







Rare shady chasmophytic habitat communities (8210) in Ukraine

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Key words: habitats, petrophytic communities, classification, chasmophytic plants, ferns, bryophytes, ecological parameters, threats.

Ključne besede: habitati, petrofitske združbe, klasifikacija, hazmofiti, praproti, mahovi, ekološki dejavniki, grožnje.

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Received: 8. 9. 2022
Accepted: 4. 4. 2023

Abstract

The characteristics of shaded chasmophytic habitats on calcareous rocks in forest conditions are described, where the forest canopy primarily acts as a shading factor that determines microclimate, humidity and light levels. These communities can be found in deciduous forests of the *Carpinion betuli*, *Fagion sylvaticae* and *Tilio-Acerion* alliances, where they are confined to steep calcareous rock faces and cliffs. Syntaxonomically, these communities belong to the *Polypodietea* class (*Ctenidio-Polypodietalia vulgaris* order, *Ctenidio-Polypodion vulgaris* alliance) and to four informal communities: *Isoheciium alopecuroides-Polystichum braunii*, *Porella platyphylla-Asplenium ruta-muraria*, *Pseudanomodon attenuatus-Chrysosplenium alternifolium* and *Pedinophyllum interruptum-Polystichum aculeatum*. We evaluated indices of environmental parameters according to the synphytoindication method using Didukh's scales. An assessment of the threat impacts and indicators of sociological significance shows that the habitat belongs to a rare type (II class), and therefore requires specific conservation measures.

Izvešček

Opisali smo značilnosti zasenčenih hazmofitskih habitatov na karbonatnih skalah v gozdovih, kjer gozd predstavlja dejavnik zasenčenosti in s tem določa mikro-klimatske, vlažnostne in svetlobne značilnosti rastišča. Take združbe najdemo v listopadnih gozdovih zvez *Carpinion betuli*, *Fagion sylvaticae* in *Tilio-Acerion*, kjer so omejene na strmih apneniških skalah in klifih. Sintaksonomsko te združbe uvrščamo v razred *Polypodietea* (red *Ctenidio-Polypodietalia vulgaris*, zveza *Ctenidio-Polypodion vulgaris*) in štiri združbe: *Isoheciium alopecuroides-Polystichum braunii*, *Porella platyphylla-Asplenium ruta-muraria*, *Pseudanomodon attenuatus-Chrysosplenium alternifolium* in *Pedinophyllum interruptum-Polystichum aculeatum*. Okoljske spremenljivke smo ovrednotili s sinfitoindikacijsko metodo z Didukhovimi indikatorji. Ocena ogroženosti in indikatorji sociološkega pomena kažejo, da habitat uvrščamo kot redek tip (razred II) in potrebuje posebne mere varovanja.

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Introduction

Petrophytic habitats and floristically poor plant communities have generally received much less attention than forests and grasslands, but they have recently become the subject of more precise analysis. They have been considered, *inter alia*, to be “ecological islands”, protected from the competition of characteristic species and the influence of various external factors (fire, human activity, grazing, climate change) (Pigott & Walters, 1954; Larson, 2000; Theurillat & Guisan, 2001; Lavergne et al., 2004; Speziale & Ezcurra, 2012; Tomaselli et al., 2019). They have also been interpreted as “ecological traps”, or unique ecological niches that provide conditions for specific, narrowly adapted species (Larson, 2000, Tomaselli et al., 2019). Nevertheless, they contribute to an increase in γ -floristic and phytosociological diversity and are thereby protected and included within the habitat definitions listed in the EU Habitats Directive (Council Directive 92/43/EEC) as 8210 “Calcareous rocky slopes with chasmophytic vegetation” or 8220 “Siliceous rocky slopes with chasmophytic vegetation”. The EUNIS classification system allocates these habitats to a separate class (H) (Rodwell et al., 1998). In the latest summary of the European vegetation classification (Mucina et al., 2016), communities of this habitat are divided into eight classes and are given high syntaxonomic status. The approaches of the classification of biotopes (Palaeartic Habitat, CORINE, EUNIS) and plant communities (EuroVegChecklist) used do not match, so from the point of view of developing a new classification, these issues need to be resolved.

Communities of this type are not large, are often fragmented, and characterized by habitat mosaics because of typological, topological and regional differences. Many questions thus arise, such as the delimitation of syntaxa and their place in the classification system, the place of the bryophyte component reflected in their name etc. At the same time, due to the paucity of species in the floristic composition, the emphasis in the classification process is not only on floristic criteria but on the specifics of the ecological conditions. The essential aspect in this context is the question of the rocky habitat assessment forming in shady conditions. According to Didukh et al. (2016), a habitat is an ecosystem at a topological level characterized by interactions between biotic and abiotic components that ensure structure, organization and integrity over an extended period and matter cycle, with metabolism, energy transformation, pedogenesis, biota existence at the population level, reproduction, species evolution and adaptation to particular conditions. Petrophytic communities in forests should therefore be

interpreted as a habitat type, different from surrounding forest habitats.

Their existence is not directly related to the forest communities: the forest canopy here acts as a shading factor that determines the peculiarities of the microclimate, humidity etc., which are different from those of open rock communities. The floristic composition, structure and organization of these habitats differ from forest habitats, and they are the habitat of specific species within the boundaries of the forest communities (Chorney et al., 2014). These chasmophyte species of rock communities develop and reproduce on shallow soils – nudilic leptosols (IUSS Working Group WRB, 2015), and are not related to the successional process of the forest ecosystems. Notably, this type of habitat forms in specific orographic conditions: with the presence of rocks and outcrops of calcareous bedrock and is not characteristic of the forest habitat type within which it occurs. According to data recorded for shaded rocks (Sádlo & Chytrý, 2009), the temperature is positive from April to the end of November, and the summer temperature does not exceed 15° C. Communities of distinctive and specific species composition (6–13 species of spermatophytes and 4–7 species of bryophytes) develop in shady and wet conditions, in contrast to those of open rock habitats.

All the available evidence indicates that evolutionary processes are weak for this habitat type; successional development here actually slows down, and when communities degrade, their recovery is probably also very slow (Sádlo & Chytrý, 2009). For example, all ferns are polyploids in these habitats (2n=72, 143, 144, 148, 160, 168) due to the evolutionary process (Onete, 2012; Chorney et al., 2014).

This habitat combines chasmophyte (*Polypodietaea* class) and bryophyte communities: epilithic (*Ctenidietea mollusci* class) and epiphytic-epigeic (*Neckeretea complanatae* class), which are reflected in the name of the *Ctenidio-Polypodietalia vulgaris* order. On the other hand, the bryophyte component of the habitat is considered independently, although in the composition of this habitat they co-exist as a whole system (Gapon, 2013). Many questions thus require complex, systematic analysis, which determines the purpose of this publication. Considering these questions, we aimed to investigate the phytosociological and ecological peculiarities of shady chasmophytic habitats in Ukraine. To achieve this aim, we addressed the following questions: i) how is a shady chasmophytic habitat described syntaxonically? ii) which ecological conditions are characteristic of shady chasmophytic habitats? iii) to what threats and risks are shady chasmophytic habitats exposed, and how can they be protected?

Study area

Our research covered 5 localities from the Pre-Carpathian region within the Ivano-Frankivsk and Chernivtsi regions and Transcarpathian region (Figure 1), where the habitat type occurs on steep rocky slopes or vertical rock faces of northern or western exposure, on ridges or large calcareous rocks and cliffs, shaded by a canopy of deciduous trees. The limiting factor that ensures constant atmospheric wet and cool summer temperatures is the dense shading by the deciduous tree canopy (mesophytic sciophytic conditions) (Didukh et al., 2016).

The Pre-Carpathian region (Prut-Dniester confluence) is situated in the western part of Ukraine and geologically combines Precambrian bedrocks (gneisses, granites and argillites), Silurian and Devon bedrocks (limestones, dolomites and marls), alluvial clays and loess loams. The geomorphology of the Prut-Dniester confluence consists of ancient and developed valleys of the Dniester and Prut Rivers and their tributaries. The soil cover in the Prut-Dniester confluence is podzolic grey soils, sod-podzolic soils, podzolic chernozems, wet-meadow soils and shallow and skeletal soils on rocks and outcrops of calcareous bedrocks with deciduous forests, meadows, dry meadow

steppes and chasmophytic communities. The climate of the Prut-Dniester confluence is moderately continental with mild winters and a relatively warm, wet summer (the average temperature for January is $-5.1\text{ }^{\circ}\text{C}$, the average temperature for July is $18.7\text{ }^{\circ}\text{C}$, and the range in annual precipitation is from 500 to 700 mm (Herenchuk, 1973, 1978).

The Transcarpathian region is also situated in the western part of Ukraine and is characterized by a mountainous relief. This region geologically combines Proterozoic (gneisses and crystalline shales), Cretaceous (flysches) and Sarmatian bedrocks (clays, sandstones, limestones and conglomerates). The hydrography of the region is provided by the Tysa, Uzh, Latorytsia rivers and their tributaries. The soil cover in the region is formed by burozems, meadow burozems, shallow and skeletal soils on rocks and outcrops of sandstones, limestones and conglomerates with deciduous and coniferous forests, sub-alpine meadows and chasmophytic communities. The climate of the Transcarpathian region is moderately continental that strongly depends on temperature fluctuations (the average temperature for January is $-4.8\text{ }^{\circ}\text{C}$, the average temperature for July is $17.1\text{ }^{\circ}\text{C}$). The range in annual precipitation is approximately 1122 mm (Herenchuk, 1981).



Figure 1: Locations of shady chasmophytic habitat communities in Ukraine.

Slika 1: Lokacije zasenčenih hazmofitskih združb v Ukrajini.

Materials and methods

The subject of this research was calcareous cliffs and rocks that occur within the deciduous forests of the south-eastern and south-western macro-slopes of the Ukrainian Carpathians (Table S1). These are confined to altitude limits of 250 ± 20 to 850 ± 20 m a.s.l., respectively. The rock faces and slopes range from a height of 1.5 m to 5–10 m, with slopes up to 90° , with narrow rock protrusions up to 30 cm.

