

Bryophyte Diversity in the Forests of the Southern Urals

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Abstract

Mountain forest monitoring is closely related to the survey of bryophyte species since it is there that these organisms are common and show very specialized ecological niches. This work is aimed to show how bryophyte richness and taxonomic and ecological categories differ in the various types of indigenous forests in the Southern Ural Mountains. The distribution of bryophytes in mountain forests of the Southern Urals was examined at about 1700 sample plots. Frequency and abundance patterns suggested that species richness, taxonomic distribution, and substrate group distribution are mostly determined by the forest type. According of bryological data, the forest associations characterized by high diversity and concentration of rare species were identified. This is mainly tall herb spruce-fir and mixed forests. The proportion of rare species in these forests is about 9%, including a significant number relicts both of European and Asian origins. The sites of these forests are most valuable for nature conservation and should be protected.

Keywords: bryophytes, biodiversity, forest vegetation, the Southern Urals, syntaxonomy, nature protection

1. Introduction

The Southern Urals is the southern part of Ural Mountains that is also called the Urals, or Ural, a mountain range in west-central Russia which borders with East European Plain to the west and West Siberia to the east. The vegetation in the Southern Urals is characterized by high diversity. It depends on a number of regional factors: unique geographic position between Europe and Asia; mountains being an important climatic boundary, causing significant differences in vegetation of the western and eastern slopes; and the absence of Pleistocene glaciation, which allowed to preserve the ancient elements of the vegetation [1].

Currently, the forests cover about 80% of the Southern Urals [2]. The modern altitudinal forest belt and floristic composition of current Urals forests were formed over the last 4500 years during the subboreal and sub-Atlantic periods of the Holocene. At the same time, the Ural ridge became a natural physical and geographical boundary for the ranges of many nemoral species due to the increasing of climate continentality from west to east [3]. The Ural ridge is a natural barrier to the path of moist and warm Atlantic air masses. For this reason, the climate on the western Ural's slope is humid and warm; it is more favorable for the deciduous forests. On the eastern slope, the climate is more continental, which led to the dominance of hemiboreal pine-birch and larch forests of West Siberian type and steppe communities. In the middle of the central elevated part of the Southern Urals, the

spruce–fir and mixed broad-leaved and dark coniferous forests are widespread. Thus, the Southern Urals is a contact area of three types of forest vegetation, that is, (1) East European broad-leaved deciduous forests, (2) mountain taiga, and (3) hemiboreal Siberian pine, larch, and birch forests. The presence of the species from three complexes, nemoral, boreal, and hemiboreal, significantly increases species richness of Ural forests [3–5].

In comparison with North European forests, where agriculture started to reduce in the forest area 3000–5000 years ago [6], the history of forest exploitation in the Southern Urals is relatively short: the large-scale felling has been carried out here for 300 years. Nevertheless, intensive cutting of the mountain forests in this area has brought about a highly mosaic structure of vegetation represented by various types of forests at different stages of regeneration and age succession [7]. Also, heavily exploitation of mountain forests causes a major part of their biodiversity value to be lost.

One of the important challenges of forest ecology is reconstruction of the picture of the original species composition and structure of the forests (in relation to overall biodiversity, space, age, thickness of trees, composition of understory vegetation, etc.). The preserved parts of indigenous forests represent an important base for knowledge about the original diversity and structure of forests of a particular region. The identification of the most vulnerable and valuable forest sites in terms of the conservation of forest biodiversity is an important conservation challenge which attracts the attention of specialists from different fields. There are several approaches to the selection of these areas, which differ by their significance, sizes, and level of conservation. In the vegetation science, there are many categories of “etalon” forest communities: forests of high conservation value, intact forest landscapes (IFA), biologically valuable forests (IVF), etc. [8]. Despite the differences in the interpretation of the terms “indigenous,” “old-growth,” or “intact” forests, most of the researches keep in mind forest communities that have developed over a long period of time (comparable to the maximum biological age of tree species or exceeding this age) without or with minimal human impact [9]. In our research, we identify these forests as “relatively indigenous,” or “indigenous,” keeping in mind that at least some of them were established in the sites that were more or less human-modified in the past. It should be noted that many types of indigenous forest communities of the Southern Urals have been preserved only by small fragments in areas difficult to access for logging or in specially protected natural areas [10, 11].

Bryophytes represent a significant component of overall forest diversity and play important roles in ecosystem processes and functions [12], but in European Russia the bryophyte diversity in particular types of forest is not well studied [13–15].

In the last three decades, we are specifically interested in the revealing of bryophyte diversity in the forests of the Southern Urals and the presence of rare species in the different forest types of the region. In particular, we intended to answer the following questions: (1) Do bryophyte diversity vary in relation to environmental variables linked to different forests types? (2) Are rare and endangered species mainly associated with particular forest types? (3) What differences exist between bryophyte diversity in indigenous and secondary forest communities established after felling?

2. Study area and characteristic of investigated forest types

The research was performed between 1991 and 2017 in the territory of the Republic of Bashkortostan and some adjacent areas of Chelyabinsk Region (Russian Federation). The climate of study area is moderately continental, with relatively

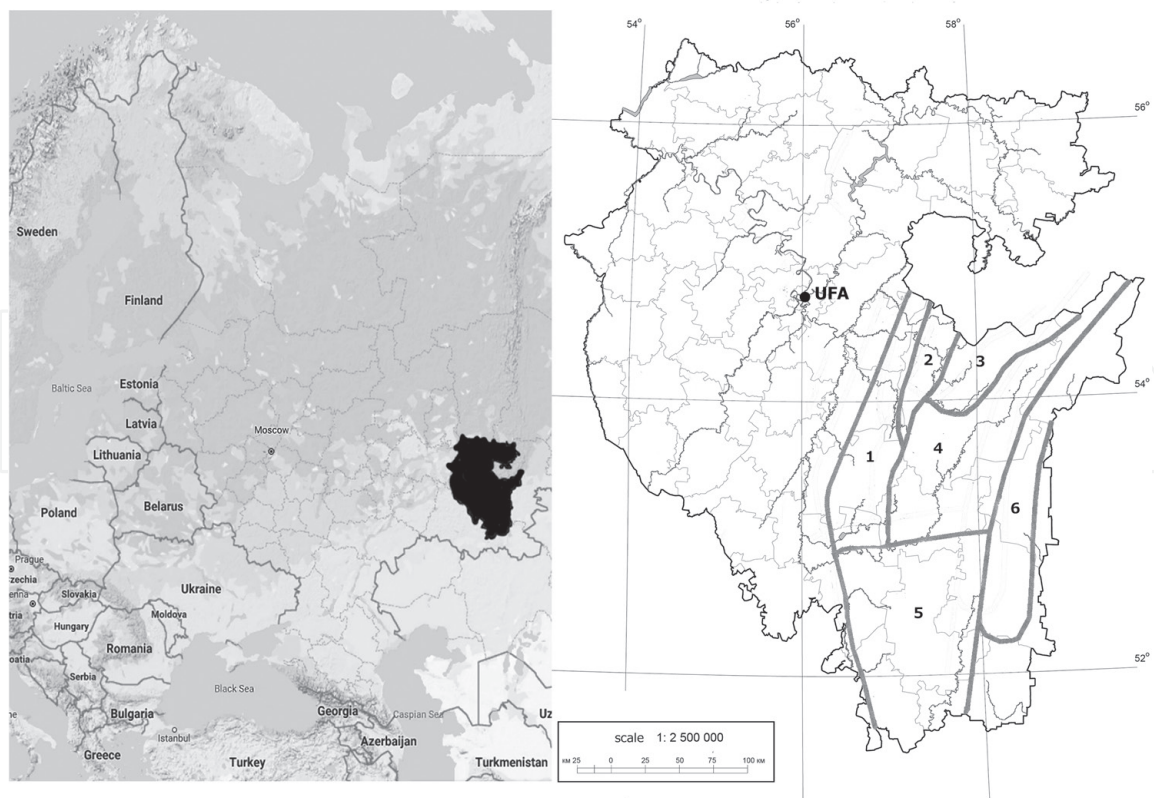


Figure 1.
Map of study area and the districts of natural zoning of the Southern Urals according to the scheme of A. Muldashev [16].

