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TO THE BRYOPHYTE FLORA OF COMMUNITIES OF STEPPES AND STEPPE SCRUBS IN THE BASHKIR CIS-URALS (THE SOUTHERN URALS REGION)

К БРИОФЛОРЕ СООБЩЕСТВ СТЕПНЫХ КУСТАРНИКОВ И СТЕПЕЙ БАШКИРСКОГО ПРЕДУРАЛЬЯ (ЮЖНО-УРАЛЬСКИЙ РЕГИОН)

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Abstract

57 bryophyte species (3 liverworts and 54 mosses) are revealed within communities of steppe scrubs and steppes in the Bashkir Cis-Urals (the Republic of Bashkortostan). The list of species annotated with occurrences in the steppe shrublands, meadow steppes, genuine dry steppes and stony (petrophytic) steppes is provided. Results of the ecological analysis of bryophyte flora are discussed.

Резюме

В сообществах степей и степных кустарников Башкирского Предуралья (Республика Башкортостан) выявлено 57 видов мохообразных (3 печеночника и 54 мха). Дан список видов с указанием встречаемости в сообществах степных кустарников, луговых степей, настоящих сухих степей и петрофитных степей. Обсуждаются результаты экологического анализа бриофлоры.

KEYWORDS: mosses, hepatics, steppe, Ural Mts., rare species

INTRODUCTION

Steppes have a high economical and conservational value around the world and are recognized as vulnerable ecosystems dramatically degraded due to the human impact during the last centuries (Smelansky & Tishkov, 2012; Hurka *et al*., 2019). Steppes of the Bashkir Cis-Urals are no exception. The agricultural development of the territory is very high. The overgrazing, recreation and other adverse environmental impacts led to fragmentation of steppe communities which remained mostly in habitats unsuitable for plowing (Yamalov *et al*., 2012).

Despite this, the steppe vegetation of the Bashkir Cis-Urals is characterized by high diversity. It depends on several regional factors: complex topography, numerous sandstone and lime outcrops, and unique geographic position between Europe and Asia. According to a European system of floristic classification of vegetation (Mucina *et al*., 2016), the steppe shrublands of the Bashkir Cis-Urals belong to the alliance ***Prunion fruticosae*** Tx. 1952 (the order ***Prunetalia spinosae*** Tx.1952, the class ***Crataego-Prunetea*** Tx. 1962), whereas grass communities are included in the orders ***Brachypodietalia pinnati*** Korneck 1974, ***Helictotricho-Stipetalia*** Toman 1969 and ***Tanaceto achilleifolii-Stipetalia lessingianae*** Lysenko et Mucina in Mucina et al. 2016 of the class ***Festuco-Brometea*** Br.-Bl. et Tx. ex Soy 1947, which combines genuine bunchgrass and forbs-bunchgrass steppes, meadow steppes, stony (petrophytic) steppes, as well as different types of human-modified steppe communities.

The earliest information on the bryophyte species found in steppes of the Bashkir Cis-Urals dates to the first half of the 20th century (Podpera, 1921; Bachurina, 1946). Later, some species were reported in the framework of syntaxonomical investigations conducted in several nature protected areas (Mirkin, 2010; Melentyev & Martynenko, 2014; Mirkin & Martynenko, 2018). Nevertheless, bryophyte flora in the steppe communities of the Bashkir Cis-Urals was still relatively unexplored.

The present study is aimed to record and analyze data on the bryophyte composition in different types of steppe scrub and steppe communities in the Bashkir Cis-Urals.

MATERIALS AND METHODS

The study was conducted in the forest-steppe zone of the Bashkir Cis-Urals. It is the south-eastern part of the East European Plain bordering the western foothills of the Southern Urals. According to zonation of Eurasian steppe (Lavrenko, 1970), the study area is located within East European forest-steppe and Transvolga-Kazakhstan steppe provinces of the Black Sea-Kazakhstan subregion. The terrain of the study area is a gently sloping and hilly plain with an average elevation of about 200–300 m a.s.l. The climate is continental with short warm summers and long and moderately cold winters. The average temperature ranges from +2.5 to +3.5°C, while the sum of effective temperatures during the growing period varies from 1900 to 2350°C. The average annual precipitation is 450–500 mm, while Selyaninov's geothermal coefficient is 0.8–1.4 (Yaparov, 2005).