We recorded 46 phytosociological relevés with a uniform plot size of 4 m^2 , using the Braun-Blanquet approach (Braun-Blanquet, 1964) and the recommendations of Chytrý & Otýpková (2003) for the plot size of rocky vegetation, which we collected from Ukraine in 2018–2019, with specific vascular plants, bryophytes and epigeic lichens. We identified habitats by the presence of chasmophyte ferns (*Asplenium* L., *Cystopteris* Bernh., *Polypodium* L.), a dense cover of mosses that grow on rocks with steep slopes, and cliffs with ledges up to 30 cm wide (such ledges can accumulate soil and have a different floristic composition). We recorded different types of slopes and focused on the typical conditions of the habitat. The distribution map was created with the help of MapInfo Professional software (MapInfo, 2007).

The nomenclature for the vascular plant species is according to the Euro+Med Database checklist (<http://www.emplantbase.org/>), while bryophytes are according to Hodgetts et al. (2020), and lichens are according to the Index Fungorum (<http://www.indexfungorum.org/>).

Syntaxa nomenclature followed Mucina et al. (2016), Stodiek (1937), Cain & Sharp (1938), Herzog & Höfler (1944), Duda (1951) and Redžić et al. (2002).

The data were analysed in JUICE software (Tichý, 2002). We used a TWINSpan modified algorithm (Roleček et al., 2009): three pseudospecies cut level -0, 5 and 25, and Whittaker's method for distinguishing the clusters. Diagnostic species for individual clusters were estimated based on the phi-coefficient (threshold of fidelity at more than 30%), tested by Fisher's exact test ($p \geq 0.01$) (Chytrý et al., 2002), with the sizes of all groups standardized to an equal size (Tichý & Chytrý, 2006). We used a threshold of constancy of more than 50% for the determination of highly constant species, and for constant species of more than 25%.

Phytoindication scales of Y. Didukh (Didukh, 2011; Didukh et al., 2021) are comparable to other environmental indicator values (Ellenberg) and reflect amplitude indices of the species characterized by the following dimensions: ecological indicator of soil humidity (Hd – 23 grades), ecological indicator of variability of damping (fH – 11 grades), ecological indicator of soil acidity

(Rc – 15 grades), ecological indicator of total salt regime (Sl – 19 grades), ecological indicator of carbonate content (Ca – 13 grades), ecological indicator of nitrogen content (Nt – 11 grades), ecological indicator of soil aeration (Ae – 15 grades), ecological indicator of thermoregime (Tm – 17 grades), ecological indicator of humidity of microclimate (Om – 23 grades), ecological indicator of continentality (Kn – 17 grades), ecological indicator of cryoregime (Cr – 15 grades) and ecological indicator of light in the community (Lc – 9 grades).

DCA analysis (Detrended Correspondence Analysis) was conducted to assess the impact of environmental factors on plant communities. Phytoindication values were passively projected onto a DCA graph. We used the R program (R Core Team, 2021) to visualize the DCA analysis. The cyclogram of the quantitative indices of leading environmental parameters dispersion and determination of ecological valence of the communities was conducted using the application of environmental parameters' calculations (Didukh & Budzhak, 2020).

Habitat-level identification was performed using the EUNIS-ESy Expert System (Chytrý et al., 2020) to identify each relevé in the phytosociological table (Table S2). The impact of threats and sociological assessment of the habitats were conducted using a four-categories impact scale (Table S4) and ultimately summing them (Table S3) (Didukh, 2014; Didukh et al., 2018). By calculating the sum of points, the indices (in percentages) of the stability degree (Stability) $S = (S*1 - 3.99) \times 8.33$ and value degree (Value) $V = (V*1 - 9.99) \times 3.33$ were evaluated. Based on these indices, the corresponding classes were selected: I – > 80%, II – 61–80, III – 41–60, IV – 21–40, and V – < 21%.

Results

Shady chasmophytic communities occur from 250–500 m a.s.l., confined to forests of the *Carpinion betuli* and *Tilio-Acerion* alliances. The dominant tree species are *Acer platanoides*, *A. pseudoplatanus*, *Carpinus betulus*, *Quercus robur* and *Tilia cordata*. In Transcarpathia, such communities occur within an altitudinal range of 520–850 (1020) m a.s.l., in beech forests of the *Fagion sylvaticae* alliance. The cover of vascular plants fluctuates from 20 to 50%, the cover of bryophytes is 50–80% and the cover of the bare surface of rocks is 10–40%. At the foot of the rocks, and on more or less horizontal surfaces, there are beds of shrubs dominated by *Sambucus nigra*, rarely by *Euonymus verrucosa*, as well as seedlings of *Acer platanoides* or *Fagus sylvatica* trees, the roots of which penetrate very deeply and disrupt the structure of the calcareous rocks. The syntaxonomical peculiarity of

these communities is the presence of chasmophyte ferns with winter-green fronds (*Asplenium trichomanes*, *A. ruta-muraria*, *A. viridis*, *Phyllitis scolopendrium* and *Polypodium vulgare*). These chasmophyte species develop rhizomes that fill screes and rock depressions, thus contributing to soil formation (Fabiszewski et al., 1997).

Description of the communities (Table 1, Table S2, Figure 3 a-d)

We obtained four well-differentiated clusters using a modified TWINSpan algorithm (Figure 2), which could be interpreted as informal communities.

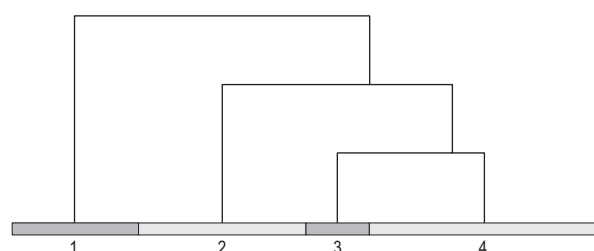


Figure 2: Dendrogram based on the modified TWINSpan algorithm classification. Cluster 1 – *Isoetecium alopecuroides*-*Polystichum braunii* community (8 relevés); Cluster 2 – *Porella platyphylla*-*Asplenium ruta-muraria* community (16 relevés); Cluster 3 – *Pseudanomodon attenuatus*-*Chrysosplenium alternifolium* community (17 relevés); Cluster 4 – *Pedinophyllum interruptum*-*Polystichum aculeatum* community (5 relevés).

Slika 2: Dendrogram na osnovi algoritma klasifikacije TWINSpan. Klaster 1 – združba *Isoetecium alopecuroides*-*Polystichum braunii* (8 popisov); Klaster 2 – združba *Porella platyphylla*-*Asplenium ruta-muraria* (16 popisov); Klaster 3 – združba *Pseudanomodon attenuatus*-*Chrysosplenium alternifolium* (17 popisov); Klaster 4 – združba *Pedinophyllum interruptum*-*Polystichum aculeatum* (5 popisov).

Cluster 1. *Isoetecium alopecuroides*-*Polystichum braunii* community

Floristical characteristics. The *Isoetecium alopecuroides*-*Polystichum braunii* community is characterized by the following diagnostic species: *Ctenidium molluscum*, *Dentaria glandulosa*, *Homalia trichomanoides*, *Isoetecium alopecuroides*, *Plagiomnium cuspidatum*, *Polystichum braunii*. The species *Ctenidium molluscum*, *Homalia trichomanoides*, *Pseudanomodon attenuatus* are dominant in the communities. The total cover of the species is 60–90% and the cover of cryptogam species is 60%.

Distribution and threats. This community occurs on Marmarosh calcareous cliffs and conglomerates (Transcarpathian region) of north-eastern and north-western slopes on which dry nudilic leptosols are formed at an elevation of 233–307 m a.s.l. According to the sociological assessment of the habitat and the impact of threats,

this community is endangered due to climbing and tourist activity (camping sites, fireplaces, litter accumulation) in the Transcarpathian region (Table S3).

Cluster 2. *Porella platyphylla*-*Asplenium ruta-muraria* community

Floristical characteristics. The *Porella platyphylla*-*Asplenium ruta-muraria* community is characterized by the following diagnostic species: *Anomodon viticulosus*, *Cardaminopsis arenosa*, *Homalothecium philippeanum*, *Porella platyphylla*, *Sagina procumbens*, *Seseli libanotis*. The species *Exerthotheca crista* and *Hedera helix* are dominant in the communities. The total species cover is 70–90%, based on bryophytes and overlapped by vascular plants.

Distribution and threats. This community forms loose mats on thin soils that are rich in nitrogen compounds, covering partially shaded calcareous rocks mainly on western, northern and north-western slopes and occupying an area of almost 40–60%, where the rest of the surface is exposed rock at an elevation from 232 to 657 m a.s.l. The community is found in the Pre-Carpathian (Chernivtsi region, Ukraine) and the Transcarpathian regions (Ukraine). According to the sociological assessment of the habitat and impact of threats, this plant community is an endangered habitat due to tourist activity and has a high constancy of synanthropic species (*Chelidonium majus*, *Geranium robertianum*, *Urtica dioica*) (Table S3).

Cluster 3. *Pseudanomodon attenuatus*-*Chrysosplenium alternifolium* community

Floristical characteristics. The *Pseudanomodon attenuatus*-*Chrysosplenium alternifolium* community is characterized by the following diagnostic species: *Campanula rapunculoides*, *Chiloscyphus polyanthos* var. *rivularis*, *Conocephalum salebrosum*, *Cystopteris fragilis*, *Lamium galeobdolon*. The species *Conocephalum salebrosum* and *Pseudanomodon attenuatus* are dominant in the communities. The total species cover is 60–80%, based on bryophytes and overlapped by vascular plants.