warm summer and long cold winter. The average annual temperature is +0.5 to +2.0; the mean temperature in January is -15.5 to -17°C and in July +16.5 to +17.5 $^{\circ}\text{C}$. The mean annual precipitation is 500–700 mm. The frost-free period is 50–90 days; the mean snow depth is 60–75 cm [2].

According to natural zonation of the Republic of Bashkortostan (**Figure 1**), the study area belongs to six districts [16]:

1. *The district of mountain broad-leaved forests of the western slope of the Southern Urals* includes Bash-Alatau, Takaty, Kyrybujan, Ulutau, Alatau, Kolu, Kanchak, and Kibiz Ranges extended mostly in the meridional direction. The relief is presented by low and middle mountains dissected by deep river canyons. The soil cover consists mostly of mountain forest gray and dark gray soils. The watersheds and mountain slopes are covered by broad-leaved forests. On the southern slopes, the oak forests are more common, and the northern slopes are covered mostly by maple woodlands. The lime forests grow in the low parts of gentle slopes of different exposure. In the river valleys, the floodplain forests with elm, alder, and bird cherry are widespread. In the valleys of Zilim and Nugush Rivers, the fragments of old-growth pine and spruce forests are preserved. The largest areas are occupied by secondary lime, birch and aspen forests, and the meadows. The territory is sparsely populated.
2. *Zil'merdak District of mixed deciduous and dark coniferous fir and spruce forests* of the middle part of the Southern Urals includes Zil'merdak Range and adjacent mountains. The relief is hills, terrain, and middle mountains. The soil cover consists mostly of mountain forest light gray soils. In the past, the spruce-fir forests with an admixture of lime, maple, elm, and oak, as well

as pine broad-leaved forests, were widely distributed here. Currently, the indigenous vegetation is preserved in small areas, on steep slopes, and in the water-protected zone of the Inzer River. Most of the district's area is covered by secondary birch, aspen, and mixed deciduous forests. Steppe communities occur on steep rocky slopes in the canyons of mountains rivers. The area is sparsely populated.

3. *Yamantau District of dark coniferous fir-spruce forests and highland vegetation* comprises the largest peaks of the Southern Urals, that is, Yamantau Mountain (1638 m.a.s.l.) and Iremel Mountain (1586 m.a.s.l.), as well as the Nary, Mashak, and Belyagush Ranges. The relief is ridges with deep depressions. Mountain sod-podzol, mountain gray forest, and mountain meadow soils are widespread. Before the forest exploitation, at the altitude of (900) 1000–1100 m.a.s.l., the mountain slopes have been covered by spruce-fir forests, sometimes with an admixture of bush form of linden. Also, the pine and larch forests were quite common in the upper and lower forest belts, respectively. The present-day vegetation is represented by different secondary successional communities, appeared after felling, mostly by birch woodlands. In the subalpine belt, up to 1150–1250 m.a.s.l., the spruce, fir, and birch (*Betula czerepanovii* Orlova) open woodlands, as well as tall-herb alpine meadows, are widespread. The tops of some highest mountains are covered by mountain tundra. In river valleys bogged birch-spruce forests are quite common. The area is very sparsely populated.
4. *The district of light coniferous pine and larch forests in the central part of the Southern Urals* includes the Jurmatau, Belyatur, Shatak and Kraka Ranges (800–1000 m.a.s.l.) and part of the Uraltau Range. Relief is ridges and inter-mountain depressions. Mountain forest gray soils are predominated. The pine forests are very common, somewhere, for example, on Kraka and Jurmatau Ranges; the large sites of larch forests bordered with petrophyte steppe communities are presented. Most of indigenous forests are replaced by secondary birch and aspen woodlands. At the altitude 850–900 m.a.s.l. near the upper border of forest belt appear larch-birch scarce woodlands and the meadows. The area is well developed and relatively densely populated.
5. *The district of forest and forest-steppe in the Zilair Plateau* has the relief consisting of the low ridges and hills with deeply embedded river valleys. The different types of chernozems and gray and dark gray forest soils are common here. Western part of plateau is covered with oak forests that are replaced with pine broad-leaved forests in an eastward direction. The coniferous forests are mostly cut down and replaced with birch woodlands. The area is fairly sparsely populated.
6. *The forest-steppe district of eastern slope of the Southern Urals* includes Krykty, Kurkak, and Irendyk Ranges and adjacent foothills. The relief is low ridges and hills. In the depressions, the lakes and mires are quite common. The soil cover consists mostly of mountain gray forest soils and leached chernozems. In the past, the upper parts of the ridges were occupied by pine, larch, and birch forests; nowadays vegetation is represented mainly by the birch forest-steppe. The region is relatively densely populated.

The main forest trees of the Southern Urals are *Picea obovata* Ledeb., *Abies sibirica* Ledeb., *Pinus sylvestris* L., *Larix sibirica* Ledeb., *Tilia cordata* Mill., *Acer*

platanoides L., *Quercus robur* L., *Ulmus glabra* Huds., *Betula pendula* Roth., *Betula pubescens* Ehrh., *Populus tremula* L., and *Alnus incana* (L.) Moench and *Padus avium* Mill. The floodplain forests are formed by *Populus nigra* L., *Populus alba* L., and *Salix* spp.; also paludified floodplain forests with predominance of *Alnus glutinosa* (L.) Gaertn. are occasionally found.

Vegetation classification of the indigenous forests of the Southern Urals consistent with the Braun-Blanquet approach [17] allowed to separate 42 associations which belonged to 10 sub-alliances, 9 alliances, 4 orders, and 4 classes [10]. In total, bryophyte richness was studied in 11 types of forest communities (F1–F11) separated at the level of alliances and sub-alliances. The syntaxonomical position of investigated forest types is given below:

Class CARPINO-FAGETEA SYLVATICAE Jakucs ex Passarge 1968 (syn. Quercofagetea Br.-Bl. et Vlieger in Vlieger 1937)—mesic deciduous and mixed coniferous-broadleaved forests of temperate Europe, the Caucasus and Southern Siberia [18].

Order FAGETALIA SYLVATICAE Pawłowski 1928.

F1—Alliance *Alnus incanae* Pawłowski et al. 1928.

