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Current State of Forest Moss Communities after Reduction of Emissions from the Middle-Ural Copper Smelter

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Abstract—The moss cover of forests in a 50 × 36 km area around the Middle-Ural Copper Smelter after the almost complete cessation of its emissions is analyzed. It is shown that moss communities in the low and high pollution zones differ significantly in the composition, number, and occurrence of species and, at the same time, are characterized by a similar cover of ground mosses. The occurrence of most species is lower in the high pollution zones than in the low pollution zones. A significant increase in the occurrence along the pollution gradient has been recorded only for *Pohlia nutans*. Species loss was more significant on the mesoscale (species richness within a community) than on the macroscale (the total number of species in a pollution zone). The elimination of species with an increase in pollution has been recorded for species with a low (up to 40%) initial occurrence. Despite the almost complete cessation of emissions from the smelter, the forest moss cover remains very damaged in the high pollution zones and is represented by a single species (*Pohlia nutans*) over a considerable area. However, localities that are characterized by a higher species richness and a higher similarity of species composition with the background communities occur even under heavy pollution conditions. The presence of these localities, combined with a considerable time lag before the disappearance of species from the whole study area, may have a significant value for recolonization of degraded areas after emission reduction.

Keywords: mosses, diversity, composition, occurrence, pollution, heavy metals

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INTRODUCTION

The study of the consequences of anthropogenic transformation of ecosystems is a topical problem in modern ecology (Cadotte et al., 2012; Cardinale et al., 2012; Bukvareva, 2017). In this context, it is extremely important to analyze the vulnerability of different groups of biota to anthropogenic impacts, which implies an assessment of both the sensitivity to the load and the recovery potential after its reduction.

Bryophytes play a huge role in the regulation of the soil microclimate, biogeochemical cycles, and other parameters of ecosystems (Turetsky, 2003; Turetsky et al., 2012). At the same time, bryophytes are very sensitive to pollution (Pescott et al., 2015; Dittrich et al., 2016; Rola and Osyczka, 2018) and changes in general environmental conditions (Oishi and Morimoto, 2016; Becker-Scarpitta et al., 2017) due to the features of their anatomical and morphological structure.

The degradation of the moss cover of forest ecosystems in the impact zone of metallurgical plants and the high sensitivity of most bryophyte species to pollution have been demonstrated in a number of studies (*Lesnye ekosistemy*..., 1990; Kabirov et al., 1992; Chernenkova et al., 1995; Gol'dberg, 1997; Yarmishko et al., 2009; Freedman and Hutchinson, 1980; Salemaa et al., 2001); however, most of them were carried out in northern regions. In turn, there are single studies on the technogenic impact on moss cover in the Middle Urals, a region with many large industrial enterprises (Gol'dberg, 1997).

Until recently, the Middle-Ural Copper Smelter (MUCS) was one of the largest sources of pollution: its annual emissions were 225000 tons of pollutants in 1980 (Vorobeichik et al., 2014). The long-term input of pollutants resulted in a significant degradation of forest ecosystems around the smelter (Vorobeichik et al., 1994). In particular, the diversity of bryophytes in dark-coniferous forests decreased from 24 to one species (Gol'dberg, 1997). The input of pollutants has gradually decreased over the past few decades (Vorobeichik and Kaigorodova, 2017), which has initiated the recovery of some groups of biota even in the immediate vicinity of the plant (Vorobeichik and Nesterkova, 2015; Mikhailova, 2017, 2020; Vorobeichik et al., 2019, 2020). At the same time, the recovery of the diversity and abundance of some other groups, e.g., plants of the herb–dwarf-shrub layer of forests, is almost completely absent in the high pollution zones (Vorobeichik et al., 2014; Trubina, 2020), which was also recorded after the reduction of emissions from other metallurgical enterprises (Yarmishko et al., 2009; Chernenkova et al., 2011). The capability of bryophytes for regeneration after emission reduction is not really known.

