

Long-Term Dynamics of Epiphytic Lichen Communities in the Vicinity of Karabash Copper Smelter

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Abstract—The long-term (2001, 2010, and 2023) dynamics of the structure of epiphytic lichen communities on birch trunks were analyzed following the reduction of emissions from the Karabash Copper Smelter (Chelyabinsk oblast, Russia). A survey conducted in 2023, 7 years after emissions nearly ceased, revealed an increase in lichen species diversity in the background and buffer zones, partly due to the emergence of highly pollution-sensitive species. At the same time, the communities of the impact area are in an impoverished state, dominated by toxic-tolerant species, whose abundance remained unchanged throughout the study period. The consistent increase in similarity between the buffer and background zones suggests that recovery has begun, though at the time of the study, it was confined to the less polluted areas.

Keywords: dynamics, recolonization, natural recovery, resistance, heavy metals, copper, sulfur dioxide, industrial pollution, South Urals

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INTRODUCTION

Reducing or stopping emissions from industrial enterprises initiates restoration processes in ecosystems that have been under long-term toxic influence. This provides an opportunity to study the patterns of recolonization in disturbed habitats. A comparative analysis of the rates of restoration of various ecosystem components in different habitats and natural zones is important. To date, extremely slow rates of restoration of communities of higher vascular plants have been demonstrated [1–4]. The reason for the significant time lag is the long-term persistence of high concentrations of metals in the soil and forest litter [5, 6]. Groups of organisms not directly linked to the pool of toxicants in the soil undergo the first stages of recolonization faster, as shown for epiphytic and epixylic lichens and epixylic mosses [7, 8]. However, subsequent stages of restoration of these groups take significantly longer: in the vicinity of the copper-nickel plant in Sudbury (Canada), where the longest-term studies to date have been conducted, restoration of the species richness of lichens to background levels was recorded only 40 years after the cessation of emissions [9]. To verify the obtained patterns, further information is necessary.

Objective—To analyze the dynamics of the composition and structure of epiphytic lichen communities

under conditions of changing emissions from a large copper smelter in the Southern Urals. The Karabash Copper Smelter (KCS), which has been operating since 1910, has long been one of the largest sources of industrial pollution not only in Russia but also in the world, and so has repeatedly attracted the attention of environmentalists [10–12]. To study the spatial distribution of metals and identify their sources in the region, lichen transplantation methodology was used [13–15]. This makes the area convenient for comparative analysis of the spatiotemporal dynamics of ecosystem components due to the dynamics of atmospheric pollution.

Our work is based on the results of three surveys of epiphytic lichen communities conducted at the same sites during periods of high, declining, and almost completely ceased emissions. This study tested the following hypotheses: (1) a reduction in the toxic load initiates the restoration of epiphytic lichen communities; (2) the rate of restoration depends on the initial degree of disturbance of the area.

RESEARCH AREA

The KCS is located within the city of Karabash (Chelyabinsk oblast, 90 km northwest of Chelyabinsk, 55°27' N, 60°12' E), on the eastern macroslope of the

Table 1. The number of trees examined and their diameter in different load zones

Indicators	Background			Buffer			Impact		
	2001	2010	2023	2001	2010	2023	2001	2010	2023
Number of trees	20	30	30	20	40	40	20	20	20
Trunk diameter, cm:									
Mean ± SD	29 ± 4	28 ± 3	32 ± 3	27 ± 5	25 ± 4	29 ± 4	25 ± 4	24 ± 4	29 ± 4
Range	23–37	22–33	26–41	13–40	19–38	21–40	20–34	20–32	24–41

Southern Urals, in the subzone of pre-forest-steppe birch-pine forests. The climate of the region is moderately continental, the average annual precipitation is 523 mm, the average annual temperature is 0.1°C, the average temperature of the warmest month (July) is 5.7°C, and the coldest (January) is –16.3°C [16].

The main components of KCS emissions are sulfur dioxide and metal-containing dust (Cu, Pb, Zn, Cd, Fe, Hg, and As). During the period of maximum emissions (1960–1970), their level reached 210000–290000 tons per year. In the late 1980s, emissions dropped to 15000–160000 t/year, after which production was suspended in 1990 until 1997. In 2000–2002, emissions were about 100000 t/year, in the mid-2000s—30000–40000 t/year, in 2010—13000–14000 t/year, and after 2015—5000–6000 t/year [17, 18]. The history of production and pollution is described in detail in [17].

