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Long-term Dynamics of Small Mammal Communities in the Period of Reduction of Copper Smelter Emissions:
1. Composition, Abundance, and Diversity

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Abstract—The long-term dynamics of the composition, total abundance, and diversity (α- and γ-diversity) of small mammal (SM) communities is analyzed in the vicinity of a large copper smelter during the periods of high (1990–1997), reduced (1998–2009), and almost terminated emissions (2010–2019). It is shown that the response of SM communities to pollution has not fundamentally changed over 30 observation years. An increase in pollution caused a significant reduction in the total abundance and α-diversity of communities and their dominance index in each of the three periods; at the same time, the γ-diversity remained similar in the background (13 species) and polluted zones (12 species). The reduction of emissions had no significant influence on the SM communities in the background (conditionally clean) zone: the species structure fluctuated insignificantly, the dominance structure did not change, and the increase in the animal abundance by the end of observations (owing to forest voles but not insectivores) was due to successional changes in the vegetation. The reduction of emissions led to a succession of dominants near the smelter and the trends of changes in abundance in this area differed from those observed in the buffer and impact zones (increase and no change, respectively). The increase in the abundance of species of different trophic groups (phytophages, granivores, and zoophages) in the moderately polluted (buffer) zone can be considered a symptom of the initial stages of recovery due to the improvement of habitat quality. Positive shifts in the SM community from the highly polluted (impact) zone are less distinct, being expressed only as an increase in the proportion of shrews.

Keywords: natural recovery, industrial pollution, relative abundance, γ-diversity, α-diversity, rodents, shrews

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The long-term operation of metallurgical enterprises leads to the formation of technogenic geochemical anomalies around them: the contents of pollutants, including heavy metals (HMs), exceed the background levels by tens and hundreds of times [1–3]. Industrial pollution affects all components of natural ecosystems both directly (leading to the elimination of the least stable links) and indirectly (through changes in habitat quality, interspecific competition, individual resistance to external factors, etc.).

In the past decades, the reduction of production volumes and/or the technological improvement have led to a significant decrease in the technogenic emission of xenobiotics in most European and North American countries. Researchers are currently particularly focused on processes of restoration of disturbed areas near production plants [1, 4–18]. Processes of spontaneous (i.e. without direct human involvement) remediation of areas are of prime interest in this context; these processes make it possible to study the mechanisms and intensity of natural recovery of natural ecosystems.

The pattern of initial stages in the recovery of biota in response to the reduction of emissions depends on the objects, duration and intensity of impact from the pollution source, and its natural and geographical location. Some researchers expect ecosystems to quickly recover to their initial state [13, 15, 17], while others believe that this will take a long time, even after the complete cessation of emissions [4, 7, 11, 14, 18]. There is also an opinion that ecosystems are modified and acquire new properties, rather than recover to their original state, after the reduction of pollution [19, 20].

The interpretation of the currently observed changes is problematic due to the lack of documented data on the dynamics of the recovery of different biota components. For correct comparison, new data should be collected in the same plots using the same methods even if information is available about the initial state of the study objects during the period of intensive pollution (it is this aspect that is often most problematic). Otherwise, spatial variation in the compared parameters can be mistaken for their temporal dynamics [4]. It is important that studies should cover a sufficiently long interval, since short-term observations(up to 10 years) do not make it possible to differentiate the recovery determined by reduction of emission from interannual fluctuations. In addition, analysis of a limited set of species does not allow one to apply the results for the whole group.

Small mammals (SMs) are often considered as model objects of different ecological and ecotoxicological studies, since they play a significant role in terrestrial ecosystems due to their wide distribution, high abundance, settled way of life, and eurybionism [21]. The study of the SM response to industrial pollution is usually limited to the analysis of species composition and population size [8, 22–26] or estimation of accumulation levels of separate elements in the organs and tissues of model species [11, 14, 27, 28], sometimes using morphological, biochemical, and genetic materials [16, 29–33]. Most studies on the SM communities cover a short period (1–3 years), thereby providing only the "instant slices" of communities, while long-term observations are rare [8–10, 34, 35]. The reduction of industrial emissions leads to positive shifts in SM communities (their species richness and the abundance of separate species increase); however, the rates of changes are low. Lack of information does not yet allow making definite conclusions about the pattern of structural alterations in SM communities under conditions of decreasing technogenic load. This determines the necessity for further studies of SMs inhabitind areas polluted from point sources in different natural zones.