The purpose of this study was to analyze the current state of the forest moss cover after the almost complete cessation of emissions from the Middle-Ural Copper Smelter. The authors tested the hypothesis of the absence of rapid regeneration of moss communities: despite the significant reduction in emissions, the number and abundance of moss species will remain lower in heavily polluted areas than in slightly polluted ones. This hypothesis is based on the assumption that the high sensitivity of mosses to environmental pollution with heavy metals (*Lesnye ekosistemy*..., 1990; Gol'dberg, 1997; Freedman and Hutchinson, 1980; Salemaa et al., 2001), combined with the retention of high metal concentrations in the litter and soil (Vorobeichik and Kaigorodova, 2017), continues to limit the regeneration of the moss cover significantly.

MATERIALS AND METHODS

This research was carried out in the vicinity of the Middle-Ural Copper Smelter, located on the outskirts of the town of Revda, 50 km west of the city of Yekaterinburg. The main ingredients of emissions are gaseous compounds of sulfur, fluorine, and nitrogen, as well as dust particles with sorbed heavy metals (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As). The enterprise has been operating since 1940; the annual gross emissions of the MUCS reached 150000–225000 tons in the 1980s; it decreased to 65000 tons by the early 2000s and 3000–5000 tons after the cardinal renewal of the enterprise in 2010 (Vorobeichik and Kaigorodova, 2017). According to the physical-geographical zoning, the territory is part of the southern taiga subzone (the province of Middle Ural low mountains); the absolute elevations are 100 to 450 m a.s.l. (Prokaev, 1976).

We analyzed the results of descriptions of the moss cover that were carried out during the period of low emissions from the enterprise (2014–2016) at 110 sample plots (SPs) (25 × 25 m), which were laid in forest phytocenoses at a distance of not less than 1 km from each other in a 50 × 36 km area around the plant. The sample plots differed in the type of landscapes (eluvial, transitional, and accumulative landscapes), soil type (gray forest, brown mountain-forest, and sod-podzolic soils), and vegetation (birch, pine–birch, pine, and spruce–fir forests of various associations). The choice of SPs was based on the following criteria: the absence of recent fires and strong anthropogenic impact not related to the pollution; the distances between the SPs and highways should exceed 100 m; and the age of the tree layer edificators should exceed 80 years.

The toxic load was estimated using the index characterizing the average excess over the regional background concentrations of acid-soluble forms of Cu, Cd, Pb, and Zn in the forest litter (Vorobeichik, 2003) (their concentrations in forests of Sysert district, Sverdlovsk oblast: 23.6 μg/g Cu, 1.1 Cd, 17.4 Pb, and 147.8 Zn). Metal concentrations were determined in samples collected in the years 1995–1998 (a sample was suspended in a tenfold volume of 5% HNO_3, shaken, and extracted over 24 h. The concentration was determined by atomic absorption on an AAS-3 spectrometer (Analytik Jena, Germany). Three averaged litter samples were taken from each SP. The toxicity index in the area studied varied from 2.3 to 132.1 arb. units. During the analysis, the gradient was divided into five zones of pollution: background pollution (I), low pollution (II), moderate pollution (III), high pollution (IV), and very high pollution (V), 21–23 SPs per each zone. The currently available data (Vorobeichik and Kaigorodova, 2017; Vorobeichik et al., 2014) indicate an extremely slow release of HMs from the soil after the reduction of emissions from the MUC plant; however, the concentration of HMs in the litter, which was used to determine the toxicity index, decreases more rapidly. Since it was necessary to assess the diversity of the former pollution zones that we previously differentiated during the period of high emissions from enterprises (Trubina and Vorobeichik, 2012) where the state of the vegetation cover (Trubina, 2020) and other components of ecosystems (Vorobeichik and Nesterkova, 2015) is monitored, we used data on the HM concentration in the samples from 1995–1998 in this study.

The variety of species was characterized using two indices: the species richness (SR) (number of species in the area of 625 m^2) and the total number of species within the pollution zone. The SR index characterizes the species diversity on the mesoscale (hundreds of meters) and total species number on the macroscale (km). The species composition of mosses in each SP was determined on the main substrates (soil, forest litter, bark of living trees, and dead wood). Twenty squares (50 × 50 cm) were randomly laid in each SP to determine the projective cover of ground mosses.

