ISSN 1067-4136, Russian Journal of Ecology, 2019, Vol. 50, No. 2, pp. 146–160. © Pleiades Publishing, Ltd., 2019.
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# Initial Stages of Recovery of Soil Macrofauna Communities after Reduction of Emissions from a Copper Smelter

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Received August 16, 2018; revised August 20, 2018; accepted August 23, 2018

**Abstract**—Analysis of natural recovery of communities after reduction of industrial emissions is important for gaining an insight into their stability. However, there is obvious deficit in observations on the course of this recovery; in particular, no data on direct comparisons of the state of communities before and after reduction of emissions are available for soil macroinvertebrates. We have studied the structure of soil macrofauna communities at the level of supraspecific taxa in southern taiga spruce–fir forests in the region exposed to emissions from the Middle Ural Copper Smelter (MUCS; Revda, Sverdlovsk oblast). The data over three periods—high, reduced, and almost terminated emissions (1990–1991, 2004, and 2014–2016, respectively)—have been compared to test the hypothesis that the communities do not recover rapidly. The results partly confirm this hypothesis. On the one hand, the response of pedobionts to pollution at a qualitative level has remained basically unchanged: in each of the three periods, their total abundance (and that of the majority of groups) decreased abruptly as the MUCS was approached, with dominance shifting from saprophages to phyto- and zoophages. On the other hand, signs of recovery have appeared during the last period: the abundance of pedobionts has increased, and pollution-sensitive groups (earthworms, enchytraeids, and mollusks) have approached closer to the MUCS. This is most likely explained by decrease in the toxicity of metals due to normalization of soil pH. Rapid recolonization of defaunated territory may be accounted for by the presence in it of microsites with more favorable conditions, compared to the surrounding area, which allow low-mobile forms to survive beyond the boundaries of their main distribution area.

*Keywords:* dynamics, stability, resilience, natural recovery, recolonization, succession, industrial pollution, heavy metals, community structure, soil macroinvertebrates, earthworms, enchytraeids, lithobiids, spiders, insects, mollusks

**DOI:** 10.1134/S1067413619020115

Soil macroinvertebrates in forest ecosystems largely determine the rate of biological turnover and plant provision with nutrients; contribute to the formation of soil structure, thereby influencing soil water regime and fertility; and modify the composition of soil microorganisms [1]. In view of such a significant role of this group, suggestions to include parameters characterizing its state in environmental monitoring [2] and environmental pollution control [3] are quite reasonable.

Various pollutants have a deleterious effect on soil macroinvertebrates [4]. Especially hazardous is soil pollution with heavy metals caused by nonferrous metal industries: some groups of these animals disappear or drastically decrease in abundance, which radically transforms the structure of communities [5–11]. Such transformations lead to retardation of organic matter decomposition and deceleration of biological turnover [12], destruction of soil aggregates [12, 13], elimination of mammals trophically connected with macroinvertebrates [14], and disbalance of mineral nutrients in plants [15] and birds [16].

Industrial emissions in many countries have been reduced in the recent period due to shutdown or overhaul of metal industries [17], which theoretically should have a favorable effect on the soil fauna. However, the recovery of pedobiont communities after such reduction has been examined in only a few studies [10, 18, 19]. Moreover, conclusions about the dynamics of communities in these studies are based not on direct observations but on the data partially obtained by other authors [10] or by space-for-time substitution [19]. Several studies on soil invertebrates in the vicinities of industrial plans shut down long ago have been performed without regard to the dynamics of their recovery [8, 20, 21]. More detailed data are available on changes in soil fauna in the course of natural overgrowing or reclamation of industrial slagheaps and abandoned mines [22–25]. However, these data characterize trends in the course of primary succession and therefore have only an indirect bearing on our subject matter, and only as regards the terminal stages of ecosystem degradation (industrial barrens). Such scarcity of information on the patterns of soil fauna recovery after reduction of industrial emissions makes studies in this field highly relevant.

The region considered here is convenient for analyzing the recovery of pedobiont communities for several reasons. First, it has been exposed to pollution by emissions from a copper smelter for more than 75 years, which has resulted in the formation of a major geochemical anomaly where metal concentrations in the center exceed the background levels by several orders of magnitude [26]. This has had disastrous consequences for the biota [27], and their evaluation is simplified due to contrasting responses to pollution in different groups of pedobionts. Second, the input of pollutants has been gradually reduced almost to zero during the past few decades [26], which should have given rise to the recovery of ecosystems. Third, the state of soil macrofauna prior to the onset of reduction of industrial emissions was described in detail 25 years ago [27–29], and these data can be taken as reference.

Moreover, information on responses to pollution from different ecosystem components is available for the study region, which is important for interpretation of the results. In particular, this information concerns vegetation [30], soil [12, 13, 31], soil microbial cenosis [32–34], soil microarthropods [35], herpetobionts [36, 37], chortobionts [38], necrobionts [39], and dendrobionts [40]. Still more important are the results of studies on the dynamics of heavy metal concentrations in the soil [26] and plants [41, 42] and on the recovery of vegetation [30], phyllophages [42], epiphytic lichens [43], and the common mole as an underground dweller [14].

Analysis of soil fauna may be performed with different degree of detail, focusing either in integral parameters of communities (their total abundance, the ratio of supraspecific taxa) or on the abundance and species diversity of certain groups. These approaches complement rather than exclude each other. Here we used the first approach, which paints the picture of dynamics in broad strokes.

The purpose of this study was to analyze the dynamics of the total abundance of soil macrofauna and the ratio of its supraspecific taxa (of family and higher rank) over a 25-period of reduction of emissions from a copper smelter. We are not aware of other studies on the impact of industrial pollution that have directly compared parameters of soil macroinvertebrate communities before and after reduction of emissions. The hypothesis tested here is that no positive dynamics in communities inhabiting the most polluted areas have occurred during this period. This hypothesis is based on the following facts: (1) the leaching rate of heavy metals from the upper soil horizons is low [44], which has also been documented for the study region [26]; (2) vegetation near the smelter remains in a suppressed state [30], indicating the absence of positive dynamics in the environment; (3) the abundance of soil macrofauna in the vicinities of industrial plans shut down long ago remains at a low level [8, 19–21].

## MATERIAL AND METHODS

**Study region.** The Middle Ural Copper Smelter (MUCS) located in the suburbs of Revda, 50 km west of Yekaterinburg, has been in operation since 1940, being until recently a major source of industrial pollution in Russia. The main toxic components of emissions from the smelter are gaseous compounds of sulfur, fluorine, and nitrogen and also dust particles with adsorbed heavy metals (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As). The annual amount of emissions in 1980 reached $225 \times 10^3$ t, being reduced to $148 \times 10^3$ t in 1990 and $106 \times 10^3$ t in 1991. Subsequent reduction was more significant: to $96 \times 10^3$ t in 1994, $63 \times 10^3$ t in 2000, $28 \times 10^3$ t in 2004, and, after an overhaul of the smelter in 2010, to only $3–5 \times 10^3$ t per year [30]. Emissions of the main pollutants—sulfur dioxide and dust—between 1980 and 2012 were reduced by factors of 116 and 44, respectively. Among metals, copper emission was reduced most strongly: by a factor of more than 3000 between 1989 and 2012 [26]. Current concentrations of heavy metals in the forest litter near the MUCS are very high: Cu, 3500–5500 μg/g; Pb, 2500 μg/g; Cd, 17–20 μg/g; Zn, 600–900 μg/g; i.e., they exceed the background values by factors of 100, 40, 7, and 3, respectively [13, 45].

