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BRYOPHYTE FLORA OF TWO PECULIAR SITES IN THE MT. PAPUK (EASTERN CROATIA)

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During ongoing bryological surveys conducted in the Mt. Papuk, two significant sites, Sokolina Gosted and Svinjarevac, have been identified. These sites are characterized by unique acidophilic forests with a predominance of peat mosses on the forest floor. Sokolina Gosted represents the first documented locality in Croatia for four taxa: *Andreaea rothii* ssp. *rothii*, *Grimmia donniana*, *G. montana*, and *Racomitrium affine*. Furthermore, *Buxbaumia aphylla* and *Dicranum spurium* were observed for the first time at both Sokolina Gosted and Svinjarevac. Additionally, several extremely rare species have been reported at one or both locations, including *Cynodontium polycarpon*, *Dicranum polysetum*, *Isopaches bicrenatus*, *Jungermannia pumila*, *Pleuridium acuminatum*, *Rhabdoweisia fugax*, *Syzygiella autumnalis* and *Ulota intermedia*. Consequently, both locations serve as important bryological hotspots, exhibiting distinctive species assemblages within unique habitats relevant to Southeast Europe. While the significance of these sites in terms of bryophyte diversity is clear, the presence of the invasive species *Campylopus introflexus* underscores the necessity for ongoing research and monitoring efforts in the area.

Keywords: acidophilic forests, bryophyte diversity, invasive species, SE Europe

Šegota, V., Deme, J., Kovács, D., Rimac, A., Purger, D., Csiky, J. & Alegro, A.: Mahovinska flora dva neobična lokaliteta na Papuku (istočna Hrvatska). Nat. Croat. Vol. 35, No. 1, 135-149, 2025, Zagreb.

Tijekom recentnih brioloških istraživanja provedenih na području Papuka, identificirana su dva značajna nalazišta, Sokolina Gosted i Svinjarevac s unikatnim acidofilnim bukovim šumama s dominacijom mahova tresetara u prizemnom sloju. Sokolina Gosted predstavlja prvo nalazište u Hrvatskoj za četiri svojte: *Andreaea rothii* ssp. *rothii*, *Grimmia donniana*, *G. montana* i *Racomitrium affine*. Nadalje, vrste *Buxbaumia aphylla* i *Dicranum spurium* su po prvi puta zabilježene na obje lokacije, Sokolina Gosted i Svinjarevac. Dodatno je na tim nalazištima zabilježeno nekoliko izuzetno rijetkih vrsta, uključujući *Cynodontium polycarpon, Dicranum polysetum, Isopaches bicrenatus Jungermannia pumila, Pleuridium acuminatum, Rhabdoweisia fugax, Syzygiella autumnalis* i *Ulota intermedia*. Obje lokacije stoga predstavljaju važna briološka nalazišta, sa specifičnim zajednicama na jedinstvenim staništima značajnim za jugoistočnu Europu. Značaj ovih lokacija u smislu raznolikosti mahovina je velik, a prisutnost invazivne vrste *Campylopus introflexus* naglašava potrebu za kontinuiranim istraživanjem i naporima praćenja u tom području.

Ključne riječi: acidofilne šume, raznolikost mahovina, invazivne vrste, Jugoistočna Europa

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INTRODUCTION

Following the publication of the most recent overviews of the bryophyte flora of Croatia (Sabovljević, 2003, 2006; Alegro *et al*., 2021) and the checklists for Southeastern Europe (Sabovljević & Natcheva, 2006; Sabovljević *et al*., 2008), numerous new species have since been recorded in Croatia (see Šegota *et al*., 2020, 2021; Rimac *et al*., 2023; Šegota & Rimac, 2025). The majority of the newly documented species have been found in the southern and central regions of Croatia, where Mesozoic limestone predominates as the primary bedrock. In contrast, areas with acidic rocks are relatively uncommon in the country. An important exception is Mt. Papuk in eastern Croatia, which is characterized by metamorphic rocks, such as granites and schists, that provide suitable habitats for various acidophilic mosses and liverworts (Pamić *et al*., 2003). Due to its significant geological diversity and numerous rock types, including igneous, sedimentary, and metamorphic, Mt. Papuk is a part of the European Geoparks network as well as the UNESCO-assisted Geoparks network. The mountain represents the largest massif in the peri-Pannonian region of Slavonia, eastern Croatia, with its highest peak reaching 953 meters above sea level. The climate is temperate and moderately warm, lacking a distinct dry season (Zaninović *et al*., 2008). The annual mean temperature ranges from 8 to 11 °C, and annual precipitation is between 1000 and 1500 mm, depending on the elevation. The majority of the mountain is covered by acidophilic communities of beech forests. Local biodiversity hotspots can be found in the relatively small, open and exposed rocky habitats.

