.) R.H. Zander	Jiménez et al., 2022a
Riella affinis M. Howe & Underw.	not mentionned	Segarra-Moragues et al., 2014
Entosthodon commutatus Durieu & Mont.	not mentionned	Brugués et al., 2010
Didymodon desertorum (J. Froehl.) J.A. Jiménez & M.J. Cano	not recognized	Jiménez et al., 2022b
Ptychostomum cellulare (Hook.) D. Bell & Holyoak	Plagiobryoides cellularis (Hook.) J.R. Spence	Holyoak, 2021

The taxonomy and nomenclature of the bryophytes mainly follow Kürschner & Frey (2020), except for the 13 names indicated in Table 2, for which specific references are provided. For vascular plants, we use Kürschner & Neef (2018). The vouchers are currently kept in the private herbarium of Vincent Hugonnot and Florine Pépin and will be transferred to the Royal Commission for AlUla's (RCU) collection in early 2025.

Several bryophyte species are taxonomically problematic, due to limited structural information (Heinrichs et al. 2009), with many species currently under review by researchers. For such taxa in this research, they have been named using up-to-date treatments, i.e. Kürschner & Frey (2020), including *Fissidens arnoldi* R. Ruthe and *Bryum sp*. Additionally, *Entosthodon commutatus* Durieu & Mont. is not mentioned in Kürschner & Frey (2020), and is a taxonomically problematic species.

The vegetation description is largely derived from the Inventory and Vegetation of AlUla Flora Project (CMEP 2023) and Kürschner & Neef (2018). Associated vascular plants are systematically noted, with a distinction made between those growing in the same microhabitat (e.g., a wet fissure, under an overhang, etc.) and those growing in the vicinity under distinct ecological conditions.

The scale of expression of tracheophytic communities is very different from that of bryophytic communities, making the correlation between the two vegetation types extremely problematic. The predictive power of tracheophytic communities is extremely limited as regard bryophytic ones. The main types of Tracheophyte vegetation units are the following (CMEP 2023; Kürschner & Neef 2018):

- *Lycium shawii–Ephedra foliata* shrubland of the runnels and wadis of the Hijaz Mountains;
- Vegetation of the sandstone canyons and sandy gullies (*Ficus salicifolia*, *F. palmata*, *Abutilon bidentatum* etc.);
- Sparse mixed herb and shrub community of the scree slopes (*Ochradenus baccatus*, *Fagonia bruguieri*, *Forsskaolea tenacissima*, *Tetraena simplex*) housing cracks and micro-communities dominated by *Parietaria alsinifolia*, *Isatis lusitanica*, *Hemionitis pteridioides*;
- *Retama raetam–Artemisia sieberi* open shrubland of the high Hijaz mountains, well developed in Jabal AlWard from 1 500 to 2 000 m;
- Palm groves housing rich assemblages of ruderal communities (*Aizoon canariense*, *Lysimachia arvensis*, *Calendula tripterocarpa*, *Malva parviflora*, *Bromus tectorum* etc.);
- Seasonal pools with *Juncus rigidus*, *Typha* sp. and *Mentha longifolia* and mainly Characeae species and green Algae;
- Seepage with *Adiantum capillus veneris*.

Each of the recognized bryological communities is described, focusing on ecological setting, tracheophytic vegetation, character species, syntaxonomy with citation of the relevant references, dynamics, distribution, phytogeographical affinities and heritage value. The basis of the heritage value estimate is the consideration of rarity, ecological specialization, sensitivity to disturbances, and the presence of rare species, conservation and management. Given the high number of relevés and the putative fragmentary nature of many of them, only the frequency table (based on the complete set of relevés) is provided. The complete frequency table containing all 207 relevés is given as supplementary electronic material. All images were taken during the present study and are intended to illustrate the overall character of each community. When communities cannot be assigned to a described syntaxon, we name them by using the name of the most typical species or family of the floristic assemblage (e.g., *Riccia cavernosa* community; *Pottiaceae* community).

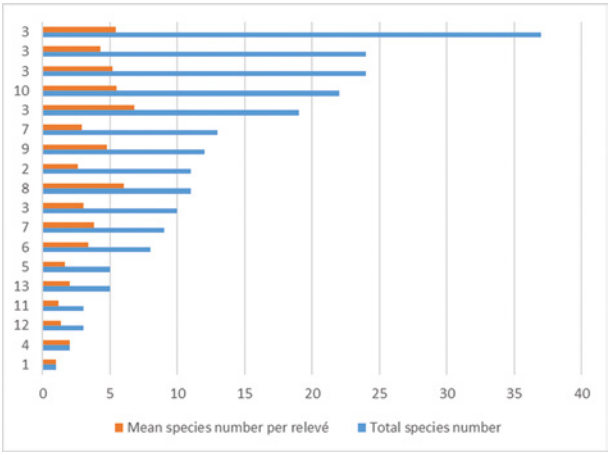

Fig. 4. Specific richness of the bryosociological relevés of AlUla County compared with the total number of species recorded in each community (x-axis: number of recorded species; community codes (Supplementary Table 1 and Fig. 17) are given including all the faciès of each community, in the y-axis).

Results

13 communities could be identified from data on the 207 surveyed vegetation relevés. The mean number of species per relevé is 4.11 (SD 2.89), and is always low (Fig. 4), regardless the community, whereas the total number of species is 51 and is highly variable across communities (from 1 to 37).

As an example, the richest community of AlUla County (number 3: *Pottiaceae* community) has 37 potential species whereas the mean number of species per relevé of this community is only 5.4.

The communities are described in the following, from terricolous communities, saxicolous and tufa-forming ones. The bryosociological relevés are provided in Supplementary Table 1. In the following section, we will describe the relevant ecological parameters, the floristic composition, the heritage value and conservation of each community.

Terricolous communities (Fig. 5)

Three terricolous communities have been identified, including one temporary aquatic, one amphibious, and the last one, highly polymorphic and xerophytic.

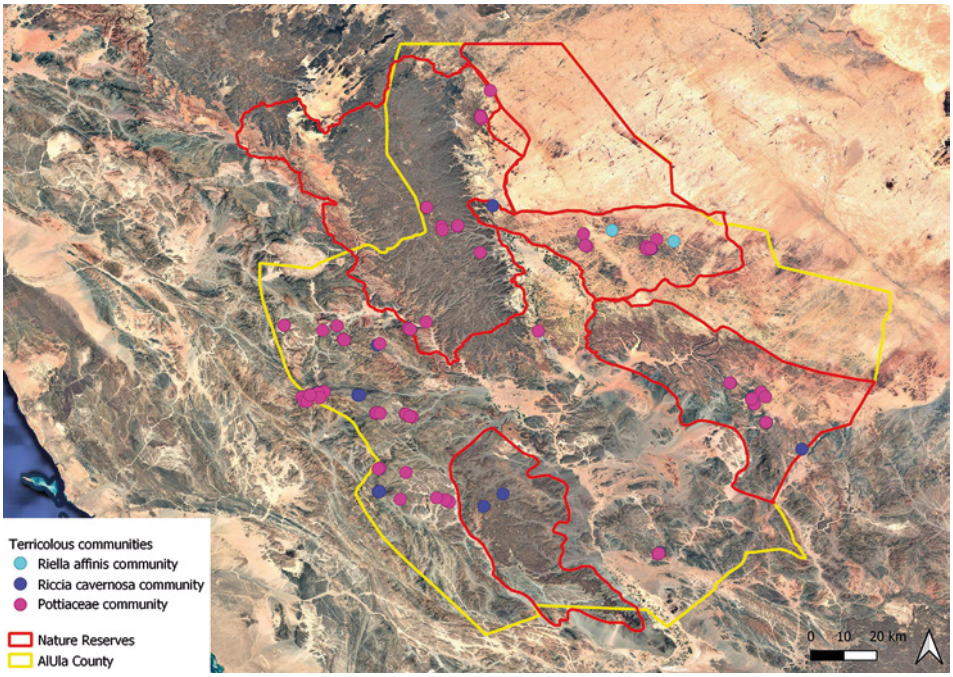

Fig. 5. Distribution of terricolous bryophytic communities in AlUla County.

Riella affinis community

An aquatic, submerged, annual, and ephemeral community developing in small temporary water bodies. Clear, shallow freshwater (around 50–100 cm maximum) pools form on a sandy substrate resulting from the disintegration of sandstone (Fig. 6). The community undergoes a period of complete desiccation, during which the species of the genus *Riella* survives in the form of spores buried in the organic-poor, sandy soil. It is a pioneer community that cannot withstand competition from any other plant. The only vascular species developing in one of the two water bodies surveyed is *Phragmites australis*, which is present as small colonies. The two water bodies in question are located in deep sandstone gorges, which significantly limits sunlight exposure. One of the two water bodies is natural and small (around ten square meters), while the other, more extensive (around 220 square meters), is the result of a small human-made dam built a few decades ago.