Distribution and threats. This community occurs in forests, mainly on shaded steep calcareous cliffs (75–90°), primarily on northern, north-western, and south-eastern slopes of the Transcarpathian region (Ukraine) at an elevation of 536–1014 m a.s.l. and is formed on dry nudilic leptosols. According to the sociological assessment of the habitat and impact of threats, this plant community is influenced by climbing and the mining of limestones in illegal quarries in the Transcarpathian region; we therefore decreased the threat impact index (3 points) (Table S3).

Cluster 4. *Pedinophyllum interruptum*-*Polystichum aculeatum* community

Floristical characteristics. The *Pedinophyllum interruptum*-*Polystichum aculeatum* community is characterized by the following diagnostic species: *Asarum europaeum*, *Campanula carpatica*, *Fissidens dubius*, *Pedinophyllum interruptum*, *Scopolia carniolica*, *Tamobryum alopecurum*. The species *Conocephalum salebrosum* and *Hedera helix* are dominant in the communities. The total species cover is 60–95%, based on bryophytes and overlapped by vascular plants.

Distribution and threats. This community occurs on steep Marmarosh calcareous cliffs (45–90°), mainly on southern and south-western slopes of the Transcarpathian region (Ukraine) at an elevation of 519–574 m a.s.l. and formed on dry nudilic leptosols. According to the sociological assessment of the habitat and impact of threats, this plant community is influenced by the colonization of forest species (*Aegopodium podagraria*, *Asarum europaeum*, *Scopolia carniolica*) in the Carpathian Biosphere Reserve (Transcarpathian region); we therefore decreased the threat impact index (3 points) (Table S3).

Table 1: Synoptic table of shadow chasmophytic communities, indicating the constancy of species expressed by their percentage frequency in the respective four clusters. Species are ranked by decreasing constancy and phi coefficient values are not shown, although species with a phi- value greater than 0.25 are accepted as differential for the syntaxa. Species of each syntaxon with a constancy of 15% or less, as well as other taxa with a constancy of 15% or less, are not shown in the table.

Tabela 1: Sinoptična tabela zasenčenih hazmofitskih združb. Prikazana je stalnost vrst s frekvenco v odstotkih v štirih klastrih.

Vrste so razvrščene glede na padajočo stalnost, vrednosti fi koeficienta niso prikazane. Kot razlikovalne vrste smo upoštevali tiste, ki imajo fi koeficient večji od 0,25. Vrste s stalnostjo, manjšo od 15% v posameznem sintaksonu in vse vrste z stalnostjo manjšo od 15%, niso prikazane v tabeli.

Number of relevés	8	16	17	5
Cluster	1	2	3	4
<i>Isoethecium alopecuroides</i>-<i>Polystichum braunii</i> community				
<i>Isoethecium alopecuroides</i>	63	6	.	.
<i>Plagiomnium cuspidatum</i>	63	.	.	.
<i>Ctenidium molluscum</i>	63	19	.	20
<i>Homalia trichomanoides</i>	50	.	.	20
<i>Acer platanooides</i> (juv.)	38	6	.	20
<i>Polystichum braunii</i>	38	.	.	20
<i>Rubus idaeus</i>	38	.	.	.
<i>Eurhynchium striatum</i>	38	19	.	.
<i>Porella platyphylla</i>-<i>Asplenium ruta-muraria</i> community				
<i>Campanula trachelium</i>	.	50	6	.
<i>Porella platyphylla</i>	.	44	.	.
<i>Fagus sylvatica</i> (juv.)	25	38	.	.
<i>Asplenium ruta-muraria</i>	.	38	18	.
<i>Sagina procumbens</i>	13	38	.	.
<i>Galium intermedium</i>	25	31	24	.
<i>Exsertiotheca crispa</i>	25	31	.	20
<i>Pseudanomodon attenuatus</i>-<i>Chrysosplenium alternifolium</i> community				
<i>Pseudanomodon attenuatus</i>	88	50	94	40
<i>Conocephalum salebrosum</i>	.	.	71	40
<i>Chrysosplenium alternifolium</i>	.	.	53	40
<i>Campanula rapunculoides</i>	.	.	35	20
<i>Pedinophyllum interruptum</i>-<i>Polystichum aculeatum</i> community				
<i>Polystichum aculeatum</i>	13	19	.	80
<i>Asarum europaeum</i>	25	.	12	80
<i>Campanula carpatica</i>	.	6	.	60
<i>Poa nemoralis</i>	13	6	29	60
<i>Pedinophyllum interruptum</i>	.	6	.	60
<i>Lunaria rediviva</i>	.	19	6	60
<i>Fissidens dubius</i>	.	.	.	40
<i>Veronica urticifolia</i>	.	6	.	40
<i>Carex montana</i>	.	13	.	40
<i>Pulmonaria obscura</i>	.	.	.	40
<i>Scopolia carniolica</i>	.	.	.	40
<i>Senecio nemorensis</i>	.	.	.	40

Number of relevés	8	16	17	5
Cluster	1	2	3	4
<i>Radula complanata</i>	25	13	.	40
<i>Salvia glutinosa</i>	.	25	18	40
<i>Aegopodium podagraria</i>	.	.	6	40
<i>Moebringia trinervia</i>	.	13	6	40
<i>Galium transcarpaticum</i>	.	6	.	40
<i>Allenella complanata</i>	.	19	.	20
<i>Ctenidio</i>-<i>Polypodium vulgare</i> alliance,				
<i>Ctenidio</i>-<i>Polypodietales vulgaris</i> order, <i>Polypodietales</i> class				
<i>Phyllitis scolopendrium</i>	88	88	100	100
<i>Polypodium vulgare</i>	88	50	59	60
<i>Asplenium trichomanes</i>	75	94	65	60
<i>Hedera helix</i>	75	19	29	80
<i>Cystopteris fragilis</i>	13	63	76	40
<i>Dryopteris filix-mas</i>	75	31	6	60
<i>Lamium galeobdolon</i>	25	25	82	80
Other vascular plants in alphabetical order				
<i>Cardaminopsis arenosa</i>	.	50	.	60
<i>Chelidonium majus</i>	.	38	29	20
<i>Geranium robertianum</i>	25	50	47	80
<i>Hepatica nobilis</i>	.	31	24	40
<i>Hylotelephium maximum</i>	.	31	18	40
<i>Mercurialis perennis</i>	.	25	6	20
<i>Mycelis muralis</i>	13	75	.	40
<i>Sambucus nigra</i> (juv.)	.	31	41	40
<i>Urtica dioica</i>	13	25	12	20
<i>Valeriana</i> sp.	.	19	.	20
Other cryptogam species in alphabetical order				
<i>Anomodon viticulosus</i>	25	63	12	60
<i>Chiloscyphus polyanthos</i> var. <i>rivularis</i>	.	.	18	.
<i>Homalothecium philippeanum</i>	.	25	.	.
<i>Lepraria membranacea</i>	13	31	.	40
<i>Metzgeria conjugata</i>	63	.	.	40
<i>Mnium stellare</i>	.	.	24	20
<i>Plagiochila porelloides</i>	50	6	6	40
<i>Thamnobryum alopecurum</i>	50	13	.	60

Proposed syntaxonomical scheme

We did not find relevant associations within the *Ctenidio-Polypodium vulgaris* alliance, *Ctenidio-Polypodietales vulgaris* order, *Polypodietales* class. However, we did not find all diagnostic bryophyte species to describe them as bryophyte associations. We therefore we propose a syntaxonomical scheme of the distinguished clusters interpreted as informal communities.

Cl. *Polypodietales* Jurko et Peciar ex Boscaiu, Gergely et Codoreanu in Ratiu et al. 1966

Ord. *Ctenidio-Polypodietales vulgaris* Jurko et Peciar ex Boscaiu, Gergely et Codoreanu in Ratiu et al. 1966

All. *Ctenidio-Polypodium vulgaris* S. Brullo et al. 2001

- 1) *Isoetes alopecuroides*-*Polystichum braunii* community
- 2) *Porella platyphylla*-*Asplenium ruta-muraria* community
- 3) *Pseudanomodon attenuatus*-*Chrysosplenium alternifolium* community
- 4) *Pedinophyllum interruptum*-*Polystichum aculeatum* community