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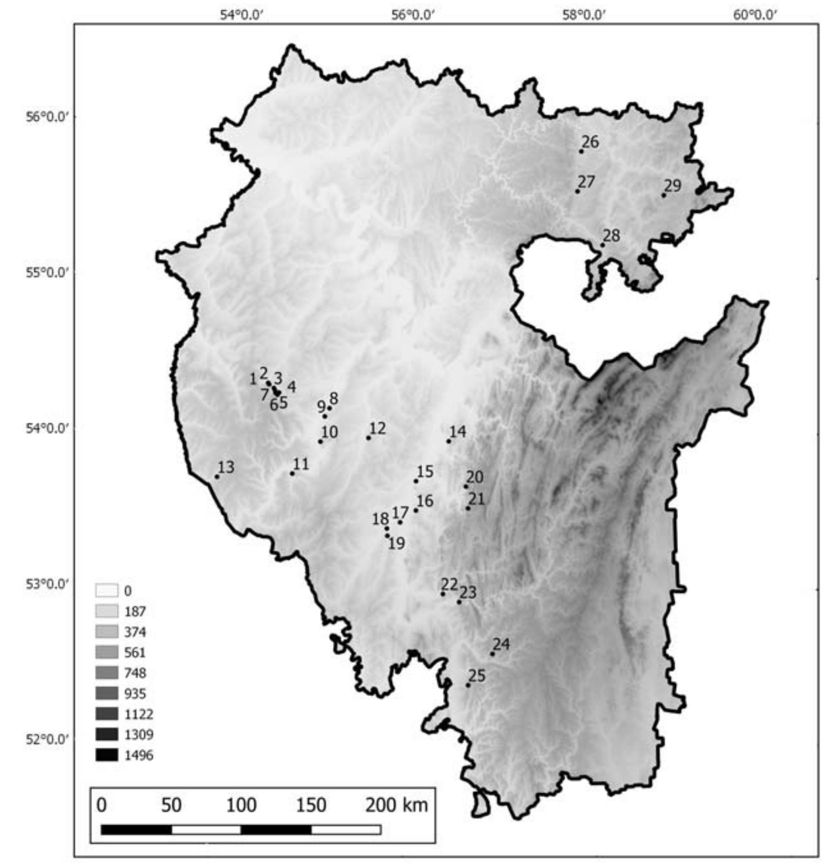

Fig. 1. Collecting localities.