Our research in the vicinity of the Middle Ural Copper Smelter (MUCS) cover 30 years, which included periods of high (1990–1997, period I), reduced (1998–2009, II), and almost terminated emissions (2010–2019, III). The resulting data make it possible to analyze the long-term dynamics of the composition and abundance of SM communities. Long-term studies on the dynamics of other biota components near the MUCS in the same sites during the same periods show that forest stands continue to die and there are no recovery processes in the grass–dwarf-shrub layer in the immediate vicinity of the emission source even after manyfold reduction in the volume of industrial emissions [4, 12]. According to [1, 36], the suppressed state of forest ecosystems is explained by an extremely slow rate of purification of the upper soil horizons from HMs and retention of a thick layer of slightly decomposed forest litter. At the same time, certain positive shifts are observed in the communities of soil invertebrates [5] and insectivorous mammals [37]: an increase in the abundance and a shift in the range of distribution of some groups (earthworms, mollusks, and mole) towards the smelter. Long-term observations on the behavior of other biota components, in particular, SMs, are relevant under these conditions.

The purpose of this study was to analyze the dynamics of the species structure of SM communities and their diversity and abundance in the vicinity of a large copper smelter during the 30-period of reduction in its emissions. We do not know any studies where the results of long-term annual observations are used to compare the key parameters of SM communities (species composition, abundance, and α- and γ-diversity) before and after the reduction of emissions. We tested the hypothesis that a decrease in technogenic load as a result of reduced industrial emissions should lead to an increase in the total abundance and diversity of SM communities; we also assumed that positive changes would be less distinct in highly polluted than in moderately polluted areas.

MATERIAL AND METHODS

Source of emissions. Studies were performed in the areas polluted by atmospheric emissions from the Middle-Ural Copper Smelter (MUCS) located in the suburbs of Revda, 50 km west of Yekaterinburg.

The MUCS has been in operation since 1940; the main toxic components of emissions are gaseous compounds of sulfur, fluorine, and nitrogen and also dust particles with adsorbed HMs (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As). In the 1980s, MUCS total emissions reached 225000 t/yr., which made this plant one of major sources of industrial pollution in Russia. During the 1990s, the volume of emissions was reduced by half, from 148000 t in 1990 to 65000 t in 1999; the next 10 years were marked by even stronger reduction: from 63000 t in 2000 to 22000 t in 2009; after the reconstruction of the smelter in 2010, total emissions have not exceeded 3000–5000 t/yr. [1, 38].

Study area. The key plots were in spruce–fir forests at distances of 1–30 km to the west of the MUCS (against the prevailing wind direction) and covered areas with different degrees of ecosystem damage. The tree layer is suppressed (decrease in the height, diameter, and stock of tree stand), and the species richness and abundance of the ground vegetation layer decrease with proximity to the smelter. The degree of suppression is not equal in different load zones: the background zone (20–30 km from the smelter) is characterized by a relatively undisturbed state, since this area is exposed only to the regional fallout of pollutants; the buffer zone (4–10 km) is characterized by structural alterations in ecosystems due to the effect of local pollution; in the impact zone (1–3 km), the structure of ecosystems fundamentally differs from their background state: extreme variants in the technogenic digression of communities are observed there [1, 39]. Until 2012, no positive shifts were recorded in the state of ground vegetation layer in the impact zone, while the diversity and abundance of vegetation increased in other areas [4, 12]. However, these changes were due not so much to the decrease in the pollution level as to the thinning of the tree canopy after the large-scale