MATERIALS AND METHODS

Between 2009 and 2016, non-systematic bryological surveys were undertaken in various forest communities across the Mt. Papuk region (Fig. 1). Among the surveyed localities with acidophilic beech forests, two sites exhibiting particularly distinct bryophyte flora were studied in greater detail: the Svinjarevac site, located near the village of Kamenski Vučjak (Fig. 2) and the Sokolina Gosted site, near the village of Doljanci, both around 2.5 ha large (Fig. 3) in the southwest part of the nature park. Additionally, the rocky outcrops overgrown with *Quercus petraea* were examined along the margins of the investigated beech forests. In both locations, a comprehensive sampling and documentation of the bryophyte and vascular flora were conducted throughout several field surveys. The collected specimens are deposited in the Herbarium of the University of Pécs (JPU) and the University of Zagreb (ZA). The nomenclature for bryophytes adheres to Hodgetts *et al.* (2020), while the nomenclature for vascular plants follows Nikolić *et al.* (2025). The nomenclature for lichens follows Verseghy (1994). Chorology and soil-pH preference of bryophytes we assigned according to Van Zuijlen *et al.* (2023).

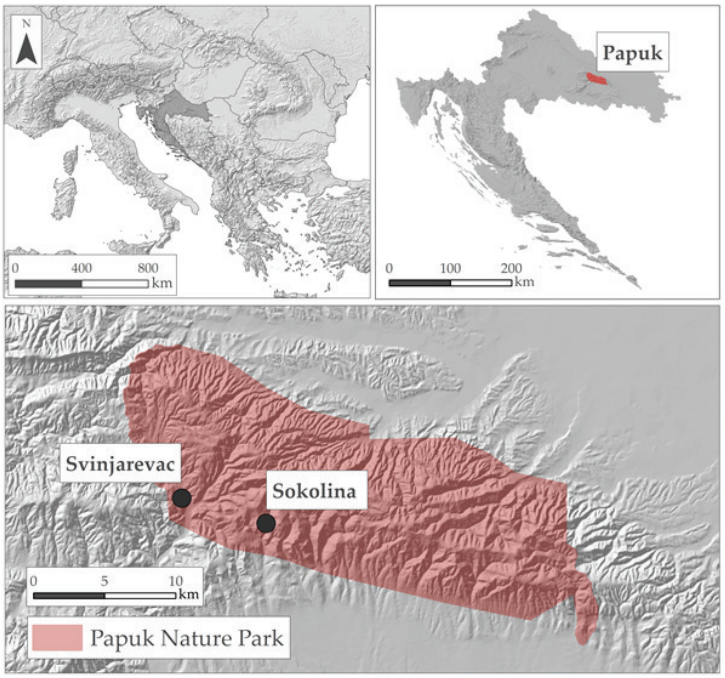


Fig. 1. Geographical position of the study area in southeast Europe and Croatia and of two investigated localities on Mt. Papuk.



Fig. 2. Svinjarevac – acidophilic beech forest with domination of reddish peat moss *Sphagnum quinquefarium* in ground layer.



Fig. 3. Sokolina Gosted – acidophilic beech forest with domination of *Vaccinium myrtillus* and *Sphagnum quinquefarium* in understory.

RESULTS AND DISCUSSION

Floristic account

The bryological surveys conducted at Svinjarevac documented 58 bryophyte species (20 liverworts and 38 mosses), while the surveys at Sokolina Gosted identified 46 bryophyte species (15 liverworts and 31 mosses). In total, 75 bryophyte species were recorded, including 23 liverworts and 52 mosses (Tab. 1). The absence of a comprehensive census, coupled with a non-systematic field survey, renders this species list for the studied localities non-final.

