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Dynamics of Epiphytic Lichen Communities in the Initial Period after Reduction of Emissions from a Copper Smelter

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Abstract—Changes in the composition and structure of epiphytic lichen communities have been analyzed over 5 years (2014–2018) after significant reduction of emissions from the Middle Ural Copper Smelter on the basis of annual observations in 22 permanent sampling plots established in spruce–fir forests of the Middle Urals. Despite the almost complete cessation of toxicant input from the atmosphere, increased Cu concentrations in the fir bark and higher bark acidity persist in the vicinity of the smelter. The number of lichen species in the heavily polluted zone rapidly increases (by 1–2 species per year) primarily on account of species with a high colonization potential that are abundant in adjacent biotopes or on other substrates in heavily polluted areas. The level of their toxitolerance is not the critical factor: both tolerant and moderately and highly sensitive species colonize tree trunks. The current community structure in the polluted zone is basically different from that in the background area: explerent species *Hypocenomyce caradocensis* dominates, while species typical for background spruce–fir forests are rare or absent.

Keywords: dynamics, recolonization, recovery, sustainability, elasticity, heavy metals, copper, sulfur dioxide, industrial pollution, community structure, Middle Urals, bark pH

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The ability of lichens to respond to changes in the chemical composition of the environment is well known. The consequences of increase in toxicant concentrations in the environment have been studied in detail at all organization levels, from subthallomic (elemental composition and biochemical and physiological parameters) to cenotic (community composition and structure) [1, 2]. The data on the patterns of their response to improvement in the habitat quality are less detailed and applies mainly to lichens in urban conditions [3–9]. However, resultant time series are very difficult to interpret due to the specificity of urban environments. For instance, a decrease in the intensity of one factor (e.g. concentration of sulfur compounds) may be accompanied by an increase in the intensity of another one (e.g. concentration of nitrogen compounds); reduction of industrial emissions may be counterbalanced by increasing emissions from motor vehicles; etc. [5, 10].

Point emission sources make it possible to analyze effects in a gradient of the stress factor itself. However, only a few studies are dealing with the recovery of lichens after reduction or cessation of emissions from large industrial sources [11, 12]; furthermore, the state of lichen communities has been assessed long after that (10, 15, or 20 years later). No studies have been performed on a smaller time scale (e.g., annually over several years), although they could provide more accurate data on the rate of changes and the sequence of recolonization by species with different life strategies and sensitivity to environmental disturbances.

The purpose of this study was to analyze, on the basis of annual observations, changes in the species composition and structure of epiphytic lichen communities in spruce–fir forests in the initial period after reduction of emissions from a major copper smelter. The study area is convenient for research on the dynamics of their recovery because data on the state of these communities in 1990–1995 (i.e., during the period of high emissions) are available [13–15]. As early as 10 years after the beginning of emission reduction, we have noted the recolonization of the former lichen desert (1–2 km from the plant) and documented initial changes in the species composition of communities in the rest of the polluted area [16].

We have tested two hypotheses. The first one is that the polluted area is recolonized primarily by species that are abundant in the surrounding biotopes (and, accordingly, produce numerous diaspores). This hypothesis is based on an analogy with postpyrogenic successions [17, 18]. The second hypothesis is that the degree of toxitolerance is not critical for successful colonization. It is supported by our previous data on the colonization of a former lichen desert by not only resistant but also by moderately tolerant species [16] and by data collected in the vicinity of a major copper smelter in Sudbury, Canada [11].

MATERIAL AND METHODS

The studies were performed in the vicinity of the Middle Ural Copper Smelter (MUCS) located near the town of Revda, Sverdlovsk oblast, and operating since 1940. The main toxic components of emissions are sulfur oxides and dust particles with sorbed heavy metals (Cu, Fe, Cd, Zn, Pb, etc.) and metalloids (As). The amount of emissions reached 225000 t of pollutants per year in 1980, 140000 t in the late 1980s, 71000–96000 t in 1995–1998, and 24000–34000 t in 2003–2008. After the fundamental reconstruction of the MUCS in 2010, the amount of emissions decreased to 3000–5000 t per year [19]. Descriptions of the study area, the degree of degradation and recovery dynamics of some objects were published previously [16, 19–21]. The long-term dynamics of lichen communities was analyzed using the data on lichen successions on fir trunks that were obtained in 1990–1992 in three zones with different pollution levels: 4, 7, and 30 km from the MUCS [14]. A total of 190 trees older than 40 years were included in the analysis. The area within a radius of 1–2 km from the polluter (a lichen desert in 1990–1992) was surveyed by the route method.