The study region lies in the southern taiga subzone. The surroundings of MUCS are occupied by uneven-aged spruce–fir forests with elements of nemoral floristic complex growing on smooth hillslopes. The ground vegetation layer in the background zone is dominated by *Oxalis acetosella*, *Aegopodium podagraria*, *Gymnocarpium dryopteris*, *Dryopteris carthusiana*, *Asarum europaeum*, *Maianthemum bifolium*, *Cerastium pauciflorum*, and *Stellaria holostea*; in the buffer zone, by *Oxalis acetosella*, *Cerastium pauciflorum*, *Maianthemum bifolium*, *Carex montana*, *Calamagrostis obtusata*, *Rubus saxatilis*, and *Linnaea borealis*. Exposure to pollution has resulted in suppressed growth of trees (decrease in the height, diameter, and stock of tree stand) and ground vegetation (decrease in species diversity and productivity). Closer to the MUCS, spruce–fir forest has survived in fragments with herbaceous communities of relatively poor species composition (*Equisetum sylvaticum*, *Deschampsia caespitosa*, *Tussilago farfara*, *Agrostis capillaris*, etc.) and a moss layer formed by *Pohlia nutans*. Despite significant reduction of emissions in recent years, vegetation in the most polluted areas is not yet being recovered, but some positive changes have already occurred in the buffer zone [30].

The soil cover is composed of mountain-forest brown, soddy podzolic, and gray forest soils transformed to different extents. Apart from heavy metal accumulation and increased acidity, soil transformation manifests itself in the enhancement of the eluvial-gleying process, degradation of soil aggregates, decrease in exchangeable potassium and magnesium, and formation of thick peaty litter [12, 13, 31, 45].

**Censuses of soil macrofauna** were taken in July and August of 2014–2016. Sampling plots 10 × 10 in size were established in four zones distinguished previously by the level of pollution and the state of vegetation: background zone (20–30 km west of the MUCS; five plots in 2014 and by two plots in 2015 and 2016); buffer-1 zone (7 km; five plots in 2014 and by two plots in 2015 and 2016), buffer-2 zone (3–6 km, six plots in 2014 and by three plots in 2015 and 2016), and impact zone (0–2 km, seven plots in 2014 and by two plots in 2015 and 2016). A total of 41 censuses were conducted.

Invertebrates with a body size over 2 mm were hand-sorted out of soil monoliths 20 × 20 cm in area and 20–30 cm in depth (depending on the occurrence of invertebrates). Ten such monoliths were collected from each plot in a random pattern, avoiding sites with visible soil perturbation and areas within 0.5 m from large tree stems. They were placed in plastic bags, delivered to the laboratory, and stored before processing at 12°C for no more than 5 days (as a rule, 1–2 days). To make sampling of invertebrates more accurate, the monoliths were divided into two layers, forest litter and mineral soil horizons (the data for these layers were pooled during further analysis). The collected invertebrates were fixed with 70% ethanol. Ants, empty earthworm cocoons, and relatively large microarthropods (springtails, oribatid mites, etc.) were left out of account.

For comparative purposes, we used the data of our previous studies performed in June and July 1990–1991 [27–29] and June–August 2004 [11]. Sampling plots used in 2014–2016 coincided with those in 2004; in 1990–1991, the plots were in approximately the same areas, with differences in their location varying within a range of 300–500 m (by three plots in the background and buffer-1 zones, nine plots in the buffer-2 zone, and three plots in the impact zone); in 2004, the number and distribution of the plots by zones were the same as in 2014, except for two instead of five plots in the buffer-1 zone and four instead of seven plots in the impact zone. The data of 76 censuses conducted in all these years were included in analysis.

The procedure of sampling and hand sorting was the same in all years, except that the size of soil monoliths in 1992 was 25 × 25 cm and the number of samples taken in 1990 reached 20–40 per plot. The material analyzed in 2016 amounted to 90 samples (4800 ind. of invertebrates); in 2015, 92 samples (9200 ind.); in 2014, 230 samples (15800 ind.); in 2004, 169 samples (6300 ind.); in 1990–1991, 306 samples (5600 ind.); on the whole, 887 samples (41700 ind.) over all these years.

**Data analysis**. Information on weather conditions was obtained from the nearest weather station in the city of Revda. In addition to average air temperature, precipitation, and the number of days with precipitation, Selyaninov hydrothermal coefficient was calculated as the ratio (multiplied by 10) of the sum of precipitation over the period with daily average temperature above 10°C to the sum of differences between this temperature and 10°C over this period.

In all cases, each sampling plot was a statistical unit. Differences between pollution zones and observation periods were evaluated using two-way ANOVA (separately for the first vs. second and second vs. third periods) with Huber–White correction for heteroskedasticity (hc3 algorithm, car v. 3.0-0 package), expressing the data on abundance in natural logarithmic form: $y = \ln(x + 1)$. The Benjamini–Yekutieli procedure was used to control false discovery rate (*FDR*) in multiple testing of statistical hypotheses (all $p$-values were calculated with *FDR* correction). Multiple comparisons were made with Tukey's test. The effect size relative to the background area was evaluated by calculating the bias-corrected natural logarithmic response ratio estimator $RR^{\Delta}$ proposed for small samples and near-zero values in experiment [46]. Ordination based on the relative abundance of taxonomic groups was performed by the principal coordinate method using the Jaccard coefficient (vegan v. 2.4-5 package). All calculations were made in R version 3.4.3.

## RESULTS

The weather markedly varied between study years: compared to the long-term average conditions, 2016 was significantly warmer and drier; 1990 and 2015 were colder and more humid; and conditions in 1991, 2004, and 2014 were close to the long-term average level (Table1).

The total abundance of soil macroinvertebrates and the abundance of almost all taxa (except for the larvae of sawflies and click beetles) were found to differ significantly between pollution zones either in both variants of comparison (the first vs. second and second vs. third periods) or in one of them (Tables 2, 3). Differences between observation periods were not so unequivocal. In the first variant, significant differences in abundance were revealed for spiders, lithobiids, sawflies, nematocerans, click beetles, and staphylinids; in the second variant, for a greater number of groups: enchytraeids, geophilids, scale bugs, lepidopterans, sawflies, click beetles, dipterans, staphylinids, and mollusks. Differences in the total abundance of pedobionts between the periods were significant in both variants. The interaction of factors "zone × period" in almost all cases had no significant effect, indicating the absence of prominent differences in the directions of changes occurring in different zones.