The significance of the influence of the load zone on the test parameters was estimated using the Kruskal–Wallace test. The occurrence of species in several pollution zones was compared using the two-way Student's *t*-test. During the comparison, we used the fourth level of significance ($p < 0.10$) to emphasize the beginning of significant changes in the occurrence of a certain species. The degree of transformation of communities along the pollution gradient was estimated by the average similarity of the species composition between the communities from different zones for all combinations (IS_1) and by the structural similarity between the communities from different zones according to the combined lists, taking into account the occurrence of the species (IS_2). The Bray–Curtis index was used as a similarity measure for the qualitative and quantitative data. The degree of differentiation of communities from different pollution zones was visualized using cluster analysis. Calculations were made in PAST v4.0 and Statistica v7.0 (StatSoft, Inc.).

RESULTS

A total of 50 moss species belonging to 32 genera, 18 families, and six orders were identified throughout the studied area (Table 1). The most representative orders are Hypnales (26 species), Bryales (ten species), and Dicranales (nine species). The dominant families were Brachytheciaceae (eight species), Dicranaceae (seven species), and Mniaceae (five species).

In the background pollution zone (I), a high occurrence (over 50%) was recorded for *Brachythecium salebrosum*, *Pleurozium schreberi*, *Dicranum montanum*, *Plagiomnium cuspidatum*, *Sanionia uncinata*, *Sciurohypnum oedipodium*, *S. reflexum*, and *Amblystegium serpens.* In the low pollution zone (II), the occurrence of most species differed little from that in zone I; however, a number of new species were recorded here. The occurrence of *Stereodon pallescens* decreased statistically significantly in this area; the occurrence of *Pylaisia polyantha*, *Climacium dendroides, Callicladium haldanianum*, *Dicranum montanum*, and *Hylocomium splendens* decreased at the trend level. In the following zones III–V, a significant decrease in the occurrence (up to elimination from the communities) was recorded for most species. *Bryum pseudotriquetrum*, *B. weigelii*, and *Oncophorus wahlenbergii* were recorded among the newly emerged species in zones III and IV; however, their occurrence was very low and they were no longer recorded in zone V. The decrease in the occurrence of a number of species (*Brachythecium salebrosum*, *Sciurohypnum oedipodium*, and *S. reflexum*) was recorded only in the zone of very high pollution (V).

An increase in the occurrence of species at intermediate pollution levels, followed by their decrease in the high pollution zone, was recorded for *Tetraphis pellucida*. The occurrence of *Ceratodon purpureus* and, in particular, *Pohlia nutans* increased along the pollution gradient (the occurrence of the latter species increased by almost two times in the high pollution zone compared to the background zone). Species with a low occurrence had statistically insignificant changes along the pollution gradient; however, negative changes were recorded for almost all of them after the increase in the load: a decrease in the occurrence and elimination from the communities (see Table 1).

The moss cover increased with growth in the pollution level (Table 2); however, these changes were statistically insignificant. The SR differed in different zones ($H_{4.109} = 55.7$; $P < 0.001$): lower values were recorded in zones IV ($P < 0.001$) and V ($P < 0.001$). The moss cover and SR varied significantly in all pollution zones and could differ by an order of magnitude. In zone V, only one species, *Pohlia nutans*, occurred on a significant part of the plots (52%); however, the SR amounted to eight–ten species in some of the plots. The total number of species was the highest in zone II and decreased only in zones IV and V. On the whole, the SR decreased by 3.3 times and total number of species, by 2.2 times in zone V compared to the background zone.

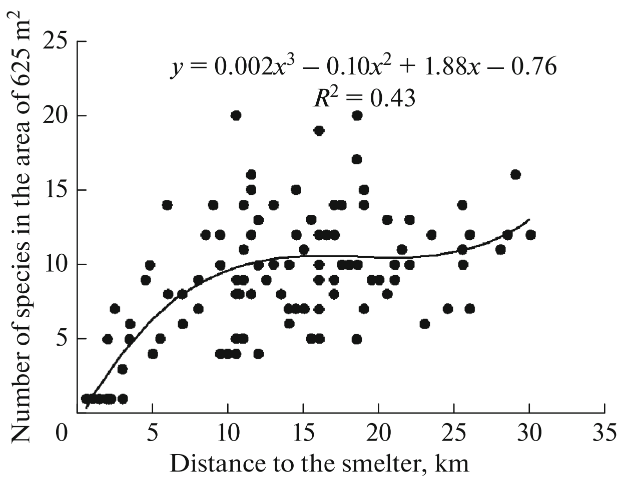

Fig. 1. Variation in the species richness of mosses depending on the distance to the smelter.