MATERIALS AND METHODS

The first survey of epiphytic lichen communities was conducted in 2001 on 12 sample plots located along transects north and south of KCS. In 2010, 9 permanent marked sample plots were established: 4 plots at a distance of 5, 11, 18, and 32 km from KCS in the northern direction and 5 plots at a distance of 4, 9, 12, 26 and 27 km from KCS in the southern direction (Fig. 1). In 2023, they were re-described. Of the 12 plots surveyed in 2001, 7 were included in the analysis, coinciding in location with the permanent plots (the difference in their location does not exceed 50–100 m). The plots are grouped into three pollution zones (background, buffer, and impact) according to the content of metals in the forest litter and the state of the vegetation cover [18].

Sample plots were established in birch forests. In the background area, the grass-shrub layer was dominated by *Pteridium latiusculum* (Desv.) Hieron. ex Fries, *Calamagrostis arundinacea* (L.) Roth, *Vaccinium myrtillus* L., *Rubus saxatilis* L., and *Carex* spp. The buffer zone was dominated by *Fragaria vesca* L., *C. arundinacea*, *R. saxatilis*, *Vaccinium vitis-idaea* L., *Brachypodium pinnatum* (L.) Beauv., *Lathyrus vernus* (L.) Bernh., *Galium boreale* L., *Veronica chamaedrys* L., and *P. latiusculum*. In the impact zone, 90% of the surface is almost devoid of vegetation, with isolated

occurrences of *C. arundinacea*, *Agrostis capillaris* L., *Deschampsia cespitosa* (L.) P. Beauv., *Festuca rubra* L., and *V. vitis-idaea* [18, 19].

Within each sample plot, descriptions of epiphytic lichen communities were made on ten birch trunks (*Betula pendula* Roth). The characteristics of the examined trees are given in Table 1. The diameter of the trunks examined in 2001 and 2010 in the impact zone was smaller than in the background and buffer zones, which is consistent with the younger age of the stands in this area: according to data from 2009 [16], the average age of the stands in the impact zone was 45–69 years, while in the buffer and background zones it was 63–78 and 68–74, respectively. On each trunk, the species composition of lichens was determined, and the frequency of species was assessed using a sliding grid [20] on the side of maximum lichen development at two levels, at the base of the trunk and at a height of 1–1.5 m. Frequency at each level was assessed as the number of grid cells (from 0 to 10) in which the species was encountered. For further analysis, the frequency values at two heights were summed up and expressed as a percentage of the maximum possible (i.e. of 20). The choice of the method for accounting for abundance is based on the results of a study [21], which revealed a higher informative value of metrics based on accounting for frequency using a grid compared to accounting for projective cover using a palette.

Based on the obtained data, the average number of species on the trunk and the sum of the frequency values of all lichen species were calculated. The same metrics were calculated for macrolichens (i.e., species with foliose, fruticose, and squamulose forms of thalli, see Table 2), for which the probability of discrepancies in field identification by different researchers who performed descriptions of communities in different years is minimal.

For the calculated metrics, an analysis of differences between pollution zones and observation periods was performed (two-way ANOVA, accounting unit – tree) and multiple comparisons were carried out using Tukey test. The significance of differences in the species composition of communities in different pollution zones was assessed using the ANOSIM (Analysis of Similarities) test; the SIMPER procedure was used to identify the species that contribute most to

