ISSN 1062-3590, Biology Bulletin, 2020, Vol. 47, No. 1, pp. 87–96. © Pleiades Publishing, Inc., 2020.
Russian Text © The Author(s), 2020, published in Izvestiya Akademii Nauk, Seriya Biologicheskaya, 2020, No. 1, pp. 85–95.

ECOLOGY

Coarse Woody Debris as Microhabitats of Soil Macrofauna in Polluted Areas

E. L. Vorobeichik[a, *], **A. I. Ermakov**[a], **D. V. Nesterkova**[a], **and M. E. Grebennikov**[a]

[a] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*

**e-mail: ev@ipae.uran.ru*

Received May 6, 2018; revised August 25, 2019; accepted September 1, 2019

Abstract—We built a map of the distribution of earthworm abundance in coniferous forests in the area affected by long-term emissions from the Middle Ural Copper Smelter. It is established that a "lumbricide desert" of about 65 km^2 without earthworms in the forest litter and soil mineral horizons has been formed near the smelter due to extremely high concentrations of heavy metals. However, we have also found that earthworms (only *Dendrodrilus rubidus tenuis*) inhabit logs of the late stages of decomposition in this area. Their abundance is comparable to that in the soil of unpolluted (background) areas; single individuals (including cocoons) were also found in the soil directly under the logs. Gastropods, which are absent in standard soil samples in this area, were also recorded in these logs (five species). We suppose that the presence of such "survival microsites" may serve as a mechanism of recolonization of polluted areas by groups sensitive to pollution after the reduction of emissions, followed by a decrease in soil toxicity.

DOI: 10.1134/S1062359020010173

INTRODUCTION

Soil pollution can be extremely high near large long-term non-ferrous smelters: the concentrations of some metals and metalloids, including particularly toxic ones (Cd, Pb, Ni, Cu, Zn, Hg, As, etc.), exceed the background values by ten and hundred folds (Dudka and Adriano, 1997). This high level of pollution (especially in combination with soil acidification) is detrimental to soil fauna, causing a decrease in the abundance of some sensitive groups (earthworms, pot worms, mollusks, diplopods, etc.), followed by their complete disappearance (Bengtsson et al., 1983; Spurgeon and Hopkin, 1996; Vorobeichik, 1998; Vorobeichik et al., 2012, 2019). In the immediate vicinity of large enterprises, the process of ecosystem degradation ends with the formation of industrial barrens: specific "moonscapes" that are almost completely devoid of higher vegetation and upper soil horizons (Kozlov and Zvereva, 2007).

The study of soil fauna in heavily polluted areas, especially at the range margins of sensitive groups, provides a better understanding of the "internal organization" of pedobiont communities, and the patterns of their functioning and stability. In this regard, such studies are similar to those performed in other extreme habitats (e.g., Arctic deserts and highlands), which have made a significant contribution to the soil zoology and ecology of communities.

The worldwide reduction of atmospheric emissions in recent years (Pacyna et al., 2009) makes it possible to analyze another important aspect, namely, the natural recovery of soil fauna. Our research near the Middle Ural Copper Smelter (MUCS), the emissions of which have sharply decreased over the last decade, has revealed an unexpected phenomenon, namely, an incredibly high rate of recolonization of the polluted area by earthworms and mollusks. Thus, comparison of materials from two sequential censuses made it possible to conclude that the rate of advancement of these groups towards the smelter was 2 km over 10 years (Vorobeichik et al., 2019). This value would not be surprising for actively flying insects, such as coleopterans; however, the groups under study have low mobility: the rate of colonization of a new area by earthworms is usually 4–6 (maximum 14–28) m/yr. (Eijsackers, 2011) and the rate of colonization by terrestrial mollusks is usually 2–5 (maximum 20) m/yr. (Kramarenko, 2014). In other words, the documented shifts in the distribution boundaries of these groups would possibly take 100 years rather than ten.