Descriptions of Lichen Communities

Permanent sampling plots (SPs) have been established in 2014 in spruce–fir forests at distances of 1, 2, 4, 7 and 30 km to the west of the smelter, i.e. opposite to the prevailing wind direction (two SPs at the distance of 1 km and five SPs at every other distance). Five Siberian fir trees (*Abies sibirica* Ledeb.) were selected in each SP, and four permanent microplots (20 × 20 cm) were marked up on each tree (at the trunk base and at the height of 1.3 m on the northern and southern sides). The state of the lichen communities was described annually from 2014 to 2018 (except at 7-km distance in 2016). All lichen species on each trunk were recorded; the abundance of each species within microplots was estimated as a number of 2 × 2 cm cells where the species occurred. The abundance of each species on the trunk (%) was calculated as the proportion of such cells in all the four microplots. The species found outside microplots were assigned abundance of 0.1. The total abundance of lichens on the trunk was calculated as the sum of abundances of individual species. As shown previously [22], this parameter is informative for assessing the state of epiphytic lichen communities along a gradient of toxic impact.

During the observation period, three model trees in background SPs and one tree at 2 km from the smelter were lost due to windfall. The data on these trees were taken into account when assessing the number of lichen species but not included in the analysis of their abundance dynamics.

Analysis of Bark Chemistry

In 2015, samples of the outer bark layer (1–3 mm) were collected from five fir trunks in each SP at heights of 1–1.3 m (evenly around the trunk). In the laboratory, the bark was cleaned of lichens and other foreign matters and ground in a laboratory mill. To measure bark pH, the samples were immersed in deionized water at a 1 : 25 ratio, placed on a shaker for 30 min, and left in closed vials for 1.5 h. Measurements were made with an inoLab740 ionometer (WTW, Germany). The total copper content was measured with an AAS 6 Vario atomic absorption spectrophotometer (Analytik Jena AG, Germany) with flame atomizer. The samples for analysis were prepared by digestion in 65% HNO_3 using the MWS-2 microwave pressure digestion system (Berghof, Germany).

Statistical Data Processing

Statistical analysis was performed using STATISTICA v. 8.0 and PAST 3.12. software packages. Mixed-effect nested ANOVA was used to assess the influence of pollution on chemical properties of the bark, with a tree taken as a statistical unit and SP as a random factor nested in the pollution zone. Multiple comparisons were made using the Tukey test. The significance of differences in species abundance in the beginning and the end of the observation period was estimated using Wilcoxon matched pairs test. The Bray–Curtis coefficient for quantitative data was used to compare species composition of the communities.

RESULTS

Bark Chemistry

The pH of the bark in the vicinity of the plant is 0.3 units lower than in the background area (Fig. 1, $F_{4;86} = 25.5$, $p < 0.001$). The differences between SPs within the polluted zone are also significant ($F_{17;86} = 2.1$, $p < 0.05$). Multiple comparisons have revealed no significant differences between SPs at distances of 7 and 30 km ($p = 0.12$), but all other SPs significantly differ from them ($p \ll 0.001$).

The Cu content in the bark in the vicinity of the smelter exceeds the background level by a factor of 7.5 (Fig. 1, $F_{4;85} = 35.2$, $p < 0.001$). Similar to pH, the random factor (i.e. SP within the zone) also significantly affects the Cu content ($F_{17;85} = 1.92$, $p < 0.05$). Multiple comparisons indicate the significance of pairwise differences between SPs at all distances except for the 2–4 km pair.