Tab. 1. Bryophyte species list of two investigated sites on Mt. Papuk

		Svinjarevac	Sokolina Gosted
Liverworts			
1.	*Bazzania trilobata* (L.) Gray	x	x
2.	*Blepharostoma trichophyllum* (L.) Dumort.	x	
3.	*Calypogeia fissa* (L.) Raddi	x	x
4.	*Cephalozia bicuspidata* (L.) Dumort.	x	
5.	*Cephaloziella divaricata* (Sm.) Schiffn.		x
6.	*Conocephalum conicum* (L.) Dumort	x	
7.	*Diplophyllum albicans* (L.) Dumort.	x	x
8.	*Frullania dilatata* (L.) Dumort.	x	x
9.	*Frullania tamarisci* (L.) Dumort.	x	x
10.	*Fuscocephaloziopsis lunulifolia* (Dumort.) Váňa & L.Söderstr.		x
11.	*Isopaches bicrenatus* (Schmidel ex Hoffm.) H.Buch	x	
12.	*Jungermannia pumila* With.	x	
13.	*Lepidozia reptans* (L.) Dumort.	x	x
14.	*Lophocolea heterophylla* (Schrad.) Dumort.	x	x
15.	*Lophozia ventricosa* (Dicks.) Dumort.	x	x

		Svinjarevac	Sokolina Gosted
16.	*Metzgeria furcata* (L.) Corda	x	x
17.	*Pedinophyllum interruptum* (Nees) Kaal.	x	
18.	*Plagiochila porelloides* (Torrey ex Nees) Lindenb.	x	x
19.	*Porella arboris-vitae* (With.) Grolle	x	
20.	*Porella platyphylla* (L.) Pfeiff.	x	x
21.	*Scapania nemorea* (L.) Grolle	x	
22.	*Sphenolobus minutus* (Schreb. ex D.Crantz) Berggr.		x
23.	*Syzygiella autumnalis* (DC.) K.Feldberg, Váňa, Hentschel & Heinrichs	x	x
Mosses			
24.	*Alleniella complanata* (Hedw.) S.Olsson, Enroth & D.Quandt	x	
25.	*Andreaea rothii* F.Weber & D.Mohr ssp. *rothii*		x
26.	*Bartramia pomiformis* Hedw.	x	
27.	*Brachytheciastrum velutinum* (Hedw.) Ignatov & Huttunen	x	
28.	*Brachythecium rutabulum* (Hedw.) Schimp.		x
29.	*Brachythecium salebrosum* (Hoffm. ex F.Weber & D.Mohr) Schimp.	x	
30.	*Buxbaumia aphylla* Hedw.	x	x
31.	*Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl.	x	x
32.	*Campylopus introflexus* (Hedw.) Brid.		x
33.	*Cynodontium polycarpon* (Hedw.) Schimp.		x
34.	*Dicranella heteromalla* (Hedw.) Schimp.	x	x
35.	*Dicranum polysetum* Sw. ex anon.	x	
36.	*Dicranum scoparium* Hedw.	x	x
37.	*Dicranum spurium* Hedw.	x	x
38.	*Diphyscium foliosum* (Hedw.) D.Mohr	x	
39.	*Eurhynchium angustirete* (Broth.) T.J.Kop.	x	
40.	*Exsertotheca crispa* (Hedw.) S.Olsson, Enroth & D.Quandt	x	
41.	*Fissidens dubius* P. Beauv.	x	
42.	*Grimmia donniana* Sm.		x
43.	*Grimmia montana* Bruch et Schimp.		x
44.	*Gyroweissia tenuis* (Hedw.) Schimp.	x	
45.	*Hedwigia ciliata* (Hedw.) P.Beauv.	x	x
46.	*Hylocomiadelphus triquetrus* (Hedw.) Ochyra & Stebel	x	
47.	*Hylocomium splendens* (Hedw.) Schimp.	x	x
48.	*Hypnum cupressiforme* Hedw.	x	x
49.	*Isothecium alopecuroides* (Lam. ex Dubois) Isov.	x	
50.	*Leucobryum glaucum* (Hedw.) Ångstr.	x	x
51.	*Orthotrichum stramineum* Hornsch. ex Brid.	x	
52.	*Oxyrrhynchium hians* (Hedw.) Loeske (s. l.)	x	
53.	*Paraleucobryum longifolium* (Hedw.) Loeske		x
54.	*Plagiothecium platyphyllum* Mönk.	x	x
55.	*Pleuridium acuminatum* Lindb.		x
56.	*Pleurozium schreberi* (Willd. ex Brid.) Mitt.	x	x
57.	*Pogonatum aloides* (Hedw.) P.Beauv.	x	
58.	*Pohlia nutans* (Hedw.) Lindb.		x
59.	*Polytrichum commune* Hedw.	x	x
60.	*Polytrichum formosum* Hedw.	x	x
61.	*Polytrichum juniperinum* Hedw.	x	x
62.	*Polytrichum piliferum* Hedw.	x	x
63.	*Pseudanomodon attenuatus* (Hedw.) Ignatov & Fedosov	x	
64.	*Pseudotaxiphyllum elegans* (Brid.) Z.Iwats.	x	x
65.	*Pterigynandrum filiforme* Hedw.	x	
66.	*Racomitrium affine* (F.Weber & D.Mohr) Lindb.		x
67.	*Racomitrium canescens* (Hedw.) Brid.		x