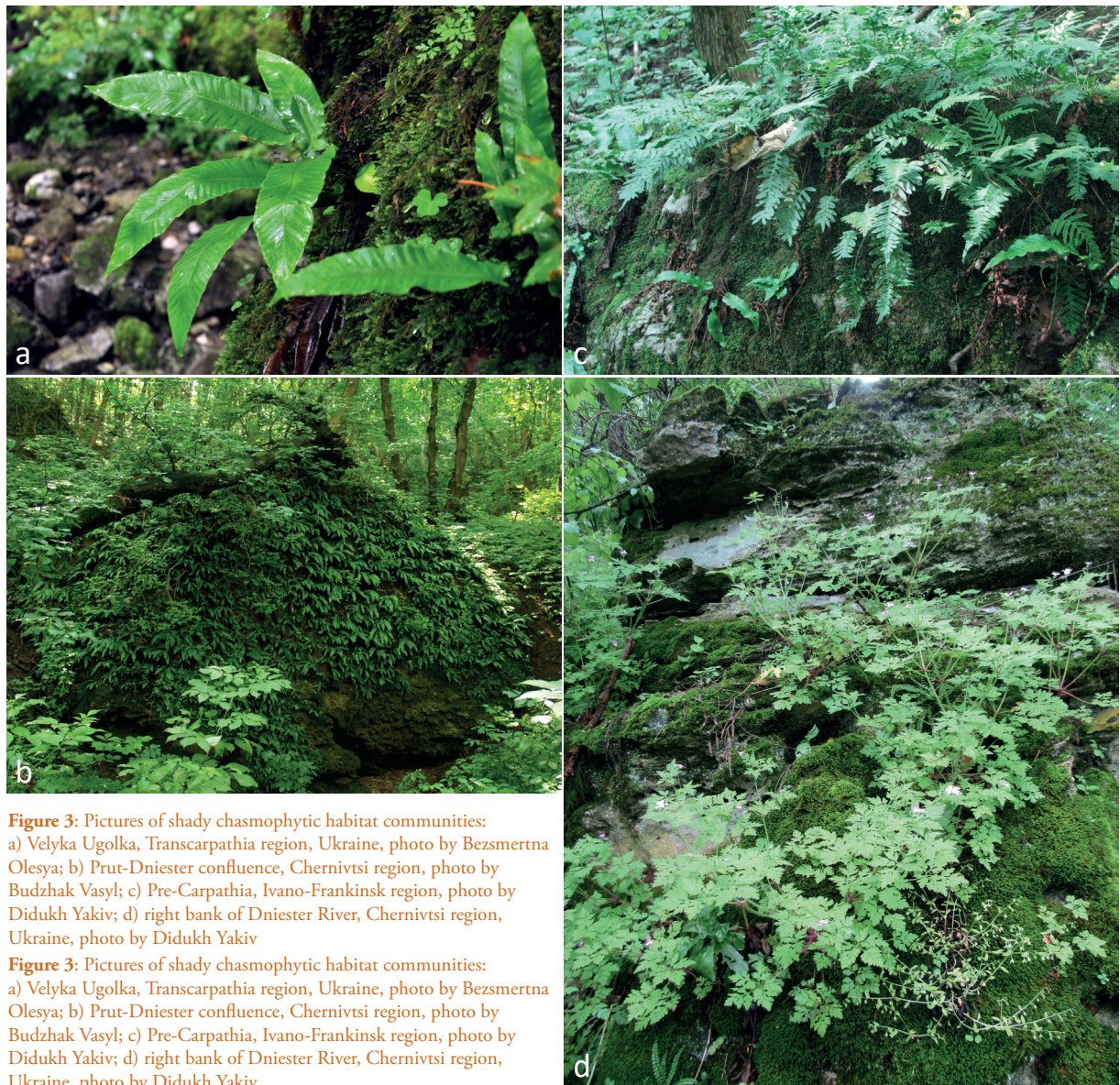


Figure 3: Pictures of shady chasmophytic habitat communities: a) Velyka Ugolka, Transcarpathia region, Ukraine, photo by Bezsmertna Olesya; b) Prut-Dniester confluence, Chernivtsi region, photo by Budzhak Vasyl; c) Pre-Carpathia, Ivano-Frankinsk region, photo by Didukh Yakiv; d) right bank of Dniester River, Chernivtsi region, Ukraine, photo by Didukh Yakiv

Figure 3: Pictures of shady chasmophytic habitat communities: a) Velyka Ugolka, Transcarpathia region, Ukraine, photo by Bezsmertna Olesya; b) Prut-Dniester confluence, Chernivtsi region, photo by Budzhak Vasyl; c) Pre-Carpathia, Ivano-Frankinsk region, photo by Didukh Yakiv; d) right bank of Dniester River, Chernivtsi region, Ukraine, photo by Didukh Yakiv

Ecological characteristics of the shadow chasmophytic habitat communities

We assessed the ecological factors' indices according to the synphytoindication methodology (Didukh, 2011). According to humidity indices, these communities can be interpreted as meso-hygromesophyte and well-wetted; according to the variability of dampness indices, these communities can be interpreted as hydro-hemicontrastophobic with uniform steady or slightly uniform hydration; according to the aeration indices, hemiaerophobic with uniform aerated substrata; according to the acidity indices – neutrophilic with pH from 6.5 to 7.1; according to the total salt regime in soil indices, semi eutrophic; according to the carbonate content indices these communities are acarbonatophilic, despite the carbonate richness of the bedrocks; according to the nitrogen content indices, heminitrophilic – nitrophilic, with high concentrations of nitrate ions. According to the thermoregime indices these communities are submesothermic; according

to the cryoregime indices, hemicyrophytic; according to the continentality indices, hemioceanic; according to the humidity of the climate indices, subbromphytic. Such climatic characteristics of this habitat correlate with the indicators of the *Carpinion betuli* and *Fagion sylvaticae* alliances (Didukh et al., 2016). They are similar to forest habitats, but deviate from zonal ones and reflect their preferences to shading by a wooded canopy.

Based on the calculation of ecological indicators' values, cyclograms illustrate the environmental niches of shady chasmophytic habitat communities, which are characterized by a narrow amplitude of environmental factors and are typical for stenotopic species. The most limited range of tolerance is prominent (Figure 4 a-d): the soil humidity (Hd) (mainly *Isoeteceum alopecuroides*-*Polystichum braunii* community and *Pedinophyllum interruptum*-*Polystichum aculeatum* community), the total salt regime (Sl) (all distinguished communities), carbonate content (Ca) (mainly *Pedinophyllum interruptum*-*Polystichum aculeatum* community) and acidity (Rc) (mainly *Pedinophyllum interruptum*-*Polystichum aculeatum* community).

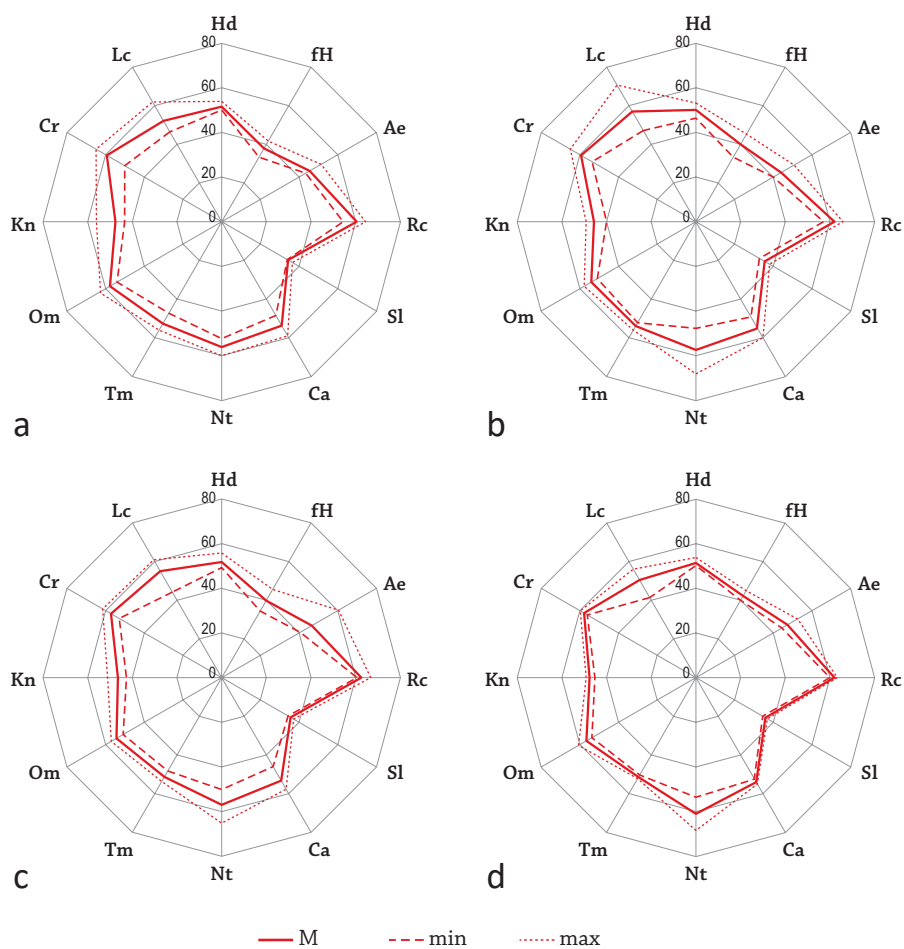


Figure 4: Cyclogram of ecological indicator values of shady chasmophytic habitats. Acronyms of the ecological indicators are the same as in the Materials and methods section. The dashed line shows the minimum and maximum of the ecological indicator indices. The solid line shows the ecological optimum of the shady chasmophytic habitat communities.

a) – *Isoeteceum alopecuroides*-*Polystichum braunii* community, b) – *Porella platyphylla*-*Asplenium ruta-muraria* community, c) – *Pseudanomodon attenuatus*-*Chryso-splenium alternifolium* community, d) – *Pedinophyllum interruptum*-*Polystichum aculeatum* community.

Slika 4: Ciklični graf ekoloških indikatorskih vrednosti zasenčenih hazmofitskih združb. Okrajšave ekoloških indikatorjev so enake kot v poglavju Material in metode. Prekinjena črta prikazuje najmanjšo in največjo vrednost indikatorja. Polna črta prikazuje optimum zasenčenih hazmofitskih združb.

Four shady chasmophytic communities were clearly distinguished on the DCA visualization (Figure 5). The main axis (DCA 1) compared to the vectors of ecological indicators (carbonate content, thermoregime, cryoregime and humidity), whereby a significant differentiation between the *Isothecium alopecuroides*-*Polystichum braunii* community and the *Pseudanomodon attenuatus*-*Chryso-splenium alternifolium* community is observable. Although the second axis (DCA 2) does not show substantial differences between the communities, it is closer to the vectors of ecological indicators (total salt regime in the soil and soil humidity).

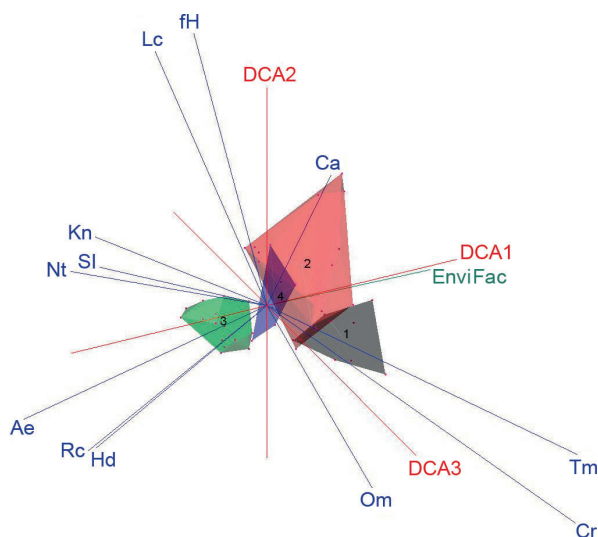


Figure 5: Detrended Correspondence Analysis (DCA) of shady chasmophytic habitat communities. 1 – *Isothecium alopecuroides*-*Polystichum braunii*, 2 – *Porella platyphylla*-*Asplenium ruta-muraria*, 3 – *Pseudanomodon attenuatus*-*Chryso-splenium alternifolium*, 4 – *Pedinophyllum interruptum*-*Polystichum aculeatum*. Acronyms of the ecological indicators are the same as in the Materials and methods section.