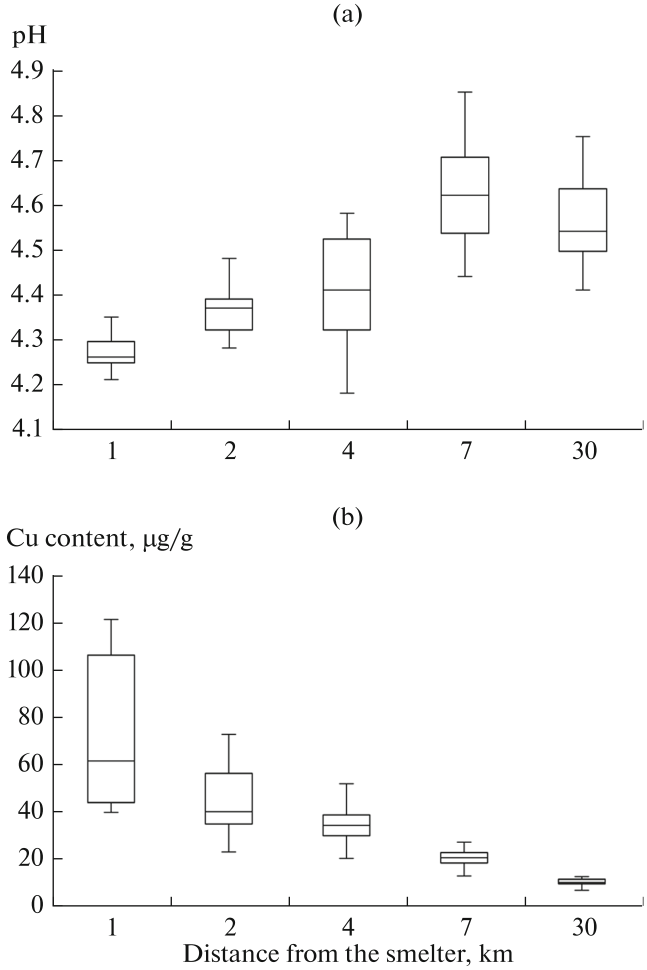

Fig. 1. Acidity of fir bark (a) and Cu content in fir bark (b) along the pollution gradient. Median values, interquartile ranges, and 95% intervals are shown.

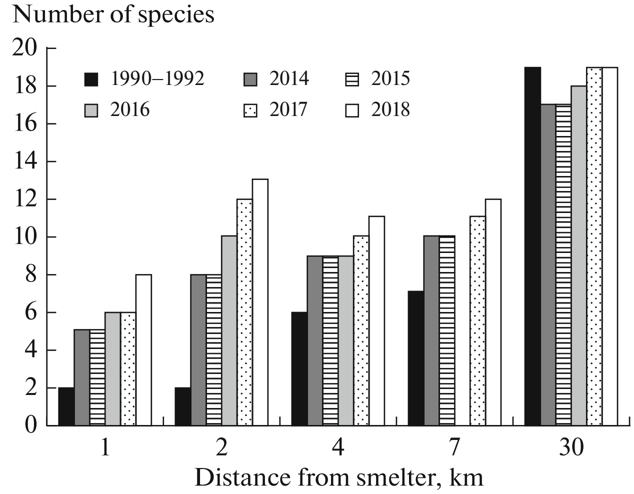

Fig. 2. Dynamics of numbers of epiphytic lichen species on fir trunks at different distances from the Middle Ural Copper Smelter throughout the study period.

Species Composition

In total, 23 lichen species have been identified on model fir trunks in the study area (Table 1). Group of crustose sorediate lichens includes *Fuscidea arboricola*, *F. pusilla, Lecidea nylanderi*, and *Ropalospora viridis*, whose young thalli are difficult to identify in the field. In the period of 2014–2018, new species appeared in the communities on model trunks (Fig. 2). It is necessary to note that the total number of species recorded in 1990–1992 includes all species found on fir trunks at the indicated distances [16], while the total number of species recorded in 2014–2018 includes only species found on model trees.

Bryoria nadvornikiana and *Hypogymnia tubulosa* appeared in the background area; the former species was noted among the background species in 1990–1992 [14, 16], but it was not found on model trees in 2014.