1. Davlekanovskiy district, 1.7 km N from Kidryachevo Village. 54.34458°N, 54.46802°E. Alt 307 m.
2. Buzdyakskiy district, 2.5 km S from Kanly-Turkeevo village. 54.35433°N, 54.45663°E. Alt 307 m.
3. Davlekanovskiy district, 2.5 km SE from Chapaevo village. 54.32253°N, 54.52072°E. Alt 210 m.
4. Davlekanovskiy district, 1.8 km NE from Burangulovo village. 54.30866°N, 54.53380°E. Alt 250 m.
5. Davlekanovskiy district, vicinity of the southern shore of Aslykul' Lake. 0.5 km W from Yangi-Turmush village. 54.29416°N, 54.58008°E. Alt 258 m.
6. Davlekanovskiy district, 4 km W from Alga village. 54.28047°N, 54.56258°E. Alt 341 m.
7. Davlekanovskiy district, 2 km E from Burangulovo village. 54.29158°N, 54.54111°E. Alt 333 m.
8. Davlekanovskiy district, vicinity of Sokolovka village. 54.20371°N, 55.13887°E. Alt 120 m. (Bachurina, 1946).
9. Davlekanovskiy district, 1 km E from Dyurtyuli village. Yaryshtau Mt. 54.14985°N, 55.09035°E. Alt 240 m.
10. Alsheevskiy district, 3 km SE from Churaevo village. Susaktau Hill. 53.98671°N, 55.04979°E. Alt 265 m.
11. Miyakinskiy district, Vicinity of Miyakitamak village. 53.77556°N, 54.75306°E. Alt 150 m.
12. Aurgazinskiy district, 2.5 km E from Turumbet village. 54.01793°N, 55.57447°E. Alt 230 m.
13. Bizhbulyakskiy district, 2.5 km E from Muradymovo village. 53.73675°N, 53.93802°E. Alt 250 m.
14. Gafuriyskiy district, 4.5 km NE from Tabynskoye village. Voskresenka Mt. 54.00333°N, 56.45122°E. Alt 202 m.
15. Sterlitamakskiy district, 2 km N from Belskoye village. Yuraktau Mt. 53.74461°N, 56.09919°E. Alt 130 m.
16. Ishimbayskiy district, 3 km NE from Urman-Bishkadak village. Tratau Mt. 53.55516°N, 56.10150°E. Alt 372 m.
17. Sterlitamakskiy district, vicinity of Vasilyevka village. 53.47749°N, 55.93300°E. Alt 150 m. (Bachurina, 1946).
18. Sterlitamakskiy district, vicinity of Ayuchevo village. 53.43625°N, 55.79115°E. Alt 140 m. (Bachurina, 1946).
19. Sterlitamakskiy district, vicinity of Murdashevo village. 53.38934°N, 55.79873°E. Alt 170 m. (Bachurina, 1946).
20. Ishimbayskiy district, 3 km NE from Sargaevo village. Ilisyntash Mt. 53.71197°N, 56.64138°E. Alt 380 m.
21. Ishimbayskiy district, 7 km E from Gumerovo village. 53.57160°N, 56.66503°E. Alt 600 m.
22. Meleuzovskiy district, 1.5 km NE from Zirikovo village. 53.01855°N, 56.40083°E. Alt 390 m.
23. Kugarchinskiy district, 4.5 NE from Nizhnebikkuzino village. 52.96723°N, 56.57630°E. Alt 420 m.
24. Kugarchinskiy district, 5 km NE from Bogdashkino village.52.63348°N, 56.93153°E. Alt 510 m.
25. Kugarchinskiy district, 5 km E from Kugarchi settlement. 52.43123°N, 56.67502°E. Alt 467 m.
26. Duvanskiy district, Northern vicinity of Yaroslavka village. Gladkaya Mt. 55.86929°N, 57.94363°E. Alt 340 m.
27. Duvanskiy district, 3.5 km SE from Elantub village. 55.61203°N, 57.89372°E. Alt 270 m.
28. Salavatskiy district, 1 km E from Iltaevo village. Kantuntau Mt. 55.26328°N, 58.16812°E. Alt 370 m.
29. Belokatayskiy district, 3.5 km S from Maygaza village. 55.57607°N, 58.8731°E. Alt 350 m.

The present publication is based on the identification of bryophytes collected in 2006–2020 within steppe communities located in fourteen districts of the Republic of Bashkortostan, including the territories that are key objects of the projected Geopark "Toratau" nominated for inclusion in the UNESCO Global Geoparks Network.

Most of the specimens were collected from different habitat niches, i. e. soil, rock substrates, decaying wood, bark of shrubs, *etc.* within 100 m^2 sample plots of geobotanical relevés. In total, bryophyte diversity was recorded for 134 geobotanical relevés, including 42 sample plots located in meadow steppes, 24 – in true dry steppes, 57 – in petrophytic variants of both meadow and dry steppes, and 11 – in steppe scrub communities. The species which could be easily recognized were recorded in the field, while the other specimens were collected for identifying in the laboratory. Some specimens were collected during floristic observations, and their labels were provided with short description of habitats. Also, literature sources were considered.

In total, about 500 specimens of bryophytes were studied. The species were identified with the microscopes Olympus CX31 and Al'tami SPM0880 using the traditional anatomical-morphological method. Specimens are kept in the Herbarium of the Ufa Institute of Biology of Ufa Research Centre of RAS (UFA). The nomenclature of species follows "An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus" (Hodgetts *et al*., 2020).

The data on bryophyte diversity within steppes and steppe shrublands of the study area are provided for localities listed in Fig.1.

Results

The study was conducted within different vegetation types. Steppe scrub communities dominated by *Caragana frutex* (L.) K. Koch, *Spiraea crenata* L., *Spiraea hypericifolia* L., *Prunus tenella* Batsch (syn. *Amygdalus nana* L.), *Prunus fruticosa* Pall. (Fig. 2 A) occur in the small hollows and on the slopes of different steepness and exposures across all study area. These communities present the order ***Prunetalia spinosae***, and their bryophyte composition was investigated in localities 14-16, 20, 21 (Fig. 1).