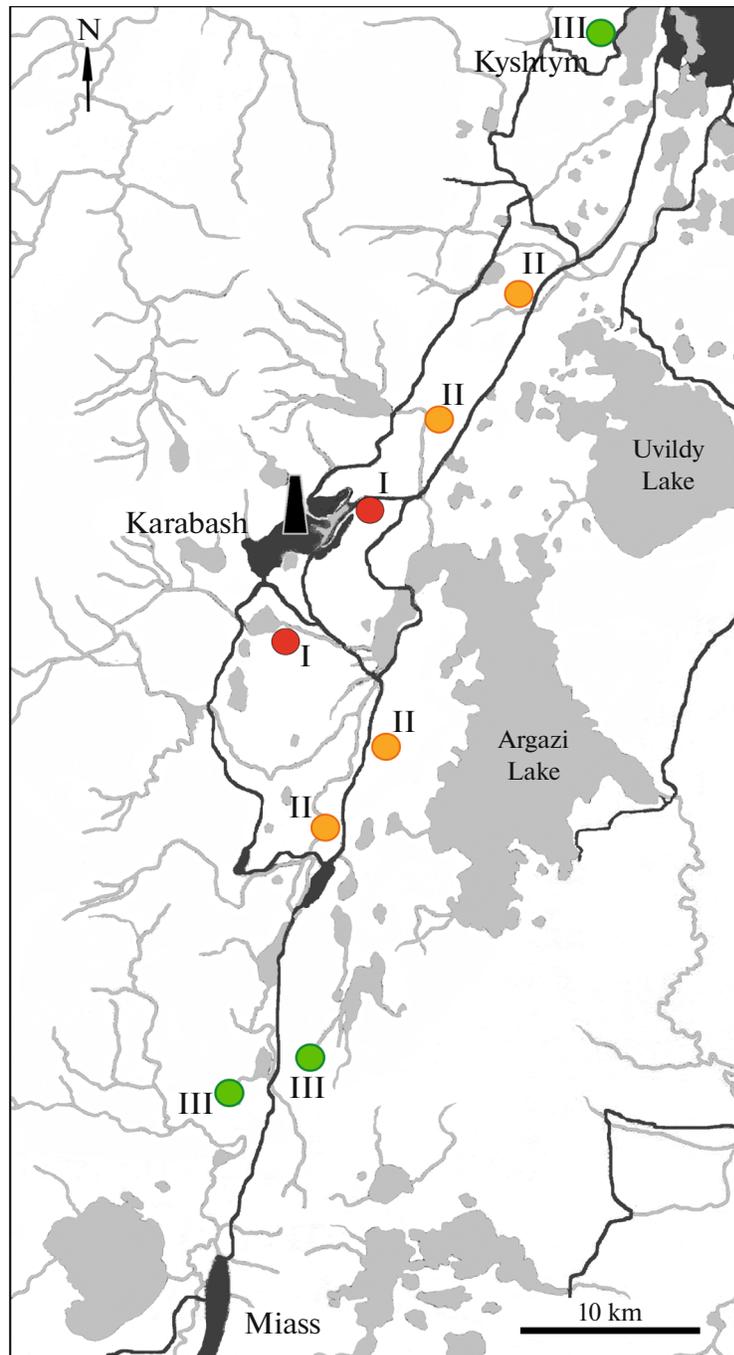


Fig. 1. Layout of sample plots within load zones: I – impact, II – buffer, and III – background.

community differences. Visualization of the dynamics of differences in species composition was performed using the non-metric multidimensional scaling (NMDS), the Bray–Curtis index was used as a distance measure. The analysis was performed using the Statistica 7 and Past 4.17 packages.

The nomenclature of lichens is given in accordance with the ITALIC 8.0 information system [22].

RESULTS

In total, 45 species of epiphytic lichens were identified on birch trunks in the KCS area for three periods (Table 2), of which 8 were recorded only once. The group *Lepraria* spp. includes *Lepraria elobata* Tønsberg, *L. jackii* Tønsberg, and small unidentified specimens. The number of species detected in the background and buffer zones increased from 2001 to 2023. In 2010 and 2023, in both zones *Bryoria nadvorniki-*

Table 2. Occurrence of lichen species in different pollution zones during different observation periods