The dependence of the SR on the distance to the smelter was nonlinear; it can be satisfactorily approximated by a third-degree polynomial (Fig. 1). The SR began to decrease significantly at a distance of 10 km. Within the radius of 2 km from the emission source, the moss cover was generally represented by only one species (*Pohlia nutans*).

The IS_1 between the communities from the background zone and other pollution zones varied in a very wide range, from 0 to 0.86 (see Table 2). Zero similarity was recorded only between the communities from the background zone and zone V. However, high IS_1 values (up to 0.82) were recorded in some plots between the communities from zone V and the background zone. On the whole, zones II and III were characterized by a high similarity of the species composition with the background zone; the lowest similarity was recorded for zone V. The IS_2 changed in a similar way with an increase in pollution. Analysis of the similarity between the combined lists, taking into account the occurrence of species, clearly differentiates three clusters: the first cluster includes zones I and II, the second includes zones III and IV, and the third

Table 1. Occurrence of moss species in several pollution zones, %

Species	Order	Family	Pollution zone				
			I	II	III	IV	V
1	2	3	4	5	6	7	8
Amblystegium serpens	Hypnales	Amblystegiaceae	52	39	48	33	10**
A. serpens var. *juratzkanum*	Hypnales	Amblystegiaceae	5	13	4	–	–
Atrichum undulatum	Polytrichales	Polytrichaceae	10	17	–	–	–
Brachytheciastrum velutinum	Hypnales	Brachytheciaceae	5	–	–	5	–
Brachythecium rutabulum	Hypnales	Brachytheciaceae	–	9	4	–	–
B. salebrosum	Hypnales	Brachytheciaceae	90	70	96	81	33***
Bryum caespeticium	Bryales	Bryaceae	–	–	9	5	–
B. pseudotriquetrum	Bryales	Bryaceae	–	–	4	–	–
B. weigelii	Bryales	Bryaceae	–	–	–	5	–
Callicladium haldanianum	Hypnales	Pylaisiaceae	33	13	4*	–*	10†
Calliergon cordifolium	Hypnales	Calliergonaceae	–	4	–	–	5
Campylidium sommerfeltii	Hypnales	Amblystegiaceae	–	4	–	–	–
Ceratodon purpureus	Dicranales	Ditrichaceae	–	9	9	–	14
Cirriphyllum piliferum	Hypnales	Brachytheciaceae	–	17	–	5	–
Climacium dendroides	Hypnales	Climaciaceae	33	17	9†	–**	–**
Dicranum bonjeanii	Dicranales	Dicranaceae	–	4	–	–	–
D. flagellare	Dicranales	Dicranaceae	10	–	4	–	–
D. flexicaule	Dicranales	Dicranaceae	–	9	–	–	–
D. fuscescens	Dicranales	Dicranaceae	14	13	9	5	5
D. montanum	Dicranales	Dicranaceae	62	39	13**	10***	10***
D. polysetum	Dicranales	Dicranaceae	–	9	9	–	–
D. scoparium	Dicranales	Dicranaceae	24	22	22	5†	–*
Eurhynchiastrum pulchellum	Hypnales	Brachytheciaceae	5	4	–	–	–
Hylocomium splendens	Hypnales	Hylocomiaceae	38	22	4**	5**	–***
Mnium spinulosum	Bryales	Mniaceae	–	4	–	–	–
Oncophorus wahlenbergii	Dicranales	Rhabdoweisiaceae	–	–	4	5	–
Oxyrrhynchium hians	Hypnales	Brachytheciaceae	–	9	13	–	–
Plagiomnium cuspidatum	Bryales	Mniaceae	76	87	52†	33**	10***
P. drummondii	Bryales	Mniaceae	10	4	9	–	–
P. ellipticum	Bryales	Mniaceae	–	17	4	5	10
P. medium	Bryales	Mniaceae	5	4	–	5	–
Plagiothecium curvifolium	Hypnales	Plagiotheciaceae	5	4	–	–	–
P. denticulatum	Hypnales	Plagiotheciaceae	5	13	4	5	–
P. laetum	Hypnales	Plagiotheciaceae	29	39	30	5*	–*
Platygyrium repens	Hypnales	Pylaisiadelphaceae	5	–	–	–	–
Pleurozium schreberi	Hypnales	Hylocomiaceae	90	91	83	52**	14***
Pohlia nutans	Bryales	Mielichhoferiaceae	48	87	87	90	95**
Polytrichum commune	Polytrichales	Polytrichaceae	–	4	–	–	–
P. juniperinum	Polytrichales	Polytrichaceae	10	13	–	–	–
Ptilium crista-castrensis	Hypnales	Pylaisiaceae	5	9	17	5	–
Pylaisia polyantha	Hypnales	Pylaisiaceae	38	13†	17	10*	–**
Rhodobryum roseum	Bryales	Bryaceae	19	30	9	10	–*

