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Bryoerythrophyllum duellii Blockeel newly recorded from Southwest Asia (Saudi Arabia), with support from molecular data

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ABSTRACT

Methods. Morphological study and DNA sequencing (ITS, *rps4*) were carried out using *Bryoerythrophyllum* specimens collected in the Asir and Mecca provinces of Saudi Arabia, and the results compared against published data for *B. duellii*.

Key results. The Arabian plants match *Bryoerythrophyllum duellii* in diagnostic morphology, although with more frequent spinose marginal teeth and occasional apiculi. The *rps4* sequence was identical to that of Greek and Cypriot accessions; the ITS sequence differed by only a few substitutions and indels, clustering with strong support in a monophyletic *B. duellii* clade. The species was found at 2100–2500 m on granitic substrates in clearings within *Juniperus procera* woodland, extending the known range nearly 2000 km southeast and representing the first record of *Bryoerythrophyllum* in the Arabian Peninsula.

Conclusions. Our morphological and molecular findings confirm the identity of the Saudi Arabian plants as *Bryoerythrophyllum duellii*. The discovery highlights its wider biogeographical potential and the need for habitat management to mitigate grazing impacts.

KEYWORDS

Asir Mountains; monsoon climate; Pottiaceae; Saudi Arabia

Introduction

Bryoerythrophyllum duellii Blockeel is a recently described moss (Blockeel et al. 2017) currently known from only five localities in Greece (including Crete) and Cyprus. It belongs to the *Bryoerythrophyllum recurvirostrum* group and differs most significantly from *B. recurvirostrum* (Hedw.) P.C.Chen and *B. rotundatum* (Lindb. & Arnell) P.C.Chen, two other members of this group, in the combination of lingulate shape of the leaves with rounded or broadly pointed apices and the rudimentary peristome teeth. Its status as a distinct taxon was confirmed by molecular data (Blockeel et al. 2017).

While surveying the bryoflora of the Asir mountain range in the southwestern Arabian Peninsula in 2024 and 2025, the first two authors found a pottiaceous moss which was at first sight referred in the field to the genus *Bryoerythrophyllum* P.C.Chen, because the habit was reminiscent of *B. recurvirostrum* (the older part of the stems with a clear red-orange coloration, and the leaves with shiny bases suggestive of well-differentiated hyaline basal cells). Some characters, however, were anomalous for this species (peculiar leaf twisting, with some leaves coiling, apical part of leaves too wide, etc.), resulting in the preliminary determination as *Bryoerythrophyllum* sp.

In the laboratory, the anatomical characteristics of the moss were examined and compared with those of *Bryoerythrophyllum duellii* from the eastern

Mediterranean basin. The Arabian specimens matched *B. duellii* reasonably well, and this observation was confirmed by the third author, to whom some material was sent. Nevertheless, considering the complexity of the genus, the limited knowledge of the species, and some morphological differences from the published description (notably the more often denticulate leaf margins frequently with spinose teeth), we decided to barcode the material molecularly to confirm the identity of the specimens.

Material and methods

Study site

The site is part of the Asir Mountains, one of the highest regions of the Arabian Peninsula, along with the Yemeni Highlands. The geological substrate consists predominantly of granite. The Asir Mountains rise steeply to elevations of 2400–2600 m, forming a pronounced escarpment to the west, dominating the Red Sea. To the east, the terrain slopes gently towards the Arabian Platform (Sayed and Masrahi 2023).

The region experiences an average temperature range of 16–18°C, characteristic of a moderately warm, semihumid montane climate. Situated on the periphery of the subtropical zone, it is influenced by monsoonal summer rains, resulting in a secondary precipitation peak during July and August, in addition to

the primary rainfall maxima in winter and spring. This increased precipitation pattern strongly influences the development of the vegetation. The total annual precipitation is approximately 500 mm (Vincent 2008).

Specimens examined

Saudi Arabia. Asir Province, Tanomah, North-West, outside but close to the border of Alsharaf Park, altitude 2500 m, 18°57'7.97"N, 42°8'32.06"E, 22 March 2024 (Private herbarium of VH and FP), KSA590; 3 km West Tanomah, altitude 2500 m, 18°58'42.39"N, 42°11'21.67"E, 23 March 2024 (Private herbarium of VH and FP), KSA612; idem 18°57'15.48"N, 42°08'30.38"E, 15 March 2024 (Private herbarium of VH and FP; duplicate in CBFS), KSA501, sequenced specimen; Mecca Province, 4 km SE Ash Shafa, altitude 2120 m, 21°2'46.1472"N, 40°21'26.8380"E, 16 March 2025 (Private herbarium of VH and FP), KSA 472; Mecca Province, 15 km W Taïf, altitude 2100 m, 40°16'0.0696"E, 21°16'39.6768"N, 12 March 2025 (Private herbarium of VH and FP), KSA451; Mecca Province, 13 km NW Taïf, altitude 2200 m, 40°17'10.5180"E, 21°19'3.2556"N, 12 March 2025 (Private herbarium of VH and FP), KSA449.