F2—Alliance *Lathyro pisiformis-Quercion roboris* Solomeshch et Grigoriev in Willner et al. 2015.

Alliance *Aconito lycoctoni-Tilion cordatae* Solomeshch et Grigoriev in Willner et al. 2016.

F3—Sub-alliance *Aconito septentrionalis-Tilienion cordatae* Martynenko 2009 prov.

F4—Sub-alliance *Tilio cordatae-Pinenion sylvestris* Martynenko et Shirokikh in Martynenko 2009 prov.

Class ASARO EUROPAEI-ABIETETEA SIBIRICAE Ermakov, Mucina et Zhitlukhina in Willner et al. 2016—cool-temperate coniferous and mixed montane forests with nemoral and hemiboreal floristic elements of the Southern Urals and Southern Siberia [18].

Order ABIETETALIA SIBIRICAE (Ermakov in Ermakov et al. 2000) Ermakov 2006.

F5—Alliance *Aconito septentrionalis-Piceion obovatae* Solomeshch, Grigoriev, Khaziakhmetov et Baisheva in Martynenko et al. 2008.

Class VACCINIO-PICEETEA Br.-Bl. in Br.-Bl. et al. 1939—holarctic coniferous forests on oligotrophic and leached soils in the boreal zone and at high-altitudes of mountains in the nemoral zone of Eurasia [18].

Order PICEETALIA EXCELSAE Pawłowski et al. 1928.

Alliance *Piceion excelsae* Pawłowski et al. 1928.

F6—Sub-alliance *Atrageno sibiricae-Piceenion obovatae* Zaugolnova et al. 2009.

F7—Sub-alliance *Eu-Piceenion abietis* K.-Lund 1981.

Order PINETALIA SYLVESTRIS Oberd. 1957.

F8—Alliance *Dicrano-Pinion sylvestris* (Libbert 1933) W. Matuszkiewicz 1962.

Class BRACHYPODIO PINNATI-BETULETEA PENDULAE Ermakov et al. 1991 hemiboreal pine and birch-pine herb-rich open forests on fertile soils of the Southern Urals and Southern Siberia [18].

Order CHAMAECYTISO RUTHENICI-PINETALIA SYLVESTRIS Solomeshch et Ermakov in Ermakov et al. 2000.

F9—Alliance *Caragano fruticis-Pinion sylvestris* Solomeshch et al. 2002.

F10—Alliance *Veronico teucarii-Pinion sylvestris* Ermakov et Solomeshch in Ermakov et al. 2000.

F11—Alliance *Trollio europaea-Pinion sylvestris* Fedorov in Ermakov et al. 2000.

Short characteristic of the investigated forest types is given in **Table 1**.

Forest type	Number of relevés	Elevation	Districts	Description	Cover of moss layer, %
F1	96	200–700	1–6	Floodplain gray alder forests	1–2
F2	115	250–720	1, 3, 5	Thermophytic oak forests	1–10
F3	287	220–630	1, 4, 5	Mesic linden-maple-oak forests	<1
F4	139	350–550	1, 4, 5	Mesic pine-linden-oak forests	<1
F5	195	500–1300	1–5	Spruce-fir and mixed forests with nemoral herb layer	1–20
F6	132	400–1400	1–5	Spruce-fir green moss—tall-forb forest	55–80
F7	52	450–1300	3	Spruce-fir green moss forest	75
F8	120	350–1100	2–4	Pine green moss forest	20–70
F9	88	400–900	1, 3–5	Hemiboreal xero-mesophytic pine and pine-larch forests	5–10
F10	101	400–750	4–6	Hemiboreal birch and birch-pine forests	1–5
F11	179	450–950	1–6	Mesophytic hemiboreal birch and larch pine forests	3–15

Table 1. Characteristic of the forest types studied (F1–F11) in the Southern Ural Mountains, Russia.

3. Field sampling

In about 400 localities, we have laid 1700 sample plots with area of 400 m² (usually, not <10 plots for each of forest association). In each plot, the phytosociological relevés, following the Braun-Blanquet method [17], were carried out. All bryophytes growing on various substrates (soil, tree trunks, rotten wood, rock outcrops, etc.) were described.

An estimate of the abundance of forest floor bryophyte species was carried out on the basis of the Braun-Blanquet scale: r, a single species is encountered (the cover is insignificant); +, the species is rare and has a small projective cover up to 1%; 1, the projective cover of species is 1–5%; 2, projective cover is 6–25%; 3, projective cover is 26–50%; 4, projective cover is 51–75%; and 5, projective cover is more than 75%. In synoptic **Table 4**, the following scale of constancy was used: r, the species was encountered in <5% of the relevés; +, in 6–10% of relevés; I, in 11–20% of relevés; II, 21–40% of relevés; III, 41–60% of relevés; IV, in 61–80% of relevés; V, in 81–100% of relevés. Classification of forest vegetation was conducted according to the Braun-Blanquet approach using the TURBOVEG database [19] and program JUICE [20]. Similarity of species diversity between different forest types was calculated using the Jaccard index with program IBIS [21].

Additionally, collections of bryophytes were made outside the sample plots of phytosociological relevés (on forest roads, banks of streams, on bare soil near the roots of fallen trees, etc.). These data were used for compiling of checklist of bryophytes revealed in the forests of the Southern Urals. The specimens are kept in the Herbarium of Ufa, Institute of Biology—Subdivision of the Ufa Federal Research Centre of the Russian Academy of Sciences (UFA), and partly in Herbarium of the Main Botanical Garden of Russian Academy of Sciences (MHA).

4. The species richness and substrate groups of bryophytes in different types of forest communities

Forest areas of the Southern Urals have a rich bryophyte flora, presenting 286 species of Bryophyta distributed across 124 genera and 44 families and 58 species of Marchantiophyta from 33 genera and 23 families. This represents 75 and 62% of the moss and liverwort richness of the Republic of Bashkortostan, respectively. High proportions of mountain forest species in the total bryophyte flora of the Bashkortostan stress the great importance of forest protection for preserving biodiversity in the republic.

The predominant families, in terms of the number of species, are Brachytheciaceae (26 species), Dicranaceae (23), Grimmiaceae (20), Amblystegiaceae (20), Sphagnaceae (18), Bryaceae (17), Mniaceae (16), Pottiaceae (14), Polytrichaceae (11), and Pylaisiaceae (12), and the leading genera are *Sphagnum* (18 species), *Dicranum* (18), *Bryum* (15), *Brachythecium* (11), *Pohlia* (10), *Schistidium* (10), *Orthotrichum* (8), *Grimmia* (7), and *Plagiomnium* (7).

Some species richness indicators within studied forest types are given in **Table 2**. The mosses have the leading position in the bryophyte flora of all investigated forests where they held 78–93% of the total species richness within different forest types (**Table 2**). The participation of liverworts is less significant; their richness increases only in the forests with dominance of dark coniferous trees (F5–F7).

The highest species richness in the dark coniferous and mixed tall-herb forests (types F5 and F6) can be explained, mainly, by the relatively high humidity in their habitats, as well as high diversity of epixylic and ground species in these communities. The lowest bryophyte diversity was revealed in the pine, birch, and larch forests (F7, F10, and F11) that developed in the more continental climate conditions of eastern slope of the Southern Urals, and in the oak forests (F2), growing on the western slope but in the forest-steppe sites.