		Svinjarevac	Sokolina Gosted
68.	*Rhabdoweisia fugax* (Hedw.) Bruch et Schimp.		x
69.	*Rhizomnium punctatum* (Hedw.) T.J.Kop.	x	
70.	*Sanionia uncinata* (Hedw.) Loeske		x
71.	*Sciuro-hypnum populeum* (Hedw.) Ignatov & Huttunen	x	
72.	*Sphagnum capillifolium* (Ehrh.) Hedw.		x
73.	*Sphagnum quinquefarium* (Braithw.) Warnst.	x	x
74.	*Thamnobryum alopecurum* (Hedw.) Gangulee	x	
75.	*Ulota intermedia* Schimp.	x	

Unique national records

To date, Svinjarevac and Sokolina Gosted represent the only documented Croatian localities for six bryophyte taxa. Of these, *Andreaea rothii* ssp. *rothii*, *Racomitrium affine*, *Grimmia donniana* and *G. montana* were exclusively found at Sokolina Gosted, while *Buxbaumia aphylla* and *Dicranum spurium* were recorded at both sites.

The black patches of moss *Andreaea rothii* ssp. *rothii* were found on a steep, north-facing cliff, occupying an area of approximately 2 × 0.5 m, at the margin of an acidophilic beech forest at Sokolina Gosted. This boreo-temperate species was found growing on bare acidic rock in association with various bryophyte species, including *Cynodontium polycarpon, Dicranella heteromalla, Dicranum scoparium, Polytrichum piliferum*, and *Rhabdoweisia fugax* (Ellis *et al*., 2016).

Racomitrium affine is a temperate acidophilic species, with cryophytic character, indicating its distinct adaptation to cold microsites (Dierssen, 2001). Well-defined dark patches were identified at the boundary of an acidophilic beech forest located at the Sokolina Gosted site. The sterile specimens were scattered across a belt of approximately 100 × 10 meters, located on the lower side of partially shaded siliceous gneiss cliffs with a predominant north-eastern aspect. Within the surveyed plots, *R. affine* represented the dominant species on the rocks; however, it was more frequently found in association with *Cynodontium polycarpon*, *Hypnum cupressiforme*, *Paraleucobryum longifolium* and various epilithic lichens (Ellis *et al*., 2018).

Grimmia donniana, a boreo-arctic, considerably acidophilic species (Dierssen, 2001), has been recorded exclusively at the Sokolina Gosted site. Historical records of this species, including specific location data, are lacking, despite its appearance in several checklists (Martinčič, 1968; Düll *et al*., 1999; Sabovljević *et al*.; 2008, Ros *et al*., 2013). These references are most probably the result of repetitive, erroneous citations. Consequently, our finding represents the first confirmed occurrence of the species in Croatia. The species was discovered on exposed, well-lit siliceous rocks at the edge of an acidophilic beech forest, occupying an area of approximately 30 × 10 m. Associated mosses in the vicinity included *Grimmia montana*, *Hedwigia ciliata*, *Hypnum cupressiforme* and *Polytrichum piliferum* (the dominant species in the moss layer), along with lichen species such as *Lasallia pustulata* (L.) Mérat and *Parmelia saxatilis* (L.) Ach.