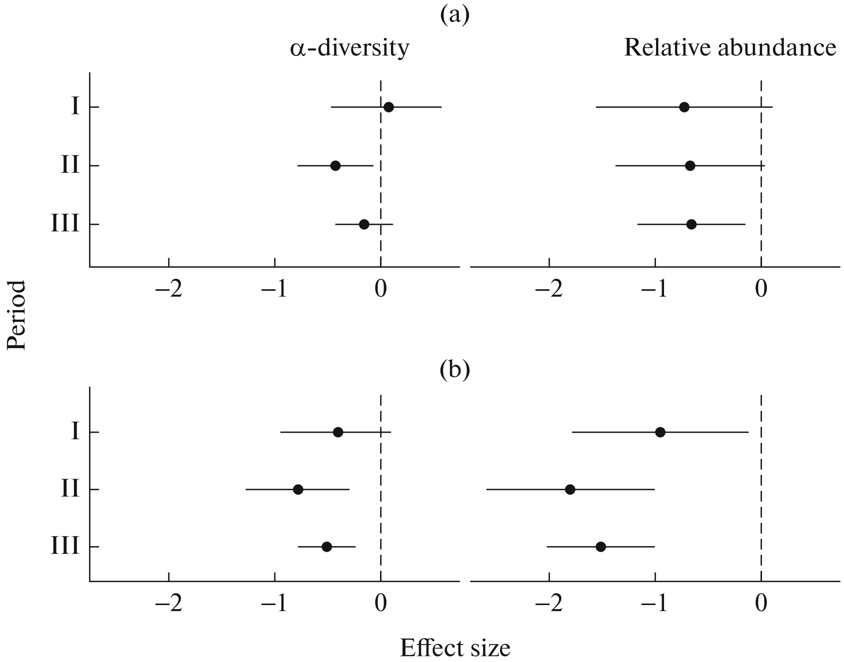

Fig. 1. Effect size relative to the background area in (a) buffer and (b) impact zones in the periods of (I) high, (II) reduced, and (III) almost terminated emissions. Horizonta bars show 95% confidence interval.

wind breakage during a hurricane in 1995. The technogenic soil transformation resulted in increased accumulation of HMs, increased acidity, and the formation of a thick peaty forest litter [36]. The soils are currently recovering to their original state, but the contents of HMs (except Cu) in the litter and humus horizon remain high in all zones [1].

Animal sampling. Small mammals were collected every year from 1990 to 2019 (except 1999 and 2001) in three rounds (from May to September) using fixed marked lines in seven key sites: three in the impact zone (1, 1.5, and 2 km from the smelter), two in the buffer zone (4 and 6 km), and two in the background zone (20 and 30 km). Some of the lines have been lost over the past years as a result of local forest fires, wind breakage, and felling operations. New lines were laid out in adjacent areas with conditions closely similar to those in their initial locations (Supplement, Fig. 1). The animals were caught using wooden snap traps arranged in lines (25 traps each) at a distance of 5–7 m from each other and exposed for 3–5 days, being inspected once a day. During each round, two to four trap lines per site were set simultaneously in all zones. The use of permanent trapping points made it possible to significantly reduce the effect of spatial heterogeneity of habitat conditions.

Taking into account limitations of the trap-line method and disadvantages of snap traps as catching gear (selective trapping of certain SM groups and dependence on weather conditions), we regularly carried out additional animal censuses in the adjacent areas using other schemes and means (live traps, cones, and Barber traps). This made it possible to more exactly determine the species composition of SM communities in different zones and assess the migratory activity of animals. However, the bulk of material for analyzing dynamic changes in the communities along the pollution gradient was obtained using the trap-line method with snap traps: this material amounted to 96800 trap–days, including 66700 trap-days in the polluted sites and 30100 trap–days in the background plots; a total of 5551 small mammals were trapped, including 2516 ind. in the polluted plots and 3008 ind. in the background sites (Supplement, Table 1). The animals were identified to the species level using appropriate identification keys [40, 41]. Latin species names are given according to *Mammals Species of the World* [42].

Data analysis. SM communities in the pollution gradient were compared with regard to (1) relative abundance, (2) the proportions of different species in the community, (3) dominance index, (4) γ-diversity, and (5) α-diversity. A key site was taken as a statistical unit in all cases. The above parameters were estimated for each year based on the pooled data from three rounds of trapping.

The relative abundance (number of individuals per 100 trap–days) was calculated both for separate species and for the whole community. The degree of species dominance was estimated from the Simpson index (D) ranging from 0 (all species are equally represented) to 1 (only one species). Species accounting for over 10% of the total community abundance were consid-

Table 1. Composition of SM communities and relative abundance of separate species (ind./100 trap-days) in the vicinity of the MUCS during the periods of (I) high, (II) reduced, and (III) almost terminated emissions