**Table 1.** Weather parameters during the period from May to September in the study years

| Parameter | Year | | | | | | Average (1981–2015) |
|---|---|---|---|---|---|---|---|
| | 1990 | 1991 | 2004 | 2014 | 2015 | 2016 | |
| Average air temperature, °C | 13.0 | 14.7 | 14.8 | 13.4 | 13.7 | 15.8 | 13.7 |
| Precipitation, mm | 445.1 | 376.3 | 341.6 | 299.3 | 528.0 | 152.2 | 343.0 |
| Number of days with precipitation | 94 | 74 | 68 | 65 | 90 | 50 | 75 |
| Hydrothermal coefficient | 5.1 | 3.8 | 3.1 | 3.7 | 5.3 | 1.1 | 3.6 |

In the period of high emissions (1990–1991), different groups of soil macrofauna showed contrasting responses to pollution (Table 2). As the MUCS was approached, the abundance of earthworms, enchytraeids, mollusks, and hemipterans decreased to the point of disappearance; the abundance of myriapods, arachnids, most of coleopterans, dipteran and lepidopteran larvae also dropped by factors of 5 to 100, but they did not disappear. In contrast, an increase in abundance upon transition between the zones with intermediate and high pollution levels was recorded in some groups (by factors of 2.2–2.5 in click beetle larvae and 7–8 in cantharids). Since a negative response to pollution was observed in groups with the highest abundance in the background area (in the first place, saprophages), the total abundance of pedobionts near the MUCS decreased drastically (by a factor of 14), and saprophages (earthworms, enchytraeids, millipedes, larvae of the majority of nematocerans) and saprophytophages (mollusks) yielded dominance to zoophages (spiders, lithobiids, geophilids, harvestmen, larval and adult carabids, cantharids, staphylinids, larvae of some brachyceran dipterans), phytophages (larvae of true weevils, sawflies, lepidopterans, and scale bugs), and mixophages (click beetle larvae).

After reduction of emissions (2004), the pattern of transformation of macroinvertebrate communities under pollution impact remained qualitatively the same, but the abundance of some groups in the buffer zone (enchytraeids, spiders, lepidopteran larvae, staphylinids, mollusks) and the impact zone (spiders, lithobiids, staphylinids) became 1.5 to 19 times higher than in the previous period.

Neither were qualitative changes in this pattern observed after emissions were reduced almost to zero (2014–2016). Compared to 2004, however, not only the abundance of earthworms, their cocoons, enchytraeids, and mollusks increased in buffer plots (by factors of 3, 12, 13, and 10, respectively), but these groups appeared in the impact zone, where they had been absent previously. Only single earthworms occurred at 4 km from the MUCS in 2004, but their abundance in this area increased by 2014–2015, and in 2015 earthworms were found as close as 2 km from the smelter. Enchytraeids and mollusks in 2004 occurred no closer than 4 km from the MUCS, whereas in 2014–2015 they were found at distances of 1 and 2 km, respectively (Table 4).

Differences in the responses of different groups and trends in recovery are well illustrated by the dynamics of effect size ($RR^{\Delta}$): this parameter in the impact zone is stable in time for the total abundance of pedobionts and the abundance of most groups, whereas in the buffer-1 and buffer-2 zones it shifts to zero upon transition from the first to the third period (Fig. 1). The abundance of several groups (earthworms, enchytraeids, carabids, staphylinids, and cantharids) in the buffer zones significantly differs from the background level in the first period, but these differences level off by the second and third period. In other words, the strength of pollution effect on pedobionts remains unchanged in the impact plots but decreases in the buffer plots.

In the ordination plot (Fig. 2), communities of the impact plots are far apart from the background communities, with communities of the buffer zones occupy an intermediate position between them. Differences in the structure of communities between the zones are accounted for mainly by earthworms, enchytraeids, mollusks, spiders, staphylinids, and larvae of brachyceran dipterans and click beetles. Differences between the periods are less noticeable in background communities than in communities of the impact and buffer plots. It is noteworthy that some plots of the buffer-2 zone (but not the impact zone) in the third period approach the background zone.

## DISCUSSION

**Response to pollution.** A detailed analysis of the character, causes, and consequences of changes in soil macrofauna communities exposed to pollution is beyond the scope of this paper (it has been partially performed in our previous studies [11, 28, 29]). In general, trends in the responses of soil macrofauna to pollution in the MUCS impact region are similar to those described for the regions exposed to emissions from other copper or nickel smelters, in particular those in the Southern Urals [7], Kola Peninsula [6, 10], Russian Far East [47], Finland [48], and France [8]. With respect to the degree of change under pollution impact (decrease in abundance by two to three orders of magnitude), soil macrofauna is different from inverte-

**Table 2.** Abundance of soil macrofauna in different pollution zones during different periods (ind./$m^2$ ± standard error)

| Taxonomic group | Pollution zone (distance from polluter, km), period | | | | | |
|---|---|---|---|---|---|---|
| | background (20–30) | | | buffer-1 (7) | | |
| | I, $n = 3$ | II, $n = 5$ | III, $n = 9$ | I, $n = 3$ | II, $n = 2$ | III, $n = 9$ |
| Lumbricidae, worms | 285.8 ± 114.8a | 261.5 ± 50.1a | 238.0 ± 25.5a | 153.5 ± 60.2a | 212.5 ± 19.4a | 330.8 ± 28.2a |
| Lumbricidae, cocoons | 178.6 ± 84.3a | 47.0 ± 7.1a | 139.6 ± 20.2a | 32.1 ± 15.0a | 27.5 ± 5.3a | 165.6 ± 27.8a |
| Enchytraeidae | 299.5 ± 112.9ab | 168.0 ± 25.8a | 1005.3 ± 137.7b | 34.5 ± 22.6a | 125.0 ± 40.7ab | 884.4 ± 207.6b |
| Aranei | 12.8 ± 4.0a | 232.0 ± 30.3b | 280.7 ± 31.6b | 9.2 ± 3.6a | 190 ± 102.5b | 172.8 ± 13.1b |
| Opiliones | 4.8 ± 2.3a | 7.0 ± 2.2a | 9.7 ± 1.7a | 1.3 ± 0.8a | 7.5 ± 3.5a | 11.1 ± 3.6a |
| Lithobiidae | 80.9 ± 27.4a | 180.5 ± 19.9a | 250.1 ± 33.4a | 41.7 ± 15.1a | 75.0 ± 7.1a | 111.9 ± 4.2a |
| Geophilidae | 35.8 ± 12.2ab | 37.5 ± 4.9a | 123.9 ± 15.7b | 14.8 ± 5.6a | 47.5 ± 10.6a | 81.9 ± 4.4a |
| Diplopoda | 5.9 ± 4.2a | 23.5 ± 5.5a | 11.3 ± 5.3a | 2.8 ± 0.3a | 5.0 ± 3.5a | 35.3 ± 26.6a |
| Heteroptera (im + l) | 32.7 ± 13.8a | 22 ± 6.3a | 6.9 ± 1.5a | 17.1 ± 9.1a | 18.8 ± 8.0a | 17.8 ± 3.5a |
| Coccoidea (im + l) | 3.2 ± 2.6a | 6.5 ± 2.2a | 42.2 ± 9.3b | 1.0 ± 0.4a | 3.8 ± 0.9a | 28.9 ± 6.2b |
| Lepidoptera (l + p) | 15.4 ± 5.8a | 10.5 ± 2.8a | 9.1 ± 1.9a | 2.9 ± 1.3a | 23.8 ± 0.9b | 4.2 ± 1.1a |
| Hymenoptera, Symphyta (l + p) | 2.8 ± 0.8a | 22.0± 6.3a | 12.4 ± 2.9a | 3.4 ± 2.5a | 23.8 ± 8.0a | 6.9 ± 1.0a |
| Diptera, Nematocera (l + p) | 19.1 ± 12.5a | 100.5 ± 61.8a | 103.8 ± 26.9a | 4.8 ± 2.7a | 5.0 ± 0.0a | 50.0 ± 9.8b |
| Diptera, Brachycera (l + p) | 111.2 ± 43.4a | 53.0 ± 13.5a | 188.4 ± 16.3a | 31.1 ± 15.8a | 56.3 ± 18.6a | 101.9 ± 15.0a |
| Carabidae (im + l) | 42.1 ± 15.4a | 10.0 ± 2.8a | 22.7 ± 7.4a | 25.2 ± 16.6a | 13.8 ± 0.9a | 17.8 ± 5.0a |
| Staphylinidae (im + l) | 108.6 ± 38.4a | 144.0 ± 21.7a | 185.3 ± 16.5a | 54.3 ± 22.8a | 136.3 ± 30.9ab | 209.7 ± 22. b |
| Cantharidae (l) | 13.9 ± 5.5a | 37.5 ± 10.5a | 35.4 ± 7.5a | 2.2 ± 1.2a | 8.8 ± 2.7ab | 26.7 ± 3.4b |
| Elateridae (im + l + p) | 24.3 ± 3.2a | 46.0 ± 9.7a | 58.3 ± 7.9a | 12.9 ± 4.7a | 85.0 ± 10.6b | 75.3 ± 17.7b |
| Curculionidae (im + l + p) | 19.0 ± 10.1a | 8.5 ± 3.6a | 6.4 ± 1.7a | 8.9 ± 5.6a | 16.3 ± 0.9a | 9.4 ± 3.2a |
| Other Coleoptera (im + l + p) | 4.2 ± 1.2a | 19.0 ± 2.8ab | 65.4 ± 10.4b | 7.5 ± 5.9a | 12.5 ± 5.3a | 76.4 ± 7.6b |
| Mollusca, Gastropoda | 73.6 ± 27.5a | 293.5 ± 97.4a | 337.4 ± 18.7a | 44.7 ± 19a | 172.5 ± 91.9ab | 348.9 ± 55.3b |
| Other invertebrates | 1.3 ± 0.3a | 13.0 ± 5.3ab | 23.4 ± 4.4b | 0.4 ± 0.2a | 2.5 ± 1.8ab | 16.1 ± 3.5b |
| Total | 1375.1 ± 497.7 ab | 1743.0 ± 224.3a | 3155.6 ± 214.0b | 506.2 ± 209.2a | 1268.8 ± 335.0ab | 2783.9 ± 298.2b |