Molecular analysis

DNA was isolated from the specimen collected on 15 March 2024 (KSA501), and the isolated genomic DNA was amplified for the nuclear ITS and chloroplast *rps4* markers, following the protocols described in Kučera et al. (2019), and sequenced in Eurofins Genomics facilities (Cologne, Germany). The resulting sequences

were manually aligned into the dataset of Blockeel et al. (2017), inspected for differences from earlier sequenced specimens, and with respect to substitution differences found in the ITS region, the alignment re-analysed using the Bayesian inference under the same settings as used by Blockeel et al. (2017).

Results

The *rps4* sequence (GenBank accession no. PX596733) from the putative Saudi Arabian *Bryoerythrophyllum duellii* is identical to that of the previously sequenced specimens from Cyprus and Greece. However, the ITS sequence (GenBank accession no. PX549046) differs in two point-substitutions and one –GG– insert in ITS1, as well as two point-substitutions and one –TG– deletion in ITS2. Nevertheless, the pairwise identity between ITS sequences from the Saudi Arabian and previously sequenced plants of *B. duellii* remains significantly higher (97.9%–98.7%) than between this sequence and ITS sequences of the most closely related *B. recurvirostrum* (93.8%–94.6%). The Bayesian phylogenetic inference from ITS data indicates nevertheless the monophyly of all three *B. duellii* accessions (posterior probability = 1), with the new Saudi Arabian accession in the sister position to the lineage formed by the two previously sequenced plants (tree not shown).

The Arabian specimens (Figures 1, 2 and 3) show the following combination of morphological characters, some of them being relatively variable. The red colouration in older parts of the stems is variously developed and is best visible in the field on examination of entire tufts. The branched rhizoids form dense bundles,



Figure 1. Habit of wet *Bryoerythrophyllum duellii* Blockeel (specimen from Saudi Arabia, Tanomah, KSA590).



Figure 2. Peristome of *Bryoerythrophyllum duellii* Blockeel (specimen from Saudi Arabia, Tanomah, KSA590).