Table 3. *Riella affinis* community relevés.

Relevé number	**91–1**	**88–1**
Surface (cm^2)	100000	30000
Taxa number	1	1
Riella affinis M. Howe & Underw.	4	2

Fig. 6. Sharaan Nature Reserve pond with abundant thallus of *Riella affinis* (26°53'55.6"N 38°19' 30.43"E).

The community is monospecific, the only characteristic species being *Riella affinis*. It is an opportunistic community, reappearing whenever hydrological conditions allow. Other aquatic communities, particularly those based on algae, may also develop if ecological conditions permit. This community has only been observed at the Sharaan Nature Reserve site and is not known elsewhere in the Arabian Peninsula. The two water bodies in question are relatively distant from each other (19 km). Other populations may be discovered within the maze of rocky canyons in the Reserve.

The heritage value and ecological interest of this community are very high, as the species is extremely rare worldwide. The maintenance of this community depends on a delicate balance, based on the seasonality of rainfall patterns, the presence of depressions at the bottom of sandstone gorges and in the minor beds of small temporary streams, and the presence of diaspore stock in the substrate.

Conserving this monospecific community is crucial and relies on maintaining the hydrological regime. Early drying is catastrophic because it prevents spore production, thereby depleting the diaspore stock. Monitoring the populations is therefore advisable. Additionally, the fragility of the masonry structure of the dam that obstructs the small watercourse, that created the *Riella* pond, should be monitored as its failure could likely lead to the disappearance of the species. Finally, the filling of the depressions should also be moni-

tored, as excessive sand accumulation at the bottom of the basins could cause the ponds to dry out. The dynamism of *Phragmites australis* should also be monitored, as it could become invasive (especially after partial filling) and threaten the *Riella*.

Riccia cavernosa community

This is an ephemeral, vernal community colonizing sandy or sandy-silty soil, the banks of wadis, and small depressions in the minor beds of small temporary watercourses. It is not found associated with sandstone outcrops, and appears to thrive in sandy-silty soils,

Fig. 7. *Riccia cavernosa* community (26°8'8.66"N 37°48'31.73"E).

Table 4. *Riccia cavernosa* community relevés.

Surface	**20000**	**10000**	**10000**	**20000**	**1500**	**2100**	**3000**	**1200**	**200**	**400**	**900**	**10000**	**1000**	**10000**	**1600**	**10000**	**3000**	**10000**	**10000**	**2500**	**20000**	**20000**
Microhabitat slope (°)	0	5	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0
Substrate depth (cm)	10	10	30	10	10	5	10	10	10	10	10	3	5	20	5	20	5	15	15	10	10	10
Taxa number	3	3	3	3	3	3	2	1	2	2	2	3	2	3	2	2	4	1	3	1	7	2
Character species																						
Riccia cavernosa Hoffm.	2	3	3	2	1	1	2	2	2	2	2	2	2	1	1	1	2	1	1	1	+	+
Psoretea and Funarietalia																						
Bryum dichotomum Hedw.	1	1	3	4	3	2	1							2	2	2	2					
Funaria hygrometrica Hedw.	1	+	+	2	1	2											+				+	
Others																						
Bryum sp.									+	+	2	2							1		+	
Entosthodon commutatus Durieu & Mont.																					1	+
Geheebia tophacea (Brid.) R.H. Zander												+	+									
Gyroweisia tenuis (Hedw.) Schimp.														+					+			

Table 4. cont.

Surface	**20000**	**10000**	**10000**	**20000**	**1500**	**2100**	**3000**	**1200**	**200**	**400**	**900**	**10000**	**1000**	**10000**	**1600**	**10000**	**3000**	**10000**	**10000**	**2500**	**20000**	**20000**
Crossidium crassinervium (De Not.) Jur.																					1	
Microbryum starckeanum (Hedw.) R.H. Zander																					1	
Fissidens arnoldi R. Ruthe																					1	
Pterygoneurum ovatum (Hedw.) Dixon																	+					

which show a greater variety of grain size and minerals. The constituent bryophytes are exposed to intense solar radiation, as the habitat generally lacks significant shading. However, in some cases, the relative removal of sediment in a watercourse or the presence of high walls provides varying degrees of shade. The community appears on the moist fine sand after the floodwaters recede and continues to develop until spore production, provided the substrate remains sufficiently moist. Frequently, the thalli abort prematurely if drought conditions set in too early in the season.

The community is characterized by the presence of *Riccia cavernosa* (Table 4) which generally exhibits relatively low cover. *Riccia cavernosa* can also be found in other temporarily moist communities that do not belong to the association described here. Eleven species comprise the floral base of this community, while the average number of species per survey is 2.59, indicating a species-poor community. *Bryum dichotomum* and *Funaria hygrometrica* are the only two species with a certain level of constancy.

The stability of the community is only maintained by disturbances caused by floods, which have a localized rejuvenating effect. In the event of environmental stabilization, the community is quickly invaded by ruderal vascular species that take advantage of the moisture to establish and proliferate.

The amphibious community with *Riccia cavernosa* is relatively common, and even sometimes quite abundant, along certain wadis, particularly in the western part of the county. More broadly, it is likely to be quite widespread along the Red Sea coast, extending into Yemen, judging from the distribution map of the nominal species provided by Kürschner (2000). This community has temperate affinities but extends widely into the subtropical zones of the Peninsula, particularly in the Tihama plain.

Although most constituent species are relatively common in the Peninsula (excluding *Pterygoneurum ovatum*), this community has significant heritage value because it reflects the seasonal functionality of watercourses. It can suffer from the effects of overgrazing (physical damage to the thallus, erosion, soil compaction etc.), especially since the edges of wadis are often favoured areas for livestock. One of the detrimental effects of frequent grazing by wandering herds is nutrient enrichment, which can lead to the trivialization of the bryoflora. Water abstraction, the construction of dams, or any other development likely to deteriorate the conservation status of watercourses should be avoided.

Pottiaceae **community (Fig. 8)**

This is a terricolous community found across a variety of different habitats across AlUla. It was recorded on scree of igneous, sedimentary, and metamorphic rock, demonstrating that this family is not restricted to rock type. It was observed at the base of rocky cliffs. The bryophytes predominantly colonize compacted, often indurated, earthy accumulations, which are inclined toward verticality and protected. The preferred situation is under the blocks, where conditions seem less severe, and where bryophytes can likely benefit

Fig. 8. *Pottiaceae* community (26°24'26.58"N 38°34'5.52"E).

from a noticeable reduction in sunlight, an increase in relative humidity, and runoff from upslope. This community is almost always observed on north-facing slopes, usually at the bottom of the slope, and on slopes located in more or less incised valleys.

Several variants can be observed. In close proximity to rocky outcrops, or in stony biotopes, saxicolous elements, particularly *Grimmia orbicularis* (Supplementary Table 2) can occupy a significant place, thus establishing a transition with true saxicolous communities. On compacted and relatively moist, organic-poor soil, often at the base of a rocky cliff or on relatively cool flats, *Microbryum starckeanum* can cover large areas, and consequently, some of the most xerophytic species may disappear or regress (for example, *Tortula atrovirens*, *Crossidium squamiferum*). In the deepest and coolest cavities between large blocks, a variant with *Fissidens arnoldii* can be observed, within which *Trichostomopsis australasiae* generally develops strongly. At the extreme end of the spectrum, in the most climatically or microclimatically challenging cases, a very poor variant with *Bryum sp.* may be present. This variant is without much bryosociological significance, however, due to its ecological characteristics, it can still be related to the community described here.

This community could potentially be recognized as an association, with its various variations linked to station characteristics considered as sub-associations. The transition to-

wards saxicolous communities could also be recognized as a sub-association. However, we have not followed this option for the following reasons:

- Our surveys were conducted in a county with a relatively modest area compared to the potential range of such an association, which could certainly extend across the arid zones of the Arabian Peninsula and perhaps beyond;
- The synsystematics of the communities within the *Aloino bifrontis-Crossidion crassinervis* Alliance is currently problematic (Marstaller 2006), highlighting the need for a large-scale revision; several associations close to the one described here have been published recently (*Crossidio crassinervis-Aloinetum aloidis* W. Frey et al. 1990; *Trichostomopso aaronis-Barbuletum trifariae* W. Frey & Kürschner 1992), so describing a new, only slightly different association would add some confusion to the Alliance;
- Frey & Kürschner (1987) themselves chose the option of not describing a new association but a synusia, which implicitly validates our choice.