	Types	Load zone and year of study												
		background			buffer			impact						
		2001	2010	2023	2001	2010	2023	2001	2010	2023				
	<i>Amandinea punctata</i> (Hoffm.) Coppins & Scheid.	-	+	-	-	-	-	-	-	-	-	-	-	-
M	<i>Bryoria nadvornikiana</i> (Gyelnik) Brodo & D. Hawksw.	-	+	++	-	++	-	++	-	++	-	-	-	-
	<i>Buellia disciformis</i> (Fr.) Mudd	+	-	-	-	-	-	-	-	-	-	-	-	-
	<i>B. schaereri</i> De Not.	-	-	+	-	-	-	-	-	-	-	-	-	-
M	<i>Cetraria sepincola</i> (Ehrh.) Ach.	++	++	++	-	++	+	++	-	++	-	+	-	-
	<i>Chaenotheca trichialis</i> (Ach.) Hellb.	-	-	-	-	++	+	++	-	++	-	-	-	-
M	<i>Cladonia botrytes</i> (KG Hagen) Willd.	-	-	+	+	+	+	+	-	++	-	-	-	-
M	<i>Cl. cenotea</i> (Ach.) Schaer.	-	++	+++*	-	++	+	++	-	++	-	-	-	-
M	<i>Cl. chlorophaea</i> (Sommerf.) Spreng.	-	+++	+	-	+++	-	+++	-	+++	-	++	++	++
M	<i>Cl. coniocraea</i> (Flörke) Spreng.	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
M	<i>Cl. digitata</i> (L.) Hoffm.	-	+	++	+	++	+	++	+	+++*	+	++	++	++
M	<i>Cl. fimbriata</i> (L.) Fr.	++	++	++	++	++	++	++	++	++	++	++	++	++
M	<i>Cl. macilenta</i> Hoffm.	-	++	++	-	++	-	++	-	++	-	++	++	++
M	<i>Cl. rei</i> Schaer.	-	-	+	-	-	-	-	-	++	-	++	++	++
M	<i>Evernia mesomorpha</i> Nyl.	+++	+++	+++*	-	+++	-	+++	-	+++*	-	+++	+++	+++
	<i>Fuscidea arboricola</i> Coppins & Tonsberg.	-	++	++	-	++	-	++	-	++	-	++	++	++
	<i>F. pusilla</i> Tonsberg	-	++	+++*	-	+++*	-	+++*	-	+++*	-	+++*	+++*	+++*
M	<i>Hypocenomyce scalaris</i> (Ach. ex Lilj.) M. Choisy.	-	+++	+++*	-	+++*	-	+++*	-	+++*	-	+++*	+++*	+++*
M	<i>Hypogymnia physodes</i> (L.) Nyl.	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
M	<i>H. tubulosa</i> (Schaer.) Hav.	-	+	++	-	++	-	++	-	++	-	++	++	++
	<i>Japewia subaurifera</i> Muhr & Tonsberg.	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Lecanora intumescens</i> (Rebent.) Rabenh.	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>L. pulicaris</i> (Pers.) Ach.	-	++	++	-	++	-	++	-	++	-	++	++	++

Table 2. (Contd.)

	Types	Load zone and year of study									
		background		buffer			impact				
		2001	2010	2023	2001	2010	2023	2001	2010	2023	
	<i>L. saligna</i> (Schrad.) Zahlbr	++++	++++	++++	+++	+++	+++	+	+	+	—
	<i>Lecidea nylanderi</i> (Anzi) Th. Fr.	+	—	—	—	—	+	—	—	—	—
	<i>Lepraria</i> spp.	—	+	++*	++	+++*	+++*	—	—	—	—
M	<i>Melanelixia glabratula</i> (Lamy) Sandler & Arup	+++	++	++	++	++	++	—	—	—	—
M	<i>Melanohalea olivacea</i> (L.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch.	+++	+++	++	++	++	++	—	—	—	++
	<i>Micarea denigrata</i> (Fr.) Hedl.	+++	++	+++	+++	+++	—	—	—	—	—
	<i>M. prasina</i> s.l.	—	+	+	++	++	—	—	—	—	—
M	<i>Parmelia sulcata</i> Taylor	++++	++++	++++	+++	+++	+++	—	—	—	—
M	<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.	++	++	++	++	++	++	—	—	—	—
M	<i>P. hyperopta</i> (Ach.) Arnold	+	++	+	—	+	—	—	—	—	—
M	<i>Physconia</i> sp.	+	+	—	—	—	—	—	—	—	—
	<i>Placynthiella icmalea</i> (Ach.) Coppins & P. James	+++	—	+*	+++	++	++	+++	++	++	+++
	<i>P. uliginosa</i> (Schrad) Coppins & P. James	++	—	—	—	+	—	—	—	—	—
	<i>Pycnora sorophora</i> (Vain.) Hafellner	—	—	+	—	—	—	—	—	—	—
	<i>Scliciosporum chlorococcum</i> (Graewe ex Stenh.) Vězda	+++	++++	++++	++++	++++	+++	+++	+++	+++	++++
	<i>Trapeliopsis flexuosa</i> (Fr.) Coppins & P. James	+++	++	++	+++	+++	+++	+++	+++	+++	+++
M	<i>Usnea subfloridana</i> Stirton	++	++	++	—	+	+	+	—	—	—
	<i>Violella fucata</i> (Stirt.) T. Sprib.	—	—	—	—	—	+	—	—	—	—
M	<i>Vulpicida pinastri</i> (Scop.) J.-E. Mattsson & MJ Lai	++++	++++	++++	+++	+++	+++	—	—	—	—
M	<i>Xylopsora caradocensis</i> (Nyl.) Bendiksby & Tímdal	—	—	+++*	+	++	+++*	—	—	—	+
	Total	20	30	34	15	28	32	9	7	7	7