By 2018, four species have expanded to the contaminated area: *Evernia mesomorpha*, *Fuscidea pusilla*, *Lecidea nylanderi*, and *Parmeliopsis ambigua*; in 2014, they were noted only in background SPs. At distances of 4 and 7 km, the number of species has increased by two between 2014 and 2018 and by five in comparison with the period of high emissions (see Fig. 2). The maximum increase in species diversity was recorded at the 2-km distance: five species appeared over the period of 2014–2018, with the difference from the period of high emissions reaching 11 species. The newly settled species represent the entire spectrum of toxitolerance: *Micarea denigrata* is one of the most tolerant epiphytes on birch trunks in the study area [15], *Cladonia fimbriata* is a moderately tolerant species [14], whereas *E. mesomorpha*, *F. pusilla*, and *L. nylanderi* were recorded in 2014 only in background SPs.

Community Structure

In the background area, *Hypogymnia physodes* and *Chaenotheca ferruginea* dominate in communities, while *Hypocenomyce caradocensis* is a subdominant (Table 1, Figs. 3, 4). During the observation period, the abundance of species typical for trunk bases (*Cladonia coniocraea* and *Lepraria elobata*) has significantly increased (see Table 1), the abundance of *H. physodes* significantly decreased, while the total abundance of all species remained unchanged.

In the polluted zone (1–7 km), the community structure is basically different from that in the background area: *H. caradocensis* dominates everywhere (see Fig. 4); its abundance has remained the same throughout the observation period (2014–2018) at the distances of 4 and 7 km and significantly increased at the distances of 1–2 km. *Cladonia coniocraea* holds the second position at the distances of 4 and 7 km, while *H. physodes* at the 2-km distance. An increase in the *C. coniocraea* abundance was noted in all SPs (see

Table 1. Abundance of epiphytic lichens on model fir trunks in zones with different pollution levels

Species	Distance from the smelter, year									
	30 km		7 km		4 km		2 km		1 km	
	2014	2018	2014	2018	2014	2018	2014	2018	2014	2018
Bryoria nadvornikiana	0	0.011	0	0	0	0	0	0	0	0
Cetraria sepincola	0	0	0	0	0	0	0.010	0.013	0	0
Chaenotheca ferruginea	43.330	46.117	0.360	0.730	0.110	0.230	0	0	0	0
Cladonia cenotea	0.010	0.089	0	0	0	0	0	0	0	0
C. coniocraea	**6.693**	**12.211****	**7.975**	**13.381****	**3.310**	**12.424*****	**0.076**	**0.384***	**0.010**	**0.025***
C. fimbriata	**0.023**	**0.640***	0	0.001	0.011	0.042	0	0.010	0	0.01
Evernia mesomorpha	+	0.047	0	0	0	0.010	0	0.017	0	0
Hypocenomyce caradocensis	16.227	17.104	60.280	58.200	31.120	32.840	**12.600**	**17.390***	**3.853**	**10.700****
H. scalaris	0.010	0.020	0.003	0.002	0	0	0	0	0	0
Hypogymnia physodes	**59.227**	**50.913****	**0.511**	**4.480*****	0.922	1.310	**1.157**	**3.413*****	**0.010**	**0.035***
H. tubulosa	0	0.013	0	0	0	0	0	0	0	0
Lepraria elobata	**5.068**	**9.340****	0.030	0.003	0	0	0	0	0	0
Micarea denigrata	0	0	0.001	0.020	0.001	0.001	0	0.018	0	0
M. prasina + *M. micrococca*	0.011	0.011	0	0	0	0	**0.001**	**0.011****	0	0
Parmeliopsis ambigua	+	0.047	0	0.001	0	0.010	0	0	0	0
Placynthiella uliginosa	0	0	0	0	0	0.00	0.001	0.002	**0.003**	**0.140***
Scoliciosporum chlorococcum	0.002	0.002	0.002	0.001	0.001	0.002	0.010	0.010	0.030	0.030
Vulpicida pinastri	0.019	0.021	0.020	0.013	0.001	0.001	0.012	0.025	0	0
Crustose sorediate lichens	**0.966**	**1.122***	**0.025**	**0.450***	**0.001**	**0.074****	0	0.045	0	0.025
Unidentified crusts	2.561	0.230	0.020	0	0	0	0	0.002	0	0
Sum of occurrences	134.147	137.938	**69.227**	**77.282****	**35.477**	**47.322****	**13.867**	**21.340****	**3.996**	**10.965****