The dynamics of this community are difficult to trace through synchronic observations. Indeed, it is subject to natural erosion (or grazing by livestock), which tends to rejuvenate it periodically, thereby creating to a cycle of reconstitution. It is possible that some relevés actually represent such pioneer phases, linked to the community's cyclic dynamics.

This community is widespread in the AlUla County and is indeed the most common bryophyte community in the region. However, it is more frequent, better developed, and richer in species in the western part of the county, in elevated areas. The Pottiaceae community gets more characterized as the altitude increases, further supporting the existence of a generally fragmentary community locally. The Pottiaceae community is much better developed and richer in species in the mountainous regions of Asir. It is a typical desert community, that colonizes particularly arid regions.

The presence of this community indicates the desert environment's potential to support groups requiring a minimum level of moisture. Therefore, the richer it is in species, the more favourable the environment, and the greater the community’s heritage value. It is also a reservoir for a bryoflora remarkable for its rarity such as *Molendoa handelii*, *Acaulon triquetrum*, and other species. The richest phases of this community may suffer from overgrazing, which can lead to the uprooting of rocks and excessive destabilization of the substrate. The microclimates generated by the arrangement of rocks are sensitive to any structural modification, which alters shading and water flow, thereby affecting humidity levels favourable to bryophytes. Moreover, this community is undoubtedly extremely sensitive to any changes in the precipitation regime and can therefore serve as a sentinel for climate change.

Notice is to be taken of the presence of a ruderal community in irrigated palm groves. These occur in market-gardening areas on packed and humid sands dominated by *Bryum sp.* (often sterile and indeterminable). This community is to be recorded, as it is often the only one to sparsely colonize agricultural areas although it does not have any bryosociological significance.

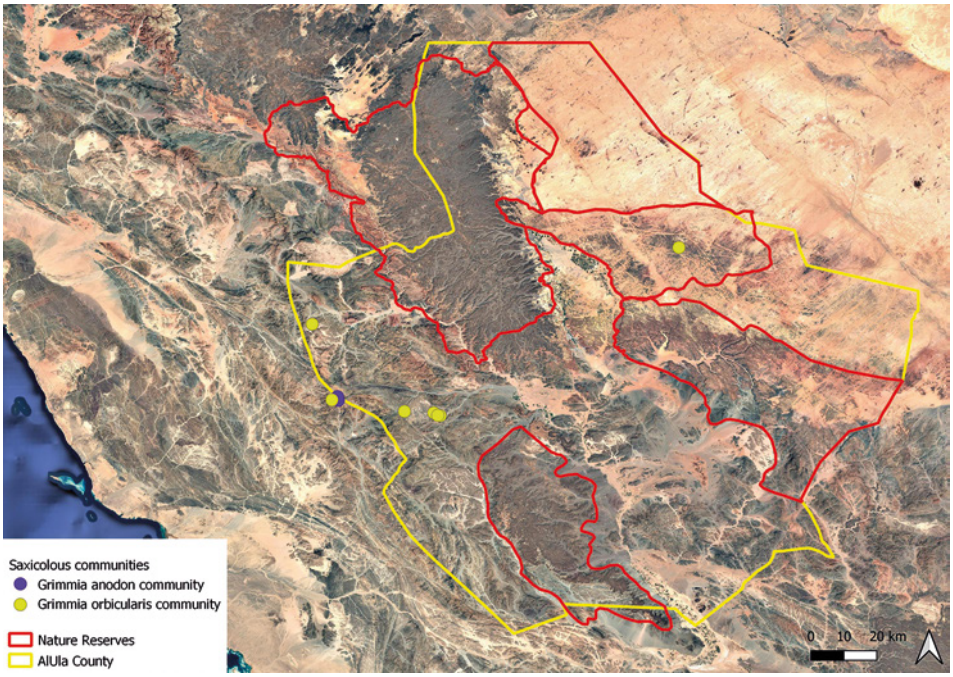

Fig. 9. Distribution of saxicolous bryophytic communities in AlUla County.

Saxicolous communities (Fig. 9)

Two rock-dwelling communities were recorded. They are both species-poor and ecologically very specialized communities.

Grimmia anodon community (Fig. 10)

A strictly saxicolous community, colonizing large granite blocks exposed to the north and benefiting from some protection against direct sunlight. The moss cushions generally colonize micro-fissures, mostly at the base of the rocks. Water supply is provided by modest runoff along the rock during rainy episodes and by capturing atmospheric moisture.

This community is particularly species-poor, with its unique characteristic being *Grimmia anodon* (Table 5). *Grimmia orbicularis* consistently accompanies it.

However, the recognition of discrete saxicolous communities is further complicated by the near-constant mixing of terricolous-saxicolous assemblages, i.e., *Grimmiaceous* rock-dwelling mosses tend to co-occur at very small spatial scales with soil-dwelling *Pottiaceous* mosses. This is particularly striking in the hyper-arid regions of Saudi Arabia, where discrete communities are hard to individualize. The putative factors are:

Fig. 10. *Grimmia anodon* community (26°24'56.86"N 37°13'4"E).

- Aridity forces species to colonize the few favourable and available micro-areas, which explains the spatial contraction of niches (i.e., most soil and rock areas are totally bare of any bryophyte); a minimal amount of substrate is necessary for bryophytes to colonize, as bare rocks are very unfavourable due to extremely low water retention;
- The intense erosive power of the climate causes severe disaggregation of rock surfaces, making them liable to retain small amounts of particles, and on the other hand, mud and sand tend to accumulate on bare rocks, thereby favouring the arrival of terricolous assemblages over rock surfaces. Given the listed limitations, it is nonetheless

Table 5. *Grimmia anodon* community relevés.

Surface	60	200
Microhabitat slope (°)	80	80
Taxa number	2	2
Grimmia anodon Bruch & Schimp.	3	3
Grimmia orbicularis Bruch ex Wilson	1	1

possible to recognize a *Grimmia anodon* community. Recognition can be attributed to the *Grimmion tergestinae* alliance, although this alliance typically concerns thermophytic communities that develop on carbonate rocks. In fact, in hyper-arid climates, the nature of the rock becomes secondary, and it is through the compensation of factors that most of the communities in Europe within this alliance are found on limestone. This is arguably because the climate is much more humid in Europe, where the syntaxonomic studies were conducted. Given the community's scarcity in AlUla County, it is advisable to defer before deciding on the attribution to any specific association.

The community shows an approach towards the Temperate-Mountain *Syntrichio calcicolae-Grimmietum anodontis* (Giacomini 1939) but cannot be attributed to this association without more information.

This is a permanent community, with no possibility of significant evolution. However, in some cases, the accumulation of detrital material from the granite disintegration can lead to the introgression and eventual replacement of the community by terricolous elements, particularly mosses of the *Pottiaceae* family.

The community is only present around the highest point of Jabal Alward, in the extreme west of the county where it is sparse locally, with a few colonized blocks. This community is also known from the summits of the Asir Mountains, around 2.800 meters a.m.s.l., at Jebel Natfa (Frey & Kürschner 1988). It has clear northern affinities and is probably very rare in the Arabian Peninsula.

The community's heritage value is therefore high. Its conservation depends on maintaining the granite summit screes. All factors contributing to artificialization are thus detrimental, particularly the deposition of rubble, concrete, and the displacement of blocks for various construction purposes.

***Grimmia orbicularis* community (Fig. 11)**

A strictly saxicolous community colonizing the surface of granite blocks, and more rarely on sandstone, as observed in Sharaan Nature Reserve, within scree complexes generally exposed to the north of Sharaan. Additionally, the micro-locational position of this community provides it with certain protection against direct sunlight. It primarily colonizes the base of the blocks, often in the shade of neighbouring large blocks. Water supply can be provided by slight runoff as well as atmospheric moisture.

A species-poor or even monospecific community. *Crossidium squamiferum*, *C. aberrans*, *Didymodon desertorum*, and *Weisia condensa* are the only species capable of colonizing the rocky surfaces (Table 6). Even then, they do so in the form of sparse and very low-cover colonies.

We consider here only the true community associated with the surfaces of rock blocks, thereby excluding relevés in which terricolous species occupy a significant place. Transitions between the two can exist, which remain difficult to place objectively, but this

Fig. 11. *Grimmia orbicularis* community (26°21'40.17"N 37°33'2.95"E).

does not hinder the recognition of true saxicolous communities. The community fits easily within the *Grimmion tergestinae*, although it is associated with non-carbonate rocks (see above). The *Grimmietum orbicularis* could correspond to it. The low abundance of terricolous elements is also clearly evident when reading the table published by Von Hübschmann (1986).

This saxicolous community can be partially or entirely covered by unslope soil, leading to its replacement by more terricolous communities, where *Grimmia orbicularis* may persist, but *Pottiaceae* species gradually take on a more prominent role.