Table 1. (Contd.)

Species	Order	Family	Pollution zone				
			I	II	III	IV	V
1	2	3	4	5	6	7	8
Rhytidiadelphus subpinnatus	Hypnales	Hylocomiaceae	24	26	9	–*	–*
Rhytidiadelphus triquetrus	Hypnales	Hylocomiaceae	5	4	–	–	–
Sanionia uncinata	Hypnales	Scorpidiaceae	90	96	91	71†	24***
Sciurohypnum oedipodium	Hypnales	Brachytheciaceae	81	78	91	86	38**
S. reflexum	Hypnales	Brachytheciaceae	100	96	100	90	38***
Sphagnum squarrosum	Sphagnales	Sphagnaceae	–	4	–	–	–
Stereodon pallescens	Hypnales	Pylaisiaceae	29	4*	4*	–**	–**
Tetraphis pellucida	Tetraphidales	Tetraphidaceae	29	61*	35	19	5*

The dash indicates the absence of the species. Significance level of differences with the background zone in the proportion of colonized sample plots: †, $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2. Moss cover parameters in several pollution zones

Parameter	Pollution zone				
	I (background pollution)	II (low pollution)	III (moderate pollution)	IV (high pollution)	V (very high pollution)
Distance to the smelter, km	11.5–30	9.5–28.5	8–26	3.5–16	0.6–8
Load index, arb. units	2.3–4.2	4.4–6.9	7.0–14.4	16.6–37.4	40.0–132.1
Cover, %	$\frac{8.9 \pm 2.9}{0.4–58.5}$	$\frac{12.9 \pm 2.1}{0.9–35.5}$	$\frac{16.8 \pm 4.2}{0.6–74.3}$	$\frac{12.4 \pm 2.1}{0.9–27.4}$	$\frac{18.2 \pm 4.0}{0.3–54.7}$
Number of species in the area of 625 m^2	$\frac{11.7 \pm 0.7}{7–20}$	$\frac{12.2 \pm 0.8}{6–20}$	$\frac{9.8 \pm 0.6}{5–15}$	$\frac{6.9 \pm 0.6}{4–14}$	$\frac{3.6 \pm 0.7}{1–10}$
Total number of species	33	43	33	25	15
IS_1 with the background zone	–	$\frac{0.56 \pm 0.01}{0.26–0.86}$	$\frac{0.58 \pm 0.01}{0.25–0.84}$	$\frac{0.52 \pm 0.01}{0.22–0.86}$	$\frac{0.25 \pm 0.01}{0.0–0.82}$
IS_2 with the background zone	–	0.80	0.78	0.67	0.35

The numerator is the arithmetic mean ± standard error, and the denominator is the limits.

includes only zone V, which is most isolated from the others (Fig. 2).

DISCUSSION

The communities from different pollution zones differed significantly in their composition, number, and occurrence of species. Despite the reduction of emissions over the past few decades, the species richness and total number of species, as well as the occurrence of most species, were significantly lower in the zones of high and very high pollution than in the background and low pollution zones (see Tables 1 and 2). This fully confirms our hypothesis.