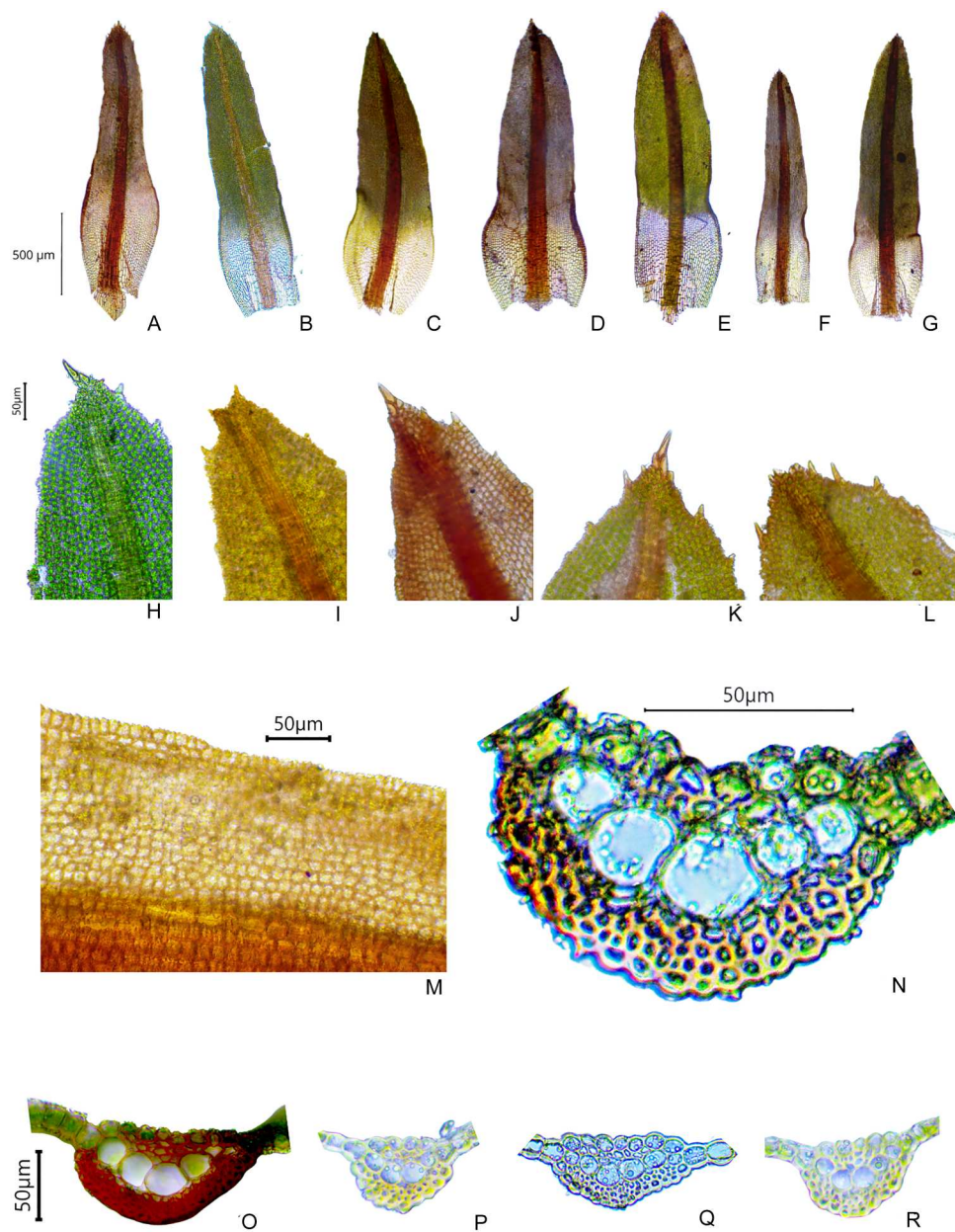


Figure 3. *Bryoerythrophyllum duellii* Blockeel (specimen from Saudi Arabia, Tanomah, KSA590). (A–G) Vegetative leaves. (H–L) Leaf apices. (M) Areolation at the leaf middle. (N–R) Vegetative leaves, transverse sections.

located in the axils of the leaves. The axillary hairs are hyaline, numerous, easy to detect, and very long (to 400 µm). The stem is rather weak, with a poorly differentiated sclerenchyma (only 1 or 2 cells with feebly thickened walls) and a relatively large, elliptic stem central strand, up to 20 cells wide, at times, however, much less developed. The leaves are mostly lingulate, with a moderately differentiated leaf base, spreading 45–70° from the stem. The leaf apex is variably obtuse or subacute. The leaves are more or less crispate when dry, with the marginal recurvature at times very indistinct, but sometimes extending to 2/3 of leaf length. The denticulation along the upper leaf margins is very variable, occasionally only in the form of notches (laterally protruding cells) reaching the middle region of the leaves, but not infrequently markedly developed with forward-directed, spinose teeth, which are at times pluricellular. The apex is occasionally apiculate, with an apiculus of 3 smooth and large cells. The nerve section shows two stereid bands (the dorsal one much more strongly developed and crescent-shaped), 1–4 very small hydroid cells, and costal epidermis differentiated. The gametangia are lateral, synoicous, reduced, consisting of 2–4 small oblong-apiculate fertile bracts, enclosing several archegonia, and often only a single antheridium. The few capsules observed are 1.5–2 mm long, with a rostrate lid, 0.9–1.1 mm long, and a rudimentary peristome. The spores are 13.5–21.5 µm in diameter.