This bryological community presents significant heritage interest due to its strong ecological specialization. Its conservation depends on maintaining the granite screes and the north-facing sandstone outcrops in their current state. Although the effects of grazing are poorly understood in the absence of precise studies, field observations tend to indicate that mechanical disturbances to the soil on steep slopes exacerbate erosion, leading to an intensified leaching. This phenomenon can lead to the disappearance of saxicolous communities through burial and invasion by terricolous elements.

Table 6. *Grimmia orbicularis* community relevés.

Surface	400	250	2400	800	900	200	300	600	1600
Microhabitat slope (°)	30	80	90	60	55	90	45	70	85
Taxa number	3	2	2	1	1	1	1	1	2
Character species									
Grimmia orbicularis Bruch ex Wilson	3	3	3	2	2	2	2	1	3
Others									
Didymodon desertorum (J. Froehl.) J.A. Jiménez & M.J. Cano			+						+
Crossidium squamiferum (Viv.) Jur.	+								
Crossidium aberrans Holz. & E.B. Bartram		+							
Weissia condensa (Voit) Lindb.	+								

Tufa communities (Fig. 12)

Tufa communities in AlUla County are diverse and difficult to characterize because they differ subtly in their floristic composition. We can recognize four well-characterized communities and 3 others that seem impoverished or fragmentary.

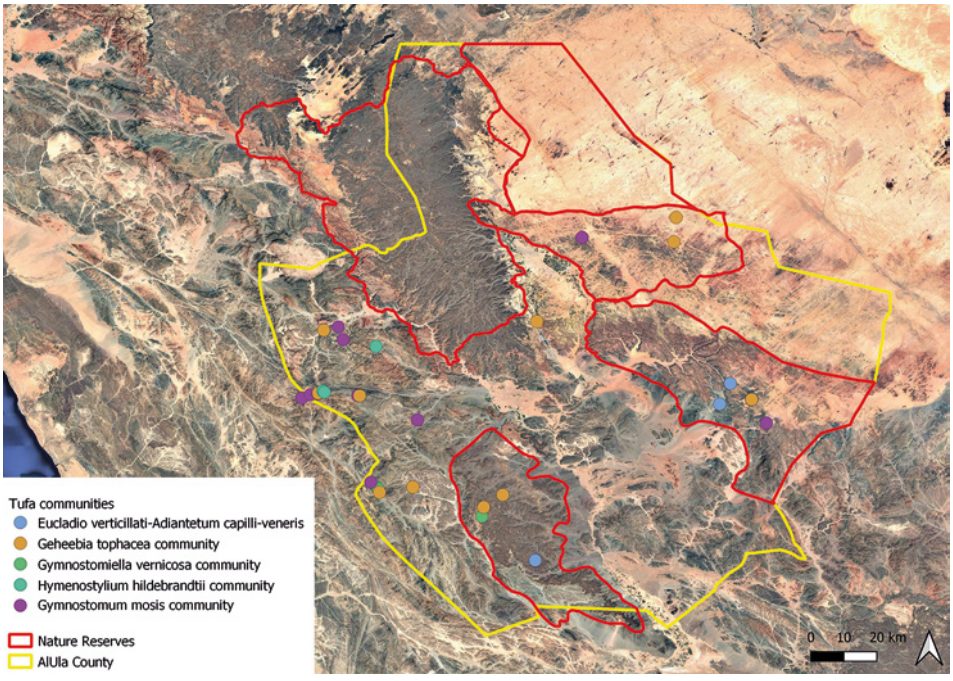

Fig. 12. Distribution of tufa bryophytic communities in AlUla County.

Eucladio verticillati-Adiantetum capilli-veneris Br.-Bl. ex Horvatiç 1934

This community is established in the South of AlUla, predominantly on metamorphic rocks. They occur on small overhangs, in seepage cavities, or at the base of walls that are permanently damp and often benefit from significant shading. The water supply is carbonate-rich. The mosses settle in the area influenced by the seepage and grow on this water source. They tend to become encrusted, and the tufaceous substrate is generally thin, no more than 1–5 cm deep.

The community is species-poor with eight taxa recorded, and is characterized by the presence of *Adiantum capillus-veneris* and *Eucladium verticillatum*. *Geheebia tophacea* may appear locally and has been observed to form extensive patches. *Ptychostomum pseudotriquetrum* is very rare. Some terricolous species can be observed but they are always infrequent.

The dynamics of this community are limited to internal changes related to erosion and minimal alterations in the flow path, leading to the localized disappearance of hygrophytic species. This community has close dynamic links with that of *Geheebia tophacea*, a species that tolerates more pronounced desiccation phases than *Eucladium verticillatum*.

Fig. 13. *Eucladio verticillati-Adiantetum capilli-veneris* (26°25'24.8"N 38° 33' 37.93"E).

Table 7. *Eucladio verticillati-Adiantetum capilli-veneris* relevés.

Surface	**6000**	**3000**	**20000**	**10000**	**8000**	**20000**	**5000**	**1800**	**10000**	**500**
Microhabitat slope (°)	70	80	90	90	90	80	90	80	80	80
Taxa number	7	5	3	2	4	4	2	1	2	4
Character species										
Eucladium verticillatum (With.) Bruch & Schimp.	2	3	3	4	2	2	3	3	3	+
Adiantum capillus-veneris L.	1	1	4	+	+	2	3			1
Geheebia tophacea (Brid.) R.H. Zander			1		2	3			1	3
Others										
Entosthodon commutatus Durieu & Mont.	+	1			1	+				1
Ptychostomum pseudotriquetrum (Hedw.) J.R. Spence & H.P. Ramsay	3	1								
Bryum sp.	2	1								
Microbryum starckeanum (Hedw.) R.H. Zander	+									
Crossidium aberrans Holz. & E.B. Bartram	+									

This community is necessarily limited by the absence of a well-developed hydrographic network. Only a few sites with permanent micro-springs are likely to host it. Therefore, it inherently has a fragmented nature in the county. Elsewhere on the Peninsula, particularly in wetter, mountainous areas, it can acquire relictual characteristics (Deil 1989). This basal community has northern affinities and a certain Mediterranean character.

The heritage value of this community is high because it is the only permanently hygrophilous bryophyte community encountered, while all others have a more or less temporary nature. Although species-poor and lacking vascular characteristics, this community harbours rare and highly ecologically specialized elements (*Eucladium verticillatum*, *Ptychostomum pseudotriquetrum*). The conservation of this community depends on the preservation of its water resources. Any withdrawal or modification of flows, as well as any changes in physico-chemical characteristics (eutrophication, etc.), will necessarily affect on the development of the community.

Geheebia tophacea community (Fig. 14)

This widespread community is found in the minor bed of wadis, often on small steps, on encrusting substrates. The water supply is sporadic, with periods of prolonged drying out. This community is sometimes found in the vicinity of the *Eucladio-Adiantetetum* community, but most often independently, at less consistently irrigated sites.

Geheebia tophacea characterizes this community (Table 8), although this species can also be observed in all other tufa communities in the county. *Funaria hygrometrica* can constitute a distinct facies in ruderalized areas, such as the bases of dams or around hydraulic developments.

In areas with a sufficient water supply, this community may evolve slowly towards the *Eucladio-Adiantetum* community, but in most cases, prolonged drying constrains significant evolution. In the event of permanent drying, the community can become enriched in soil elements and drift towards the xerophytic soil community rich in *Pottiaceae* previously described (thus accounting for its relative floristic richness compared with more hygrophytic communities).

Fig. 14. *Geheebia tophacea* community (26°53'57.04"N 38°13'32.39"E).

Table 8. *Geheebia tophacea* community relevés.

Surface	**20000**	**2000**	**400**	**1000**	**2000**	**10000**	**10000**	**1600**	**900**	**400**	**200**	**3500**	**1200**	**1000**
Microhabitat slope (°)	90	80	90	70	90	0	90	0	90	90	30	40	40	20
Taxa number	3	3	3	8	2	3	7	2	1	1	2	5	3	2
Character species														
Geheebia tophacea (Brid.) R.H. Zander	3	1	+	2	4	2	1	2	1	1	1	2	3	+
Others														
Funaria hygrometrica Hedw.	3	1	2	+	+									
Bryum sp.			1	2			1					2	1	
Bryum dichotomum Hedw.	3	4						2						3
Entosthodon commutatus Durieu & Mont.				+		1						2		
Riccia cavernosa Hoffm.												+	+	
Tortula muralis Hedw.				1			1							
Microbryum davallianum (Sm.) R.H. Zander				+			+							
Adiantum capillus-veneris L.						1								
Gyroweisia tenuis (Hedw.) Schimp.												+		
Entosthodon duriaei Mont.							1							
Crossidium crassinervium (De Not.) Jur.											1			
Microbryum starckeanum (Hedw.) R.H. Zander				1										
Tortula mucronifera W. Frey, Kürschner & Ros							1							
Timmiella barbuloides (Brid.) Mönk.							1							
Geheebia siccula (M.J. Cano, Ros, García-Zam. & J. Guerra) J.A. Jiménez & M.J. Cano				+										

This community is widespread throughout the county but less common in the west, where wadis are more abundant and less temporary. It is probably widespread in the Arabian Peninsula and has a Nordic and Mediterranean character.