Grimmia montana, a temperate, considerably to moderately acidophilic species (Dierssen, 2001), was found at Sokolina Gosted, where we observed well-developed dense, compact cushions and patches with sporophytes, inspite capsules are being infrequently found elsewhere (Erzberger, 2009). The species occurred on the same

exposed, well-lit siliceous rocks as *G. donniana*. An old literary reference of *G. montana* in Croatia originates from Senjska Draga (Mt. Velebit) (Degen, 1938), and this information has been cited in subsequent works by Pavletić (1955) and Sabovljević (2006), although it was not included in Sabovljević *et al.* (2008) and remains unconfirmed to this day. The old record in Senjska Draga was made by Hungarian botanist Árpád Degen, who routinely sent his *Grimmia* collections to other bryologists for identification. Erzberger (2009) notes that many of the *Grimmia* records published or specimens collected in Hungary during the early to mid-20th century, including *G. montana*, were often misidentified. It appears that bryologists of that period lacked a clear understanding of the taxonomic boundaries of this species. Therefore, this early Croatian record, which is not supported by a voucher specimen, should be regarded as uncertain, rendering our observation the first confirmed occurrence of *G. montana* in Croatia. In neighbouring Hungary, based on our observation, the species is extremely rare and critically endangered (CR) (Papp *et al*., 2010), known only from the Jakab-hegy mountain (Mt. Mecsek, 78 km from Sokolina Gosted).

Buxbaumia aphylla is a rare circumpolar boreal-montane moss species (Hill & Preston, 1998). In Europe, it is present in the majority of western and northern countries, but its frequency decreases towards the southern regions of the continent (Charissou & Happe, 2016). In Southeast Europe, the species is recorded in most countries, with the exceptions of Greece, Serbia, and Kosovo (Hodgetts & Lockhart, 2020). At Svinjarevac and Sokolina Gosted, the species was found occurring on bare acidic soil as well as on *Sphagnum* peat, primarily in shaded areas beneath beech (*Fagus sylvatica*) or oak (*Quercus petraea*) trees (Ellis *et al*., 2017). The species was accompanied by lichens *Cladonia* spp. (incl. *C. fimbriata* (L.) Fr., *C. furcata* (Huds.) Schrad., *C. gracilis* (L.) Willd. and *C. squamosa* (Scop.) Hoffm.) and bryophytes *Dicranella heteromalla, Dicranum scoparium, Diphyscium foliosum, Hypnum cupressiforme, Leucobryum glaucum, Polytrichum formosum* and *Scapania nemorea*. Only a few predominantly acidophilic vascular plant species (*Deschampsia flexuosa* (L.) Trin., *Genista pilosa* L., *Gentiana asclepiadea* L., *Hieracium sabaudum* L., *Luzula luzuloides* (Lam.) Dandy et Wilmott, *Lychnis viscaria* L. and *Vaccinium myrtillus* L.) were present. *Buxbaumia aphylla* has recently been reported from a single locality on Dilj Gora, a low mountain in eastern Croatia, situated north of Slavonski Brod, as well as on six new sites on Mt. Papuk (Ellis *et al*., 2017; Doboš & Šegota, 2023). Additionally, the most recent revision of the previously overlooked historical bryophyte collection at Herbarium Croaticum (ZA) has identified two specimens of *B. aphylla* from the village of Dubravica in Hrvatsko Zagorje Region (Horvat, 1950; Šegota *et al*., 2022; Bučar *et al*., 2023).

Dicranum spurium, a boreal-montane and highly acidophilic species (Dierssen, 2001), has been found on both investigated localities – Svinjarevac (Ellis *et al*., 2014) and Sokolina Gosted. At both sites, the species was recorded within a rare type of acidophilic beech forest with a dense layer of peat moss *Sphagnum quinquefarium* on the forest floor. The habitat was characterized by steep slopes, shallow soil, and a geological substrate comprised of quartzite and gneiss.