Slika 5: Korespondenčna analiza z odstranjenim trendom (DCA) Detrended Correspondence Analysis zasnečenih hazmofitskih združb. 1 – *Isothecium alopecuroides*-*Polystichum braunii*, 2 – *Porella platyphylla*-*Asplenium ruta-muraria*, 3 – *Pseudanomodon attenuatus*-*Chryso-splenium alternifolium*, 4 – *Pedinophyllum interruptum*-*Polystichum aculeatum*. Okrajšave ekoloških indikatorjev so enake kot v poglavju Material in metode.

Discussion

Syntaxonomical revision

Chasmophytic communities are often a mosaic in structure, due to variations in the microrelief. They typically have a lower level of floristic richness, with a combination of different taxa (vascular plants, bryophytes, lichens) and their syntaxonomy is described differently (Valachovič, 1995; Sádlo & Chytrý, 2009).

In the Prodom of the Vegetation of Europe, the classification of these communities has undergone significant changes (Mucina et al., 2016). The chasmophytic vegetation of rocks and screes belongs to 8 classes, 36 orders and 146 alliances. However, at the same time, many questions arise regarding the delimitation of syntaxa and their place in the classification system, especially when the bryophyte component, which plays a significant role in certain classes and has high diagnostic value, is not taken into account. We must emphasize the division of two classes *Asplenieta trichomanis* and *Polypodieta*. This division is based on the chemical characteristics of substrata, humidity and shading. The *Polypodieta* class, which consists of 3 orders and 13 alliances and represents communities of shady rocks and crevices, with characteristic species: chasmophyte, sciophyte plants and a high cover of bryophytes, which occupy rock surfaces and crevices where a small amount of detritus accumulates (Tomaselli et al., 2019).

Finding the syntaxonomical affiliation of the bryophyte component generally causes discussion (Cain & Sharp, 1938). On the one hand, if the bryophyte communities are interpreted as a part of the whole, synusia or mero-coenos, within the shady chasmophytic habitat, then the opinion of Berg et al. (2019) is fully justified. Following this claim of Berg et al. (2019), bryophyte communities should not be considered separate classes at the level of holocoenoses, which can be reflected in their name by introducing the appropriate suffixes. On the other hand, Mucina et al. (2016) claimed that synusia (micro-communities) are elements within plant associations or separate syntaxonomic units; we therefore preliminarily consider the distinguished clusters to be informal communities within the *Ctenidio*-*Polypodion vulgaris* alliance, *Ctenidio*-*Polypodietalia vulgaris* order, *Polypodieta* class (Table 1).

Moreover, we did not aim to investigate the bryophyte communities as separate syntaxonomical units and used a traditional approach to describe the vascular plants' communities. Based on this, we omitted some species that could be diagnostic in some bryophyte associations.

The first cluster was interpreted as the *Isothecium alopecuroides*-*Polystichum braunii* community, which had related connections with the association *Tortello-Ctenidietum mollusci* (Gams 1927) Stodiek 1937, which was described by Stodiek (1937) with the presence of diagnostic bryophyte species (*Ctenidium molluscum*, *Isothecium alopecuroides*, *Plagiomnium cuspidatum*) that belong to the alliance *Ctenidion mollusci* Ștefureac 1941, order *Ctenidietalia mollusci* Hadač et Šmarda in Klika et Hadač 1944, class of *Ctenidietea mollusci* von Hübschmann ex Grgić 1980. On the other hand, there is a

significant presence of vascular plants (*Acer planatoides* (juv.), *Denatria glandulosa*, *Polystichum braunii*) and the absence of numerous diagnostic species (*Brachythecium glareosum*, *Ditrichum flexicaule*, *Fissidens dubius*) of the *Ctenidion mollusci* alliance (Ştefureac, 1941; Klika, 1948; Ragulina & Orlov, 2021).

We classified the second cluster as the *Porella platyphylla-Asplenium ruta-muraria* community, with the presence of ferns (*Asplenium ruta-muraria*, *Phyllitis scolopendrium*, *Polypodium vulgare*) and spermatophytes (*Campanula trachelium*, *Fagus sylvatica*, *Sagina procumbens*) as the diagnostic species. It should be added that the distinguished cluster has two diagnostic species (*Porella platyphylla* and *Exsertotheca crispa*) of the bryophyte association of *Homalothecio sericei* – *Porelletum platyphyllae* Stormer 1938 ex Duda 1951, which was described by Duda (1951) within the alliance *Neckerion complanatae* Šmarda et Hadač ex Klika 1948, order *Neckeretalia complanatae* Jezek et Vondracek 1962 and class *Neckeretea complanatae* Marstaller 1986. However, since we have diagnostic species of the association (Ragulina & Orlov, 2021), we did not observe numerous diagnostic species of the *Neckerion complanatae* alliance (*Metgeria conjugata*, *Sciuro-hypnum populeum*, *Thamnobryum alopecurum*).

In the third cluster, there were some diagnostic bryophyte species (*Pseudanomodon attenuates*, *Conocephalum salebrosum*), which could lead us to the association *Anomodontetum attenuati* Cain & Sharp 1938, which has also been considered within the alliance *Neckerion complanatae*, order *Neckeretalia complanatae* and class *Neckeretea complanatae* (Peciar 1965). The fourth cluster, designated the *Pedinophyllum interruptum-Polystichum aculeatum* community, has the features of *Pedinophyllum interrupti* Herzog & Höfler 1944, which was considered by Vadam (1983). However, it cannot currently be treated as the *Pedinophylletum interrupti* association since we do not have a clear group of diagnostic bryophyte species (*Cololejeunea calcarea*, *Fissidens pusillus*, *Pedinophyllum interruptum*). Moreover, we did not find evidence of the presence of the *Pedinophylletum interrupti* association in Ukraine (Ragulina & Orlov, 2021).

Additionally, it must be noted that the high constancy of *Phyllitis scolopendrium* within all distinguished communities may indicate *Asplenio-Phyllidetum scolopendrii* Redžić et al. 2002, first described by Redžić et al. (2002) and confirmed within the Carpathian Mountains (Beskydy Mountains) by Świerkosz (2004). However, it can only be confirmed after collecting appropriate data and providing a comprehensive analysis within the Carpatho-Pannonian region in Central Europe.

Ecological assessment of shady chasmophytic communities

Calcareous rocks in the Pre-Carpathian and Transcarpathian regions obviously have various chemical compositions of rocks (thin-bedded limestones, sandstones, flysches and conglomerates): a different content of carbonate anions, calcium/magnesium cations and soil acidity indices that have apparently (Hnylko et al., 2015) generated a differentiation of the shady chasmophytic habitat communities (Didukh et al., 2016).

The distribution of species within the shady chasmophytic habitat communities is irregular – they grow in local spots, mats, and have vascular plants that occur in small beds and patches, determined by the range of variation of the microrelief (Sádlo & Chytrý, 2009). Moreover, they are heated unequally, which also causes unequal transpiration and humidity loss on the different faces of rocks (Larson et al., 2000; Pășcuț, 2018). The cryo- and thermoregimes, as the microclimate indices, also caused a differentiation of the plant communities in the microrefugia formed on the rock cliffs (Garcia et al., 2020).

Conservation status of the shady chasmophytic habitat communities

Shady chasmophytic habitats are protected in accordance with Resolution 4 of the Bern Convention (Council of Europe, 2018) as H3.252 Communities of shady, cool, often moist rockfaces of the Alps and neighbouring regions, of the Carpathians, of the Jura, the Hercynian ranges, the British Isles, with many ferns, including [*Cystopteris fragilis*], [*Cystopteris regia*], [*Asplenium viride*], [*Asplenium scolopendrium*], [*Asplenium trichomanes*] and with [*Carex brachystachys*] and 8210 Calcareous rocky slopes with chasmophytic vegetation in accordance with NATURA 2000 (Table S3).

According to the classification of Ukrainian habitats (UkrBiotop), the equivalent of this habitat has been described for the Crimea Mountains: H:2.114 Shaded chasmophyte communities with a complex of lichens and bryophytes (Didukh et al., 2011). Thereafter Didukh et al. (2018) considered a single habitat K5.2 “Chasmophyte and bryophyte communities of shaded calcareous cliffs”, which combined communities of the *Polypodietea* class, *Ctenidio-Polypodium vulgare* alliance, which is distributed in the Carpathian Mountains and adjacent lowlands of Ukraine (Table S3).

It must be added that the results of the ESy-EUNIS expert system evaluation (Table S2) showed undefined expectations: many relevés were identified with a question mark “?”. On the other hand, the last cluster has

been assigned as R55 (Lowland moist or wet tall herb and fern fringe dominants) and R57 (Herbaceous forest clearing vegetation) habitats, although the elements of these habitats are present in shady chasmophytic communities. It should be mentioned that these shady chasmophytic habitat communities are described as H32c (Temperate lowland to montane base rich inland cliff) according to the modern EUNIS classification (Chytrý et al., 2020); however, the group of characteristic species of H32c is missing in our results.

The main threat to this habitat's existence is deforestation, which increases light levels, warming and a moisture deficiency of the substrata, and eutrophication, as a result of which nitrophilic species invade these communities (Didukh et al., 2016). Moreover, in our opinion, some other kinds of threats could include climbing, tourist activity and mining of dolomites and limestones (Świerkosz et al., 2011; Świerkosz & Reczynska, 2012), when, due to mechanical disturbance, the restoration of the communities is very slow (Didukh et al., 2012).