The meadow steppes of the order ***Brachypodietalia pinnati*** usually occur in relatively small and not so extremly dry sites on gentle slopes (< 20°) or near foot of northern slopes (Fig. 2 C). The floristic composition of these communities includes *Stipa pulcherrima* K. Koch, *Stipa pennata* L., *Adonis vernalis* L., *Campanula sibirica* L., *Galium verum* L., *Veronica spicata* L., *Thalictrum minus* L., *Trifolium montanum* L., *Fragaria viridis* Weston (Fig. 2 B) These steppes were explored in localities 1-8, 11-19, 21-29 (Fig. 1).

Genuine (true) dry steppes with *Helictotrichon desertorum* (Less.) Pilg., *Festuca valesiaca* Schleich. ex Gaudin, *Carex supina* Willd. ex Wahlenb., *Euphorbia caesia* Kar. & Kir. (Fig. 2 C) belong to the order ***Helictotricho-Stipetalia*** and usually cover dry plain surfaces and gentle southern and east-southern slopes of hills. These communities were studied in localities 1-7, 9, 10, 14–16 (Fig. 1).

The petrophytic variants of meadow and genuine dry steppes (Fig. 2 D, E) occupy steep southern and eastern slopes (>30–40°) with stony soils and different bedrock types including chalks, gypsum, limestones and sandstones (localities 2–6, 9, 10, 13–16, 20–23, 26, 27). The projective cover of stones within these habitats may reach up to 80 %. Such typical for dry steppe species as *Stipa lessingiana* Trin. & Rupr., *Kochia prostrata* (L.) Schrad., *Stipa sareptana* Beck and petrophytes (*Hedysarum razoumovianum* DC, *Artemisia salsoloides* Willd., and *Orostachys spinosa* (L.) Sweet) usually grow there.

Semi-arid steppe communities of the order ***Tanaceto achilleifolii-Stipetalia lessingianae*** are rare in the study area, and their bryophyte diversity was not investigated.

The list of species annotated with occurrences in the different community types is provided (Table 1).

The bryophyte flora of investigated steppes and steppe shrublands includes 57 species (3 liverworts and 54 mosses). To determine the differences between bryophyte compositions of studied communities, an ecological analysis was conducted. The proportions of taxa with different life strategies, life forms, ecological groups associated with different habitat and vegetation types, as well as in relation to water regime and light are presented as a share (in percentage terms) of the total number of species recorded in each type of community (Table 2). The assessment of ecological groups was based on expert knowledge of the habitat preferences of each species in the Southern Urals region.

Discussion

The diversity of bryophytes in steppes of the study area (57 species) is lower than bryophyte richness in steppes of the Central Russian Upland (80 species) (Popova, 2019), but similar with data on similar vegetation described in other regions of Russia, i. e. the Republic of Altay (47 species) (Pisarenko & Korolyuk, 2003), the Bashkir Trans-Urals (42 species) (Aznabayeva & Baisheva, 2017), south-western shore of Baikal Lake (62 species) (Prelovskaya, 2012). In the more restricted areas, i. e. Orenburg State Nature Reserve, the number of bryophytes growing in steppe communities was even lower (24 moss species) (Afonina *et al*., 2006).

The number of bryophytes revealed in different types of communities is from 16 to 35 species, being the richest, as expected, in the petrophyte steppes (Table 1). In the Urals, these communities have a high level of floristic and phytocoenotic diversity (Korolyuk *et al*., 2018). In the Central Russian Upland, the bryophyte flora of meadow petrophyte steppes with limestone and chalk outcrops was also highest compared to other types of steppes and consists of 46-50 species (Popova, 2019).

In studied communities, the bryophytes were found mainly on rocks or soil. 22 species are terrestrial (e.g.