Species found: (+)—single, (++)—<25% of trunks, (++++)—25–74.9%, (++++)—75–100%; dash—absence of species; *—significant differences between 2001 and 2023 (Fisher's exact test, $p < 0.05$); M—macrolichens.

Table 3. Results of ANOVA for the parameters of epiphytic lichen communities in different pollution zones and observation periods

Indicator	Source of variability		
	zone ($df = 2$)	period ($df = 2$)	zone \times period ($df = 4$)
Full list of species:			
number of species on the trunk	199.46	44.67	10.12
sum of frequency values	181.00	14.71	8.78
Macrolichens:			
number of species on the trunk	269.43	20.44	8.33
sum of frequency values	200.64	19.09	5.19

F-ratio, $p < 0.001$ in all cases.

ana, *Hypogymnia tubulosa*, and *Fuscidea arboricola* were registered, which were not found in 2001. These species are considered to be highly sensitive to atmospheric pollution in the Urals [23]. *Evernia mesomorpha*, a highly sensitive species that in 2001 was noted only in the background area, was recorded in the buffer zone in 2010 and 2023. In the background area, the richness of facultative epiphytes of the genus *Cladonia* increased from two to seven species.

In the impact area, the total number of species has remained virtually unchanged from 2001 to 2023: communities are composed predominantly of *Cladonia coniocraea*, *Placynthiella icmalea*, *Scoliciosporum chlorococcum* and *Trapeliopsis flexuosa*, typical for impact areas of the Urals [7, 20]. In 2001, small (2–3 mm) thalli of pollution-sensitive species including *Hypogymnia physodes* (on two trunks), and *Usnea subfloridana* and *Cetraria sepincola* (both single) were noted, but they were not detected in subsequent observation periods.

Both studied factors, “pollution zone” and “observation period,” have a significant impact on the average number of species on the trunk, both when taking into account all species and only macrolichens (Table 3, Fig. 2). The decrease in the average number of species on a trunk as one approaches the emission source persists in all periods, with all pollution zones differing in pairs in 2001 and 2010, and no significant differences between the background and buffer zones in 2023. The significance of the “observation period” factor is due to the dynamics of the communities of the background and buffer zones, where the number of species on the trunk in 2023 increased significantly compared to previous periods, while in the impact zone this metric remained at the same level over all periods. The visually noticeable, although statistically insignificant, “dip” in the diagram in the background and buffer zones in 2010 is mainly due to a drop in occurrence on trunks *Placynthiella icmalea*: in 2001, the species was noted in the background zone on 35% of trunks, in 2010 it was absent from the list of species, and in 2023 it was noted only once. In the buffer zone, the frequency of this species on trunks also falls from 60% in 2001 to 15% in 2010 and 7.5% in 2023.

The analysis of the sum of frequency values of both the full list of species and macrolichens also demonstrated a significant influence of the factors “pollution zone” and “observation period” on this metric (see Table 3 and Fig. 3). In the impact zone, the frequency of macrolichens in all observation periods is close to zero, and the sum of the frequency of the full list of species is significantly lower ($p < 0.001$) than in other