Abundance of national rarities

The two studied sites on Mt. Papuk host several exceptionally rare bryophyte species, with only a limited number of recent occurrences documented in Croatia – *Syzygiella autumnalis*, *Jungermannia pumila, Rhabdoweisia fugax, Cynodontium polycarpon*,

Dicranum polysetum, *Isopaches bicrenatus*, *Pleuridium acuminatum*, *Ulota intermedia*, *Buxbaumia viridis* and invasive alien *Campylopus introflexus*.

Syzygiella autumnalis, a highly to considerably acidophilic liverwort, was documented in Croatia only once, nearly 80 years ago, on Mt. Velebit (Bakovac Valley near Kosinj) by Degen (1938), with no subsequent confirmations. The two newly identified localities, Svinjarevac and Sokolina Gosted, thus represent the only recently known occurrences within the Croatian territory. Here, the species has been found in acidophilic beech forest stands with peat mosses. The liverwort was growing in peat moss cushions over acidic soil. The abundance was greater at the Sokolina Gosted site, where the peat moss carpet was less dense compared to Svinjarevac, which facilitated the colonization of other bryophytes.

Jungermannia pumila, a considerably acidophilic to basophilic liverwort, is native to the temperate zone of Europe with montane character. It grows on moist sites on boulders and rock outcrops or thin soil over rocks and cliff ledges, in crevices and on shallow peat (Dierssen, 2001). It has been relatively recently recorded in Croatia for the first time, on limestone rocks in the Slunjčica River near the town of Slunj (Alegro *et al.*, 2014). Our observation from Svinjarevac represents the second documented occurrence in Croatia.

Rhabdoweisia fugax, a moderately acidophilic moss, is a European boreal-montane species (Hill & Preston, 1998), documented on only two occasions in Croatia so far. Both records were made relatively recently on Mt. Papuk, the first at Sokolina, near the Radovanka Stream in the village of Velika (Papp *et al.*, 2013), and the second on the eastern slopes of Mališćak Hill (Alegro *et al.*, 2019). It is typically found growing in shaded crevices of siliceous rocks, on cliff ledges, beneath overhanging boulders, in gullies, and within wooded ravines (Dierssen, 2001). During this study, we have recorded *Rhabdoweisia fugax* at Sokolina Gosted site.

Cynodontium polycarpon, an acidophilic moss, is a boreal-montane species that thrives on sheltered, siliceous rocks and screes, with a preference for the forest belt (Dierssen, 2001). Old historical records indicate that the species was previously reported from only two locations in Croatia: Ludvić Stream in the Samoborsko Gorje Hills and the second from Vrapčanska Gora on Mt. Medvednica (Horvat, 1932), both characterized by siliceous geology. Within our research, the species has been recorded at Sokolina Gosted site.

Dicranum polysetum, a highly to moderately acidophilic moss, is a boreal-montane species species. It typically thrives in coniferous forests, heaths and acidic mires (Dierssen, 2001). Remarkably, we have confirmed its presence in Croatia after more than a century, with previous records limited to forests around Zagreb (Klinggräff, 1861–1862) and the Istrian Peninsula (Głowacki, 1902). At the Svinjarevac site, it grew in small clusters among other moss species, primarily alongside *Dicranum scoparium*, *Pleurozium schreberi* and *Polytrichum formosum*, often found outside the main *Sphagnum* habitats, particularly on more sun-exposed slopes. This species is also reported in all neighbouring countries, with a notable abundance in Hungary, particularly in coniferous plantations on acidic soils, such as the nearby Juniper Woodland of Barcs (within 50 km) and the Mt. Mecsek (within 75 km) (Boros, 1968; Galambos, 1981).

Isopaches bicrenatus, a highly to moderately acidophilic liverwort, is a boreo-temperate species typically found in peaty or sandy soils, as well as on boulders, rocky stream sides and heathlands (Dierssen, 2001). Historical records of the species in Croatia are limited to two instances: the first from the Mediterranean *Quercus ilex* forest in Kalifront on the island of Rab (Schiffner, 1909, 1915), and the second from Mt. Velebit near Pazarište (Degen, 1938). Within our research, the species has been found at the Svinjarevac site.