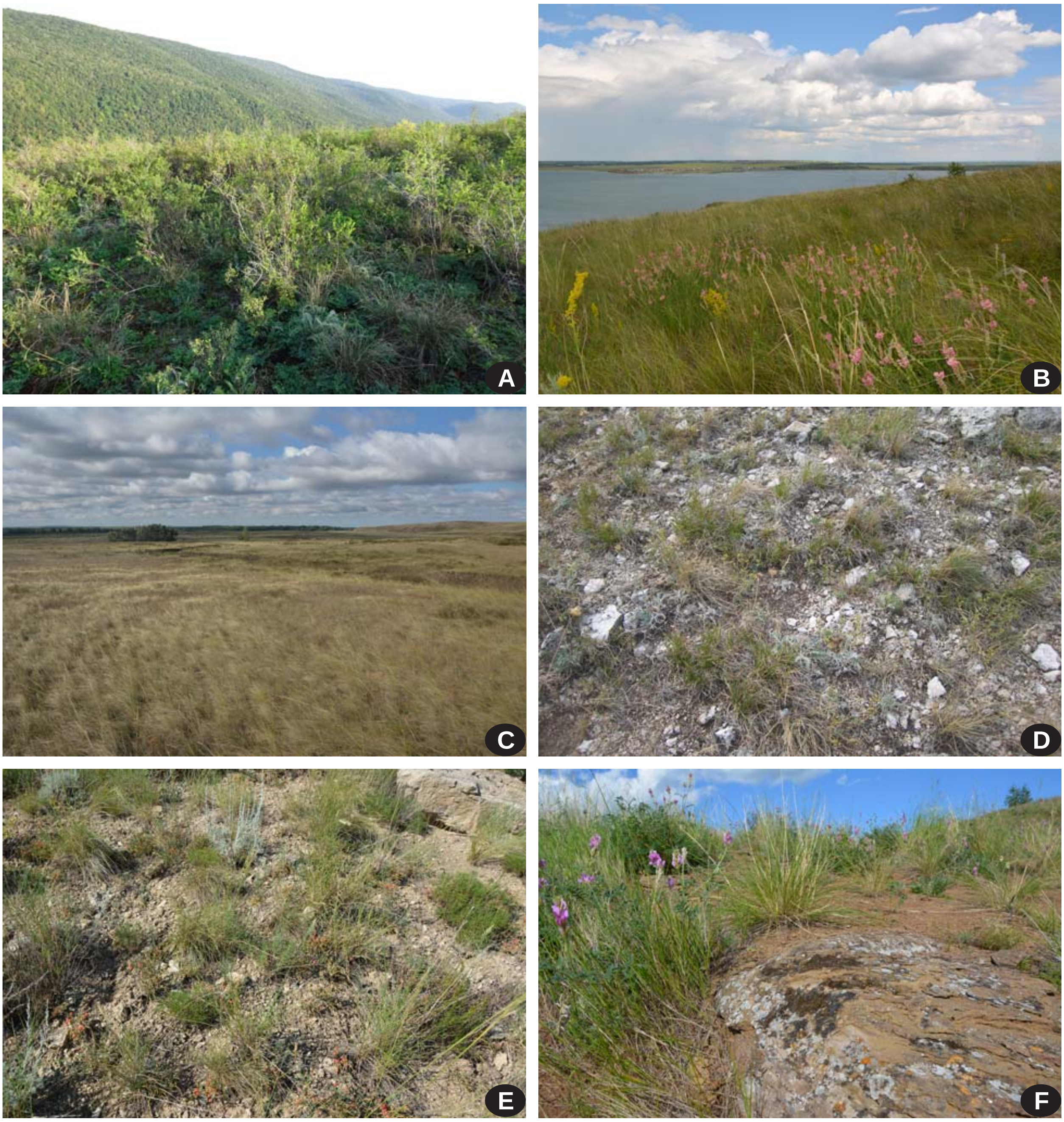

Fig. 2. Vegetation of steppe shrublands and steppes in the Bashkir Cise-Urals (photos of Baisheva). A: steppe scrub communities, habitat of *Dicranum dispersum* on the top of Ilisyntash Mt.; B: meadow steppe; C: true dry steppe; D, E: stony steppes; F: habitat of *Grimmia plagiopodia* and *Jaffueliobryum latifolium* near the southern shore of Aslykul' Lake.

Pterygoneurum ovatum, P. subsessile, Weissia brachycarpa), 26 species are saxicolous and grow on rock outcrops and boulders (e.g. *Grimmia spp., Schistidium spp., Syntrichia intermedia*), and 9 species were found on both substrates (e.g. *Abietinella abietina, Brachythecium albicans, Syntrichia ruralis*). Obligate epilithic species have the larger representation in stony steppes and steppe scrub communities (45–50 % of total species number within vegetation type) (Table 2).

Human and animal disturbances are common and typical for steppe ecosystems, particularly grazing and fire (Smelansky & Tishkov, 2012). The effect of grazing and recreation is more evident in terrestrial bryophyte communities, whereas saxicolous communities are rarely affected by these disturbance factors (McIntosh, 1986). To reflect the response of bryophyte composition towards different environmental conditions, we used the system of bryophyte life strategies including the seven main categories distinguished at present (e.g., annual shuttle species, colonists, fugitives, geophytes, perennial shuttle species, perennial stayers, short-lived shuttle species) (Kürschner & Frey, 2012).