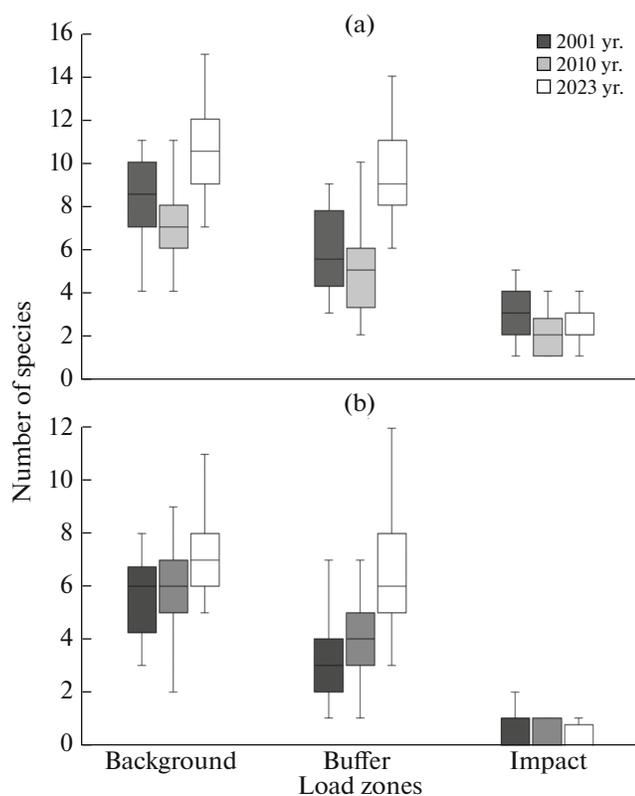


Fig. 2. Dynamics of the average number of lichen species on a trunk: (a) full list of species, (b) macrolichens. The median, first quartile, third quartile, minimum and maximum values are shown.

load zones. No significant differences were found between the observation periods in the impact area.

In the buffer zone, the sum of frequency values of macrolichens is significantly ($p < 0.001$) lower than the background level in all study periods, whereas for the sum of the frequencies of the full list of species, the decrease compared to the background zone is significant only in 2010 (see Fig. 3). In the background area from 2001 to 2023, there has been a consistent increase in the lichen frequency, both when taking into account all species and only macrolichens. In the buffer zone, the sum of frequency values in 2023 exceeds the figures for 2001 and 2010, but in 2010 there is a small “dip,” followed by a sharp increase in figures by 2023 (both according to the full list of species and only macrolichens).

Not only the persistence but also the increasing differences in the species composition of communities along the pollution gradient are confirmed by the results of ANOSIM ($R = 0.53$ in 2001 and 2010, 0.61 in 2023, $p \leq 0.001$). Since the impact zone communities did not undergo changes in any of the analyzed parameters during the observation period, we will pay attention to the dynamics of differences between the communities of the buffer and background zones. In 2001, equality of the sum of occurrences of the full list of species in the background and buffer zones was achieved due to crustose forms, which accounted for 25.9% of the sum of frequency values in the buffer zone compared to 16.8% in the background area. The SIMPER test showed the highest contribution (24.4%) of *Scoliciosporum chlorococcum* in the significance of differences in communities: the frequency of the species was 87% in the buffer zone and only 37% in the background zone. Over subsequent periods, the frequency of the species in the background and buffer zones was almost equal and amounted to 73.5% and 80.5%, respectively, in 2010, and 79.5% and 91% in 2023. In all observation periods, a significant contribution (SIMPER, 18.4%, 24.4%, and 24.1% in 2001, 2010, and 2023, respectively) to the dissimilarity of communities was made by the difference in the abundance of the dominant species *Hypogymnia physodes*: The frequency of the species increased in both zones, but at the same time, 2.5–3-fold differences between the zones remained. A significant contribution to the dissimilarity of communities was also made by *Parmelia sulcata* (from 7.5% to 11.2% in different years), *Lecanora saligna* (12.8–20.8%), *Vulpicida pinastri* (6–11.5%), the abundance of which in the background zone exceeded the buffer values during all observation periods. Thus, the differences between the background and buffer zones are due not so much to differences in species composition as to differences in the abundance of the same species.

The described changes are clearly demonstrated by the NMDS ordination diagram of communities of load zones and survey periods (Fig. 4). The correlation