**Table 2.** (Contd.)

| Taxonomic group | Pollution zone (distance from polluter, km), period | | | | | |
|---|---|---|---|---|---|---|
| | buffer-2 (3–6) | | | impact (0–2) | | |
| | I, $n = 3$ | II, $n = 5$ | III, $n = 9$ | I, $n = 3$ | II, $n = 2$ | III, $n = 9$ |
| Lumbricidae, worms | 8.2 ± 3.4a | 32.9 ± 21.3ab | 93.3 ± 32.4b | 0.0a | 0.0a | 1.0 ± 1.0a |
| Lumbricidae, cocoons | 7.9 ± 3.5ab | 4.2 ± 3.4a | 50.8 ± 23.9b | 0.0a | 0.0a | 0.0a |
| Enchytraeidae | 19.1 ± 9.4a | 25.0 ± 15.3a | 300.6 ± 124.4a | 0.5 ± 0.4a | 0.0a | 4.1 ± 2.3a |
| Aranei | 6.6 ± 2.9a | 165.8 ± 40.8b | 179.8 ± 18.9b | 3.7 ± 1.2a | 24.6 ± 5.9ab | 51.1 ± 10.3b |
| Opiliones | 0.7 ± 0.4a | 1.7 ± 0.8ab | 4.0 ± 0.7b | 0.5 ± 0.4a | 0.6 ± 0.5a | 1.1 ± 0.7a |
| Lithobiidae | 17.2 ± 5.3a | 32.5 ± 10.6a | 40.8 ± 10.1a | 1.1 ± 0.4a | 16.6 ± 1.9b | 41.1 ± 14.1b |
| Geophilidae | 8.3 ± 1.9a | 16.7 ± 5.5a | 43.3 ± 9.1a | 1.1 ± 0.4a | 0.6 ± 0.5a | 3.6 ± 1.1a |
| Diplopoda | 3.6 ± 1.1a | 13.3 ± 8.1a | 8.5 ± 6.7a | 1.6 ± 0.8a | 3.8 ± 3.2a | 3.4 ± 1.9a |
| Heteroptera (im + l) | 5.7 ± 2.3a | 6.7 ± 1.5a | 6.5 ± 1.9a | 0.0a | 1.9 ± 0.6ab | 3.6 ± 0.9b |
| Coccoidea (im + l) | 0.5 ± 0.4a | 7.5 ± 4.3ab | 20.0 ± 6.3b | 1.1 ± 0.9a | 1.3 ± 1.1a | 14.0 ± 7.2a |
| Lepidoptera (l + p) | 3.6 ± 1.7a | 9.6 ± 5.2a | 7.1 ± 2.1a | 1.1 ± 0.4a | 3.8 ± 1.9a | 3.4 ± 1.2 a |
| Hymenoptera, Symphyta (l + p) | 1.3 ± 0.5a | 13.8 ± 4.5ab | 6.5 ± 1.2b | 1.6 ± 1.3a | 23.2 ± 8.8a | 7.0 ± 2.9a |
| Diptera, Nematocera (l + p) | 1.9 ± 1.3a | 4.6 ± 1.6a | 98.8 ± 26.6b | 1.1 ± 0.4a | 5.2 ± 1.6ab | 34.2 ± 9.8b |
| Diptera, Brachycera (l + p) | 28.6 ± 13.2a | 50.4 ± 21.4a | 129.6 ± 56.1a | 19.7 ± 7.9ab | 1.9 ± 0.5b | 53.7 ± 26.3a |
| Carabidae (im + l) | 6.4 ± 2.0a | 8.8 ± 1.8a | 9.6 ± 1.7a | 2.7 ± 1.6a | 4.5 ± 1.1a | 5.4 ± 1.3a |
| Staphylinidae (im + l) | 17.9 ± 4.2a | 74.2 ± 9.2b | 137.9 ± 16.8b | 11.2 ± 5.4a | 61.4 ± 5.7b | 53.8 ± 9.4b |
| Cantharidae (l) | 12.0 ± 3.8a | 28.3 ± 9.3a | 22.3 ± 4.0a | 6.9 ± 1.6a | 9.7 ± 3.4 a | 9.3 ± 3.0a |
| Elateridae (im + l + p) | 26.3 ± 7.7a | 48.8 ± 5.3ab | 71.3 ± 6.0b | 24.5 ± 12.4ab | 17.8 ± 5.0a | 71.7 ± 14.9b |
| Curculionidae (im + l + p) | 4.5 ± 1.3a | 8.3 ± 2.0a | 3.8 ± 1.0a | 2.7 ± 1.2a | 0.0a | 2.0 ± 0.7a |
| Other Coleoptera (im + l + p) | 0.7 ± 0.5a | 41.7 ± 6.4b | 61.5 ± 8.4b | 0.5 ± 0.4a | 13.3 ± 4.3b | 24.7 ± 4.6b |
| Mollusca, Gastropoda | 3.4 ± 2.2a | 7.5 ± 4.5a | 74.8 ± 27.4b | 0.0a | 0.0a | 0.4 ± 0.3a |
| Other invertebrates | 0.7 ± 0.5a | 11.3 ± 4.4b | 4.4 ± 1.3ab | 0.0a | 0.0a | 3.4 ± 1.8a |
| Total | 185.0 ± 49.9a | 613.3 ± 63.3b | 1375.0 ± 256.6b | 81.6 ± 12.1 | 190.2 ± 15.9a | 392.1 ± 43.2b |

Observation periods: (I) 1990–1991, (II) 2004, (III) 2014–2016; developmental stages: (im) adult, (l) larva, (p) pupa or pseudopupa; a sampling plot (average of 10 samples) is taken as a statistical unit, n is the number of surveys; similar letter indices indicate the absence of significant differences (Tukey's test) between periods within a zone for each group (here and in Table 3 and Figs. 1, 2).