Community description	Zone and period								
	background zone (20–30 km)			buffer zone (4–6 km)			impact zone (1–2 km)		
	I	II	III	I	II	III	I	II	III
Common shrew (*Sorex araneus*)	0.93 ± 0.10	0.39 ± 0.06	0.73 ± 0.08	0.20 ± 0.04	0.01 ± 0.02	0.28 ± 0.06	0.28 ± 0.04	0.03 ± 0.02	0.03 ± 0.01
Laxmann's shrew (*S. caecutiens*)	0.17 ± 0.04	0.17 ± 0.04	0.60 ± 0.08	0.27 ± 0.05	0.34 ± 0.08	0.87 ± 0.10	0.20 ± 0.04	0.14 ± 0.04	0.58 ± 0.06
Even-toothed shrew (*S. isodon*)	0.26 ± 0.05	0.21 ± 0.05	0.14 ± 0.04	0.02 ± 0.01	–	0.03 ± 0.02	0.01 ± 0.01	–	–
Pygmy shrew (*S. minutus*)	0.03 ± 0.02	–	0.03 ± 0.02	0.01 ± 0.01	–	0.01 ± 0.01	0.03 ± 0.01	–	0.01 ± 0.01
European mole (*Talpa europaea*)	0.05 ± 0.02	0.02 ± 0.01	0.02 ± 0.01	–	–	–	–	–	–
Ural field mouse (*Apodemus uralensis*)	0.32 ± 0.06	0.42 ± 0.06	0.71 ± 0.08	0.27 ± 0.05	0.68 ± 0.10	0.93 ± 0.10	0.62 ± 0.06	0.26 ± 0.06	0.33 ± 0.04
Striped field mouse (*A. agrarius*)	–	–	0.01 ± 0.00	0.03 ± 0.02	0.03 ± 0.02	–	0.02 ± 0.01	–	–
House mouse (*Mus musculus*)	–	–	–	–	–	–	0.01 ± 0.01	–	–
Common vole (*Microtus arvalis*)	0.13 ± 0.04	0.10 ± 0.03	0.08 ± 0.03	0.01 ± 0.01	0.07 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
Field vole (*M. agrestis*)	0.17 ± 0.04	0.10 ± 0.03	0.03 ± 0.02	0.08 ± 0.03	0.01 ± 0.005	0.13 ± 0.04	0.05 ± 0.02	0.01 ± 0.01	0.09 ± 0.02
Root vole (*Alexandromys oeconomus*)	0.03 ± 0.02	0.01 ± 0.01	0.04 ± 0.02	–	–	–	–	–	–
Northern red-backed vole (*Myodes rutilus*)	–	0.70 ± 0.07	0.67 ± 0.08	0.51 ± 0.07	0.56 ± 0.06	1.76 ± 0.14	0.34 ± 0.05	0.55 ± 0.09	1.20 ± 0.08
Bank vole (*M. glareolus*)	6.97 ± 0.28	6.11 ± 0.24	9.25 ± 0.30	2.55 ± 0.15	2.55 ± 0.19	3.33 ± 0.19	1.87 ± 0.11	1.01 ± 0.12	0.40 ± 0.05
Grey red-backed vole (*M. rufocanus*)	–	0.23 ± 0.04	0.05 ± 0.01	0.05 ± 0.02	0.18 ± 0.06	0.07 ± 0.03	–	0.04 ± 0.02	–
Number of analyzed trap-days									
Number of captured animals, *N*	8755	10800	10525	10945	6790	8900	14785	7150	16950
Total abundance, ind./100 trap–days	793	914	1301	438	301	661	510	156	447
Simpson's index of dominance, *D*	9.1 ± 0.3 *ab* (0.3 – 23.7)	8.5 ± 0.3 *ab* (0.9 – 26.3)	12.4 ± 0.4 *a* (0.4 –38.7)	4.0 ± 0.2 *bc* (0.8 – 9.2)	4.4 ± 0.3 *bc* (0.5 – 13.6)	7.4 ± 0.4 *b* (1.0 – 25.8)	3.4 ± 0.4 *bc* (0 – 10.7)	2.0 ± 0.2 *c* (0 – 6.3)	2.6 ± 0.2 *bc* (0 – 8.7)
Observed γ-diversity, *S* (recorded number of species per zone)	0.72 ± 0.07 *a*	0.54 ± 0.05 *ab*	0.59 ± 0.05 *ab*	0.55 ± 0.07 *ab*	0.50 ± 0.06 *ab*	0.42 ± 0.05 *b*	0.59 ± 0.04 *ab*	0.68 ± 0.06 *a*	0.42 ± 0.04 *b*
Interpolated γ-diversity, *S** (calculated number of species per zone)	10	11	13	11	9	10	11	8	8
α-diversity (average number of species per key site)	9.8 [9.3–10.2]	9.1 [8.2–9.9]	10.2 [10.0–12.1]	11.0 [10.8–11.2]	7.7 [6.9–8.6]	9.3 [8.6–10.0]	10.8 [10.4–11.2]	8.0 [7.9–8.1]	8.0 [7.7–8.2]

Data are presented as mean ± error, with minimum and maximum values in parentheses; values in square brackets show 95% confidence interval; dash, no species; The key plot was taken as a statistical unit. Values with the same letters do not differ significantly between the zones (($p < 0.05$, Tukey's test).