The decrease in the number of species and the corresponding increase in the toxic load towards the source of emissions, as well as the high sensitivity of most moss species to pollution, have been demonstrated in many works (*Lesnye ekosistemy*..., 1990; Freedman and Hutchinson, 1980; Chernenkova et al., 1995; Yarmishko et al.., 2009; Salemaa et al., 2001), and our results are quite consistent with them. An increase in the occurrence along the load gradient was revealed only for two species, *Ceratodon purpureus* and *Pohlia nutans* (postfire succession pioneers) (Dyachenko, 1999; Uotila and Kouki, 2005; Uotila et al., 2005), which is also consistent with the findings about their high tolerance to environmental pollution with heavy metals (Freedman and Hutchinson, 1980; Gol'dberg, 1997; Salemaa et al., 2001; Rola and Osyczka, 2018). It is important to note that some species occurred less frequently even under moderate pollu-

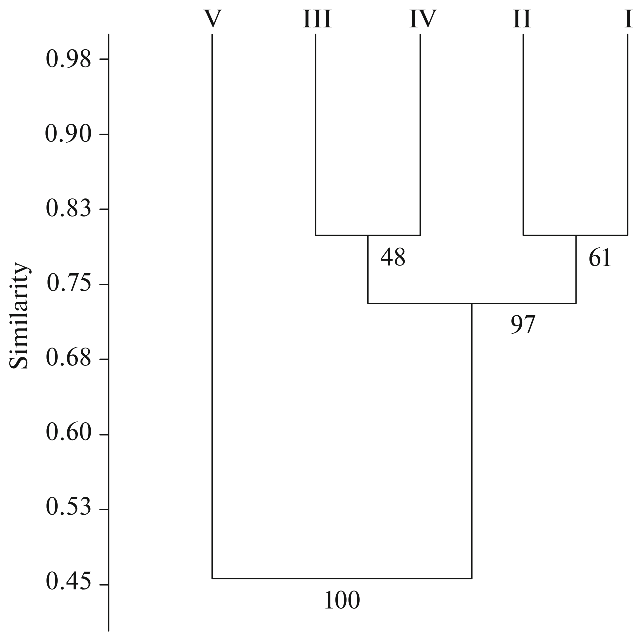

Fig. 2. Similarity dendrogram of moss communities from several pollution zones; the bootstrap support numbers are given under the lines.

tion conditions. As a result, the moderate pollution zone was more similar to the high pollution zone, rather than to the low pollution zone, with respect to the composition and structure of communities (see Table 1, Fig. 2).

The pattern of change in moss diversity along the toxic load gradient (the decrease in the number of species only in the high load zone and the less significant decrease in the total number of species (the diversity on the macroscale) than the decrease in the species richness (the diversity on the mesoscale)) is similar to changes in the diversity of vascular plants of the herb–dwarf-shrub layer in the area studied (Trubina and Vorobeichik, 2012; Trubina, 2020).

Unlike the moss diversity, the ground moss cover slightly increased along the load gradient. In heavily polluted habitats, this was determined by the overgrowth of a single species, *Pohlia nutans*. These results are fully consistent with the earlier data for dark-coniferous forests near the MUCS (Gol'dberg, 1997). The increase in the ground moss cover may be related to a significant decrease in the number and abundance of species of the herb–dwarf-shrub layer in these plots along the load gradient (Trubina, 2020), since the competition between mosses and vascular plants for resources is a well-known phenomenon (Van der Wal et al., 2005; Turetsky et al., 2012; Soliveres et al., 2018). This explanation is indirectly confirmed by the above-described transition of *Pohlia nutans* to the new substrate along the pollution gradient: in unpolluted habitats, the species grows on decaying wood, stem bases, and tree roots protruding from the soil and actively colonizes litter and soil with an increase in pollution (Gol'dberg, 1997). In this study, we did not evaluate the moss cover on trunks of living trees and decaying wood; however, it should be emphasized that changes in the cover on these substrates along the pollution gradient may differ from changes in the ground moss cover.