Table 1. Bryophyte composition of steppe scrub and steppe communities in the Bashkir Cis-Urals (Republic of Bashkortostan).

Community types	I	II	III	IV	LS	Localities
			Liverworts			
Lophocolea minor	Rar				PSs,as	15
Mannia fragrans	Rar			Rar	PaS	15, 22
Porella platyphylla				Rar	PeS	15
			Mosses			
Abietinella abietina		Com	Com	Sp	PSm	
Aloina rigida				Rar	Cs	6
Barbula unguiculata				Rar	Cs	2
Brachytheciastrum velutinum		Rar			PSs	14
Brachythecium albicans	Com	Sp		Sp	PSm	
Brachythecium campestre	Rar	Rar	Rar	Rar	PSm	
Brachythecium capillaceum				Rar	PSs	14
Brachythecium glareosum			Rar	Rar	PSm	15
Brachythecium laetum				Rar	PSm	15
Bryoerythrophyllum recurvirostrum	Rar				Cs	15
Bryum argenteum			Com	Com	Cs	
Buckia vaucheri			Sp	Sp	PSm	
Campyliadelphus chrysophyllus	Rar	Sp	Sp		PSs	
Ceratodon purpureus		Com	Com	Sp	Cs	
Didymodon rigidulus		Rar			Cas	4
Dicranum dispersum	Rar				PSm	20
Encalypta ciliata		Rar			PeS	5
Encalypta rhaptocarpa			Sp		PeS	
Encalypta vulgaris		Sp		Sp	PeS	
Eurhynchiastrum pulchellum		Sp		Sp	PSm	
Flexitrichum flexicaule		Sp			PSm	
Grimmia anodon				Rar	Cpa	6, 15, 16
Grimmia plagiopodia			Rar	Rar	Cpa	5, 7, 9
Grimmia teretinervis				Rar	PSm	2
Homomallium incurvatum		Rar			PSs	5
Hypnum cupressiforme			Sp	Sp	PSm	
Jaffueliobryum latifolium			Rar		Cs	5
Orthotrichum anomalum	Rar			Sp	Cpa	
Pleuridium subulatum		Rar			PaS	17
Polytrichum juniperinum		Rar			PSs	24
Pseudoamblystegium subtile				Rar	PSs,as	15
Pseudoleskeella catenulata	Sp	Sp		Sp	PSm	
Pseudoleskeella nervosa	Sp				PSs,as	
Pseudoleskeella tectorum				Sp	PSm	
Pterygoneurum kozlovii				Rar	PaS	5
Pterygoneurum ovatum			Sp	Sp	PaS	
Pterygoneurum subsessile			Sp	Sp	PaS	
Ptychostomum creberrimum				Rar	Cs	15
Ptychostomum imbricatulum		Sp	Com	Sp	Cs	
Ptychostomum moravicum				Rar	Cas	14, 15
Rhytidium rugosum		Sp		Sp	PSm	
Schistidium apocarpum				Rar	Cpa	6
Schistidium submuticum	Sp			Sp	Cpa	
Sciuro-hypnum reflexum			Rar		PSs	4
Syntrichia caninervis			Sp	Sp	PSm	
Syntrichia montana	Rar				PSm	20
Syntrichia ruralis	Sp	Sp	Com	Com	PSm	
Tortella tortuosa	Sp		Sp	Sp	PSm	
Tortula acaulon	Rar	Rar	Rar		AnS	11, 14
Tortula muralis		Rar			Cs	8
Tortula protobryoides	Rar		Rar		PeS	19
Tortula truncata			Rar		PaS	17
Weissia brachycarpa			Rar		Cpa	18, 19
Weissia longifolia			Rar		Cs	11, 17
Total number of species	16	20	23	35		

Explanations: Community types: I = steppe scrub communities; II = meadow steppes; III = genuine dry steppes; IV = stony steppes. The indices in columns are occurrence calculated for each species per community type according to the following scale: Rar = rare (1-3 localities), Sp = sporadic (4-15 localities); Com = common (>15 localities). LS – life strategy: AnS = annual shuttle species, PaS = short-lived shuttle species, PeS = perennial shuttle species, Cs = colonists with sexual reproduction, Cas = colonists with high asexual reproductive effort, Cpa = pauciennial colonists, PSm = perennial stayers with moderate or rare reproductive effort, PSs = perennial stayers with sexual reproduction, PSs,as = perennial stayers with sexual and asexual reproduction. Localities according to Fig. 1 are indicated for species with rare occurrences within studied communities.