Table 2. Results of ANOVA for the main parameters of SM communities

Parameter	Source of variability					
	Zone (*df* = 2)		Period (*df* = 2)		Zone × period (*df* = 4)	
	F	*p*	F	*p*	F	*p*
Relative abundance	16.04	**<0.0001**	3.41	**0.036**	0.77	0.569
Index of dominance	3.37	**0.038**	5.91	**0.004**	2.54	**0.043**
α-diversity	9.33	**0.0002**	1.11	0.332	0.94	0.442

Boldface indicates significant differences in the test parameters ($p < 0.05$).

ered dominant, and species accounting for less than 1% were considered rare. The index of γ-diversity characterizes the total number of species in the zone. Since the direct comparison of species richness (*S*) in the study areas was incorrect due to unequal catch efforts in different zones, we also used an interpolated number of species S^* (a multiple of 10) for the abundance that was closest to the maximum value in one of the zones. The α-diversity was characterized using the average number of species in the key site.

A two-way ANOVA with log-transformed data was used to estimate the differences between the pollution zones and between the periods. Multiple comparisons were performed using Tukey's test. The effect size relative to the background area was calculated as the logarithm of the response ratio (ln Response Ratio, RR^{Δ}). In statistical tests, differences were considered significant at $p < 0.05$. Calculations were made in PAST 4.0 [43] and JMP v.11 [44].

RESULTS

Total abundance. The total abundance of SM communities proved to depend significantly both on the pollution level and the observation period (I–III), decreasing by a factor of 2–4, on average, as pollution increased (Tables 1, 2). The dynamics of this parameter in the studied zones had different patterns: there were no distinct changes in the impact sites, while the SM abundance in the buffer sites increased twofold along with reduction of emissions (from period I to III), and an approximately 30% increase was observed in the background area. Dominant species contributed most to the dynamics of abundance within each zone. Changes in the abundance of animals in the polluted sites relative to the background area showed different trends: in the buffer zone, the effect strength (RR^{Δ}) did not vary with time, while it shifted to the region of negative values in the impact zone during the transition from period I to period III (Fig. 1).

Composition of communities. Fourteen SM species, including nine rodent species (Rodentia) of two families (Muridae and Cricetidae) and five insectivorous species (Soricomorpha) of two families (Soricidae and Talpidae) were recorded in the study area over the 30 years. The use of additional census methods provided evidence for the presence of northern birch mouse (*Sicista betulina*) in the background and buffer zones and of water shrew (*Neomys fodiens*) in the background zone, but these two species were excluded from further analysis.

The SM communities in all zones were dominated by rodents, which accounted for more than 80% of total abundance (see Table 1). The bank vole (*Myodes glareolus*) was dominant in all areas (Table 2). The proportion of this species decreased with growth in pollution level: from 75% in the background area to 53% in the moderately polluted zone and 38% in the impact sites. On the contrary, the proportions of Ural field mouse (*Apodemus uralensis*) and northern red-backed vole (*My. rutilus*) increased from 5% in the background zone to 15–27% near the smelter. The proportion of voles *Microtus* spp. and *Alexandromys* spp. did not exceed 2.5% in most of the sites during the 30-year study period, except the area near the smelter (1 km) where it reached 8%. The proportion of insectivores was 12–13% of the total abundance in the background and buffer zones and 17% in the impact zone. The species composition of this group was similar in all zones, except for the European mole (*Talpa europaea*) which was captured only in the background sites.

Dominance structure. An increase in pollution leads to fundamental changes in the structure of SM communities: they are transformed from monodominant into polydominant ones. Communities of the background sites were dominated by a single species, *M. glareolus*, which accounted for 73–77% of total abundance, while dominance in the polluted sites was shared by two–three species (Table 1). The proportion of rare species was comparable between different parts of the pollution gradient, varying from 25 to 54% of the total species number in different periods. These features were reflected in the dynamics of the *D* index: its values significantly increased with distance from the smelter (see Table 2) and also changed significantly depending on the observation period: after reduction of emissions, they decreased by factors of 1.2 in the background plots and of 1.3–1.4 in the impact plots.