The shady chasmophytic habitat is thus rare (Table S3) and has limited distribution, with a low potential for restoration. These communities are sensitive to the influence of anthropogenic factors and require targeted protection measures, which must be taken into account when management plans for habitat protection are created.

Acknowledgments

We warmly appreciate Neil Lockhart and Martin Creegen for proofreading the text and improving the English spelling. We are also grateful to Dr. Marina Ragulina and Dr. Vitalii Virchenko for the determination of the bryophyte difficult groups. We are grateful to the Editor-in-Chief Urban Šilc, Milan Chytrý and two anonymous referees for their valuable comments and suggestions. Notably, we want to express our gratitude to the Armed Forces of Ukraine for providing the opportunity for us to undertake our research activity in safety.

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References

- Braun-Blanquet, J. (1964). *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Springer.
- Cain, S. A. & Sharp, A. J. (1938). Bryophytic unions of certain forest types of the Great Smoky Mountains. *American Midland Naturalist*, 20, 249–301.
- Chorney, I., Budzhak, V., Tokaryuk, A., Volutsa, O. (2014). *Khorolohiya raryetnoho bioriznomanityta Bukovyny. Chastyna I. Arkhehoniaty*. DrucArt.
- Chytrý, M., Tichý, L., Holt, J. & Botta-Dukát, Z. (2002). Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, 13, 79–90. <https://doi.org/10.1111/j.1654-1103.2002.tb02025.x>
- Chytrý, M., Tichý, L., Hennekens, S.M., Knollová, I., Janssen, J.A.M., Rodwell, J.S., Peterka, T., Marcenò, C., Landucci, F., Danihelka, J., Hájek, M., Dengler, J., Novák, P., Zúkal, D., Jiménez-Alfaro, B., Mucina, L., Abdulkhak, S., Acíć, S., Agrillo, E., Attorre, F., Bergmeier, E., Biurrun, I., Boch, S., Böllöni, J., Bonari, G., Braslavskaya, T., Bruelheide, H., Campos, J.A., Čarni, A., Casella, L., Čuk, M., Čušterevska, R., De Bie, E., Delbosc, P., Demina, O., Didukh, Y., Dítě, D., Dziuba, T., Ewald, J., Gavilán, R.G., Gégout, J.-C., Giusso del Galdo, G.P., Golub, V., Goncharova, N., Goral, F., Graf, U., Indreica, A., Isermann, M., Jandt, U., Jansen, F., Jansen, J., Jašková, A., Jiroušek, M., Kački, Z., Kalníková, V., Kavgaci, A., Khanina, L., Korolyuk, A.Yu., Kozhevnikova, M., Kuzemko, A., Kuzmič, F., Kuznetsov, O.L., Laiviņš, M., Lavrinenko, I., Lavrinenko, O., Lebedeva, M., Lososová, Z., Lysenko, T., Maciejewski, L., Mardari, C., Marinšek, A., Napreenko, M.G., Onyshchenko, V., Pérez-Haase, A., Pielech, R., Prokhorov, V., Rašomavičius, V., Rodríguez Rojo, M.P., Růsina, S., Schrautzer, J., Šibík, J., Šilc, U., Škvorc, Ž., Smagin, V.A., Stančić, Z., Stanisci, A., Tikhonova, E., Tonteri, T., Uogintas, D., Valachovič, M., Vassilev, K., Vynokurov, D., Willner, W., Yamalov, S., Evans, D., Palitzsch, Lund M., Spyropoulou, R., Tryfon, E. & Schaminée, J.H.J. (2020). EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. *Applied Vegetation Science*, 23, 648–675. <https://doi.org/10.1111/avsc.12519>
- Council of Europe. (2018). *Revised Annex I to Resolution 4 (1996) of the Bern Convention on Endangered Natural Habitat Types using the EUNIS Habitat Classification (Adopted by the Standing Committee on 30 November 2018)*. <https://rm.coe.int/16807469e7>
- Didukh, Y. (2011). *The ecological scales for the species of Ukrainian flora and their use in synphytoindication*. Phytosociocentre.
- Didukh, Y., Phytosailo T., Korotchenko, I., Iakushenko, D., Pashkevych, N., Alioshkina, U. (2011). *Biotopy lisovoyi ta lisostepovoyi zon Ukrainy*. PP Makros.
- Didukh, Y. (2014). Assessment of stability and risk of loss of ecosystems. *Scientific notes of National University of Kyiv-Mohyla Academy*, 158. *Biology and ecology*, 54–60.
- Didukh, Y., Chorney, I., Khodosovtsev, O. (2018). K5.2 Chasmophyte and moss communities of shaded carbonate rocks. In: Kuzemko, A., Didukh, Y., Onyshchenko, V. et al. (Eds.). *National habitat catalogue of Ukraine*. PP Klymenko.
- Didukh, Y., Chorney, I., Budzak, V. et al. (2016). *Climatogenic Changes of Plant Life of the Ukrainian Carpathians*. DrucArt.

- Didukh, Y., Kagalo, O., Prots, B. (Eds.). (2012). *Biotopy (oselyshcha) Ukrainy: naukovi zasady yikh doslidzhennya ta praktichni rezultaty inventaryzatsii. Materialy robochoho seminaru. Kyiv, 21–22 bereznya 2012 roku.* M.G. Kholodny Institute of Botany. National Academy of Sciences of Ukraine.
- Didukh, Y., Kuzemko, A., Vakarenko, L. (2018). Otsinka znachymosti ta kadastr ridkisnykh biotopiv Ukrainy dlia zberezhennia bioriznomanittia ta monitorynhu dovkillia. *Klasyfikatsiia roslynnosti ta biotopiv Ukrainy.* M.G. Kholodny Institute of Botany. National Academy of Sciences of Ukraine.
- Didukh, Y., Budzhak, V. (2020). *Probrama dlya avtomatyzatsii protsesu rozrakhunku balnykh pokaznykiv ekolohichnykh faktoriv: metodychni rekomendatsii.* Chernivtsi National University.
- Didukh, Y. (2021). Climate Change Assessment Based on Synphytoindication Method. In M. Lackner et al. (Eds.). *Handbook of Climate Change Mitigation and Adaptation.* Springer Science+Business Media, LLC, part of Springer Nature 2021. https://doi.org/10.1007/978-1-4614-6431-0_137-1
- Duda J. (1951). Spolecenstva Bryophyt na piskovcovych skalach v Beskydach. *Prirodoredecky Sbornik ostravskeho Kraje, 12*, 323–334.
- Euro+Med. (2006–2020). *Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity.* <http://ww2.bgbm.org/EuroPlusMed/query.asp>
- Fabiszewski, J., Koła, W. & Kwiatkowski, P. (1997). *Phyllitis scolopendrium* (L.) Newm. in the Sudeten Mountains. *Annales Silesiae, 27*, 49–62.
- Gapon, S.V. (2013). Methodological aspects of the moss vegetation studies. *Ukrainian Botanical Journal, 70(3)*, 392–397. <https://doi.org/10.15407/ukrbotj70.03.392>
- Herzog, T. & Höfler, K. (1944). Kalkmoosgesellschaften um Golling. *Hedwigia, 82 (1/2)*, 2–90.
- Herenchuk, K.I. (1973). *Pryroda Ivano-Frankivskoi oblasti.* Vyshcha shkola.
- Herenchuk, K.I. (1978). *Pryroda Chernivetskoj oblasti.* Vyshcha shkola.
- Herenchuk, K.I. (1981). *Pryroda Zakarpatskoj oblasti.* Vyshcha shkola.
- Hill, M. (1979). *TWINSPAN – A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Cornell University, Ithaca.
- Hnylko, O., Krobicki, M., Feldman-Olszewska, A., Iwanczuk, J. (2015). Geology of the volcano-sedimentary complex of the Kamyany Potik Unit on Chyvhyn Mount (Ukrainian Carpathians): preliminary results. *Geological Quarterly, 59 (1)*, 145–156. <http://dx.doi.org/10.7306/gq.1220>
- Hodgetts, N. G., Söderström, L., Blockeel, T. L., Caspari, S., Ignatov, M. S., Konstantinova, N. A., Lockhart, N., Papp, B., Schröck, C., Sim-Sim, M., Bell, D., Bell, N. E., Blom, H. H., Bruggeman-Nannenga, M. A., Brugués, M., Enroth, J., Flatberg, K. I., Garilleti, R., Hedenäs, L., Holyoak, D. T., Hugonnot, V., Kariyawasam, I., Köckinger, H., Kučera, J., Lara, F., Porley, R. D. (2020). An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology, 42 (1)*, 1–116. <https://doi.org/10.1080/03736687.2019.1694329>
- IUSS Working Group WRB. (2015). *World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports № 106.* FAO.
- Klika, J. (1948). *Rostlinna sociologie (Fytocoenologie).* Melantrich.
- Larson, D.W., Matthes, U. & Kelly, P.E. (2000). *Cliff ecology. Pattern and process in cliff ecosystems.* Cambridge University Press.
- Lavergne, S., Thompson, J.D., Garnier, E. & Debussche, M. (2004). The biology and ecology of narrow endemic and wide-spread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos, 107*, 505–518. <https://doi.org/10.1111/j.0030-1299.2004.13423.x>
- MapInfo. (2007). *MapInfo Professional v. 9.5.* Pitney Bowes MapInfo. <https://mapinfo-professional.software.informer.com/9.5/>
- Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Dengler, J., Čarni, A., Šumberová, K., Raus, T., di Pietro, R., Gavilan Garcia, R., Chytrý, M., Yakushenko, D., Schaminée, J.H.J., Bergmeier, E., Santos Guerra, A., Daniëls, F.J.A., Ermakov, N., Valachovic, M., Pignatti, S., Rodwell, J. S., Pallas, J., Capelo, J., Weber, H.E., Lysenko, T., Didukh, Y.P., Capelo, J., Weber, H., Solomesh, A., Dimopolous, P., Aguiar, C., Freitag, H., Hennekens, S.M. & Tichý, L. (2016). Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen and algal communities. *Applied Vegetation Science, 19 (1)*, 3–264. <https://doi.org/10.1111/avsc.12257>
- Onete, M. (2012). Assessment and conservation status of ferns from Buila-Vânturaria National Park. *Oltenia Studii și comunicări Științele Naturii, 28 (2)*, 144–148.
- Pășcuț, C.G. (2018). Phytocoenological study of rocky vegetation from Codru-Moma Mountains based on ecological indices. *Annals of the University of Oradea, Fascicle: Environmental Protection, 30*, 145–156. <https://doi.org/10.5281/zenodo.4362296>
- Peciar, V. (1965). Epiphytische Moosgesellschaften der Slowakei. *Acta Botanica Facultatis Rerum Naturalium Universitatis Comenianae, 12*, 371–471.
- Pigott, C.D. & Walters, S.M. (1954). On the interpretation of the discontinuous distributions shown by certain British species of open habitats. *Journal of Ecology, 42*, 95–116.
- R Core Team. (2021). *R: A language and environment for statistical computing. R Foundation for Statistical Computing.* Vienna, Austria. <https://www.R-project.org/>
- Ragulina, M.E., Orlov, O.L. (2021). Mokhova roslynnist skelnykh vykhodiv lisovogo zakaznyka “Chortova skelya” ta yiyi antropogenna dunamika. *Naukovi Zapysky Derzhavnogo Pryrodnychoho Muzeiu, 37*, 137–142.
- Redžić, S. (Ed.). (2002). *Evaluation of Natural Values of Environment of Brcko District.* Center of ecology and natural resources of the Faculty of Science University of Sarajevo & Counterpart International.
- Rodwell, J.S., Schaminée, J.H.J., Mucina, L., Pignatti, S., Dring, J. & Moss, D. (1998). The Scientific Basis of the EUNIS Habitat Classification. Report to the European Topic Centre on Nature Conservation. Unit of Vegetation Science, Lancaster
- Roleček, J., Tichý, L., Zelený, D. & Chytrý, M. (2009) Modified TWINSPAN Classification in