Table 2. Ecological structure of bryophyte composition of steppe shrubland and steppe communities in the Bashkir Cis-Urals, Republic of Bashkortostan, Russia. I = steppe scrub communities; II = meadow steppes; III = genuine dry steppes; IV = stony steppes.

Community types	I	II	III	IV
Floristic indices			Scores (%)	
Substrate groupes				
Saxicolous species	50.0	35	21.7	45.7
Species found on both rock and soil substrates	12.5	35	26.1	22.9
Terrestrial species	37.5	30	52.2	31.4
Life strategies				
Annual and short-lived shuttle species (AnS+Pas)	12.5	10	17.4	11.3
Perennial shuttle species (PeS)	6.2	10	8.7	5.7
Colonists with sexual reproduction (Cs)	6.2	15	21.7	17.1
Colonists with high asexual reproductive effort (Cas)	-	5	-	2.9
Pauciennial colonists (Cpa)	12.5	-	8.7	14.3
Perennial stayers with moderate or rare reproductive effort (PSm)	43.8	40	34.8	42.9
Perennial stayers with sexual reproduction (PSs)	6.3	20	8.7	2.9
Perennial stayers with sexual and asexual reproduction (PSs,as)	12.5	-	-	2.9
Life forms				
Cushions	18.7	15	13	25.6
Turfs (short turfs +tall turfs)	31.2	50	56.6	34.3
Mats	37.5	25	21.7	34.3
Wefts	6.3	10	8.7	2.9
Thalloid mats	6.3	-	-	2.9
Species associated with different habitat and vegetation types				
Petrophytic steppe and forest-steppe species	12.5	15	17.4	17.1
Petrophytic forest species	12.5	20	8.6	17.1
Petrophytic species growing in different vegetation types	6.3	5	-	5.7
Steppe species	31.3	15	43.6	22.9
Forest-steppe species	18.7	15	8.7	11.4
Forest species	18.7	5	4.3	11.4
Eurytopic species	-	25	17.4	14.3
Ecological groups of species in relation to water regime				
Xerophytes	50.0	40	52.2	40.0
Xero-Mesophytes	43.8	30	34.8	31.4
Mesophytes	6.2	10	-	11.4
Indifferent to water regime species	-	20	13.0	17.2
Ecological groups of species in relation to light				
Heliophytes	56.2	55	65.2	40.0
Helio-Sciophytes	37.6	40	26.1	48.6
Light and shade tolerant species	6.2	5	8.7	11.4

In bryophytes, tolerance and avoidance of environmental stress are two main alternative possibilities to survive within a plant community (Kürschner & Frey, 2012). The dominance of bryophytes within some unproductive habitats of low biomass (for instance, bogs or rock outcrops) is related not any exceptional ability to monopolize resource capture in competition with neighbours; rather they have assumed dominance slowly through the capacity to retain and protect captured resources (Grime *et al.*, 1990).

The species with such types of strategies as annual shuttles (AnS), fugitives (F) and geophytes (G) follow an avoidance strategy, while other species seem to be following tolerance strategy (Kürschner & Frey, 2012). The species with strategies fugitives and geophytes were absent in studied communities. Shuttle species have large spores (>25 µm in diameter) and are typical for unstable habitats with the disturbed ground (During 1979; Kürschner & Frey, 2012). The proportion of annual and short-lived shuttle species (e.g. *Tortula acaulon, Pterygoneu-*

ron spp.) is significant only in genuine dry steppes, subject to grazing (26%). Perennial shuttle species (e.g. *Encalypta vulgaris, Tortula protobryoides*) are not numerous. In total, the proportion of species with shuttle strategy varies from 17 to 26 %, being lowest in petrophyte steppes and communities of steppe scrubs (Table 2).