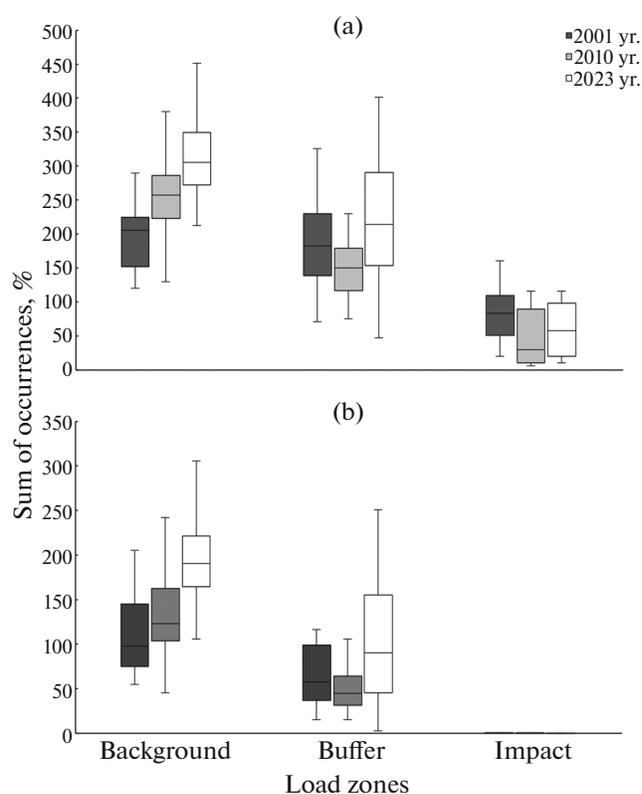


Fig. 3. Dynamics of the sum of lichen frequency values: (a) full list of species, (b) macrolichens. For designations see Fig. 2.

of the x -axis with the pollution level is 0.94; accordingly, the communities of the impact zone are located in the region of positive values and are maximally isolated from the communities of the buffer and background zones. A gradual “convergence” of the communities of the buffer and background zones is clearly visible.

The lack of dynamics in the degree of similarity between communities in the impact and background areas is indicative: the Bray–Curtis index is the same in all three periods (0.30–0.31). At the same time, the similarity of communities in the buffer and background areas increases: the Bray–Curtis index increased from 0.57 in 2001 to 0.68 in 2023.

Thus, in the period from 2001 to 2023, an increase in the number of lichen species and their abundance was observed on the birch trunks of the background and buffer areas in the vicinity of the KCS, while in the impact area the lichen communities remained unchanged.

DISCUSSION OF RESULTS

The dynamics of epiphytic lichen communities in natural conditions is determined by a complex of factors, among which the age of the stand and the specific

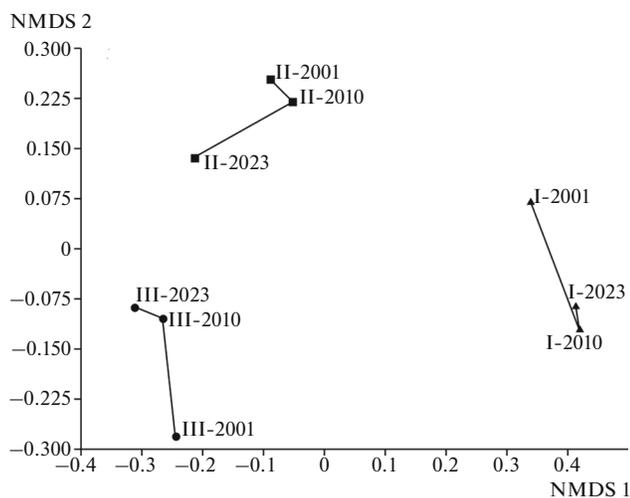


Fig. 4. NMDS ordination of communities from three pollution zones over three survey periods: I—impact, II—buffer, and III—background.

phorophyte are of primary importance. Numerous studies [24–26] have shown an increase in the number of lichen species (including due to the appearance of rare species – indicators of old-growth forests) as the age of the forest stand increases and a typical forest microclimate is formed. The leading role of age and/or diameter of a tree in the dynamics of species richness and structure of epiphytic communities has also been shown by many authors [25, 27–29]. An increase in the age of the substrate and its surface area increases the probability of colonization by lichen diaspores. As the tree ages, the bark becomes more fissured, providing an increase in the number of potential microhabitats [30]. The destruction of the bark in the basal part can explain the increase in the diversity of facultative epiphytes of the genus *Cladonia*, which move to the base of the trunks from the soil and rotting wood. The increase in the number of species during epiphyte succession is also determined by the insignificance of interspecific competition: it is not the replacement of some species by others that is characteristic, but the addition of species to the community [31]. Thus, the dynamics of lichen communities observed by us in undisturbed and slightly disturbed birch forests of the study area match the expected patterns of microsuccessions in epiphytic communities.