**Table 3.** Results of ANOVA for differences in the abundance of soil macrofauna between pollution zones and observation periods

| Group | Source of variation | | | | | |
|---|---|---|---|---|---|---|
| | periods I and II | | | periods II and III | | |
| | zone, $df = 3$ | period, $df = 1$ | zone × period, $df = 3$ | zone, $df = 3$ | period, $df = 1$ | zone × period, $df = 3$ |
| Lumbricidae, worms | 522.2 (<0.001) | 0.0 (1.000) | 0.6 (0.761) | 619.4 (<0.001) | 4.5 (0.079) | 0.7 (0.718) |
| Lumbricidae, cocoons | 224.7 (<0.001) | 2.0 (0.276) | 0.4 (0.84) | 728.4 (<0.001) | 0.0 (1.000) | 11.4 (<0.001) |
| Enchytraeidae | 256.5 (<0.001) | 0.1 (0.843) | 0.9 (0.624) | 306.6 (<0.001) | 48.8 (<0.001) | 0.5 (0.792) |
| Aranei | 8.6 (0.001) | 66.5 (<0.001) | 1.9 (0.263) | 20.6 (<0.001) | 1.7 (0.311) | 0.1 (0.992) |
| Opiliones | 2.1 (0.212) | 1.1 (0.448) | 0.4 (0.843) | 13.8 (<0.001) | 2.8 (0.185) | 0.4 (0.843) |
| Lithobiidae | 51.2 (<0.001) | 17.4 (0.001) | 1.7 (0.311) | 60.1 (<0.001) | 4.7 (0.073) | 0.8 (0.654) |
| Geophilidae | 21.9 (<0.001) | 0.7 (0.542) | 0.9 (0.576) | 48.3 (<0.001) | 30.1 (<0.001) | 0.4 (0.840) |
| Diplopoda | 1.1 (0.501) | 0.1 (0.840) | 0.4 (0.855) | 3.5 (0.048) | 0.4 (0.654) | 0.4 (0.855) |
| Heteroptera | 12.5 (<0.001) | 5.5 (0.056) | 0.7 (0.718) | 7.4 (0.001) | 1.1 (0.448) | 0.8 (0.654) |
| Coccoidea | 1.2 (0.468) | 4.5 (0.086) | 0.4 (0.843) | 6.4 (0.003) | 22.4 (<0.001) | 0.3 (0.906) |
| Lepidoptera | 6.9 (0.004) | 4.7 (0.079) | 1.1 (0.503) | 4.8 (0.013) | 24.8 (<0.001) | 3.9 (0.036) |
| Hymenoptera, Symphyta | 1.2 (0.464) | 13.8 (0.003) | 0.5 (0.837) | 1.2 (0.468) | 6.2 (0.038) | 1.3 (0.42) |
| Diptera, Nematocera | 3.7 (0.05) | 5.9 (0.048) | 0.1 (1.000) | 4.2 (0.025) | 125.5 (<0.001) | 2.1 (0.198) |
| Diptera, Brachycera | 6.4 (0.006) | 0.0 (0.926) | 2.0 (0.246) | 19.2 (<0.001) | 21.3 (<0.001) | 2.0 (0.222) |
| Carabidae | 5.8 (0.009) | 1.1 (0.448) | 1.2 (0.468) | 7.8 (0.001) | 0.0 (1.000) | 0.3 (0.86) |
| Staphylinidae | 5.8 (0.009) | 34.1 (<0.001) | 0.5 (0.792) | 11.7 (<0.001) | 5.8 (0.044) | 2.3 (0.161) |
| Cantharidae | 2.7 (0.124) | 4.4 (0.09) | 0.6 (0.761) | 5.3 (0.008) | 0.1 (0.840) | 1.2 (0.459) |
| Elateridae | 3.3 (0.074) | 11.2 (0.007) | 1.2 (0.464) | 1.9 (0.248) | 6.1 (0.040) | 2.8 (0.093) |
| Curculionidae | 411.7 (<0.001) | 1.0 (0.464) | 2.2 (0.194) | 408.9 (<0.001) | 0.2 (0.792) | 7.3 (0.001) |
| Other Coleoptera | 1.7 (0.311) | 125.6 (<0.001) | 5.0 (0.018) | 11.6 (<0.001) | 21.4 (<0.001) | 2.1 (0.194) |
| Mollusca, Gastropoda | 65.7 (<0.001) | 0.0 (1.000) | 0.9 (0.624) | 301.0 (<0.001) | 5.9 (0.044) | 2.9 (0.090) |
| All groups | 47.1 (<0.001) | 30.5 (<0.001) | 0.8 (0.654) | 109.6 (<0.001) | 34.6 (<0.001) | 0.0 (1.000) |

Values of Fisher's F-test and *FDR*-adjusted significance levels (in parentheses) are shown; *df*, the number of degrees of freedom for a factor; $df_{Error}$ is 27 for comparison between periods I and II, and 50 for comparison between periods II and III.

**Table 4.** Occurrence (%) of indicator groups of soil macrofauna in samples taken at different distances from polluter in different years

| Year | Distance from polluter, km | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 20–30 | 7 | 5–6 | 4 | 3 | 2 | 1 | 0–0.5 |
| Lumbricidae (worms and cocoons) | | | | | | | | |
| 1990–1991 | 80 | 66 | 41 | 25 | 0 | 0 | – | 0 |
| 2004 | 98 | 100 | 70 | 27 | 0 | 0 | 0 | – |
| 2014 | 100 | 100 | 75 | 77 | 0 | 0 | 0 | 0 |
| 2015 | 100 | 100 | 100 | 100 | 60 | 45 | 0 | – |
| 2016 | 100 | 95 | 100 | 10 | 20 | 0 | 0 | 0 |
| Enchytraeidae | | | | | | | | |
| 1990–1991 | 55 | 22 | 34.8 | 15 | 40 | 10 | – | 0 |
| 2004 | 90 | 70 | 40 | 16.7 | 0 | 0 | 0 | – |
| 2014 | 100 | 92 | 60 | 83.3 | 0 | 10 | 10 | 0 |
| 2015 | 100 | 100 | 100 | 100 | 40 | 45 | 0 | – |
| 2016 | 100 | 90 | 80 | 60 | 0 | 20 | 0 | 0 |
| Mollusca | | | | | | | | |
| 1990–1991 | 48 | 45 | 21 | 2 | 0 | 0 | – | 0 |
| 2004 | 92 | 75 | 20 | 17 | 0 | 0 | 0 | – |
| 2014 | 100 | 98 | 50 | 60 | 30 | 3 | 0 | 0 |
| 2015 | 100 | 100 | 100 | 90 | 70 | 9 | 0 | – |
| 2016 | 100 | 100 | 100 | 60 | 40 | 0 | 0 | 0 |
| Number of samples | | | | | | | | |
| 1990–1991 | 60 | 100 | 66 | 40 | 10 | 10 | 0 | 20 |
| 2004 | 50 | 20 | 20 | 30 | 10 | 29 | 10 | 0 |
| 2014 | 50 | 50 | 20 | 30 | 10 | 30 | 10 | 30 |
| 2015 | 21 | 20 | 10 | 10 | 10 | 11 | 10 | 0 |
| 2016 | 20 | 20 | 10 | 10 | 10 | 10 | 10 | 10* |

* Additional samples taken near permanent plots for comparison with coarse woody debris [66]; (–) no data.

brates inhabiting other layers—herpetobionts [36, 37], necrobionts [39], and dendrobionts [40]—whose abundance near the MUCS is decreased by a factor of only 2–3.