In the five populations, the species predominantly develops in clearings within dense forests belonging to *Myrsino africanae*–*Juniperetum procerae* (Deil and al Gifri 1998), which correspond to evergreen montane juniper woodland, on a north-facing slope. Within these clearings, of several tens of square metres, flat outcrops accumulate quantities of particulate detritus, mixed with organic matter, that form a relatively spongy substrate with (temporarily) percolating water among small stones. On other occasions, it colonises a mineral substrate among boulders. *Bryoerythrophyllum duellii* primarily colonises the edges of earthy ridges, characterised by low vascular plant cover, consequently with virtually no shade, and, by contrast, an almost continuous cover of bryophytes. These are mostly mosses, the only thallose liverwort being *Targionia lorbeeriana* Müll. Frib. occurring in small quantities. Mosses tend to form dense colonies that are mutually exclusive, probably due to competitive interactions. The dominant species are mostly Pottiaceae with Mediterranean affinities, such as *Brachymerium exile* (Dozy & Molk.) Bosch & Sande Lac., *Timmiella barbuloidea* (Brid.) Mönk., *Tortella squarrosa* (Brid.) Limpr., *Trichostomopsis australasiae* (Hook. & Grev.) H. Rob. and *Trichostomum cf. meridionale* Ros, O. Werner & R. D. Porley, with, as accompanying species, *Anoetangium* sp., *Bartramia aprica* Müll. Hal., *Buckia vaucheri* (Lesq.) D. Ríos, M. T. Gallego & J. Guerra,

Didymodon cordatus Jur., *Encalypta vulgaris* Hedw., *Gymnostomum mosis* (Lorentz) Jur. & Milde and *Vinealobryum vineale* (Brid.) R. H. Zander.

The areas occupied by the species were approximately 5 m², 1 m², 20 m², 10 m² and 2 m², with a coverage of about 30%. Sporophytes were observed in small groups of 5–10, but they were never abundant, most colonies in each population being sterile.

Discussion

Despite slight morphological differences from the Mediterranean specimens of *Bryoerythrophyllum duellii* and several differences in the ITS sequence, the overall evidence confirms the conspecificity of the newly discovered Saudi Arabian specimens with *B. duellii*.

Bryoerythrophyllum duellii is very similar to *B. pseudomarginatum* J. Kou, X.-M. Shao & C. Feng in gametophytic characters. However, according to the protologue (Kou et al. 2016), *B. pseudomarginatum* is dioicous, a clear distinction from the synoicous *B. duellii*. Admittedly, it is not possible to know from the protologue, which is based on a single specimen, whether this is a stable character in the species. Another apparent difference is found in the structure of the inner basal leaf cells, which are described as ‘transversely thick-walled’ in *B. pseudomarginatum*. This appears to be confirmed by the accompanying figure (figure 2 in Kou et al. 2016). The inner basal cells of *B. duellii* are evenly thin-walled, both in European and Arabian material. Strangely, the dorsal and ventral surfaces of the costa of *B. pseudomarginatum* are described in the same terms: ‘ventral cells of costa in upper half rectangular, papillose; dorsal surface cells of costa in upper half rectangular, papillose’. It seems unlikely that the cells on both surfaces are identical. The ventral costa cells of *B. duellii* are ± quadrate and densely papillose, while the dorsal cells are elongate and ornamented with scattered simple papillae. The presence of a discontinuous border of one to several weakly papillose/transparent marginal cells in the leaves of *B. pseudomarginatum* is an uncertain difference, being a potentially variable character in its development. Very occasionally, two such adjacent marginal cells have been observed together in *B. duellii*. On present evidence, we conclude that *B. duellii* is not synonymous with *B. pseudomarginatum*, but a reassessment will be appropriate if further populations of the latter species can be found.

Bryoerythrophyllum duellii was known previously only from the initial description and pictures in Blockeel et al. (2017); the photographs from the same specimens appeared in Lüth (2019). All diagnostic morphological characters of *B. duellii* have been verified in the Saudi Arabian material. Although the