The use of the Jacquard index (**Table 3**) determining the proportion out of the total species list for two forest types which is common to both revealed low

Forest type	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11
Number of species	74	65	71	81	121	124	69	91	82	64	67
% of liverworts	13	14	7	10	19	17	22	14	9	8	15
% of mosses	87	86	93	90	81	83	78	86	92	92	85
Marchantiophyta											
Number of species	10	9	5	8	23	21	15	13	7	5	10
Number of genera	8	8	4	7	18	15	12	9	5	4	10
Number of families	7	6	4	6	14	10	8	7	5	4	8
Bryophyta											
Number of species	64	56	66	73	98	103	54	78	75	59	57
Number of genera	47	40	42	55	67	68	36	55	53	40	42
Number of families	23	22	25	28	32	34	20	29	27	21	22
% of pleurocarpous	66	59	61	59	54	49	46	45	55	53	60
% of acrocarpous	34	41	39	41	46	52	56	55	45	48	40

Table 2. Some bryophyte richness indicators of the forest types studied (F1–F11) in the Southern Ural Mountains, Russia.

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11
F1		0.34	0.37	0.45	0.39	0.36	0.25	0.33	0.26	0.33	0.37
F2	0.34		0.46	0.46	0.41	0.31	0.30	0.44	0.47	0.48	0.47
F3	0.37	0.46		0.46	0.39	0.34	0.28	0.38	0.39	0.44	0.37
F4	0.45	0.46	0.46		0.52	0.49	0.35	0.48	0.48	0.51	0.48
F5	0.39	0.41	0.39	0.52		0.64	0.38	0.49	0.44	0.40	0.45
F6	0.36	0.31	0.34	0.49	0.64		0.40	0.46	0.39	0.39	0.38
F7	0.25	0.30	0.28	0.35	0.38	0.40		0.40	0.30	0.33	0.36
F8	0.33	0.44	0.38	0.48	0.49	0.46	0.40		0.49	0.55	0.49
F9	0.26	0.47	0.39	0.48	0.44	0.39	0.30	0.49		0.51	0.48
F10	0.33	0.48	0.44	0.51	0.40	0.39	0.33	0.55	0.51		0.51
F11	0.37	0.47	0.37	0.48	0.45	0.38	0.36	0.49	0.48	0.51	

Table 3. Jaccard index (similarity matrix) of bryophytes for different forest types in the Southern Ural Mountains, Russia.

similarity of bryophytes of different forests: the values of the index varied from 0.25 to 0.64. Species compositions of spruce-fir and dark coniferous broad-leaved forests (F5 and F6) are more similar as well as of various pine forests (F8–F10).

These relatively low values of Jaccard index can be explained by the high proportion of species with low constancy (**Table 4**), because, in general, the bryophytes have the scattered distribution within landscapes and vegetation types [22]. In the investigated forests, about 25% of species were revealed from one to three times. The proportion of species that were found less in 10 sample plots was higher in the xero-mesophytic oak, pine, larch, and birch forests growing on the border of forest and steppe (F2, 66%; F10, 66%; F9, 60%). Species with high frequency are few and consist of 5–15% of the bryophyte flora of different forest types.

Bryophytes are well adapted to the forest habitats and can be classified according to the substrate they live on as ground or epigeic (growing on the soil), epiphytic (on the bark of living trees), epixylic (on deadwood), or epilithic (on rock surfaces). Many bryophyte species are able to live on different substrates [23, 24]. It was shown that tree bases are a transition zone between the species growing on the rotten wood (two-thirds of epixylic bryophytes were found there) and epiphytic species growing on upper part of trunks. Also, almost one-third of species of the forest floor were revealed on decaying wood [11].

In all studied forests, xero-mesophytic species *Hypnum pallescens* (Hedw.) P. Beauv., *Sanionia uncinata* (Hedw.) Loeske, *Dicranum montanum* Hedw., *Sciurohypnum reflexum* (Starke) Ignatov & Huttunen, *Ptilidium pulcherrimum* (Weber.) Vain., *Brachythecium salebrosum* (Hoffm. ex F. Weber & D. Mohr) Schimp., *Callicladium haldanianum* (Grev.) H. A. Crum, and some others were found mainly on tree bases and the logs and stumps of initial stages of decaying. These species often grow on the bark of birch and are able to survive in relatively xeric environmental conditions of forest-steppe. The group of epixylic bryophytes growing on rotten wood of the last stages of destruction is not large. These species (*Blepharostoma trichophyllum* (L.) Dumort., *Lepidozia reptans* (L.) Dumort., *Lophozia longidens* (Lindb.) Konstant. et Vilnet, *Lejeunea cavifolia* (Ehrh.) Lindb., *Dicranum flagellare* Hedw., *Tetraxis pellucida* Hedw., etc.) are typical mainly for old-growth spruce-fir and mixed forests (F5 and F6), where the proportion of epixylic species is higher (as compared with other forest types).

Forest type	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11
Number of relevés	96	115	287	139	195	132	52	120	88	101	179
Number of bryophytes	74	65	71	81	121	124	69	91	82	64	67
Epiphytes											
<i>Pylaisia polyantha</i> (Hedw.) Schimp.	III	III	III	II	II	I	+	I	I	III	II
<i>Pseudoleskeella nervosa</i> (Brid.) Nyholm	II	III	III	II	II	I	.	+	I	I	I
<i>Orthotrichum speciosum</i> Nees	I	+	I	I	I	.	.	r	r	r	r
<i>Orthotrichum obtusifolium</i> Brid.	r	r	I	r	r	I
<i>Neckera pennata</i> Hedw.	I	r	I	I	I
<i>Homalia trichomanoides</i> (Hedw.) Brid.	I	.	I	r	I	I
<i>Leucodon sciuroides</i> (Hedw.) Schwaegr.	.	I	III	I	I	.	.	.	I	.	.
<i>Anomodon longifolius</i> (Schleich. ex Brid.) Hartm.	.	r	I	I	I	I	.	.	+	+	.
<i>Anomodon viticulosus</i> (Hedw.) Hook. & Taylor	.	+	I	.	I	.	.	r	+	r	.
<i>Serpoleskea subtilis</i> (Hedw.) Loeske	.	r	I	I	+	+	I	r	.	+	.
<i>Dicranum viride</i> (Sull. & Lesq.) Lindb.	.	.	I	I	I	+	.	I	r	r	.
<i>Frullania bolanderi</i> Austin	.	r	.	r	I	+	r	.	.	.	I
<i>Anomodon attenuatus</i> (Hedw.) Huebener	.	.	r	r	.	I
<i>Leskea polycarpa</i> Hedw.	II	.	r	r
<i>Haplocladium microphyllum</i> (Hedw.) Broth.	.	.	r	r	r	.	r
Species occurring on the bases of trunks and rotten wood											
<i>Hypnum pallescens</i> (Hedw.) P. Beauv.	III	III	III	IV	V	II	III	III	V	IV	III
<i>Ptilidium pulcherrimum</i> (Weber.) Vain.	I	r	I	II	III	IV	IV	III	II	I	III
<i>Lophocolea heterophylla</i> (Schrad.) Dumort.	I	r	I	II	IV	II	II	I	r	+	II
<i>Sanionia uncinata</i> (Hedw.) Loeske	III	r	I	II	IV	IV	III	III	III	II	III
<i>Sciuro-hypnum reflexum</i> (Starke) Ignatov & Huttunen	III	II	IV	IV	IV	III	III	+	II	II	III
<i>Dicranum montanum</i> Hedw.	I	I	II	IV	IV	V	IV	IV	III	II	III
<i>Brachythecium salebrosum</i> (Hoffm. ex F. Weber & D. Mohr) Schimp.	III	II	III	III	III	I	r	II	II	III	II
<i>Callicladium haldanianum</i> (Grev.) H. A. Crum	II	r	II	IV	III	II	+	I	I	I	II
<i>Amblystegium serpens</i> (Hedw.) Schimp.	III	I	II	III	II	I	r	I	r	II	+
<i>Platygyrium repens</i> (Brid.) Schimp.	II	I	II	II	II	II	.	I	I	+	+
<i>Campylidium sommerfeltii</i> (Myrin) Ochyra	II	r	I	I	I	I	.	I	I	r	I
<i>Plagiothecium laetum</i> Schimp.	I	r	I	r	II	II	II	I	I	r	I
<i>Plagiothecium denticulatum</i> (Hedw.) Schimp.	I	r	I	r	II	II	I	I	r	.	.
<i>Lophocolea minor</i> Nees	I	r	II	I	II	I	+	+	+	r	r
<i>Pohlia nutans</i> (Hedw.) Lindb.	r	r	I	I	I	II	I	III	II	II	II
<i>Brachytheciastrum velutinum</i> (Hedw.) Ignatov & Huttunen	I	II	I	I	II	I	I	I	I	I	+