Analysis of changes at the level of higher-rank taxa makes it possible to explain the diversity of responses to pollution in different groups by differences in the mode of life. For groups such as earthworms, millipedes, mollusks, and harvestmen, decline in abundance and subsequent elimination can be attributed to direct toxic effect of heavy metals ingested with food or taken in through contact with soil. Soil concentrations of metals in the MUCS region far exceed safe levels for soil animals [5, 49], with metal toxicity being even higher under conditions of acidification in naturally acidic soils. Other taxa (lithobiids, geophilids, spiders, hemipterans, carabids, staphylinids) are apparently more vulnerable to indirect effects of pollution, such as pessimization of microclimate and depletion of trophic resources as a result of degradation of vegetation. Groups indifferent to pollution or positively responding to it (e.g., click beetle larvae) are likely to have mechanisms that either successfully prevent the intake of toxicants or effectively remove them from the body. Factors driving the recovery of these groups are also different.

**Community dynamics.** Analysis of long-term dynamics is hindered by interference from several factors that are especially significant in the case of soil macrofauna, namely, multiscale spatial variation, interannual fluctuations, and differences in the accuracy of censuses. The use of permanent sampling plots (as in our study) makes it possible to reduce the risk that analysis of temporal dynamics will be substituted by analysis of spatial patchiness on a several-hundred-meter scale. Unfortunately, this approach also cannot completely eliminate the interfering effect of microscale variation (on a several-meter scale).

It is more difficult to level off the influence of interannual variation. A possible solution is to analyze the parameters of interest in several years with con-

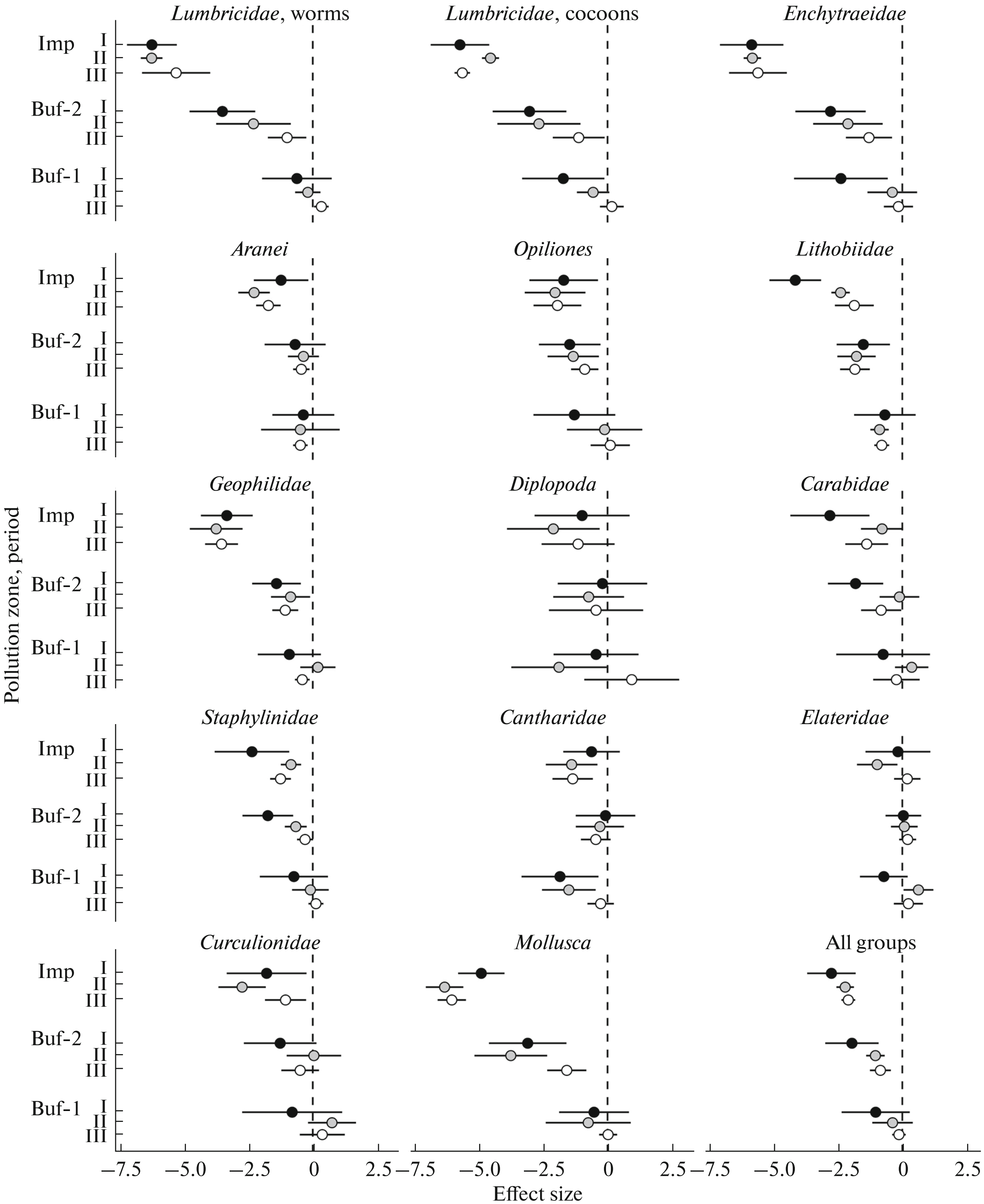


**Fig. 1.** Effect strengths (with 95% confidence intervals) in impact (Imp), buffer-1 (Buf-1), and buffer -2 (Buf-2) zones relative to background area in periods I (black circles), II (gray circles), and III (white circles). Developmental stages of invertebrates are indicated in Table 2.

trasting weather conditions within each time section. This approach has been only partially implemented in our study. Nevertheless, consideration of several pollution zones in each of the three periods allowed us to use the level of abundance in the background zone as an internal standard and analyze the dynamics of abundance in polluted plots not only in absolute values but also in values normalized relative to this stan-