In the impact area, despite a sharp decrease in the toxic load, an increase in the age of the tree stand and the size of the trees examined, no significant changes in the species richness and structure of lichen communities were recorded. The only thing that attracts attention is the fact that small specimens of *H. physodes* and *U. subfloridana* were registered in 2001 and subsequently disappeared from the community. Production was stopped in 1990–1997; a time interval of 6–7 years after the cessation of emissions

(complete or almost complete) is indicated in the literature as sufficient for the beginning of the recolonization of lichen deserts near non-ferrous metallurgy plants [32, 33]. The recolonization that began during the plant's downtime was likely stopped by the resumption of KCS operations in 1997. However, in 2023, 7 years after emissions had almost completely ceased, no signs of recolonization were recorded in the same sample plots.

The results provide data for comparative analysis of the duration of lag periods after which the first signs of recolonization of disturbed areas appear. The dynamics of recovery of epiphytic communities was studied in detail in the area of the Middle Ural Copper Smelter (MUCS), located near the city of Revda (Sverdlovsk oblast), an enterprise similar to KCS in composition, volume, and dynamics of emissions (except for the interruption of KCS operations in 1990–1997). As in the KCS region, the near-total cessation of MUCS emissions was preceded by a 10-year period of gradual decline. In the immediate vicinity of MUCS (1–2 km) in spruce-fir forests, small (4–5 mm) thalli *H. physodes* were registered 4 years after the almost complete cessation of emissions [7]. Considering the low rates of development of diaspores and juvenile thalli in spruce-fir forests [34], it should be assumed that the colonization occurred at the stage of decreasing emissions. During detailed mapping of the state of epiphytic communities in birch forests in the MUCS area 5–6 years after the cessation of emissions *H. physodes* thalli were recorded in 51% of the sample plots in the territory of the former “lichen desert” [32], which indicates a high spatial mosaic of the recolonization process. Differences in the rates of recolonization of different habitats within the same stress zone in the MUCS region have also been shown for some species of higher plants [35].

Studies of vascular plants in the KCS area in 1997 did not reveal any signs of recovery in the sparsely vegetated birch forests of the impact zone, but in the mixed-herb birch forests of the background and slightly polluted zones, an increase in the number of species and phytomass was recorded [11]. In the MUCS region, positive shifts in the condition of higher vascular plants during the first 10 years after the almost complete cessation of emissions were also noted mainly in the buffer zone [35]. The observed shift of the lichen community parameters in the KCS buffer zone to the background level (in particular, the appearance of species highly sensitive to pollution) can also be considered as an initial sign of the recovery process. It is possible that the appearance of previously unrecorded highly sensitive species in the communities of the background area is also due to the almost complete cessation of emissions. Many emission components have a significant dispersion radius: this applies primarily to gaseous pollutants (SO_2 , HF, NO_x) [36]. However, long-distance transport of

small-sized solid particles has also been recorded: on thalli *H. physodes* in 2001, at a distance of 30 km from KCS, small (<4 µm) predominantly Zn-containing spherical particles were discovered [37]. An increase in the abundance of lichen species in the background area after the almost complete cessation of emissions was also noted in the MUCS region [32].

Thus, the reduction of industrial emissions to a negligible level leads to a decrease in the regional background level of pollution, which in turn contributes to the natural dynamics of communities in background areas.

CONCLUSIONS

Our research confirmed the tested hypotheses. Cessation of the toxic load initiates the process of restoration of lichen communities in the former contaminated areas. The rate of recolonization is determined by many factors, among which the degree of initial disturbance of the habitat predominates. In the KCS area, 7 years after the almost complete cessation of emissions, recovery was recorded only in the slightly polluted area. The increased similarity of buffer zone communities with background ones is due to the establishment of sensitive species and an increase in the abundance of species typical of slightly disturbed and undisturbed habitats. Lichen communities of the impact area are still impoverished. Further research is needed to refine estimates of the time lag between the cessation of toxic load and the onset of recolonization of the highly contaminated area.

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AUTHOR CONTRIBUTION

I.N. Mikhailova – planning of work, collection of field material, and identification of lichens in 2001 and 2023, processing of material, generalization of results, and writing of the article; O.W. Purvis – planning of work, collection of field material, and identification of lichens in 2001; I.V. Frolov – collection of field material and identification of lichens in 2010.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

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