Gamma-diversity. The generalized data over the 30 years show that γ-diversity did not depend on the level of pollution but differed between the observation periods. During the period of high emissions (I), the maximum number of species was recorded in the buffer and impact zones, while γ-diversity in periods II and III was higher in the background area (see Table 1). The values of observed and interpolated species richness in the impact zone were the same, while the interpolated value (number of species) in the background zone was lower than the observed one, especially in periods II and III.

Alpha-diversity. An increase in pollution level entailed a significant reduction of α-diversity (on average, by a factor of 1.2–1.7), regardless of observation period (see Tables 1 and 2). Species saturation changed insignificantly (by less than 10%) in the background sites, while its value near the smelter varied by a factor of 1.5 between observation periods. The effect size (RR^{Δ}) was insignificant in periods I and III in the buffer zone and only in period I in the impact zone (see Fig. 1).

DISCUSSION

It is known that anthropogenic impacts of various genesis cause structural alterations in SM communities, with their extent and direction depending on the type of impact, its intensity and duration, and on specific features of the species forming the community [8, 22, 26, 40, 45, 46]. Industrial pollution, particularly from nonferrous metal industries, has a very strong effect on the biota [47]. The generally accepted opinion is that there is no permanent SM community in areas adjacent to pollution sources [23, 26, 48]. The species richness and abundance of SMs decrease with proximity to emission sourses [8, 9, 23, 26]. These changes may be monotonic [9, 19, 34, 35] or nonlinear, reaching the maximum in the zone of moderate loads. Thus, studies in the vicinities of copper (nickel) smelters in the Southern Urals [23], Kola Peninsula [26], and Finland [25] showed that the total abundance of SMs differed by a factor of 1.2–5 between the buffer and background sites and by a factor of 5–20 between the buffer and impact sites. The pattern of changes in the total abundance largely depended on the number of key plots in the pollution gradient: the recorded changes were nonlinear when their number was large (over 10) and monotonic when their number was smaller. The authors consider that general deterioration of habitat quality (in particular, with respect to food resources and protective properties) is the main factor responsible for the depletion of SM species composition and reduction in abundance near the smelters.

In studies performed without strictly confining the plots to certain biotopes, the γ-diversity of SM communities in the impact zones slightly differed from that in the background areas or even exceeded it, but their abundance in the impact zone was found to be 2–5 times lower [22, 49]. The results of our studies in the impact zone of the Karabash Copper Smelter (the Southern Urals) show that the involvment of habitat heterogenity in the analysis fundamentally changes the conclusions about the response of SM communinies to pollution. The data on SMs studied in the same biotope provided evidence for significant depletion of the species composition (from seven to two species) and a 10-fold decrease in the total abundance under increased technogenic load [23]. When the analysis covered different habitats, the diversity of communities was found to be similar in the background and impact zones (seven and eight species, respectively) and the total abundance of animals near the smelter was only two times lower [24].

Although long-term observations near the MUCS were carried out according to the traditional “single-biotope” scheme, no abrupt drop in γ-diversity was revealed with increase in pollution level. During the 30-year study period, we recorded 13 SM species in the background zone, 11 species in the buffer zone, and 12 species in the impact zone; nine, eight, and seven SM species were regularly (i.e., during all three periods) recorded in catches from the respective zones (see Table 1). The observed differences are insignificant, which may be explained by the long period of observations combined with large volume of regular catches and covering a wide range of areas (especially near the smelter), which made it possible to take into account rare species. Therefore, the expected effect of sharp depletion of the species composition of communities under the influence of industrial pollution proved to be shaded. In other words, long-term observations within the same type of biotope are comparable to a single survey of a wide range of biotopes.

The decrease in α-diversity and total abundance under the impact of pollution may due to reduction both in the area of suitable habitats and in their ecological capacity (in particular, protective conditions and food resources). The data on *My. glareolus* indicate that animal abundance is more dependent on the first factor: the local population density in the impact sites habitable for the species was comparable to the background population density [25, 34]. On the contrary, the ecological capacity of habitats is more important for α-diversity: it allows different species to successfully coexist owing to more complete utilization of resources.