Pleuridium acuminatum, a moderate acidophilic to subneotrophilic moss, is a temperate species, commonly colonizing bare patches of sandy or clayey soils (Dierssen, 2001). In Croatia, its occurrence has been documented only on the island of Rab (Düll, 1999) and, more recently, in Vrhovinsko Polje near the Plitvice Lakes National Park (Alegro *et al*., 2014). In the current research, the species has been found at the Sokolina Gosted site.

Ulota intermedia represents a moss species with a currently unknown distribution in Croatia. Namely, the recent study employing both morphological and molecular analyses has revealed that *Ulota crispa* complex comprises three species which can be differentiated by comprehensive qualitative and quantitative morphological characters – *U. crispa* s.s., *U. crispula* and *U. intermedia* (Caparrós *et al*., 2016). We found *U. intermedia* growing on the bark of an old sessile oak within the acidophilic beech forest at Svinjarevac. This represents the first documented occurrence of the species in Croatia. However, a revision of specimens in Croatian collections, is necessary to clarify the presence and distribution of the species within the *Ulota crispa* complex in Croatia.

Buxbaumia viridis is a boreal montane species that inhabits large, well-decaying wood within consistently humid forest ecosystems. It serves as an indicator species for old-growth evergreen forests, which are considered a rare habitat in the European context. This species is included in the Bern Convention (Council of Europe, 1982) and Habitat Directives (Annex II) (Council of Europe, 1992) and is categorized as Least Concern (LC) in the European Red List (Hodgetts *et al*., 2019). Recent monitoring efforts have revealed multiple populations in the mixed beech and fir, as well as spruce forests of the Croatian Dinaric Alps. Notably, our findings from Svinjarevac and Sokolina Gosted on Mt. Papuk represent the first documented occurrences of this species in Eastern Croatia. The species was here observed to grow on humus-rich soil and moss peat, indicating a substrate preference that differs from that of most regions in Europe, but is common substrate in the Pannonian Basin (Deme *et al*., 2020).

Moss *Campylopus introflexus*, native to the Southern Hemisphere, is one of only three invasive bryophyte species (along with *Orthodontium lineare* Schwägr. and *Scopelophila cataractae* (Mitt.) Broth.) recorded in Europe to date. Its initial establishment in Southeast Europe has been observed in two specific regions of Croatia: the Dinaric Region (Vrhovinsko Polje, Lika) and the peri-Pannonian Region (Mt. Papuk, Slavonia) between 2013 and 2015 (Alegro *et al*., 2018). Furthermore, five additional records of this species have been identified across Croatia but remain unpublished. In neighbouring Slovenia and Serbia, the species has been also found rather recently (Ellis *et al*., 2014; Sabovljević *et al*., 2020, 2023). Within our research, the species has been located at Sokolina Gosted, growing on a bare gneiss cliff with a northeastern-facing

slope of 10°. The population extends over an area of approximately 2 × 0.5 m, with the largest contiguous patch measuring around 0.5 m². The compact cushions of this moss develop on thin layers of dry bedrock debris and decomposed organic matter. *Campylopus introflexus* is spreading at the expense of the dominant *Polytrichum piliferum* and other native moss species within the area.

Rare habitats with distinctive ecology supporting a specific floristic assemblage

The bryophyte survey conducted at Svinjarevac and Sokolina Gosted reveals that both localities are significant bryological hotspots, featuring distinctive and unique species assemblages. Acidophilic beech forests occurring on steep slopes, where they develop on shallow acidic soils over siliceous bedrock, are particularly rare in Croatia, rendering both sites notable from pedological and phytogeographical perspectives. The harsh environmental conditions result in stands of lower density, with shorter trees and relatively open canopies (Alegro *et al*., 2015). Notably, the forest floor is predominantly occupied by peat mosses, specifically *Sphagnum quinquefarium* (at both sites) and *Sph. capillifolium* (at Sokolina Gosted), creating extensive, reddish, occasionally green carpets. These are the only documented locations of peat mosses in Eastern Croatia. Based on floristic composition and ecological attributes, this forest community can be assigned to the suballiance *Luzulo luzuloidis-Fagenion* (Lohm. Et Tx. 1954) Oberd. 1957 (*Fagion sylvaticae* Luquet 1926, *Querco-Fagetea* Br. - Bl. et Vlieger 1937). However, due to its distinctive characteristics, it warrants consideration as a separate association of high biogeographic and conservation significance. This forest serves as a refugium for several relict taxa from both warm (e.g., *Grimmia montana*) and cold climatic periods (e.g., *Andreaea rothii*, *Dicranum spurium*, *Sphagnum* spp.), although the majority of species likely colonized the area during the late-glacial and Holocene periods.