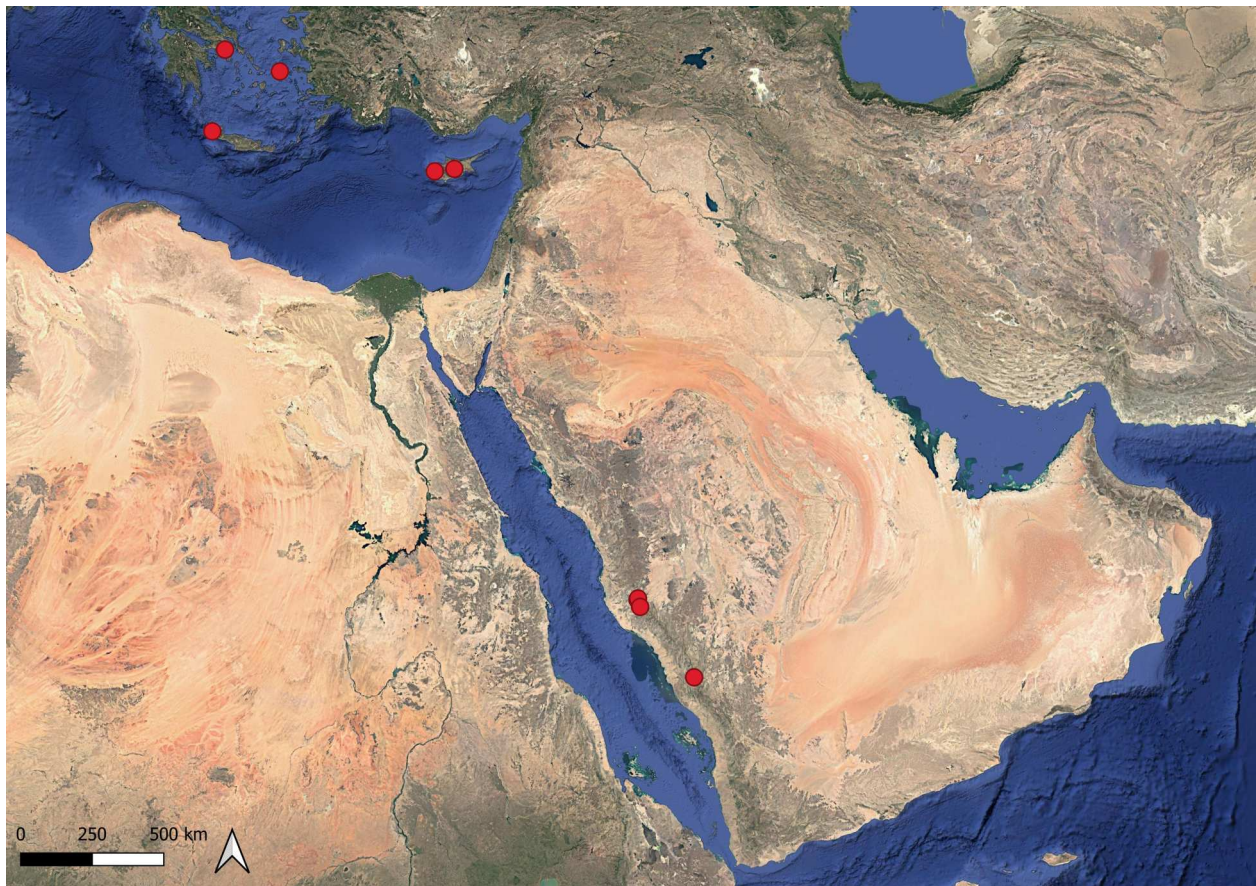


Figure 4. Global distribution of *Bryoerythrophyllum duellii* Blockeel (red dots). Map data © Google Earth.

five Arabian populations demonstrate a certain morphological variation, none of the observed morphological characters appears to deviate significantly from the usual variability of *Bryoerythrophyllum* species, ensuring that other possible future Arabian populations can be safely identified morphologically. The recognition of *B. duellii* from *B. recurvirostrum* is relatively easy, even though the key diagnostic taxonomic characters are macromorphological (shape of leaves, development of peristome teeth), while most of the microscopic features (nerve anatomy, areolation) are of lesser value. The differences between the Arabian and Mediterranean specimens are slight, and they show similar variation in leaf morphology. However, a sharp apiculus of 1–3 cells is frequently present at the leaf apex in Arabian plants (usually absent in the Mediterranean specimens), and similarly the marginal teeth of Arabian plants are more often spinose. The capsules are a little larger in Arabian plants but were found only in small quantity. They were plentiful at the sites on Ikaria, Greece, and in the Paphos Forest, Cyprus.

The species has not been recorded in southwest Asia (Taha 2019; Kürschner and Frey 2020), and the new discovery also marks the first record since the initial description of the species. The Saudi Arabian record extends the known distribution range by almost 2000 km southeastwards (Figure 4). It is also

the first generic record of *Bryoerythrophyllum* in the entire Arabian Peninsula. The nearest occurrences of the genus hitherto known in Southwest Asia (Kürschner and Frey 2020) are in Turkey (*B. recurvirostrum*, *B. ferruginascens* (Stirt.) Giacom. and *B. rubrum* (Jur. ex Geh.) P.C.Chen) and Iran (*B. recurvirostrum* only). This demonstrates that the range of *B. duellii* is obviously underestimated at present. While Blockeel et al. (2017) suggested that the species could occur in Turkey, the new record opens a substantially wider potential distribution area, probably extending to Eastern Africa within an Afromontane archipelago-like centre of endemism (Sayed and Masrahi 2023). Some specimens of *B. duellii* may be concealed in herbaria under other names, likely candidates being the habitually similar *Bryoerythrophyllum alpigenum* (Venturi) P.C.Chen recorded in Kenya, Tanzania, Uganda (Kis 1985) and Ethiopia (Sollman 2008), or *B. campylocarpum* (Müll.Hal.) H.A.Crum, which is widespread in tropical mountains and occurs, for instance, in the Ethiopian highlands (Wigginton 2001).