The studied communities also significantly differed in the structure of dominance. The community in the background zone remained monodominant over the 30-year study period, while the community in the polluted areas included two–three dominant species every year, and the reduction of emissions was accompanied by their rotation. It is known that communities in natural conditions become polydominant when habitats are characterized by structural diversity [50]. Since habitat heterogeneity is higher near the MUCS, it can be expected that the number of dominants will be greater in the community inhabiting the polluted areas than in the background zone with more uniform conditions. This is confirmed by the dynamics of *D* index in the pollution gradient (see Table 1). The decrease in its value with reduction of emissions is probably explained by successional changes in phytocenoses.

For better understanding the dynamics of SM communities in the pollution gradient, let us consider its features in different zones. The ecosystem degradation reached its maximum in the immediate vicinity of the smelter (especially during the period of high emissions). The MUCS area and adjacent sites (up to 0.5 km to the west and 2 km to the east) is a technogenic wasteland almost completely devoid of higher vegetation and upper soil horizons and is therefore unsuitable for SM habitation. The key sites in the impact zone partially border on the wasteland, and the species composition of SMs is usually depleted in this area: the number of annually recorded species varied from zero to four, increasing up to seven species only in some years (see Table 1). The response to the technogenic transformation of the habitat proved to be dual: on the one hand, stenobiont species disappeared (*T. europaea*) or their abundance decreased (*M. rufocanus*); on the other hand, there appeared synanthropes (*Mus musculus*) and species preferring to colonize open and/or sparse areas (*A. agrarius* and *M. arvalis*). During the period of high emissions, the economic activity was maximal near the MUCS and the species richness also reached a maximum (11 species). During the periods of reduced emissions (II and III), γ-diversity decreased by 40%; however, these changes can hardly be related to the reduction of emissions, since rare species most likely were not lost (except *M. musculus*) but rather moved to other parts of the impact zone. This assumption is based on the presence of *M. rufocanus*, *A. agrarius*, and *S. minutus* near the smelter, which were caught using additional long trap lines (longer than 750 m) crossing the impact zones with different microhabitats, as well as other gear (live traps and cones) (our unpublished data).

The average total abundance of SMs was four times lower in the impact than in the background zone, and its minimum values were recorded in spring. This suggests the absence of a permanent community (i.e., a community living in the same habitat during a full life cycle) in these areas. Thus, the population of *M. glareolus* during the period of high emissions consisted only of transitional individuals throughout the snowless season, which indirectly confirms our assumptions [51]. During the period with almost terminated emissions, the proportion of transitional individuals in the population reached 100% only in spring, decreasing by half by autumn (our unpublished data). This may indicate possible positive shifts in the habitat quality as a result of the gradual recovery of herbaceous vegetation after emission reductions.

During the 30-year study period, the community of the impact zone remained polydominant, and the reduction of emissions (from period I to period III) was accompanied by rotation of dominant species: *M. glareolus* was replaced by *M. rutilus*, and *S. araneus* by *S. caecutiens*; these successions were very sharp, with the proportions of *M. rutilus* and *S. caecutiens* increasing almost fourfold. The total abundance of voles (genus *Myodes*) has hardly changed over the past 20 years, whereas the abundance of shrews has become three times higher during this period. The positive shifts in the community of small insectivores in response to reduction of emissions could be stimulated by gradual improvement of food supply to them near the smelter. This is indirectly confirmed by the results of 25-year studies on the fauna of large soil invertebrates near the MUCS. The total abundance of pedobionts in the impact sites where SMs were captured increased fivefold after the almost complete cessation of emissions; in addition, some groups (earthworms, enchytraeids, and mollusks), which were previously absent in the impact zone, moved closer to the smelter [5]. At the same time, the rate of vegetation recovery near the MUCS was low [4, 12]; therefore, there was no significant improvement in food resources for phytophages, which explains the stability of the total abundance of voles.