The absence of data on the state of the moss cover for the plots studied during the period of high emissions does not allow us to characterize directly the recovery dynamics after the reduction of emissions. However, comparison of our data on the correlation between species richness and the distance to the emission source with the results of studies that were carried out in dark-coniferous forests in 1994 (Gol'dberg, 1997) shows the absence of any significant positive changes in the species richness of mosses in the immediate vicinity of the smelter. Thus, only one species, *Pohlia nutans*, was recorded within a radius of 2 km from the smelter and ten species were recorded at a distance of 4 km (two to six species per SP) in 1994, i.e., during the period of high emissions from the MUCS. According to our data, only *Pohlia nutans* was recorded in all SPs within a radius of 2 km (five species were found in only one case); within a radius of 4 km, the maximum number of species was 7 in the SPs (see Fig. 1). All of this indicates the long-term preservation of the degraded state of the moss cover in the zone of very high pollution and is quite consistent with the findings about the extremely slow regeneration of the forest ground cover after the reduction of industrial emissions (Yarmishko et al., 2009; Chernenkova et al., 2011; Vorobeichik et al., 2014; Trubina, 2020). One of the possible causes of this slow regeneration may be the retention of high concentrations of heavy metals in the soil and litter for decades after the reduction of emissions (Vorobeichik and Kaigorodova, 2017). A significant decrease in the number and abundance of species (the low number of diasporas) combined with a high level of habitat fragmentation (the increase in the distance to the sources of diasporas) may also serve as a limiting factor for the species colonization after the reduction of emissions.

The results of the study indicate a high variation of the parameters of the moss cover in all pollution zones. The diversity and abundance of mosses can be influenced significantly by a number of factors (Turetsky et al., 2012; Oishi and Morimoto, 2016), and assessment of their contribution to the dynamics of the number and abundance of species under conditions of long-term pollution requires separate analysis. The observed very high pollution of localities of quite a large number of species and the great similarity of the species composition with the communities from the low pollution zone (see Table 2) seem to be of particular importance. We previously recorded a similar situation in the area studied for vascular plants of the herb–dwarf-shrub layer (Trubina and Vorobeichik, 2012; Trubina, 2020). The presence of these localities may be determined not only by a high uneven distribution of toxicants in the area, but also by the heterogeneity of environmental conditions (different shading and moisture conditions, the presence of substrates suitable for colonization, etc.).

CONCLUSIONS

The above-presented registration of the current state of the moss cover shows that the moss communities in the zones of low and high pollution by MUCS emissions differ significantly in the composition, number, and occurrence of species and, at the same time, are characterized by a similar cover of ground mosses. The occurrence of most species, including many typical representatives of forest communities (*Hylocomium splendens*, *Pleurozium schreberi, Plagiomnium cuspidatum*, *Dicranum montanum*, *Sanionia uncinata, Tetraphis pellucida, Amblystegium serpens*, *Callicladium haldanianum*, *Climacium dendroides*, *Rhytidiadelphus triquetrus*, etc.) decreased in the high pollution zones compared to the background and low pollution zones. The elimination of species from communities with an increase in pollution was generally recorded for species with a low initial occurrence (up to 40%). For frequently occurring species (above 50%), we observed only a decrease in their involvement in communities rather than their elimination. A significant increase in the occurrence along the pollution gradient was recorded only for *Pohlia nutans.*

The total number of species in the pollution zone (i.e., the diversity on the macroscale) decreases less significantly than the species richness within a sample plot (i.e., the diversity on the mesoscale). Under very high pollution, more than half of the species disappear from the communities and the moss cover is represented by a single species, *Pohlia nutans*, in almost half of the plots.

The long-term extremely low species diversity and occurrence of most species in the polluted areas despite the multiple reduction of industrial emissions over the past decades, indicates a significant stability of the degraded state of the forest moss cover under these conditions. At the same time, the composition and number of species and the ground moss cover vary significantly in all pollution zones, including zones of high pollution, where there are localities with a relatively larger number of species and higher similarity of the species composition with communities from background and low pollution zones. The presence of these localities may be important for the further recolonization of degraded areas and moss cover regeneration.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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