The Arabian habitat has evidently much in common with the ecological setting of the species in Greece and Cyprus described by Blockeel et al. (2017). *Bryoerythrophyllum duellii* is a pioneer moss species that thrives in open or lightly shaded Mediterranean habitats, typically on thinly vegetated soils in rocky mildly acidic to slightly basic terrain. Although

we do not have pH measurements, the soil is very likely acidic in Saudi Arabia, due to the granitic nature of the bedrock. Generally, species of the genus *Bryoerythrophyllum* are basiphilous. It is probable that, like many other species reputedly calciphilous and growing in arid environments under acidic conditions, the climate explains this observation. The factors at play are probably complex and would benefit from further study.

The species grows in environments with varying light availability, from unshaded ledges to partially shaded slopes, benefitting from the protection provided by steep banks against prolonged insolation. The favoured habitats are steep banks and slopes, often in valleys or near stream gullies, rocky ledges and areas among boulders, and forest roadsides. It is found among low shrubby vegetation, such as *Erica arborea* L. heath in Crete and phrygana in Greece, which physiognomically closely resemble South Arabian evergreen montane juniper woodland.

The populations in the Arabian Peninsula were found at a significantly higher elevation (2500 m) as compared with the known sites in Crete and Cyprus (300–600 m). The climate prevailing at this altitude probably shows certain similarities with a Mediterranean climate, as temperatures remain mild throughout the year, with a relatively wet winter and a summer drought that exists but is moderated compared with the arid and even hyper-arid areas located at lower altitudes.

Conservation

Bryophyte assemblages, as described earlier, are highly sensitive to the effects of overgrazing. Grazing by livestock – primarily sheep, goats and donkeys – poses a dual threat to these communities. Directly, trampling can physically damage or dislodge bryophyte colonies, while, indirectly, it alters the microhabitats by compacting the soil and modifying the surface structure. In arid environments, bryophytes, particularly those in the Pottiaceae family, depend on soil substrates stabilised by the presence of rocks. Temporary stabilisation, a critical factor for their survival, is often supported by the establishment of a vascular plant layer. This layer, which may include woody plants, contributes to the creation of semishaded conditions that are essential for bryophyte growth. However, mechanical disturbances, such as the movement of rocks caused by livestock activity, disrupt this stabilisation, ultimately threatening these sensitive species. Thus, bryophytes rely not only on partial shade but also on environmental stability provided by a combination of physical and vegetative factors, underlining their vulnerability to overgrazing and habitat disruption.

Conversely, the pioneer species could benefit from the repeated passage of animals and soil compaction, but these disturbances must remain low in intensity

and short in duration. The sensitivity of bryophytes to grazing highlights the need for careful management of grazing intensity and timing in the ecosystems the high mountains of Arabia, to prevent irreversible damage. Strategies such as rotational grazing, limiting livestock numbers, and establishing grazing exclusion zones could help mitigate the impact of grazing and support bryophyte conservation.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Vincent Hugonnot is an independent bryologist based in France. He is involved in research on bryophyte taxonomy, ecology, biogeography and conservation, with contributions on bryophyte records, floristic surveys and ecological assessments across France and beyond.

Florine Pépin is an independent researcher in France. Her research focuses on the taxonomy, ecology and conservation of bryophytes. She is also engaged in bryofloristic and habitat surveys in France and abroad, particularly in the Arabian Peninsula, with an emphasis on the documentation and conservation of rare and threatened species.

Tom Blockeel is an independent field naturalist with a lifelong interest in bryophytes, especially concerning their taxonomy and floristics. In addition to his studies on the British and Irish flora, he has explored many parts of Greece and published widely on the bryophytes of that country.

Jan Kučera is an associate professor at the Department of Botany, Faculty of Science, University of South Bohemia, Czech Republic. His main research activities are the taxonomy and molecular phylogeny of bryophytes. He is further actively pursuing the biology of rare bryophytes and local bryofloristic research.

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