Colonists are mainly pioneer species able to colonize a new substrate. They dominate sites during primary successional stages and also can often be seen as an indicator of disturbance (Kürschner & Frey, 2012). The proportion of colonists is highest in genuine dry steppes (30 %) and petrophyte steppes (34 %). This strategy includes both terrestrial (*Aloina rigida, Bryum argenteum, Ceratodon purpureus, Ptychostomum creberrimum, Jaffueliobryum latifolium*) and saxicolous (*Bryoerythrophyllum recurvirostrum, Grimmia anodon, Schistidium submuticum*) bryophytes (Tables 1, 2).

Species with perennial stayers strategy (*Brachythecium laetum, Buckia vaucheri, Dicranum dispersum, Eurhynchiastrum pulchellum, Pseudoleskeella catenulata, Syntrichia ruralis, Tortella tortuosa*) have a significant presence in all communities. Their proportion is maximal in meadow steppes and steppe scrub communities (60-62 %), and minimal in genuine dry steppes (43 %) (Table 2). These species are most frequent in long-lasting habitats under more or less constant environmental conditions, but also can tolerate environmental stress (Kürschner & Frey, 2012).

The range of life-forms of revealed bryophytes is not wide. The proportion of acrocarpous bryophytes with life-forms cushions (mostly saxicolous species – *Orthotrichum anomalum, Schistidium spp., Grimmia spp*.) and turfs (terrestrial species *Aloina rigida, Ceratodon purpureus, Bryum argenteum, Encalypta spp., Ptychostomum spp*.) ranges from 49 to 69 %, being highest in genuine dry steppes and lowest in steppe scrub communities. Mat-forming species (e.g. *Brachythecium spp., Pseudoleskeella spp., Homomallium incurvatum*) are also prominent (21-37 %) (Table 2). Species with life-forms of weft (e.g. *Abietinella abietina, Campyliadelphus chrysophyllus*) and thalloid mat (*Mannia fragrans*) are not numerous.

Among groups of species associated with different habitat and vegetation types, proportion of petrophytic bryophytes (*Grimmia spp., Schistidium spp., Flexitrichum flexicaule*) is quite high and varies from 26 % (in genuine dry steppes) to 40 % (in petrophyte and meadow steppes) of the total number of species recorded in each vegetation type. The share of steppe (*Abietinella abietina, Brachythecium glareosum, Pterygoneurum* spp.) and forest-steppe (*Brachythecium albicans, Dicranum dispersum, Pleuridium subulatum*) species is highest in genuine dry steppes (52 %) and communities of steppe scrubs (50 %), whereas the part of forest species (*Brachythecium capillaceum*, *Pseudoamblystegium subtile, Pseudoleskeella nervosa*) is more or less significant only in steppe scrublands (18 %) and petrophyte steppes (11 %). Eurytopic species (*Bryum argenteum, Barbula unguiculata, Ceratodon purpureus, Ptychostomum imbricatulum*) were revealed only in steppes (Table 2). Heterogeneity of bryophyte composition, which includes species associated with different habitat and vegetation types, may be explained by fragmentation and the small area size of investigated communities, that are surrounded by agricultural lands and forests in study area.

As expected, the range of ecological groups in relation to light and water regime shows the high proportion of xerophytes and heliophytes among bryophytes of almost all studied communities. The share of indifferent to water regime species (*Rhytidium rugosum, Ceratodon purpureus*) is considerable only in meadow (20%) and petrophytic (17 %) steppes (Table 2).

Several species, which are rare for Europe and the Southern Urals, are associated with investigated communities. *Mannia fragrans* (VU), *Dicranum dispersum* (EN), *Grimmia plagiopodia* (VU), *Grimmia teretinervis* (NT), and *Pterygoneurum kozlovii* (CR) are listed in the European Red List of Mosses, Liverworts and Hornworts (Hodgetts *et al*., 2019). *Brachythecium laetum* is included into Red Data Book of the Republic of Bashkortostan (Mirkin, 2011). *Jaffueliobryum latifolium* is known from only one locality in Europe (Ellis *et al*., 2019). It grows on the stony sites with steppe vegetation together with *Grimmia plagiopodia* (Fig. 2 F). The population size of these species was not investigated but it seems to be not large. Usually, the number of mature individuals per subpopulation do not exceed 25-50 (considered as 1 m^2), except recently found subpopulation of *Dicranum dispesum* (locality 20, Fig. 2 A), which cover is about 250 m^2. In the Republic of Bashkortostan, all these species are probably relict, and their habitats need protection.

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