Forest type	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11
<i>Radula complanata</i> (L.) Dumort.	r	I	II	I	II	I	r	I	+	r	I
<i>Sciuro-hypnum starkei</i> (Brid.) Ignatov & Huttunen	.	.	I	r	I	II	+	r	r	r	I
<i>Tetraphis pellucida</i> Hedw.	r	.	r	r	I	II	I	I	.	.	r
<i>Lepidozia reptans</i> (L.) Dumort	.	r	.	.	+	II	r	.	.	.	r
<i>Dicranum fragilifolium</i> Lindb.	.	.	I	.	r	II	.	.	I	.	.
<i>Blepharostoma trichophyllum</i> (L.) Dumort	I	II	II
<i>Lophozia longidens</i> (Lindb.) Konstant. & Vilnet	I	I	II	r	.	.	r
<i>Bryum capillare</i> Hedw.	I	r	r	r	.	.	.	r	r	r	.
<i>Lophozia ventricosa</i> (Dicks.) Dumort.	r	r	.	r	I	I	I	r	.	r	r
<i>Bryum moravicum</i> Podp.	.	r	I	r	I	I	I	+	+	r	.
<i>Dicranum flagellare</i> Hedw.	.	.	I	I	I	I	.	II	I	+	II
<i>Cynodontium strumiferum</i> (Hedw.) Lindb.	.	.	.	r	I	I	I	I	.	.	.
<i>Orthocaulis attenuatus</i> (Nees) A. Evans	+	I	I	r	.	.	.
<i>Cephaloziella hampeana</i> (Nees) Schiffn. ex Loeske	r	.	I	I	r	.	I
<i>Eurhynchiastrum pulchellum</i> (Hedw.) Ignatov & Huttunen	r	r	.	I	II	I	.	I	+	.	I
Epilithic species											
<i>Paraleucobryum longifolium</i> (Hedw.) Loeske	.	I	I	r	I	II	III	I	r	r	+
<i>Tortella tortuosa</i> (Hedw.) Limpr.	.	II	.	r	I	I	.	r	II	I	I
<i>Schistidium apocarpum s.l.</i> (Hedw.) Bruch & Schimp.	.	+	r	.	I	II	.	r	II	r	r
<i>Homomallium incurvatum</i> (Schrad. ex Brid.) Loeske	.	r	r	r	I	I	.	.	+	+	r
<i>Hedwigia ciliata</i> (Hedw.) P. Beauv.	.	I	.	r	.	I	.	I	+	r	r
<i>Campyliadelphus chrysophyllus</i> (Brid.) R. S. Chopra	.	.	.	r	I	II	.	II	r	r	.
<i>Hypnum cupressiforme</i> Hedw.	.	.	r	r	I	I	r	r	I	.	.
<i>Pohlia cruda</i> (Hedw.) Lindb.	I	II	.	I	r	r	r
<i>Ditrichum flexicaule</i> (Schwaegr.) Hampe	.	.	.	r	r	+	.	I	II	.	.
<i>Oxystegus tenuirostris</i> (Hook. & Taylor) A. J. E. Sm.	r	r	r	.	I
<i>Sciuro-hypnum populeum</i> (Hedw.) Ignatov & Huttunen	r	I	r	.	.	.	I	r	.	.	.
<i>Pseudoleskeella tectorum</i> (Funck ex Brid.) Kindb. ex Broth.	.	+	.	.	r	.	.	.	r	.	r
<i>Distichium capillaceum</i> (Hedw.) Bruch & Schimp.	.	.	.	r	I	I	.	.	+	.	.
<i>Entodon schleicheri</i> (Schimp.) Demet.	.	.	.	r	r	r	.	.	r	.	.
<i>Bryoerythrophyllum recurvirostrum</i> (Hedw.) P. C. Chen	r	+	.	r	r	.	.
<i>Encalypta procera</i> Bruch	r	r	.	.	+	.	.