The heritage value of this community is lower than that of the *Eucladio-Adiantetum* community, because it reflects a discontinuous water supply and remains poor in flora. Its conservation is based on maintaining a healthy hydrographic network.

Gymnostomiella vernicosa community (Fig. 15)

This community is found in the minor bed of small temporary wadis, on steps in the most durable runoff. Mosses colonize superficial tufa substrates (no more than 1–5 cm deep) in well-lit conditions, but sometimes with some shade cast by neighbouring slopes or walls.

The community is species poor with 11 taxa recorded and is very well characterized floristically, by the presence of *Ptychostomum cellulare* and *Gymnostomella vernicosa* (Table 9). Occasionally, only one of these two species is present, and often one dominates in coverage. Accompanying species are classic tuficoles such as *Geheebia tophacea* or *Gymnostomum mosis*.

Fig. 15. Gymnostomiella vernicosa community (26°10'19.29"N 37°24'45.89"E).

Table 9. *Gymnostomiella vernicosa* community relevés.

Surface	**10000**	**20000**	**30000**	**20000**	**4000**	**4000**	**10000**	**4000**
Microhabitat slope (°)	70	70	90	80	70	50	90	80
Taxa number	4	4	6	6	5	4	4	6
Character species								
Ptychostomum cellulare (Hook.) D. Bell & Holyoak	1	2	2	2	3	3	1	
Gymnostomiella vernicosa (Hook. ex Harv.) M. Fleisch.			2	2	1	4		4
Others								
Geheebia tophacea (Brid.) R.H. Zander		+	1	1	2	2	+	
Entosthodon commutatus Durieu & Mont.	1	1		3	+			+
Bryum sp.	1			2	1			2
Gymnostomum mosis (Lorentz) Jur. & Milde	1		+					+
Riccia cavernosa Hoffm.			1	+			+	
Entosthodon duriaei Mont.			3				2	
Fissidens arnoldi R. Ruthe		1				+		
Trichostomopsis australasiae (Hook. & Grev.) H. Rob.								1
Timmiella barbuloides (Brid.) Mönk.								1

This is potentially a new original association but additional surveys will have to be conducted in the potential core of the community area in the southwest of the Peninsula. We are not aware of any close communities described from a bryosociological point of view. Like the other encrusting communities of the county, it probably belongs to the *Adiantetea*.

The community is subject to significant internal dynamic phenomena linked to changes in the flow path. Periodic drying limits the development of more water-demanding flora, so that the community can be considered permanent as long as the water supply is maintained. Otherwise, the community is invaded by soil elements and drifts towards the xerophytic community rich in *Pottiaceae*.

This community is only known in the west of the county, in deep valleys and seems to have a relict character. Indeed, the species with tropical affinities that develop there only find favourable locations much further south, in the higher parts of Yemen and Oman.

The heritage value of this community is exceptional. This is a community with tropical affinities, which could have been more widespread during the humid phases of the Quaternary. Climate change saw its area contract until it colonized only relict micro-populations in rare favourable places. The conservation of this community is essential but faces the same problems as other hygrophytic communities: the scarcity of water resources and its sensitivity to all external agents. It is therefore necessary to be vigilant regarding any hydraulic development project, even modest, upstream of localized communities. Water quality is of particular importance. It could be appropriate to protect the sites concerned from the effects of grazing.

Gymnostomum mosis community (Fig. 16)

This community is less strictly hygrophytic than the previous ones, and can therefore be broadly described as mesophytic. It can endure longer periods of drought, the water supply is often discontinuous, and in low volumes with water generally not visible on the surface. The water supply would be acquired, at least in certain cases, by slow diffusion in the substrate rather than by runoff. The community is petrifying and, like other tufa communities, the tuff thicknesses are low (maximum 10 cm, often less).

Gymnostomum mosis characterizes this community and often colonizes the tuff surfaces en masse. It is accompanied by a relatively large group of ephemeral species (*Entosthodon*, *Riccia cavernosa*) and xerophytic *Pottiaceae* (Table 10) from the soil-dwelling community widespread in the county. This makes this community one of the few relatively species-rich (22 taxa recorded) communities of the county.

This community can easily drift toward the more terrestrial, *Pottiaceae*-rich community under the effects of excessive drying. The community appears permanent if no disturbance occurs.

It is widespread in the county but more concentrated in the western part, due to a denser hydrographic network composed of less ephemeral streams. It could be widespread in the arid areas of the Peninsula. This community has a certain Mediterranean character.

The community's heritage value is high. Its conservation is essentially based on preserving the resource, guaranteeing a sufficient water supply in terms of quality and quantity. This community is also very sensitive to trampling and should be protected from overgrazing.

Fragmentary communities

Within the tufa communities, two groups appeared particularly poor in species and probably fragmentary; therefore, it will be necessary to complete their study in the future:

Fig. 16. *Gymnostomum mosis* community (26°36'12.28"N 37°19'35.27"E).

- *Hymenostylium hildebrandtii* community: colonizes the tuffs and seeping cracks in the minor bed of the wadis; perhaps corresponds to an impoverished form of *Eucladio-Adiantetum* or an original phase of the *Geheebia tophacea* community; remarkable community with tropical affinities, not very widespread in the county (western sector); to study again in the southwest of the Peninsula;
- The other recognized communities practically correspond to monospecific populations whose bryosociological significance is not clear: *Gyroweisia tenuis* community and that with *Entosthodon duriaei* community; in both cases, the moss colonizes superficial, humid tufa layers in the minor bed of the wadis.

Table 10. *Gymnostomum mosis* community relevés.

Surface	**20000**	**10000**	**10000**	**1500**	**5000**	**10000**	**10000**	**20000**	**6000**	**10000**	**4500**	**1200**
Microhabitat slope (°)	60	70	0	60	80	20	90	50	90	70	95	30
Taxa number	4	8	6	3	5	5	6	10	8	3	5	3
Character species												
Gymnostomum mosis (Lorentz) Jur. & Milde	3	4	3	2	2	1	1	2	4	3	3	1
Geheebia tophacea (Brid.) R.H. Zander	2	2	1	2	1	3	1	2				
Others												
Bryum sp.	1	1	1	1	1		2	1				2
Timmiella barbuloides (Brid.) Mönk.		+			3			+	+	2		
Entosthodon commutatus Durieu & Mont.	2		2					3	2			
Entosthodon duriaei Mont.		2			3	+					+	
Riccia cavernosa Hoffm.						1	1	2				1
Gyroweisia tenuis (Hedw.) Schimp.			+			+	+					
Trichostomopsis australasiae (Hook. & Grev.) H. Rob.		1							2		2	
Fissidens arnoldi R. Ruthe		+									+	
Gymnostomum calcareum Nees & Hornsch.								+	2			
Ptychostomum cellulare (Hook.) D. Bell & Holyoak							+					
Funaria hygrometrica Hedw.			1									
Hymenostylium hildebrandtii (Müll. Hal.) R.H. Zander								1				

Table 10. cont.

Surface	**20000**	**10000**	**10000**	**1500**	**5000**	**10000**	**10000**	**20000**	**6000**	**10000**	**4500**	**1200**
Microbryum starckeanum (Hedw.) R.H. Zander								+				
Entosthodon sp.										+		
Bryum dichotomum Hedw.									2			
Tortula mucronifera W. Frey, Kürschner & Ros		+										
Tortula muralis Hedw.											2	
Targionia hypophylla L.									1			
Vinealobryum vineale (Brid.) R.H. Zander									+			
Plagiochasma rupestre (J.R. Forst. & G. Forst.) Steph.								+				

Table 11. *Gyroweisia tenuis* community relevés.

Surface	500	5000	30000	400	500	900
Microhabitat slope (°)	0	30	20	70	30	0
Taxa number	1	1	2	2	1	1
Gyroweisia tenuis (Hedw.) Schimp.	4	3	1	1	1	2
Entosthodon duriaei Mont.				1		
Bryum sp.			2			

Table 12. *Entosthodon duriaei* community relevés.