Boldface indicates statistically significant differences (Wilcoxon matched pairs test): *$p < 0.05$, **$p < 0.01$, *$p < 0.001$; (+) species recorded in 2014 on model trunks subsequently lost due to windfall;

Table 1); at the distance of 4 km, this parameter has increased almost fourfold. The proportion of all other species is negligibly small.

A distinctive feature of communities inhabiting the heavily contaminated zone (1–2 km) is the presence of species not typical for fir trunks in background habitats: *Placynthiella uliginosa* (a toxitolerant epixylic species often occurring on bare soil surface and trunk bases in industrial barrens) 15]; *Cetraria sepincola* (occurs only on fir branches and only in thinned sites or at forest edges); and aforementioned toxitolerant *M. denigrata*. In addition, the abundance of *Scoliciosporum chlorococcum*, one of the most toxitolerant species, is also higher than that in the background area.

The total abundance of lichens has increased between 2014 and 2018 in all polluted plots; the maximum increase was noted at the distance of 1 km. The newly settled species do not contribute significantly to the total abundance: its increase is determined by species already present there. The very low abundance at the distances of 1–2 km is also caused by another factor: almost all species inoculate the lower part of the trunk, close to the ground, and between exposed roots (i.e. outside the marked microplots).

The above changes are well illustrated by the similarity dendrogram (Fig. 3). Communities in the background area remained almost unchanged during the observation period; communities at the distances of 4 and 7 km are also grouped into separate clusters. The maximum changes occurred in communities at the distance of 1 km: in 2014–2015, they formed a separate cluster, but in the two subsequent years, they became similar to communities at the distance of 2 km.

The dynamics of the similarity of communities inhabiting the polluted zone and background area is also illustrative (see Table 2). By 2018, the similarity coefficient for communities at the distance of 1 km has increased threefold in comparison with 2014 and equaled the value characteristic of communities at the distance of 2 km back in 2014. Concurrently, the similarity of communities at the distance of 2 km with the background area became close to that featured by communities at the distances of 4 and 7 km back in 2014.

DISCUSSION

Epiphytic lichen communities in the background area remain in stable condition; their dynamics is limited to the introduction of relatively rare species that do not play any significant role in the community structure. The factors responsible for reduction in the abundance of *H. physodes*, the dominant of lichen communities, are unclear; this phenomenon requires further sudy.

The recovery of lichen communities in the polluted zone is in progress, which follows from increase both in the number of species and in their total abundance. The latter is due mainly to the explerent species *Hypocenomyce caradocensis,* which in the absence of interspecies competition colonizes vacant parts of tree trunks. At present, disturbed communities basically differ from background ones in their composition: species typical for undisturbed spruce–fir forests, primarily *C. ferruginea* and *L. elobata*, are absent or rare in the polluted zone. The formation of a so-called technogenic ecotone at the distance of 2 km from the plant is of interest: species typical both for polluted sites and for undisturbed or slightly disturbed areas are present there. It is quite possible that this is a temporary phenomenon: with time, species typical for polluted sites will be displaced from these communities as a result of competition with superior competitors from undisturbed and slightly disturbed areas.

The quick growth of the number of lichen species (by 1–2 species per year) in the most polluted part of the gradient is in contrasts with the stable level of species diversity in the herb–dwarf shrub layer in the same area; the number of species in this layer has remained almost unchanged since the period of heavy emissions [19]. A number of other studies [23–25] also demonstrate the very slow recovery of plant communities after the cessation of industrial emissions. The persistent environmental toxicity determined by the low rates of removal of heavy metals from soil is considered the primary factor impeding their recovery [21].