The documented flora exhibits significant diversity in boreal species, which include boreo-arctic montane (*Sphenolobus minutus*, *Blepharostoma trichophyllum*, *Sanionia uncinata*, *Grimmia donniana* and *Racomitrium canescens*), wide-boreal (*Jungermannia pumila*, *Lophozia ventricosa*, *Brachythecium salebrosum*, *Dicranum scoparium*, *Hylocomium splendens*, *Pohlia nutans*, *Polytrichum commune*, *P. juniperinum* and *P. piliferum*), and boreal montane element (*Buxbaumia aphylla*, *B. viridis*, *Cynodontium polycarpon*, *Dicranum polysetum*, *D. spurium*, *Paraleucobryum longifolium*, *Plagiothecium platyphyllum*, *Pterigynandrum filiforme*, *Rhabdoweisia fugax* and *Sphagnum quinquefarium*), as well as boreo-temperate species (e.g. *Andreaea rothii* ssp. *rothii*, *Isopaches bicrenatus*, *Syzygiella autumnalis*, *Sphagnum capillifolium* etc.). A recent study of forest bryophytes on Mt. Papuk revealed that acidophilic forests growing on silicate bedrock were predominantly characterized by boreal chorotypes, which indicate cooler habitats and nitrogen-deficient soils (Alegro *et al*., 2023). The observed higher prevalence of boreal species at Sokolina Gosted in comparison to Svinjarevac is attributed to the peat moss carpet, which is more frequently interrupted by rocks, facilitating the colonization of other northern bryophytes.

The examined forests exhibit a significant presence of acidophilic bryophyte species, which are indicative of soils with low nutrient availability. Species that indicate extreme acidity include *Syzygiella autumnalis*, *Leucobryum glaucum*, *Paraleucobryum*

longifolium and *Racomitrium affine*. Additionally, species associated with high acidity are liverworts *Bazzania trilobata, Fuscocephaloziopsis lunulifolia, Diplophyllum albicans, Lepidozia reptans, Isopaches bicrenatus, Scapania nemorea* and mosses *Andreaea rothii* ssp. *rothii, Buxbaumia aphylla, Campylopus introflexus, Cynodontium polycarpon, Dicranella heteromalla, Dicranum spurium, Grimmia montana, Hedwigia ciliata, Pleurozium schreberi, Pohlia nutans, Polytrichum formosum, P. piliferum, Rhabdoweisia fugax* and *Sphagnum capillifolium*. Similarly, species associated with moderate acidity include liverworts *Sphenolobus minutus, Blepharostoma trichophyllum, Calypogeia fissa, Cephalozia bicuspidata, Jungermannia pumila, Lophocolea heterophylla* and mosses *Sanionia uncinata, Pogonatum aloides* and *Polytrichum juniperinum*. The environment is clearly characterized as highly acidophilic, featuring shallow soils over steep siliceous bedrock.

CONCLUSIONS

The significance of the investigated sites on Mt. Papuk is underscored by the acidophilic forests with the predominance of peat mosses on the forest floor. These forests, with their unique ecology, provide a suitable habitat for a very diverse bryoflora. Based on the floristic composition and ecological characteristics, this forest community can be categorized within the suballiance *Luzulo luzuloidis-Fagenion*; however, its unique attributes justify its recognition as a distinct association of considerable biogeographic and conservation importance. Quite numerous new national records and records of rare taxa can be attributed to the siliceous geological conditions, which are relatively uncommon in limestone-dominated regions of Croatia. Accordingly, these localities should be afforded increased protection as designated botanical reserves. Furthermore, the occurrence of the invasive moss *Campylopus introflexus* underscores the need for continuous ecological monitoring.

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