Surface	1500	20000	20000	500	5000
Microhabitat slope (°)	40	90	90	70	90
Taxa number	1	2	2	2	4
Entosthodon duriaei Mont.	2	3	1	1	1
Geheebia tophacea (Brid.) R.H. Zander				+	
Fissidens arnoldi R. Ruthe					+
Bryum sp.		3	1		1
Tortula muralis Hedw.					1

Discussion

In total, no fewer than 13 bryophytic communities have been recognized and described. Although some are considered xerophytic, all are more or less strongly linked or limited in their expression by the water factor. This observation explains the overall rarity of these communities due to the scarcity of annual rainfall. While some of them can be considered relatively widespread geographically, all are, to varying degrees, limited in space to a few favourable sites. These are essentially north-facing scree and deeply cut wadis that provide protection from solar radiation which can prevent bryophyte growth. Bryophytes, by their biology, require some form of protection to counteract the extreme aridity of the climate. This protection can be temporal for ephemeral communities that complete their cycle during the short wet period, or it can be structural (bryophytes hidden in micro-niches of extremely limited spatial extent, such as cavities, undersides of blocks, cliff bases). The latter are essentially *Pottiaceae*, which comprise many drought-adapted species, typical of the xeropottioid life syndrome (Frey & Kürschner 1988; Frey & Kürschner 1998; Kürschner 2004a), and reflect the overall aridity of AlUla County. It is an essential feature of the bryophytic vegetation of AlUla County that it is difficult to discover either because it is limited in its temporal or spatial expression: it is not widespread and never strikes the observer's eye.

The bryosociological approach has proven useful in providing a formal and structured framework for a better understanding of local bryocoenotic diversity. Many of the communities detected are insufficiently described and will require further study. Additional studies are to be conducted in sectors of comparable aridity outside AlUla County, to provide a basis for comparison. Or, alternatively, surveys in less arid sectors in order to complete the study of communities considered fragmentary, and probably better developed in the south of the Hijaz or even in the Asir.

The taxonomy of ephemeral communities with *Riella* has only been the subject of a single publication (Cirujano et al. 1993). Only two associations, which are regarded as invalid due to the absence of a designated holotype, are described within the class *Rielletea helicophyllae* – one typical of saline waters and the other of freshwater. The second of these is characterized by *Riella notarisii*, a collective species that requires revision. Neither of these two associations correspond to the one observed at AlUla. A new association could potentially be described, but pending further studies and additional surveys, we prefer to defer this decision at present.

No terricolous amphibious community has been reported so far in the Arabian Peninsula. They are included in the *Physcomitrellion patentis* alliance. At present, it is not possible to determine the specific association of the community observed in AlUla (*Riccia cavernosa* community), and any description of a new community would be hindered by the fragmentary nature of our observations. From our unpublished data, other comparable communities do exist in the Asir mountains. They are characterized by *Riccia cavernosa* and the rare *Physcomitrium niloticum* and other species of *Physcomitrium*.

With 40 taxa recorded, the *Pottiaceae* community is the most speciose community of the county. This is also the most variable from a floristic perspective, with often only five taxa occurring within the same relevé. This community is similar to the synusia previously recognized and described by Frey & Kürschner (1987) in the limestone cuesta of Jebel Tuwayq, named *Tortula atrovirens-Crossidium squamiferum*. The terricolous community observed in the AlUla County is notably distinguished by the almost complete absence of Marchantioid liverworts, the presence of species belonging to the genera *Entosthodon* and *Fissidens*, and its occurrence on non-carbonate rocks (mainly granites, sandstones, and metamorphic rocks). For now, only a single unique community can be recognized. It is considered highly variable in terms of floristics, often impoverished and fragmentary.

Pioneer saxicolous communities have not been previously considered separately. For example, in the Asir Mountains, a *Grimmia trichophylla-Targionia* stage is recognized, where *G. trichophylla* is the first species to invade bare rock surfaces where water drains quickly (Kürschner 1984b). In the central and southern parts of the Arabian Peninsula, under arid conditions, a cushion-building community is suggested to occur ‘growing on minute fissures on fully exposed rocks’ (Kürschner & Ghazanfar 1998), featuring *Grimmia orbicularis*, *G. pulvinata*, and *G. trichophylla*. Such communities have not been described from a strict bryosociological perspective but they are not present in AlUla County.

The *Grimmia orbicularis* community is widespread in the AlUla County but is very rare due to its high degree of specialization. It is certainly more widespread, though not recognized as such, in the central or southern parts of the Peninsula (Frey & Kürschner 1987; Kürschner & Ghazanfar 1998). The *Grimmietum orbicularis* is a community with northern affinities, that displays a Mediterranean character. Its existence at low altitude and in hyper-arid areas in AlUla County is remarkable.

Within tufa communities, species-poor ones, considered as basal (Deil 1996), are generally attributed to the *Eucladio-Adiantetum*, although this community is not mentioned in the synthesis on the Arabian Peninsula by the same author (1989). In the southern part of the Peninsula, two associations are recorded: *Adianto-Epipactidetum veratrifoliae* Deil 1989 along permanent watercourses in the Musandam mountains in U.A.E. and Oman, and the *Adianto-Primuletum verticillatae* Deil 1989 in rock cavities with dripping water in the montane belt of the escarpment in southwest Arabia. Outside the areas most favourable to the expression of these hygrophytic communities i.e. in hyper-arid areas, the community loses its characteristics and becomes merely a basal community, the phytosociological significance of which has been extensively discussed by Deil (1996).

The *Geheebia tophacea* community is a species-rich community with16 taxa recorded and is of interest as it is frequently observed. It corresponds to a young, pioneering, and less hygrophytic phase of the *Eucladio-Adiantetum* as specified in Deil (1996). This community has previously been individualized syntaxonomically under various names: *Eucladio-Adiantetum didymodetosum tophacei* (Raimondo et al. 1981) or *Eucladio-Didymodontetum* in the southeast of France (Hébrard 1973). The community observed in AlUla County corresponds to the ultimate stage of floristic impoverishment in relation to aridity and climatic constraints.

The *Gymnostomum mosis* community could take its place in the *Cephaloziello baumgartneri-Southbyon nigrellae* alliance, which brings together groups of relatively dry tufa protosols (Guerra & Gil 1982; Ros & Guerra 1987). There is currently no association with *Gymnostomum mosis* as character species. It will be appropriate to extend the observations to other regions of the Arabian Peninsula to determine the value of the community observed in AlUla County.

As a result, the syntaxonomic scheme of the bryophytic vegetation of AlUla County is as follows:

Terricolous communities

Rielletea helicophyllae Cirujano, Velayos, García-Murillo 1993

Rielletalia helicophyllae Cirujano, Velayos, García-Murillo 1993

Riellion helicophyllae Cirujano, Velayos, García-Murillo 1993

1 – *Riella affinis* community

Psoretea decipientis Matt. ex Follm. 1974

Funarietalia hygrometricae v. Hübschm. 1957

Physcomitrellion patentis v. Hübschm. 1957

2 – *Riccia cavernosa* community

Barbuletalia unguiculatae v. Hübschm. 1960

Aloino bifrontis-Crossidion crassinervis Ros & Guerra ex Marst. in Marst. 2006

3 – *Pottiaceae* community

Saxicolous communities

Grimmietea anodontis Had. & Vondr. in Jež. & Vondr. 1962

Grimmietalia anodontis Šm. & Van. ex Kl. 1948

Grimmion tergestinae Šm. ex Kl. 1948 [nom. cons. propos. (Marstaller, 2006)]