Epiphytic lichens are not directly connected with the toxicant pool in the soil; apparently, this accounts for higher rates of their recovery in comparison with other ecosystem components, including lichens growing on other substrates. Studies in the vicinity of the copper smelter near Sudbury, Canada, have revealed higher recovery rates in epiphytic lichens than in epigeic and epilithic ones [11, 23]. Still, the chemical composition of the substrate (i.e. bark of phorophytes) has a significant effect on epiphytic lichens. The significance of substrate pH for lichen development and growth is well known [26, 27]. The residual acidity of the oak bark is considered one of the factors responsible for slow recovery of lichen communities in London

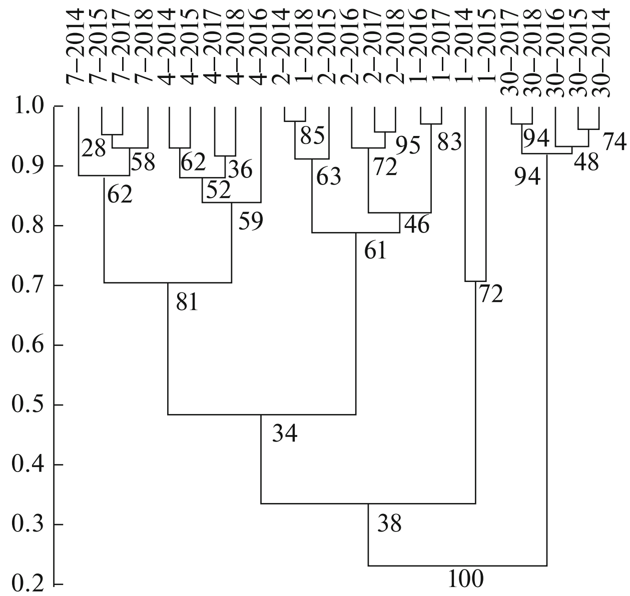

Fig. 3. Dendrogram of similarity in species composition for lichen communities located at different distances from the plant (1, 2, 4, 7, and 30 km) and in different observation periods (2014–2018) plotted using the Bray–Curtis index and UPGMA. Values at the nodes show percent bootstrap support at 1000 replicates.

[5]. Laboratory experiments have confirmed the adverse effect of metals and sulfur present in the culture medium on the germination of soredia [28–30]. A comparison of our results with the data collected in 2004 [31] shows that the Cu concentration in the bark has significantly decreased by 2015: the concentrations at distances of 1 and 2 km (331.2 and 162.6 μg/g in 2004) decreased by factors of 3.7 and 4.5, respectively; at 7 km (128.1 μg/g), by a factor of 6; and at 30 km (24.3 μg/g), by a factor of 2; i.e., Cu concentration became half lower even in the background area. Still, the current content of toxicants in the bark of phorophytes is significantly different from the background level (see Fig. 1). Although the total Cu content in the bark cannot be directly translated into toxicological parameters, its combination with high bark acidity

Table 2. Dynamics of similarity between epiphytic lichen communities and the control (Bray–Curtis indices for quantitative data, %)

Observation year	Distance from the plant, km			
	1	2	4	7
2014	5.6	18.7	24.4	25.7
2015	9.9	17.7	25.0	24.4
2016	19.2	27.8	33.7	–
2017	21.2	25.8	30.4	28.0
2018	18.6	26.5	33.7	32.4