Which the Hierarchy Respects Cluster Heterogeneity. *Journal of Vegetation Science*, 20, 596–602. <https://doi.org/10.1111/j.1654-1103.2009.01062.x>

Sádlo, J. & Chytrý, M. (2009). Vegetace skal, zdí a stabilizovaných sutí (*Asplenietea trichomanis*). Vegetation of rocks, walls and stable screes. In: Chytrý M. (Ed.). *Vegetace České republiky. 2. Ruderální, plevelová, skalní a sutová vegetace*. Academia.

Speziale, K.L. & Ezcurra, C. (2012). The role of outcrops in the diversity of Patagonian vegetation: Relicts of glacial palaeofloras. *Flora*, 207, 141–149. <https://doi.org/10.1016/j.flora.2011.09.002>

Stodiek, E. (1937). Soziologische und ökologische Untersuchungen an den xerotopen Moosen und Flechten des Muschelkalkes in der Umgebung Jenas. *Repertorium specierum novarum regni vegetabilis. Beiheft*, 99, 1–46.

Ștefureac, T. I. (1941). Cercetări sinecologice și sociologice asupra Bryophytelor din codrul secular Slătioara (Bucovina). *Analele Academiei Române, Memoriile Secțiunii & Ibreve; Științifice*, 3 (16), 1–197.

Świerkosz, K. (2004). Notes on the syntaxonomy of the *Asplenietea trichomanis* class in Poland. *Polish Botanical Journal*, 49(2), 203–213.

Świerkosz, K., Reczyńska, K., Kulpiński, K., Tyc, A. (2011). Udział gatunków obcych w zbiorowiskach z klasy *Asplenietea trichomanis* (Br.-Bl. in Meier & Br.-Bl. 1934) Oberd. 1977 w południowej Polsce. *Acta Botanica Silesiaca*, 6, 97–114.

Świerkosz K., Reczyńska K. (2012). Wapienne ściany skalne ze zbiorowiskami *Potentilletalia caulescentis*. In: W. Mróz (Ed.). *Monitoring siedlisk przyrodniczych. Przewodnik metodyczny*. GIOŚ.

Theurillat, J.-P. & Guisan, A. (2001). Potential impact of climate change on vegetation in the European Alps. *Climatic Change*, 50, 77–109. <https://doi.org/10.1023/A:1010632015572>

Tichý, L. (2002). JUICE, software for vegetation classification. *Journal of Vegetation Science*, 13, 451–453. <https://doi.org/10.1111/j.1654-1103.2002.tb02069.x>

Tichý, L. & Chytrý, M. (2006). Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science*, 17, 809–818. <https://doi.org/10.1111/j.1654-1103.2006.tb02504.x>

Tomaselli, M., Foggi, B., Carbognani, M., Gennai, M., & Petraglia, A. (2019). The rock-face vegetation in the northern Apennines and neighbouring mountain areas, from the coast line to the highest summits. *Phytocoenologia*, 49(1), 7–70. <https://doi.org/10.1127/phyto/2018/0117>

Vadam, J.-C. (1983). Les groupements muscinaux des escarpements et rochers calcaires des environs de Montbéliard (Doubs). *Ann. Sc. Univ. Franche-Comté, Besançon, Biol. Vég.*, 4 (4), 55–96.

Valachovič, M. 1995: *Asplenietea trichomanis* (Br.-Bl. in Meier et Br.-Bl. 1934) Oberd. 1977. In: M.Valachovič (Ed.). *Rastlinné spoločenstvá Slovenska. 1. Pionierskavegetácia*, Veda.

Appendix

Table S1: Geographical references of shady chasmophytic habitat communities in Ukraine.

Tabela S1: Geografski podatki za zasenčene hazmoftske združbe v Ukrajini.

Relevé ID	Date (year/month/day)	Latitude	Longitude	Relevé area (m ²)	Altitude (m)	Aspect (degrees)	Slope (degrees)	Cover total (%)	Cover herb layer (%)	Cover moss layer (%)	Author
1	29.07.2018	49.002238	24.877798	8	263	45	40	90	40	90	BV
2	29.07.2018	49.000647	24.835605	10	283	45	30	80	70	80	ChI
3	28.05.2008	48.496594	27.437630	15	233	180		80	80	30	ChI
4	28.07.2018	49.021633	24.784517	–	287	350	80	60	30	50	DY
5	28.07.2018	49.021633	24.784517	–	287	360	80	80	20	80	DY
6	28.07.2018	49.021633	24.784517	–	287	270	90	70	20	70	DY
7	28.07.2018	49.021633	24.784517	–	287	360	90	70	20	70	DY
8	29.07.2018	48.990813	24.857666	–	307	360	80	80	50	40	DY
9	29.07.2018	48.990813	24.857666	–	307	270	70	50	40	40	DY
10	29.07.2018	48.990813	24.857666	–	247	360	80	90	45	80	DY
11	29.07.2018	49.134067	24.700400	–	232	320	80	60	40	40	DY
12	28.07.2018	49.021633	24.784517	–	284	360	90	70	35	70	DY
13	29.07.2018	48.990813	24.857666	–	247	360	80	85	20	80	DY
14	28.07.2018	49.021308	24.768802	10	273	–	–	80	40	80	ChI
15	12.07.2013	48.529253	24.446425	14	233	45	50	60	60	50	ChI
16	28.07.2018	49.021633	24.784517	–	284	360	80	70	30	70	DY
17	29.07.2018	48.990813	24.857666	12	307	180	60	50	50	10	DY
18	01.08.2018	47.942574	24.115118	10	486	120	90	90	20	50	VI/BO/RG
19	01.08.2018	47.940410	24.111568	10	521	320	90	95	20	55	VI/BO/RG
20	01.08.2018	47.936740	24.104383	10	426	300	90	95	40	55	VI/BO/RG
21	31.07.2018	47.950290	24.091400	10	657	290	87	80	20	60	VI/BO/RG
22	31.07.2018	47.950330	24.090490	10	645	275	90	70	15	55	VI/BO/RG
23	01.08.2018	47.938880	24.109010	10	439	20	90	95	40	55	VI/BO/RG
24	01.08.2018	48.458617	26.103283	–	334	360	80	70	40	40	VI/BO/RG
25	31.07.2018	47.950170	24.089620	10	638	280	20	80	20	60	VI/BO/RG
26	31.07.2018	47.950450	24.083850	10	635	350	90	80	20	60	VI/BO/RG
27	31.07.2018	47.950290	24.090760	10	651	310	85	90	20	70	VI/BO/RG
28	03.08.2019	48.266350	23.634320	10	564	80	5	60	60	0	VI/BO/RG
29	03.08.2019	48.263900	23.629190	10	1014	300	90	60	20	40	VI/BO/RG
30	03.08.2019	48.266880	23.629290	10	598	120	90	60	20	40	VI/BO/RG
31	05.08.2019	48.256430	23.677520	10	827	200	90	80	20	60	VI/BO/RG
32	05.08.2019	48.256550	23.677540	10	807	210	85	80	30	50	VI/BO/RG
33	05.08.2019	48.256430	23.677500	10	846	210	90	80	5	75	VI/BO/RG
34	05.08.2019	48.256430	23.677870	10	842	223	75	70	10	60	VI/BO/RG
35	05.08.2019	48.256970	23.678410	10	835	270	90	60	5	55	VI/BO/RG
36	05.08.2019	48.256300	23.677300	10	840	140	90	70	20	50	VI/BO/RG
37	03.08.2019	48.266350	23.634320	10	557	100	90	80	20	60	VI/BO/RG
38	04.08.2019	48.268990	23.633700	10	565	160	30	80	30	50	VI/BO/RG
39	03.08.2019	48.264850	23.642230	10	754	290	90	80	20	60	VI/BO/RG
40	03.08.2019	48.270900	23.629260	10	602	300	90	70	20	50	VI/BO/RG
41	03.08.2019	48.257540	23.531370	10	536	10	90	60	20	40	VI/BO/RG
42	04.08.2019	48.268970	23.630950	10	547	270	90	90	20	70	VI/BO/RG
43	04.08.2019	48.269050	23.633440	10	547	250	87	95	10	85	VI/BO/RG
44	04.08.2019	48.276870	23.640530	10	557	140	90	90	10	80	VI/BO/RG
45	05.08.2019	48.268910	23.633920	10	519	240	90	80	2	78	VI/BO/RG
46	03.08.2019	48.267120	23.629600	10	574	40	45	60	20	40	VI/BO/RG