4 – *Grimmia anodon* community

5 – *Grimmia orbicularis* community

Tufa communities

Adiantetea capilli-veneris Braun-Blanq. ex Braun-Blanq., Roussine & Nègre 1952

Adiantetalia capilli-veneris Braun-Blanq. ex Horvatić 1934

Adiantion capilli-veneris Braun-Blanq. ex Horvatić 1934

6 – *Eucladio verticillati-Adiantetum capilli-veneris* Br.-BI. ex Horvatiç 1934

7 – *Geheebia tophacea* community

8 – *Gymnostomiella vernicosa* community

9 – *Hymenostylium hildebrandtii* community

Psoretea decipientis Matt. ex Follm. 1974

Barbuletalia unguiculatae v. Hübschm. 1960

Cephaloziello baumgartneri-Southbyon nigrellae Guerra & Gil 1982

10 – *Gymnostomum mosis* community

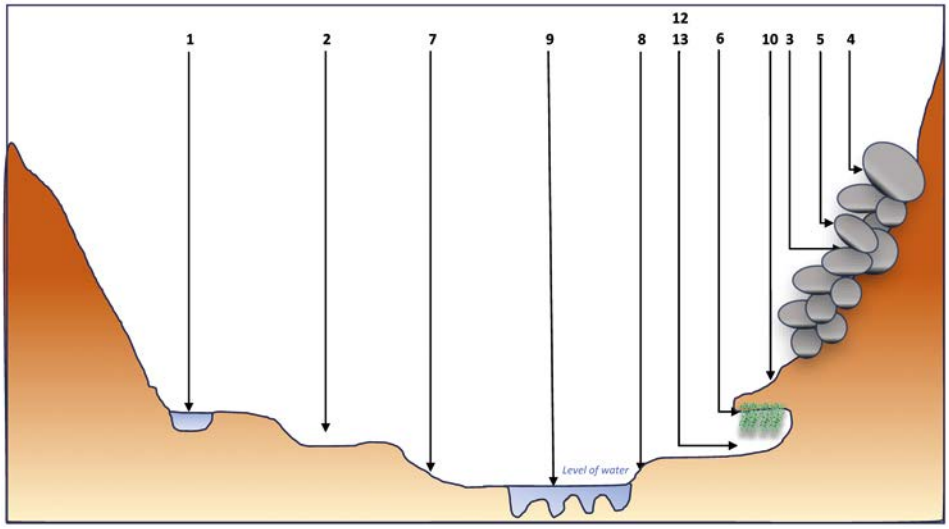

Fig. 17. Vegetation transect indicating the topographic position of main bryophytic communities. Numbering correspond to the syntaxonomic scheme and Table 3.

Incertae saedis

11 – *Bryum sp.* community

12 – *Gyroweisia tenuis* community

13 – *Entosthodon duriaei* community

The vegetation transect is intended to position each recoginzed unit along a theoretical wadi profile (Fig. 17 and Table 2).

The communities observed in AlUla are, for some, unique and original (although not described here for the reasons mentioned above), and for others, already known and widely distributed, particularly in the Mediterranean region. The original communities are primarily associated with tufa and are likely to exist in the wetter areas of the southwestern Arabian Peninsula. Their floristic composition remains to be studied and compared with that of AlUla. In contrast, saxicolous communities are widely distributed (Marstaller 2006) in the southern temperate domain and are richer in species the more humid the climate. Terricolous communities, similarly, are significantly impoverished compared to their Mediterranean or North African counterparts (Ros & Guerra 1987; Ros et al. 1990).

It should be noted that there are certain difficulties in analysing bryophytic vegetation in hyper-arid environments. Communities are structured around a small number of species due to climate constraints, complicating the description of clearly defined units. On the other hand, the small size of favourable stations makes them prone to a concentration of species in the same area, which tends to blur the boundaries between communities. Finally, the absence of global studies on bryophytic vegetation in the Arabian Peninsula

further complicates the approach. Knowledge of this vegetation is certainly in its infancy and much work remains to be done before a complete and coherent syntaxonomic scheme can be obtained.

The communities generally exhibit a certain floristic richness at the county level. In contrast, individual community surveys generally exhibit low species diversity. There is no clear link between the overall richness of a community and the specific richness of the corresponding relevés. This can be interpreted as an indication of particularly challenging environmental conditions. The ecological conditions are rarely met for the community to become saturated with the species associated with it. Furthermore, it is likely that these communities would become more saturated with species (unknown in AlUla County) in more favourable regions of the Peninsula. These observations validate our approach, which aims not to describe new communities in this hyper-arid region.

The conservation of the extraordinary communities (including several relict ones) poses serious problems in the face of the depletion of water resources. The vast majority of the communities described are directly dependent on this resource, which makes them highly vulnerable to any environmental change. With improved knowledge, it will become possible to develop a red list of the most threatened communities. A red list would make it possible to objectively prioritize, on the basis of a recognized method, the degree of threat weighing on each of them. The improvement and expansion of bryological knowledge of the Arabian Peninsula should therefore be prioritised.

Acknowledgements

The research was co-initiated by the Royal Commission for AlUla (RCU) and the French Agency for AlUla Development (AFALULA). The project was funded by AFALULA in the framework of the ‘AlUla Bryological Survey project’ and implemented in partnership with the RCU.

The authors would like to thank for their support in the completion of this work: Dr Rana El Zein (AFALULA), Dr Stephen Browne (Vice President of Wildlife and Natural Heritage WNH department, RCU), Lourens van Essen (Director of Research and Advisory, WNH-RCU) and his team in particular Ayman Abdulkareem and Manar Alsubhi, the rangers team and Reserves division of WNH-RCU, in particular Mohammed Zaarour, Khaldoun Alomari and Shujaa Alenezi; and Dr Benjamin Lee (Director of Habitat regeneration and landscaping division at WNH-RCU).

References

Alahuhta, J., Alahulkko, T., Tukiainen, H., Purola, L., Akujärvi, A., Lampinen, R., & Hjort, J. (2018). The role of geodiversity in providing ecosystem services at broad scales. *Ecological Indicators, 91*, 47–56. https://doi.org/10.1016/j.ecolind.2018.03.068

Alataş, M., Ezer, T., Erata, H., & Batan, N. (2023). Updated Checklist of Turkish Bryophyte Vegetation. *Anatolian Bryology, 9*(1), 1–10. https://doi.org/10.26672/anatolianbryology.1084591

Al-Bassam, A. M., Kahlil, A. R., & Kassem, O. M. (2014). *Using updated DurovPwin Program for hydro-chemical data processing: Case study of Al-Ula area* (pp. 75–81). Saudi Arabia: Recent Advances in Environmental Science and Geoscience.

Altherr, R., Mertz-Kraus, R., Volker, F., Kreuzer, H., Henjes-Kunst, F., & Lange, U. (2019). Geodynamic setting of Upper Miocene to Quaternary alkaline basalts from Harrat al 'Uwayrid (NW Saudi Arabia): Constraints from K-Ar dating, chemical and Sr-Nd-Pb isotope compositions, and petrological modeling. *Lithos, 330–331*, 120–138. https://doi.org/10.1016/j.lithos.2019.02.007

Baierle, H. U. (1993). Vegetation und Flora südwestlichen Jordanien. [Stuttgart.]. *Dissertationes Botanicae, 200*, 1–254.

Braun-Blanquet, J. (1964). *Pflanzensoziologie, Grundzüge der Vegetationskunde, 3. Aufl.* Wien, New York.

Chaudhary, S. A. (2001). *Flora of the Kingdom of Saudi Arabia* (Vol. III). Riyadh, Saudi Arabia: Ministry of Agriculture and Water.

Cirujano, S., Velayos, M., & García Murillo, P. (1993). Rielletea helicophyllae, una nueva clase fitosociológica de plantas acuáticas. *Botanica Complutensis, 18*, 203–211.

CMEP (2023). *Inventory and Vegetation of AlUla Flora Project* (115 pp.). Centre for Middle Eastern Plants, part of the Royal Botanic Garden Edinburgh, Royal Commission for AlUla.

Comer, P. J., Pressey, R. L., Hunter, M. L., Schloss, C. A., Buttrick, S. C., Heller, N. E., . . . Shaffer, M. (2015). Incorporating geodiversity into conservation decisions. *Conservation Biology : The Journal of the Society for Conservation Biology, 29*(3), 692–701. https://doi.org/10.1111/cobi.12508

Deil, U. (1989). Adiantetea-Gesellschaften auf der Arabischen Halbinsel, Coenosyntaxa in dieser Klasse sowie allgemeine Überlegungen zur Phylogenie von Pflanzengesellschaften. *Flora (Jena), 182*(3–4), 247–264. https://doi.org/10.1016/S0367-2530(17)30414-0

Food and Agriculture Organization of the United Nations. (1989). *Arid Zone Forestry: A Guide for Field Technicians*. Food and Agriculture Organization of the United Nations.

Frey, W., & Kürschner, H. (1981). The bryological literature of southwest Asia. *The Journal of the Hattori Botanical Laboratory, 50*, 217–229.

Frey, W., & Kürschner, H. (1987). A desert bryophyte synusia from the Jabal Tuwayq mountain systems (Central Saudi Arabia) with the description of two new Crossidium species (Pottiaceae). Studies in Arabian Bryophytes 8. *Nova Hedwigia, 45*, 119–136.

Frey, W., & Kürschner, H. (1990). Das Fossombronio-Gigaspermetum mouretii ass. nov. in der Judaïschen Wüste. 1. Verbreitung und Soziologie. *Cryptogamic Botany, 2*, 56–63.

Frey, W., Herrnstadt, I., & Kürschner, H. (1990). Verbreitung und Soziologie terrestrischer Bryophytengesellschaften in der Judaïschen Wüste. *Phytocoenologia, 19*, 233–265. https://doi.org/10.1127/phyto/19/1990/233

Frey, W., & Kürschner, H. (1992). Bryosoziologische Untersuchungen in Jordanien: Terrestrische und epilithische Gesellschaften. *Nova Hedwigia, 54*, 355–378.