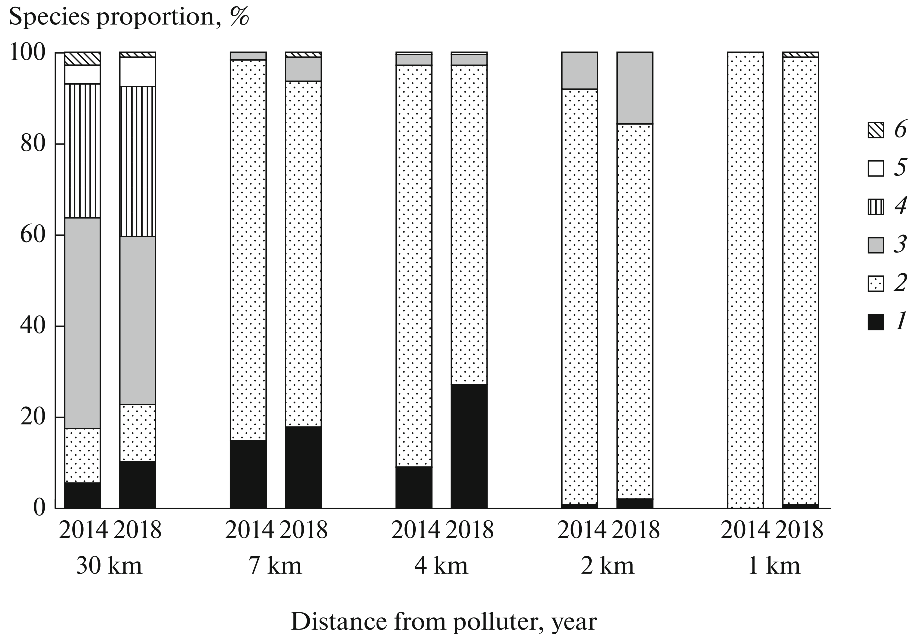

Fig. 4. Structures of epiphytic lichen communities at different distances from the plant in the beginning and end of the study period: (*1*) *Cladonia* spp., (*2*) *Hypocenomyce caradocensis,* (*3*) *Hypogymnia physodes,* (*4*) *Chaenotheca ferruginea,* (*5*) *Lepraria elobata,* (*6*) other species.

indicates partial persistence of the toxic pressure on epiphytic lichen communities, despite almost complete cessation of toxicant input into the ecosystems from the atmosphere.

The recovery of communities to their background state involves the establishment and successful development of species sensitive not only to environmental pollution but also to habitat microclimate. Such species include inter alia calicioid lichens [32] (in the study area, *C. ferruginea*). The microclimate of spruce–fir forests in the vicinity of the copper smelter is currently significantly altered due to the thinning of tree stand and poor development of the herb–dwarf shrub layer. An indicator of such changes is the presence of lichen species not typical for fir trunks: *C. sepincola* and *M. denigrata* prefer better insolation regimes [33, 34] and occur more frequently on birch trunks in the study area [14, 35]. The low abundance of *Cladonia* species on fir trunks, despite their high abundance on the soil and rotting wood, indirectly indicates xerophytization of the habitat.

On the whole, at least two factors may impede further recovery of epiphytic lichen communities: persistence of toxicants in the bark of phorophytes and altered microclimate of habitats. Most probably, the high lichen recolonization rates are typical only for the initial stages of recovery, while its subsequent stages will follow the scenario described for the vicinity of Sudbury. The onset of colonization of the lichen desert was noted within the first decade after the cessation of emissions [11]; however, the complete recovery of the lichen diversity was recorded only 40 years later [12]. Interestingly, some sensitive species (*Usnea hirta* and *E. mesomorpha*) have settled in the area earlier than one could expect based of their high sensitivity to pollution [11].

CONCLUSIONS

The relief of toxic pressure on natural communities due to the reduction of industrial emissions provides researchers with a unique opportunity to study the ecosystem elasticity phenomenon (i.e. their capability to return to the original state after the termination of a disturbance).

The results of our study show that the successful recolonization of polluted areas depends on many factors, both internal (biological and ecological features of species) and external (habitat condition and residual contamination of substrates) ones. Both our initial hypotheses have been confirmed. Explerent species with high colonization potential and abundant in adjacent biotopes or on other substrates in heavily polluted zones form the basis of pioneer communities. The hypothesis of weak connection between the colonization rate and toxitolerance of species has also been confirmed: highly sensitive species have appeared in the former lichen desert within the first decade after significant reduction of emissions.

Further studies involving data on the recovery of other ecosystem components, including the tree and herb–dwarf shrub layers, and on the dynamics of toxicant contents in substrates will make it possible to evaluate the significance of different factors for the survival of species in a changing environment.

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