Forest type	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11
<i>Dicranum spadiceum</i> J. E. Zetterst.	I	.	I	r	.	.
<i>Dicranum flexicaule</i> Brid.	.	.	.	r	.	r	r	.	r	r	.
<i>Hypnum recurvatum</i> (Lindb. & Arnell) Kindb.	r	r	.	.	r	r	r	.	r	.	r
<i>Mnium stellare</i> Hedw	.	.	.	r	+	I	.	+	.	.	.
Epigeic species sometimes found on stones and fallen trees											
<i>Brachythecium mildeanum</i> (Schimp.) Schimp.	II	.	.	r	I	r	.	.	.	r	.
<i>Brachythecium rivulare</i> Schimp.	II	.	I	.	.	r
<i>Calliargonella lindbergii</i> (Mitt.) Hedenaes	II	.	.	r	r	+
<i>Plagiomnium ellipticum</i> (Brid.) T. J. Kop.	II	.	r	r	+	r	.	r	.	r	.
<i>Calliargon cordifolium</i> (Hedw.) Kindb.	II	.	.	.	r	r
<i>Campylium stellatum</i> (Hedw.) Lange & C. E. O. Jensen	r	.	.	.	r	r	.	.	r	.	r
<i>Rhizomnium pseudopunctatum</i> (Bruch & Schimp.) T. J. Kop.	r	.	.	r	I	+	r
<i>Fissidens taxifolius</i> Hedw.	I	.	II	r	I	r	.	r	.	.	I
<i>Oxyrrhynchium hians</i> (Hedw.) Loeske	I	.	I	.	II	I	.	r	r	r	.
<i>Plagiomnium cuspidatum</i> (Hedw.) T. J. Kop.	III	II	IV	II	IV	II	+	I	+	I	II
<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.	I	r	r	II	IV	V	V	V	V	IV	V
<i>Ptilium crista-castrensis</i> (Hedw.) De Not.	r	.	.	II	II	IV	V	III	III	I	II
<i>Dicranum polysetum</i> Sw. ex anon.	r	r	.	II	I	III	II	IV	IV	II	II
<i>Dicranum scoparium</i> Hedw.	r	I	I	II	III	IV	V	IV	IV	II	III
<i>Hylocomium splendens</i> (Hedw.) Schimp.	.	.	.	II	III	V	V	IV	III	II	II
<i>Rhytidadelphus triquetrus</i> (Hedw.) Warnst.	.	.	r	II	III	III	r	III	II	I	III
<i>Plagiochila porelloides</i> (Torr. ex Nees) Lindenb.	I	.	.	r	I	III
<i>Sciuro-hypnum curtum</i> (Lindb.) Ignatov	I	r	I	I	III	II	I	II	I	I	III
<i>Rhodobryum roseum</i> (Hedw.) Limpr.	I	I	.	r	II	II	.	I	.	+	III
<i>Hylocomiastrum pyrenaicum</i> (Spruce) M. Fleisch.	.	r	r	.	II	I	I	r	.	.	.
<i>Hylocomiastrum umbratum</i> (Hedw.) M. Fleisch.	.	.	.	r	II	II	II
<i>Cirriphyllum piliferum</i> (Hedw.) Grout	I	r	.	r	II	I	.	r	.	.	r
<i>Thuidium assimile</i> (Mitt.) A. Jaeger	r	.	.	.	I	II	.	I	.	r	.
<i>Climacium dendroides</i> (Hedw.) F. Weber & D. Mohr	I	.	r	r	I	r	.	+	.	+	r
<i>Atrichum undulatum</i> (Hedw.) P. Beauv.	r	.	r	.	I	I	+	r	r	.	.
<i>Plagiomnium rostratum</i> (Schrad.) T. J. Kop.	I	.	r	r	+	r

Forest type	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11
<i>Plagiomnium medium</i> (Bruch & Schimp.) T. J. Kop.	r	.	.	.	I	I	.	r	.	.	I
<i>Brachythecium rutabulum</i> (Hedw.) Schimp.	.	r	r	.	I	r	.	.	.	r	.
<i>Polytrichum juniperinum</i> Hedw.	.	+	.	r	+	I	I	II	+	+	+
<i>Dicranum fuscescens</i> Sm.	.	.	.	r	I	I	I	I	II	+	I
<i>Rhytidiadelphus subpinnatus</i> (Lindb.) T. J. Kop.	r	.	.	.	I	II	.	r	.	.	.
<i>Barbilophozia lycopodioides</i> (Wallr.) Loeske	I	I	II
<i>Barbilophozia hatcheri</i> (A. Evans) Loeske	I	I	II
<i>Barbilophozia barbata</i> (Schmidel ex Schreb.) Loeske	.	I	.	r	I	I	.	I	+	.	.
<i>Polytrichastrum longisetum</i> (Sw. ex Brid.) G. L. Sm.	I	I	I
<i>Dicranum majus</i> Sm.	.	.	r	.	.	I	I
<i>Polytrichastrum densifolium</i> Wilson ex Mitt.	I	.	I
<i>Atrichum flavisetum</i> Mitt.	r	.	.	r	I	I	r
<i>Abietinella abietina</i> (Hedw.) M. Fleisch.	.	I	.	r	I	I	.	I	II	+	r
<i>Rhytidium rugosum</i> (Hedw.) Kindb.	.	r	.	r	.	.	.	III	I	.	.
<i>Polytrichum piliferum</i> Hedw.	r	II	.	r	.
<i>Ceratodon purpureus</i> (Hedw.) Brid.	.	+	r	r	I	.	.	I	II	II	I
<i>Brachythecium albicans</i> (Hedw.) Schimp.	.	I	I	.	r	.	.	I	r	+	r
<i>Syntrichia ruralis</i> (Hedw.) F. Weber & D. Mohr	.	I	I	+	.
<i>Leptobryum pyriforme</i> (Hedw.) Wilson	r	r	.	r	.	r
<i>Dicranella heteromalla</i> (Hedw.) Schimp.	r	.	r	I	.	.	r

Note: The species with low constancy are excluded.

Table 4.

Shortened synoptic table of bryophytes revealed in forest communities in the Southern Ural Mountains, Russia.

The “real” epiphytes, growing on the bark of the living trees at a height of 1 m and above, are *Pylaisia polyantha* (Hedw.) Schimp., *Pseudoleskeella nervosa* (Brid.) Nyholm, *Orthotrichum obtusifolium* Brid., and *O. speciosum* Nees. These species are xero-mesophytic and often may be found on the trees of settlements and in contour strip forests surrounded by agricultural lands. There is another group of mesophytic epiphytes growing mainly on the bark of old broad-leaved trees. These species (*Leucodon sciuroides* (Hedw.) Schwaegr., *Neckera pennata* Hedw., *Homalia trichomanoides* (Hedw.) Brid., *Anomodon longifolius* (Schleich. ex Brid.) Hartm., *Dicranum viride* (Sull. & Lesq.) Lindb., and some others) are quite sensitive to the fluctuations in temperature and humidity of habitats. An analysis of the distribution of these species using ecological scales showed that they have a narrow ecological amplitude, especially in relation to the factor of continentality [25, 26]. Many of these species are basophilous and can grow on limestone outcrops. Probably, the

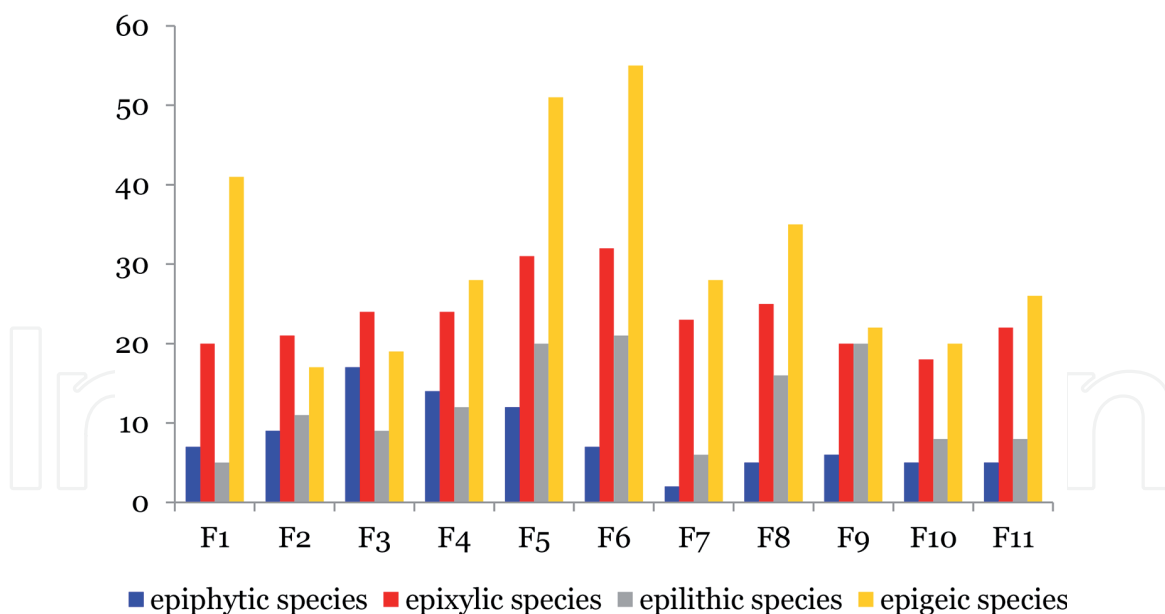


Figure 2.
 Substrate groups of bryophytes in the different forest types of the Southern Ural Mountains, Russia.