Frey, W., & Kürschner, H. (1995). Soziologie und Lebensstrategien epiphytischer Bryophyten in Israel und Jordanien. *Nova Hedwigia, 61*, 211–232. https://doi.org/10.1127/nova.hedwigia/61/1995/211

Frey, W., & Kürschner, H. (1988). Bryophytes of the Arabian Peninsula and Socotra. Floristics, phytogeography and definition of the xerothermic Pangaean element. Studies in Arabian Bryophytes 12. *Nova Hedwigia, 46*, 37–120.

Frey, W., & Probst, W. (1973). Die Polstermoosvegetation im Karadj-Tal (Elbursgebirge, Iran). *Botanische Jahrbücher für Systematik, 93*, 404–423.

Gilli, A. (1941). Ein Beitrag zur Flora des Elburs-Gebirges in Nord-Iran. *Feddes Repertorium, 50*, 263–283.

Gilli, A. (1969). Afghanische Pflanzengesellschaften. *Vegetatio, 16*(5–6), 307–375. https://doi.org/10.1007/BF00257022

Gilli, A. (1971). Afghanische Pflanzengesellschaften. II. Die mesophilen und hygrophilen Pflanzengesellschaften im sommertrockenen Gebiet. *Vegetatio, 23*(3–4), 199–234. https://doi.org/10.1007/BF02350622

Gilli, A. (1975). Afghanische Ruderal- und Segetalgesellschaften. *Feddes Repertorium, 86*(3), 171–197. https://doi.org/10.1002/fedr.19750860303

Gilli, A. (1977). Die Waldgebiete im Osten Afghanistans. *Feddes Repertorium, 88*(5–6), 375–387. https://doi.org/10.1002/fedr.19770880505

Guerra, J., & Gil, J. A. (1982). Communidades briofíticas mediterráneas de protosuelos calcáreos húmedos. *Folia Botanica Miscellanea, 3*, 87–94.

Hadley, D. G. (1987). *Explanatory notes to the geological map of the Sahl Al Matran quadrangle, sheet 26C*. Kingdom of Saudi Arabia: Saudi Arabian Deputy Ministry for Mineral Resources.

Heinrichs, J., Klugmann, F., Hentschel, J., & Schneider, H. (2009). DNA taxonomy, cryptic speciation and diversification of the Neotropical-African liverwort, Marchesinia brachiate (Lejeuneaceae, Porellales). *Molecular Phylogenetics and Evolution, 53*(1), 113–121. https://doi.org/10.1016/j.ympev.2009.05.032

Hébrard, J. P. (1973). Étude des bryoassociations du Sud-Est de la France et leur contexte écologique. Thèse, Université de Provence, Marseille.

Hübschmann von A. (1986). Prodromus der Moosgesellschaften Zentraleuropas. *Bryophytorum Bibliotheca, 32*, 1–413.

Kürschner, H. (1984a). Epiphytic communities of the Asir Mountains (SW Saudi Arabia). Studies in Arabian Bryophytes 2. *Nova Hedwigia, 39*, 177–200.

Kürschner, H. (1984b). An epilithic bryophyte community in the Asir Mountains (SW Saudi Arabia). Studies in Arabian Bryophytes 4. *Nova Hedwigia, 40*, 423–434.

Kürschner, H. (1988). Studies in the bryophyte vegetation of Saudi Arabia: terrestrial, epilithic and epiphytic communities. Studies in Arabian Bryophytes 14. Proceedings of the Sixth CEBWG Meeting, Liblice, Czechoslovakia, 1988, 149–163.

Kürschner, H. (1998). Biogeography and Introduction to Vegetation. In S. A. Ghazanfar & M. Fisher (Eds.), *Vegetation of the Arabian Peninsula* (pp. 63–98). Springer. https://doi.org/10.1007/978-94-017-3637-4_4

Kürschner, H. (2000). Bryophyte Flora of the Arabian Peninsula and Socotra. *Bryophytorum Bibliotheca, 55*, 1–131.

Kürschner, H. (2003a). Epiphytic bryophyte communities of southwestern Arabia – phytosociology, ecology and life strategies. *Nova Hedwigia, 77*(1–2), 55–71. https://doi.org/10.1127/0029-5035/2003/0077-0055

Kürschner, H. (2003b). The Riccietum jovet-astii – argenteolimbatae ass. nov. of the Jabal Arays area, Yemen. Life strategies of a remarkable xerotropical African bryophyte community. *Nova Hedwigia, 76*(3–4), 399–413. https://doi.org/10.1127/0029-5035/2003/0076-0399

Kürschner, H. (2004a). Life Strategies and Adaptations in Bryophytes from the Near and Middle East. *Turkish Journal of Botany, 28*, 73–84.

Kürschner, H. (2004b). Phytosociology, ecology and life strategies of a remarkable epiphytic bryophyte community of Socotra Island, Yemen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie, 125*(3), 377–395. https://doi.org/10.1127/0006-8152/2004/0125-0377

Kürschner, H. (2006). Syntaxonomy, synecology and life strategy of a saxicolous bryophyte community of Socotra Island, Yemen. *Englera, 28*(28), 163–174. https://doi.org/10.2307/20358186

Kürschner, H. (2008). Bryogeography of South-West Asian Bryophytes – with special emphasis on the Tropical element. *Turkish Journal of Botany, 32*, 433–446.

Kürschner, H., & Frey, W. (2020). Bryophyte novelties from the Arabian Peninsula and Socotra Island. *Nova Hedwigia, 110*(3–4), 281–286. https://doi.org/10.1127/nova_hedwigia/2020/0574

Kürschner, H., & Ghazanfar, S.A. (1998). Bryophytes and Lichens. In S. A. Ghazanfar, & M. Fisher (Eds.), *Vegetation of the Arabian Peninsula*, 99–124. Dordrecht: Springer-Science+Business Media. https://doi.org/10.1007/978-94-017-3637-4_5

Kürschner, H., & Neef, R. (2018). Tayma oasis (Saudi Arabia) and its surroundings – a first synthesis of the flora, vegetation, natural resources, and floral history. In A. Hausleiter, R. Eichmann, & M. Al-Najem (Eds.), *Tayma I. Archaeological exploration, Palaeoenvironment, Cultural contact* (pp. 88–125). Oxford: Archaeopress.

Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., . . . Weiss, S. B. (2015). The theory behind the challenges of conserving nature's stage in a time of rapid change. *Conservation Biology : The Journal of the Society for Conservation Biology, 29*(3), 618–629. https://doi.org/10.1111/cobi.12505

Marstaller, R. (2006). Syntaxonomischer Konspekt der Moosgesellschaften Europas und angrenzender Gebiete. *Haussknechtia Beiheft*, 13, 191 pp.

Raimondo, F. M., Dia, M. D., & Rossito, M. (1981). L'Eucladio-Adiantetum Br.-Bl. 1931 in Sicilia. *Atti della Accademia Nazionale delle Scienze, Serie 4, 1*, 87–94.

Rasul, N.M.A., Stewart, I.C.F., & Nawab, Z.A. (2015). Introduction to the Red Sea: Its Origin, Structure, and Environment. In N. Rasul, & I. Stewart (Eds.), *The Red Sea*. Berlin, Heidelberg: Springer Earth System Sciences.

Ros, R. M., & Guerra, J. (1987). Vegetación briofítica terrícola de la Región de Murcia (sureste de España). *Phytocoenologia, 15*(4), 505–567. https://doi.org/10.1127/phyto/15/1987/505

Ros, R. M., Jiménez, M. N., & Guerra, J. (1990). On the chorology, synecology and syntaxonomy of some terricolous bryophytic communities from northern Africa. *Nova Hedwigia, 50*(1–2), 65–79. https://doi.org/10.1127/nova.hedwigia/50/1990/65

Wood, A. J. (2007). The nature and distribution of vegetative desiccation-tolerance in hornworts, liverworts, and mosses. *The Bryologist, 110*(2), 163–177. https://doi.org/10.1639/0007-2745(2007)110[163:IENFIB]2.0.CO;2

Zohary, M. (1973). *Geobotanical Foundations of the Middle East*. Stuttgart: Fischer Verlag.

Manuscript received: November 26, 2025
Manuscript accepted: December 20, 2025
Responsible editor: J. Engel

The pdf version of this paper includes an electronic supplement

Electronic Supplementary Material (ESM)

Supplementary Table S1

Supplementary Table S2

Supplementary Table S3

Please save the electronic supplement contained in this pdf-file by clicking the blue frame above. After saving rename the file extension to .zip (for security reasons Adobe does not allow to embed .exe, .zip, .rar etc. files).