Acronyms:

BV – Budzhak Vasyl, ChI – Chorney Illia, DY – Didukh Yakiv, VI – Vasheniak Iuliia, BO – Bezmertna Olesya, RG – Gleb Ruslan

1 – *Isoetecium alopecuroides*-*Polystichum braunii* community, 2 – *Porella platyphylla*-*Asplenium ruta-muraria* community, 3 – *Pseudanomodon attenuatus*-*Chrysosplenium alternifolium* community, 4 – *Pedinophyllum interruptum*-*Polystichum aculeatum* community

Taxa that rarely occurred in the table

Vascular plants:

Acer pseudoplatanus (11:+; 34:+), *Aruncus dioicus* (28:4), *Asplenium viride* (9:1; 11:+), *Athyrium filix-femina* (4:+; 11:+; 27:+), *Atropa bella-donna* (14:+; 24:1; 25:+), *Bromopsis* sp. (13:+), *Campanula persicifolia* (12:1; 28:+), *Carex digitata* (36:r; 38:r), *Carex* sp. (12:+; 13:+), *Circaea lutetiana* (27:2), *Corylus avellana* (25:1), *Daphne mezereum* (9:1), *Dentaria glandulosa* (2:+; 4:+), *Dryopteris carthusiana* (4:+), *D. expansa* (6:1), *Epipactis helleborine* (17:+), *Equisetum palustre* (43:r), *Euonymus europaea* (27:3), *E. verrucosa* (38:3; 45:3), *Fraxinus excelsior* (17:+), *Galium aparine* (31:+), *G. odoratum* (6:+; 21:+; 26:r), *Gentiana asclepiadea* (25:+), *Geranium lucidum* (44:5), *Glechoma hederacea* (28:+), *Hieracium murorum* subsp. *sylvularum* (31:+), *Impatiens noli-tangere* (13:1; 17:1), *Luzula luzuloides* (6:+), *Maianthemum bifolium* (9:+), *Melandrium dioicum* (21:+), *Melica picta* (17:+), *M. uniflora* (15:+), *Melittis melissophyllum* subsp. *carpatica* (9:+), *Orthilia secunda* (9:+),

Oxalis acetosella (6:1; 18:1; 36:3), *Paris quadrifolia* (18:+; 26:r), *Phegopteris connectilis* (6:+), *Pilosella echiooides* (16:1; 29:+), *Polygonatum multiflorum* (17:+), *Prenanthes purpurea* (9:+), *Quercus robur* (10:r), *Rosa pendulina* (9:+), *Seseli libanotis* (12:+; 17:+; 23:+), *Silene* sp. (17:+; 23:+), *Solidago virgaurea* (36:1; 38:1), *Sorbus aucuparia* (10:+), *Stachys sylvatica* (11:+; 12:+), *Symphytum cordatum* (27:1), *Tilia cordata* (5:+), *Ulmus glabra* (41:+), *Valerianella dentata* (16:1; 29:1), *Vincetoxicum hirundinaria* (17:+; 23:+), *Viola riviniana* (15:+).

Cryptogam species:

Atrichum undulatum (6:1), *Brachythecium rivulare* (6:1; 7:3) *B. rutabulum* (30:1), *B. salebrosum* (7:3), *Campyliadelphus chrysophyllus* (29:1), *Campylophyllopsis calcarea* (37:1), *Cololejeunea rossetina* (29:+), *Conocephalum conicum* (18:+), *Dicranum scoparium* (9:3), *Ditrichum flexicaule* (10:1), *Eurhynchium angustirete* (7:+), *Homalothecium lutescens* (11:+; 12:+; 37:3), *Hypnum cupressiforme* (6:1; 10:2), *Lejeunea cavifolia* (14:+; 28:+), *Lescurea incurvata* (13:+; 17:+), *Leucodon sciuroides* (10:+; 12:+), *Lophocolea bidentata* (29:+), *Mannia fragrans* (39:1), *Metzgeria furcata* (2:r), *M. pubescens* (14:+), *Plagiomnium rostratum* (14:+), *Polytrichum* sp. (27:1), *Porella arboris-vitae* (28:2), *Ptychostomum capillare* (17:+), *Rhizomnium punctatum* (1:5; 3:+; 30:5), *Sciuro-hypnum populeum* (39:1), *Thuidium recognitum* (2:+; 7:1), *Tortella tortuosa* (11:+; 17:+).

Table S3: Impact of threats and sociological assessment of the shady chasmophytic communities.

Tabela S3: Vpliv groženj in sociološka ocena za zasenčene hazmofitske združbe.

Cluster ID	UkrBiotop (2011)	National Habitat Catalogue (2018)	Natura 2000	EUNIS	1	2	3	4	Sum of the threats	Stability, %	Class	5	6	7	8	9	10	11	12	13	14	Sum of the sociological assessment	Value, %	Class
1	H2.114	K5.2	8210	H3.252	2	2	2	4	10	66.77	II	4	4	4	4	4	4	4	3	1	2	34	79.95	II
2	H2.114	K5.2	8210	H3.252	2	2	2	4	10	66.77	II	4	4	4	4	4	4	4	3	1	2	34	79.95	II
3	H2.114	K5.2	8210	H3.252	3	2	2	4	11	77.88	II	4	4	4	4	4	4	4	3	1	2	34	79.95	II
4	H2.114	K5.2	8210	H3.252	3	2	2	4	11	77.88	II	4	4	4	4	4	4	4	3	1	2	34	79.95	II

1 – *Isoetecium alopecuroides*-*Polystichum braunii* community, 2 – *Porella platyphylla*-*Asplenium ruta-muraria* community, 3 – *Pseudanomodon attenuatus*-*Chrysosplenium alternifolium* community, 4 – *Pedinophyllum interruptum*-*Polystichum aculeatum* community.

1 – results of threats' impact; 2 – scale of the negative impact; 3 – degree of the negative influence of external factors; 4 – degree and speed of recovery (plastic, dynamic stability); 5 – position in the successional series is the final steady climax and subclimax stages; 6 – regional representativity; 7 – nature of the distribution; 8 – ecological amplitude (scales); 9 – environmental parameters of distribution; 10 – presence of invasive species; 11 – degree of hemerobity, 12 – ratio of species between strategy types stress-tolerant/expellerant species; 13 – sociological significance; 14 – synsociological state.

Table S4: Categorization of habitat characteristics for assessing the impact of threats and sociological assessment (Didukh et al., 2018)
Tabela S4: Kategorije habitatnih značilnosti za oceno vpliva groženj in sociološko oceno.

Name of the factor	Impact of threats			
	Category			
	4	3	2	1
Results of the threats' impact	(EX) damaged habitats; (CR) habitats under critical threat of extinction	(EN) endangered habitats	(VU) vulnerable habitats	(TC) habitats that are not threatened with extinction
Scale of the negative impact	General (global)	Regional	Local	Absent negative impact
Degree of the negative influence of external factors	Very powerful (destructive), destroyed completely, and recovers from pioneer stages	Significant, the structure of dominants is changing	Moderate, changing species composition	Changes are invisible, or biotopes are formed under the direct influence of an anthropogenic factor
Degree and speed of recovery (plastic, dynamic stability)	Very weak (more than 100 years)	Weak (more than 10 years)	Tolerable (more than 15 years)	Good (several years)
Sociological assessment				
The position in the successional series is the final steady climax and subclimax stages	Permanent climax and sub-climax stages	Long-term stages of endoecogenesis affecting change in the microclimate and soil	Medium-term serial syngenetic stages that do not affect change in soil and microclimate characteristics	Pioneer and short-term stages
Regional representativity	Spread within one or two geobotanical regions or districts	Spread within one geobotanical province	Spread within one geobotanical area or geographical zone	Spread within several geobotanical area or geographical zones
Nature of the distribution	Some small localities are known	Habitat has disjunctive distribution	Habitat is sporadically spread on the border of its area	Habitat is usually spread within its area
Ecological amplitude (scales)	Narrow amplitude (less than 5%) of all environmental factors	Narrow amplitude (less than 5%) for one environmental factor; and the amplitude is less than 10% for other environmental factors	Wider amplitude (less than 10%) of more than one environmental factors	Wide amplitude (more than 10%) of all environmental factors
Environmental parameters of distribution	Specific, extreme environmental conditions	Narrow distribution of rare habitat	Sporadical distribution within optimal conditions	Common distribution within optimal conditions
Presence of invasive species	Absence of invasive species	Presence of invasive species	Presence of invasive species as diagnostic species with high constancy	Invasive species are dominant in the habitat
Degree of hemerobity	Ahemerobic and oligohemerobic habitats (ha less than 25)	Mesoheerobia habitats (ha=25–50)	Euheerobia habitats (ha=50–75)	Polyheerobic and metaheerobic habitats (more than 75)
Ratio of species between strategy types stress-tolerant / expellerant species	More than 1.7	1.2–1.7	0.7–1.2	Less than 0.7
Sociological significance	Presence or dominance of CR, EN species or a large number of red-listed species	Dominant species are VU, LC, DD categories or red-listed species	Presence of VU, LC, DD species, or a couple of red-listed species	Absence of rare species
SYnsociological estate	Habitat listed in Resolution 4 of the Bern Convention, Habitat Directive and in the Green Book of Ukraine	Habitat is listed in the Green Book of Ukraine	Habitat is listed in Resolution 4 of the Bern Convention, Habitat Directive	Habitat is not listed and not protected