presence of limestones helps preserve the local subpopulations of these species in the felling areas. The proportion of epiphytic species in the bryophyte flora of different forest types is more significant in broad-leaved and mixed pine broad-leaved forests (F3 and F4) (Figure 2).

Projective cover of epigeic bryophytes varies greatly depending on the forest type, being insignificant in broad-leaved forests (<1%) and reaching the higher values in boreal spruce-fir and pine forests (up to 80%) (Table 1). The high species richness of epigeic bryophytes in tall-herb dark coniferous and mixed forests (F5 and F6), as well as in floodplain alder forests (F1), may be explained by high humidity of soil in these habitats. In relatively dry habitats of thermophytic oak forests (F2) with dense herb layer and in shaded mesic linden-maple-oak forests (F3), the diversity of epigeic species is quite low (Figure 2).

Boreal species *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Dicranum polysetum* Sw. ex anon., *Dicranum scoparium* Hedw., and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. are almost completely absent in the oak forests (F2), occasionally occur in floodplain forests (F1), and are quite common in other forest types. In “typical” boreal green-moss coniferous forests (F7 and F8), they grow mostly on the forest floor, but in other forest types, these species were found mainly on logs, bases of trees, and stones where they avoid the competition with vascular plants.

In many forests of the Southern Urals, there are numerous rock outcrops. The proportion of epilithic species is high in the hemiboreal xero-mesophytic pine and pine-larch forests (F9) growing on steep southern and southeastern slopes with lime outcrops, where these species consist of 33% of bryophyte flora, but total species richness of epilithic bryophytes is highest in the dark coniferous forests (Figure 2).

5. The peculiarities of bryophyte composition in the secondary forests

Epiphytic, epixylic, and epilithic bryophytes are particularly responsive to microclimatic as well as physical and chemical substrate properties, which directly depend on tree age and diameter, bark texture, or decay stages of deadwood. Many bryophytes

are sensitive to forest management practices [27, 28], but in Russia, the influence of felling on these components of forest vegetation has not been well studied [8].

A multitude of restoration practices are currently being used in the Southern Ural forests, but in spite of the government recommendations to establish in the felling areas the forest plantations through human-induced direct planting or seeding, the large felled areas are overgrown by deciduous pioneer tree species, for example, birch and aspen due to natural regeneration. Understanding how secondary forests differ from the indigenous forests in terms of diversity, structure, and function provides the basis for forest restoration ecology. The availability of mountain boreal forests in different stages of succession provides an opportunity for comparing of plant diversity and the structural and functional elements in the Ural's indigenous forests as well as in the secondary forests established after clear-cutting. Such data are crucial for planning monitoring and restoration of unique mountain forests [29].

In the Southern Urals, the study of reforestation processes has been only recently begun, but some preliminary results concerning dynamic of bryophyte diversity during natural forest regeneration were obtained [11, 26, 30].

The study of secondary plant communities originated after clear-cutting in the pine and broad-leaved forests [26, 30] has shown that bryophytes of various substrate groups respond to felling in different ways. Xero-mesophytic epiphytic and epixylic species (*Pylaisia polyantha* (Hedw.) Schimp., *Pseudoleskeella nervosa* (Brid.) Nyholm, *Brachythecium salebrosum* (Hoffm. ex F. Weber & D. Mohr) Schimp., *Amblystegium serpens* (Hedw.) Schimp., *Sciuro-hypnum reflexum* (Starke) Ignatov & Huttunen, and *Hypnum pallescens* (Hedw.) P. Beauv., etc.) seem to be more tolerant to habitat changes after felling. Usually, these species sharply reduce their constancy after felling but begin to grow actively after 3–4 years on stumps and felling residues and on the bases of young tree trunks. In secondary forests they restore or even increase their constancy.

The light-demanding colonists (*Ceratodon purpureus* (Hedw.) Brid., *Bryum caespiticium* Hedw., *Funaria hygrometrica* Hedw., *Pogonatum urnigerum* (Hedw.) P. Beauv., *Dicranella heteromalla* (Hedw.) Schimp, *Leptobryum pyriforme* (Hedw.) Wilson, and some others) have a relatively high constancy during the first 7–20 years after felling, but later they belong to the category of sporadically occurring species, growing on the soil near the roots of fallen trees and forest roadsides.

The nemoral species *Orthotrichum speciosum* Nees., *Leucodon sciuroides* (Hedw.) Schwaegr., *Dicranum viride* (Sull. & Lesq.) Lindb., *Neckera pennata* Hedw., *Homalia trichomanoides* (Hedw.) Brid., *Anomodon longifolius* (Schleich. ex Brid.) Hartm., *Oxyrrhynchium hians* (Hedw.) Loeske, and *Fissidens taxifolius* Hedw. are vulnerable to tree felling. They either disappear or have little constancy in the early succession communities.

Boreal species *Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Hylocomium splendens* (Hedw.) Schimp. are more resistant against changes in ecological regimes of habitats. *Ptilium crista-castrensis* (Hedw.) De Not., *Dicranum polysetum* Sw. ex anon., and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. are more vulnerable [26].

In general, changing of bryophyte diversity in the felled areas seems to be as follows:

During 1–4 years after felling, the species richness is sharply reduced, in some cases by 50–70%. The cover of herb layer increases due to disturbances of the forest floor and high illumination. These processes are particularly intense after summer clear-cutting connected with strong disturbances of the forest floor. Usually, species richness of bryophytes begins to rise only after 7 years or more, when young trees appear and shading becomes more or less significant.

Nearly 60–90 years after felling, the similarity of the bryophyte composition in the indigenous and mature secondary forests still remains quite low due to the

differences in species composition. Considering the fact that a significant number of bryophytes have a low abundance and scattered distribution, it is often difficult to say whether the disappearance of particular species is due to the felling or for some other reason.