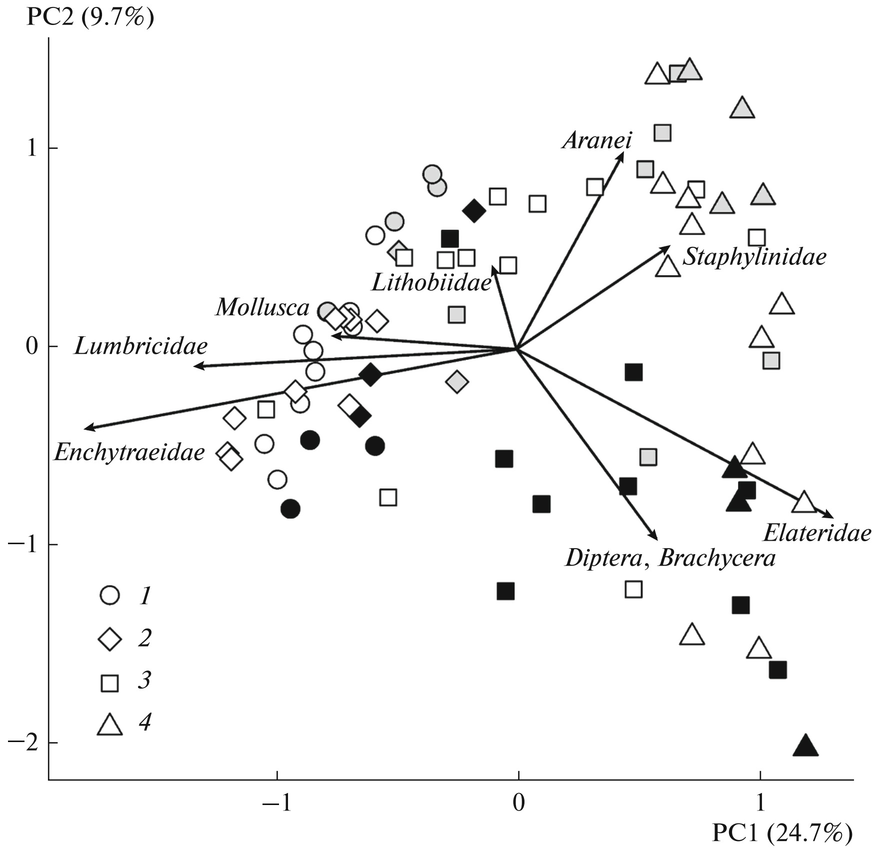


**Fig. 2.** Ordination of sampling plots in the plane of the first and second principal axes (PC1 and PC2, with percentages of explained variants in parentheses). Pollution zones: (1) background, (2) buffer-1, (3) buffer-2; (4) impact. Periods I, II, and III are indicated by black, gray, and white markers, respectively. Vectors are shown for groups whose absolute factor loading value exceeds 0.4. Developmental stages of invertebrates are indicated in Table 2. For Lumbricidae, data on the abundance of worms and cocoons are summed up.

dard. Thus, effect size estimate $RR^{\Delta}$ (Fig. 1) has proved to level off the influence of not only interannual variation but also of technical bias that have an effect on the completeness of invertebrate census.

The comparison of data on the periods of high (1990–1991), reduced (2004), and almost zero emissions (2014–2016) provides evidence for stability in the response of soil macrofauna to pollution, which has remained qualitatively the same over 25 years. The pattern of changes observed upon approaching the smelter was reproduced in each of the three periods: an abrupt drop in the total abundance of macroinvertebrates; disappearance of several taxa, including those crucial for the functioning of forest ecosystems (earthworms); and shift in the ratio of trophic groups, with sapro- and saprophytophages yielding dominance to phyto-, zoo-, and mixophages. In this respect, our hypothesis that the communities recover slowly has been confirmed.

Studies on the Kola Peninsula also have not revealed any appreciable recovery dynamics of soil macrofauna over 14 years after reduction of emissions from a nickel smelter [10]. Indirect evidence for the stability of the depressed state of geo- and chortobiont communities near smelters is provided by data on significant differences in their diversity and abundance between impact and background areas persist for a long time after the smelters were permanently shut down; e.g., such observations were made after shutdown periods of 40 years in Canada [18, 19], 50 years in France [8, 20], and 15 years in Brazil [21].

On the other hand, some changes observed in the study region may be regarded as symptoms of community recovery, which contradicts our hypothesis. Two interrelated processes are developing over time: first, an increase in the abundance of macroinvertebrates takes place in the buffer and impact zones (Table 2) and second, the distribution boundaries of groups formerly absent in the most polluted plots (earthworms, enchytraeids, and mollusks) are shifting closer to the smelter (Table 4). The first process is insufficiently reliable as a basis for conclusions about recovery, since it may reflect fluctuations of abundance between years. The second process is more reliable in this respect, as it indicates the onset of qualitative changes, but this may also be partly due to a fortunate combination of circumstances such as favorable weather conditions. As a result, differences between the polluted and background plots are leveled off to some extent, and this concerns both the structure of communities (Fig. 2) and the abundance of certain groups (Fig. 1).

As for the dynamics of groups more sensitive to indirect effects of pollution, a relevant fact is that the recovery of forest vegetation and corresponding microclimate has not yet occurred in the most polluted plots [30]. However, a more detailed taxonomic resolution is necessary for discussing this aspect.

**Putative drivers of dynamics.** It is well known that the abundance of pedobionts depends on temperature and moisture in their habitats. Therefore, the observed temporal trends may theoretically result solely from differences in heat and moisture supply between the study periods. In our case, however, the dynamics of communities cannot be explained in this way: some years in the periods of high emissions (1990) and almost zero emissions (2015) were closely similar with respect to temperature and precipitation, whereas the abundance and structure of macroinvertebrate communities markedly differed between these years (Table 1). The same follows from the comparison of data on 1991, 2004, and 2014. Symptoms of community recovery were obvious even in 2016, the driest of all years, although they were less expressed than in 2014 and 2015 (Table 4). All this gives grounds to attribute the observed trends to reduction of emissions rather than to changes in weather conditions.

Analysis of putative factors accounting for the recovery dynamics should logically be based primarily on temporal changes in toxic impact on pedobionts. Reduction of emissions from the MUCS has not yet resulted in a significant decrease in soil concentrations of metals [26]. Thus, the contents of Cd, Pb, and Zn in the forest litter and humus soil horizon remained unchanged between 1989 and 2012 or even increased by the end of this period (because of pH-dependent decrease in their mobility and some other mechanisms). On the other hand, Cu concentrations in the litter decreased by a factor of 1.5–3.0 over 25 years in all zones, and such a decrease (1.5-fold) in the immediate vicinity of the MUCS was also observed in the humus horizon [26]. However, a decrease in the concentration of one component of the "toxic cocktail," with the concentration of others remaining high, is unlikely to play any significant role, because all these metals are harmful to soil animals [50]. The retention of the high pollution level in the study region is confirmed by fact that metal contents in the diet of rodents (mainly herbaceous plants) has not decreased during the 25-year period [41]. A decrease in metal concentrations during the past few years has been revealed in birch leaves [42], but this is explained by reduced dust deposition on leaf blades, as is also documented for other regions [15].

Of special significance in the context of our discussion is that reduction of emissions (primarily of sulfur dioxide) and consequent intensification of sod process and forest regeneration due to the establishment of deciduous species in polluted areas have provided for normalization of pH in the forest litter and humus soil horizon [26]. It is well known that pH is the main factor influencing the mobility and, hence, toxicity of metals in the soil [51, 52], which decrease abruptly at pH > 5. The pH of the litter in the buffer and impact zones has almost approached this value, having increased from 3.5–3.8 units in 1989 to 4.8–5.0 units in 2012 [26]. As a consequence, the toxicity of metals may decrease while their total contents remain high. In particular, this has been demonstrated for phytotoxicity of the litter in the MUCS region [53].