The mosaic structure of the environment is particularly high in the buffer zone because of many factors: degradation of forest phytocenoses due to pollution, local economic activities (selective felling, construction of power lines, reforestation in burned-out areas, and meadow mowing), and natural disturbances (wind breakage and fires). All these increased the diversity and ecological capacity of habitats within the dominant type of biotope, which was reflected in higher total abundance and α-diversity, compared to the impact zone, with their values approaching the background level (see Table 1). Throughout the study period, the community remained polydominant and the reduction of emissions was accompanied by the rotation of dominants: the proportions of *M. rutilus*, *A. uralensis*, and *S. caeutiens* increased almost twofold (with an equivalent increase in their abundance), while the proportion of *M. glareolus* decreased by a factor of 1.4. Therefore, the total abundance of SMs in the buffer zone increased almost twofold between 1990 and 2019, with positive trends being observed in different trophic groups: zoophages, phytophages, and granivores. These changes may probably result from the gradual improvement of the habitat quality (in particular, the abundance and diversity of food resources). This is consistent with the course of restoration of other biota components (vegetation [4, 12] and invertebrates [5]) in the buffer areas.

Fir–spruce forests in the background zone occupied significantly larger areas and were more homogeneous with respect to microhabitat conditions for SMs than in the other key sites [34]. One to nine species were annually recorded there, and a significant proportion of the community was represented by typically forest species. Conditions in these forests satisfied all the habitat requirements of *M. glareolus*, which remained superdominant for all the 30 years. Small areas with sparse vegetation (forest edges and clearings) within fir–spruce stands were preferred by *M. arvalis*, *A. oeconomus*, and *A. agrarius*. The good protective properties and food resources combined with other features suitable for of different SM species accounted for the maximum values of diversity and abundance in the background area, compared to other zones (see Table 1). The total abundance of SMs became one-third higher by the end of the study period on account of rodents, while the abundance of insectivores remained unchanged. In our opinion, these changes were mainly determined by successional processes in the plant communities. As a result of regular wind breakage, old trees disappear in mature fir–spruce forests. This leads to the thinning of forest canopy, with consequent intense development of herbaceous vegetation under canopy gaps, and, on the other hand, contributes to the improvement of protective habitat properties and enrichment of food resources with conifer seeds, which become easily accessible to terrestrial species.

The use of the effect size parameter (see Fig. 1) allowed us to minimize the influence of interannual fluctuations and possible methodological errors that could affect the completeness of SM censuses. The opposite changes in the SM abundance under conditions of reduced emissions (with this parameter increasing in the background and buffer zones but remaining low in the impact zone) accounted for the absence of distinct trends toward the recovery of total abundance in the buffer zone and its negative dynamics near the smelter.

Therefore, the comparison between the periods of high, reduced, and almost terminated emissions shows that the response of the communities to the pollution has not basically changed over the past 30 years. The increase in pollution level caused a significant decrease in the total abundance and α-diversity of SM communities and their dominance index in each of the three periods. At the same time, γ-diversity remained similar in the background (13 species) and polluted plots (12 species) throughout the 30 years of study.

CONCLUSIONS

We are unaware of any long-term studies involving direct comparisons of annual data on the abundance and diversity of SM communities at different distances from the source of industrial emission in the periods before, during, and after the reduction of emission. The tested hypothesis about positive changes in the abundance and diversity of communities in polluted sites as a result of emission reduction was confirmed partially, only for the buffer zone (moderate pollution), while changes observed in the impact zone were less distinct, as expected.

The γ-diversity of SM communities was similar for all studied pollution zones during the 30 years. This is explained by the long observation period, significant catch efforts, and a large survey area, which made it possible to take into account rare species in all plots of the pollution gradient. The α-diversity of SM communities near the smelter was lower than the background value throughout the study period: apparently, the initial stages of habitat recovery have not yet led to a noticeable increase in their ecological capacity.

The studied SM communities fundamentally differed from each other in the dominance structure. In the background zone, the community remained monodominant and the fluctuations in the species structure were insignificant. By the end of the study period, the total abundance of animals increased (owing to *Myodes* voles but not insectivores), which was due to successional changes in vegetation. The SM communities in the polluted areas were characterized by polydominance and their total abundance was 2–4 times lower than the background value. The reduction of emissions led to a succession of dominants; however, trends in the abundance differed between the buffer zone (increase) and impact zone (no change). The increase in the proportion of shrews in the SM community from the impact zone can be considered a sign of initial recovery stages. The positive shifts are even more distinct in the buffer zone: the increase in the abundance of species of different trophic groups (phytophages, zoophages, and granivores) may indicate an improvement of the habitat quality for different species. The observed changes are well consistent with the beginning of the recovery processes of other biota components (vegetation and soil fauna).

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COMPLIANCE WITH ETHICAL STANDARDS

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

CONFLICT OF INTEREST

The author declares that she has no conflict of interest.

SUPPLEMENTARY INFORMATION

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