6. Rare bryophytes in the forests of the Southern Urals

As mentioned above, about 25% of bryophyte species revealed in the sample plots within indigenous forests of the Southern Urals were found one to three times and formally may be considered as “rare” species. This group comprises *Riccia rhenana* Lorb. ex Muell. Frib., *Racomitrium aciculare* (Hedw.) Brid., *R. aquaticum* (Brid. ex Schrad.) Brid., *Odontoschisma denudatum* (Mart.) Dumort., *Tetraplodon angustatus* (Hedw.) Bruch & Schimp., *Philonotis seriata* Mitt., *Myrinia pulvinata* (Wahlenb.) Schimp., *Jungermannia pumila* With., *Rhizomnium magnifolium* (Horik.) T. J. Kop., *Brachythecium laetum* (Brid.) Schimp., and many other species, some of whom are not typical for the forests. Also, it should be noted that the small number of their known localities may be explained with insufficient botanical knowledge of the region. In this connection, the selection of indicator species for identifying forest areas that need protection constitutes the important challenge.

There are two aspects—the identification of indicator species of old-growth and primeval forests. Often, these two concepts are confused, which is not quite justified due to the differences in the life strategies of bryophytes and duration of the undisturbed existence of forests. The identification of areas where ecological conditions of habitats (especially humidity and illumination) were not changed for a very long time is very important for the conservation of bryophytes. Such areas are called zones of ecological continuity [31]. Not all old-growth forests are suitable for this purpose. Usually the term “old-growth forest” is defined as the forest in which the age of tree stand is more than 120–260 years (depending on the dominant tree species and the region) [8]. At the same time, the survival of relic populations of bryophytes having a limited dispersal activity and high demands on the stability of ecological regime in the habitats is possible mostly in primeval or ancient forests.

In authors’ opinion, under selection of such criteria, both reproduction and the reasons of rarity of species should be taken into account. Among the bryophytes considered as indicators of old-growth forests in North-West European Russia [8], there are the species with different reproduction characteristics and dispersal ability. For instance, according to the system of life strategy [32], such species as *Homalia trichomanoides* (Hedw.) Brid., *Orthotrichum affine* Schrad. ex Brid., and *Haplocladium microphyllum* (Hedw.) Broth. may be considered as colonists and *Leucodon sciuroides* (Hedw.) Schwaegr., *Frullania bolanderi* Austin, and *Lejeunea cavifolia* (Ehrh.) Lindb. as shuttles. There are some species that may be considered as perennial stayers because of their low sporophyte frequency or lacking of sporophyte in study area but have vegetative propagules (*Dicranum viride* (Sull. & Lesq.) Lindb., *Barbilophozia attenuata* (Mart.) Loeske, etc.).

Most of these species are epiphytic or epixylic and can spread to a new site from the nearby forest area, if the suitable substrates are available. These species may be considered as indicators of old-growth forests. On the other hand, stayer species that have no vegetative propagules and prefer to grow on the soil or stones could be seen as indicators of both old-growth and primeval forests. This group includes the species that are very rare in the Southern Urals (*Eurhynchium angustirete* (Broth.) T. J. Kop., *Dicranum drummondii* Muell. Hal., *Entodon schleicheri* (Schimp.) Demet., *Plagiomnium confertidens* (Lindb. & Arnell.) T. J. Kop., etc.). Some of them may be considered as relicts.

Species	Reproduction features	Reasons of rarity
Indicators of old-growth forests		
<i>Neckera pennata</i> Hedw.	1	2, 4
<i>Homalia trichomanoides</i> (Hedw.) Brid.	1	2, 4
<i>Haplocladium microphyllum</i> (Hedw.) Broth.	1	2, 3
<i>Dicranum viride</i> (Sull. & Lesq.) Lindb.	3	1, 2, 4
<i>Anomodon longifolius</i> (Schleich. ex Brid.) Hartm.	4	2, 4
<i>Lejeunea cavifolia</i> (Ehrh.) Lindb.	3	1, 3
<i>Calypogeia integristipula</i> Steph.	3	3, 4
<i>Orthocaulis attenuatus</i> (Nees) A. Evans	3	3, 4
<i>Lepidozia reptans</i> (L.) Dumort.	4	3, 4
<i>Polytrichastrum pallidisetum</i> (Funck) G. L. Sm.	4	4
<i>Eurhynchium angustirete</i> (Broth.) T. J. Kop.	4	4
<i>Dicranum drummondii</i> Muell. Hal.	4	1
<i>Hylocomiastrum umbratum</i> (Hedw.) M. Fleisch.	4	1
<i>Iwatsukiella leucotricha</i> (Mitt.) W. R. Buck & H. A. Crum	4	1
Rare species with disjunctive area of distribution		
<i>Entodon schleicheri</i> (Schimp.) Demet.	1	1, 4
<i>Brachythecium geheebii</i> Milde	4	1
<i>Anomodon rugelii</i> (Muell. Hal.) Keissl.	4	1, 4
<i>Orthothecium intricatum</i> (Hartm.) Schimp.	4	1
<i>Myurella sibirica</i> (Muell. Hal.) Reimers	4	1
<i>Plagiomnium confertidens</i> (Lindb. & Arnell) T. J. Kop.	4	1
<i>Campylidium calcareum</i> (Crundw. & Nyholm) Hedenaes	4	1, 4
<p>Note: Reproduction features: 1, sporophytes are frequent, and vegetative propagules are absent; 2, sporophytes are frequent, and vegetative propagules are present; 3, sporophytes are rare or unknown in study area, and vegetative propagules are present; 4, sporophytes are rare or unknown in study area, and vegetative propagules are absent.</p> <p>Reasons of rarity: 1, rare species growing at the border of the range (or with a disjunctive area); 2, species preferring to grow on old broad-leaved trees; 3, species growing on decaying wood of last stages of destruction; 4, sciophytic and hygrophilous species disappearing during the felling and clearing of the forests.</p>		

Table 5.
Hemerobic bryophytes in the forests of the Southern Ural Mountains, Russia.

In **Table 5**, some species that may be considered as hemerobic in the Southern Urals are shown. It should be noted that the indicator value of these taxa is regional and may be different in the other areas where climatic conditions are not such continental as in the Southern Urals.

The forest associations characterized by high diversity and concentration of rare bryophytes were identified. There are mainly tall-herb and mixed forests (F5 and F6) where regionally rare species (*Brachythecium geheebii* Milde, *Eurhynchium angustirete* (Broth.) T. J. Kop., *Plagiomnium confertidens* (Lindb. & Arnell) T. J. Kop., *Haplocladium microphyllum* (Hedw.) Broth., *Polytrichastrum pallidisetum* (Funck) G. L. Sm., *Iwatsukiella leucotricha* (Mitt.) W. R. Buck & H. A. Crum, and some others) were found. The proportion of rare species in these forests is about of 9%. In contrary, the bryophyte flora of pine forests seems to be well adapted to regular disturbances, that is, fires, and contain a significant number of species with high

reproduction activity. Also, these forests are characterized by a low number of rare species that consists of about 1% of bryophyte flora.

In the Pleistocene, refugia of the nemoral flora of the western slope of Southern Urals contained both the nemoral and the black taiga floristic elements [33]. Our previous research had shown some similarities between bryophyte flora of tall-herb broad-leaved dark coniferous forests of the Southern Urals and the black taiga of Salair Ridge in Siberia [11], as well as the availability of a significant number of relicts both of European and Asian origins in these forests. The sites of these forests are most valuable for nature conservation and should be protected.

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Appendices and nomenclature

The species names are given in accordance with the checklists for the territory of Russia [34, 35] and some later sources [36].

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