We emphasize that it is the combined action of metals and soil acidity, rather than the separate action of each individual agent, that should be considered responsible for elimination of earthworms (and probably other saprophages) under pollution impact [29]. Earthworms can survive at high metal concentrations in the soil, but only if its pH is initially close to neutral and does not shift to lower values [54], and the same is true of enchytraeids [55]. Therefore, the expected decrease in toxicity due to normalization of soil pH may theoretically allow saprophages to recover their abundance.

**Recolonization of polluted territory.** The phenomenon of rapid advance of earthworms and mollusks toward the MUCS deserves special attention. Comparing the data on the first and second periods (no earthworms and mollusks occurred closer than 4 km from the smelter) and on the third period (both groups found at 2 km from it), we find that they advance at a rate of 2 km per 10 years, which is unbelievably high. A similar estimate has been obtained in the study region by analyzing shifts in the distribution boundaries of the common mole, which is almost obligatorily connected with earthworms [14].

Such a rate would be of no surprise, e.g., in flying coleopterans [56]. Rapid recolonization of "lichen deserts" by epiphytic lichens is also readily explainable, because their propagules are transferred by wind from less polluted areas [43]. However earthworms and mollusks are among the least mobile groups [57]. In most cases, the rate of colonization of vacant territory by earthworms (e.g. during invasion of European species in North American forests) is only 4–6 m per year [58, 59], with the maximum recorded values ranging from 14 [58] to 28 m per year [60]. The respective values for terrestrial mollusks are 2–5 m per year [61] and, for large land snails, 20 m/year [62]. At the above rates, the observed advance for 2 km toward the smelter would have taken not 10 but 100 years.

An alternative explanation that cannot be definitely ruled out is that these groups inhabited polluted areas in the previous periods but had not been found because of very low abundance and insufficient sample sizes. If so, their finding in 2015 is evidence not for recolonization proper but for increase of abundance above the detection limit. We consider this explanation hardly probable, since earthworms and mollusks have not been observed during four censuses in strongly polluted plots (1990, 1991, 2004, and 2014; a total of 179 samples) which was also confirmed by additional surveys.

A more likely explanation is that earthworms and mollusks not only advanced toward the smelter in a "continuous front line" but also expanded in a network pattern from certain microsites that usually remain beyond the scope of standard soil-zoological censuses, e.g., moist areas near small streams or logs and stumps at late stages of decay. It may be expected that not only moisture conditions in such microsites are more favorable than in the surrounding areas but also metal toxicity is lower due to high contents of organic matter. It is known that metal concentrations tolerable for earthworms in substrates rich in organic matter are much higher than those in poor substrates [49]. Therefore, it is possible that earthworms and mollusks can live for a long time in such microsites located far beyond their distribution boundaries drawn based on their occurrence in standard soil samples.

An important fact is that a high patchiness in the distribution of total metal contents in the soil is usually observed in polluted areas [45], with spatial variation in soil acidity making the distribution of metal toxicity still more uneven [53]. Such a patchiness of toxicity distribution can account for the spatial patterns of soil microflora [32, 33] and fauna [63, 64], partly because soil invertebrates actively avoid patches with high contents of pollutants [65]. Therefore, the aforementioned microsites can be justly regarded as "safety islands" not only in view of increased mortality of pedobionts in the surrounding areas but also because of their attractiveness to invertebrates.

If our assumption concerning these microsites is correct, then a decrease in soil toxicity in the surrounding areas, especially in combination with good weather, may provide for rapid recolonization of the polluted territory. It cannot be excluded that the dispersal of soil invertebrates is facilitated by other mechanisms, such as phoresy on birds and passive migration (e.g., on plant fragments transferred by wind and water streams).

A special survey of coarse woody debris in 2016 confirmed this assumption: earthworms and mollusks were found within decaying logs in plots that had been included in the zone of "lumbricid desert" [66]. This may be regarded as direct evidence for the existence of such microsites.

There are other observations that also provide arguments in favor of the proposed explanation. Thus, snails were found in nesting material collected from pied flycatcher nests at 1 km from the MUCS [16], although standard soil samples from the same zone contained no mollusks [27, 11]. It is hardly probable that birds were more successful in picking up soil macrofauna than specialists who sorted soil samples. Most probably, snails were collected in sites where they were highly abundant, such as overmoistened biotopes. Since pied flycatchers collect food in close vicinity of the nest, rarely moving father than 50 m from it [67], these findings also confirm the existence of microsites near the MUCS.

## CONCLUSIONS

As far as we know, this study is the first to directly compare the state of soil macroinvertebrate communities before and after reduction of industrial emissions. In view of the very slow rate of soil purification of heavy metals, we did not expect that reduction and, in the past few years, almost complete cessation of the input of pollutants would immediately provide for the recovery of these communities. Indeed, the response of soil macrofauna to pollution at a qualitative level has remained basicaly similar over 25 years, with the pattern of changes observed upon approaching the smelter being reproduced in the periods of high (1990–1991), reduced (2004), and almost zero emissions (2014–2016): an abrupt drop in the total abundance of macroinvertebrates (by two orders of magnitude) at the expense of the majority of taxa and a radical shift in the ratio of trophic groups, with saprophages yielding dominance to zoo- and phytophages.

On the other hand, some symptoms of community recovery are observed in the study region: the abundance of pedobionts in polluted plots has increased, and the distribution boundaries of groups formerly absent in the most polluted zone (earthworms, enchytraeids, and mollusks) have shifted closer to the smelter. This is most likely explained by normalization of soil pH and consequent decrease in the mobility (and, hence, toxicity) of metals in the soil, and it may well be that the combination of these factors with favorable weather conditions contributed to the positive dynamics of communities.

The observed phenomenon of the extremely rapid advance of earthworms and mollusks into the strongly polluted zone around the smelter (for 2 km in 10 years) may be due to spatial heterogeneity in the distribution of pollutants. It is probable that there are certain microsites within this territory in which conditions are less pessimal than in the surrounding areas. Such microsites allow low-mobile forms of invertebrates to survive beyond the boundaries of their main distribution area and then rapidly recolonize polluted plots as soil toxicity decreases, especially under favorable weather conditions. To test this hypothesis, it is necessary to continue monitoring and perform a special analysis of the microscale distribution of pedobionts.

We have considered only the initial stages of the recovery of soil macroinvertebrate communities, which will obviously continue for a very long time. Further direct observations on their dynamics, combined with studies on the recovery of other ecosystem components will provide an insight into the underlying mechanisms of progressive succession, which is important for the development of the theory of community stability. An analysis of communities at the species level, which is planned for our future research, will help to elucidate these mechanisms.

## ACKNOWLEDGMENTS

The authors are grateful to M.P. Zolotarev for his participation in field studies, V.S. Mikryukov for his help in data analysis, and E.A. Belskaya and O.V. Dulya for their comments on the manuscript. The material collection in 2014–2016 was supported by the Russian Foundation for Basic Research, project no. 14-05-00686. Data analysis and manuscript preparation were performed under the state contract of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, and partially supported by the Russian Foundation for Basic Research, project no. 18-04-00160).

## COMPLIANCE WITH ETHICAL STANDARDS

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

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*Translated by N. Gorgolyuk*