We assumed that the revealed phenomenon may be due to the recolonization of the previously defaunated area not only from the outside but also from the inside, namely, from some "survival microsites" that exist in heavily polluted areas. Presumably, the main "candidate" for the role of such microsites is coarse woody debris (CWD) of the late stages of decomposition, since soil invertebrates can actively colonize these sites using them as a refuge and a trophic resource (Harmon et al., 1986). We do not know any publications that analyze CWD colonization by pedobionts under severe industrial pollution.

The purpose of this study was to test the hypothesis about the possibility of earthworms and mollusks dwelling in CWD in areas with extremely high concentrations of heavy metals, where these groups are absent in the forest litter and mineral soil horizons.

MATERIALS AND METHODS

The material was collected in the area near the MUCS exposed to long-term pollution, which has affected soil (Kaigorodova and Vorobeichik, 1996; Korkina and Vorobeichik, 2016; Vorobeichik and Kaigorodova, 2017; Korkina and Vorobeichik, 2018), soil microbiocenosis (Vorobeichik, 2007; Mikryukov et al., 2015; Mikryukov and Dulya, 2017), vegetation (Vorobeichik et al., 2014; Bergman and Vorobeichik, 2017), ground running invertebrates (Ermakov, 2004; Bel'skaya and Zolotarev, 2017), and soil-dwelling macroinvertebrates (Vorobeichik, 1998; Vorobeichik et al., 2012, 2019), as well as mammals trophically related to them (Vorobeichik and Nesterkova, 2015). In addition to the accumulation of heavy metals and an increase in acidity (Vorobeichik and Pishchulin, 2016; Korkina and Vorobeichik, 2018), the technogenic transformation of soils is expressed in the strengthening of the eluvial-gleyed process, as well as the destruction of soil aggregates, a decrease in the content of exchangeable calcium and magnesium (Kaigorodova and Vorobeichik, 1996), and the formation of a thick forest litter due to the suppression of large soil saprophages and inhibition of the microbial destruction of organic matter (Vorobeichik, 2007; Korkina and Vorobeichik, 2016; Korkina and Vorobeichik, 2018).

Study area. The MUCS is located on the outskirts of the city of Revda, Sverdlovsk oblast (50 km west of Yekaterinburg). The main ingredients of its emissions are gaseous S, F, and N compounds, as well as dust particles with adsorbed heavy metals (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As). The smelter has been operating since 1940 and has until recently been one of the largest sources of industrial pollution in Russia. Its emissions were 225000 ton pollutants per year in 1980, 148000 t in 1990, 96000 t in 1994, 63000 t in 2000, 28000 t in 2004, and 3000–5000 t after the radical renewal of the smelter in 2010 (Vorobeichik and Kaigorodova, 2017).

Despite the reduction of the MUCS emissions in recent years, vegetation has not yet recovered in the most polluted areas (Vorobeichik et al., 2014) and the content of heavy metals has still not decreased in the upper soil horizons (Vorobeichik and Kaigorodova, 2017). At the same time, one can clearly observe signs of recovery in sensitive to atmospheric pollution groups that do not live in soil, e.g., epiphytic lichens (Mikhailova, 2017).

The concentration of metals in the forest litter is currently very high near the smelter: Cu, 3500–5500; Pb, 1400–2500; Cd, 17–20; and Zn, 600–900 μg/g, which exceeds the background values by 100, 40, seven, and three times, respectively; the pH of the litter (4.5–4.9) is lower than the background level by more than one (Vorobeichik and Pishchulin, 2016; Korkina and Vorobeichik, 2018).

The smelter is located in the subzone of the southern taiga on the border of the western and eastern macroslopes of the Urals. Prior to the industrial development of the area (about 300 years ago), spruce–fir forests with nemoral flora species prevailed on the western macroslope and pine forests were dominant on the eastern slope. Today, in addition to these species, significant areas are occupied by secondary birch and aspen forests on both macroslopes. The soil cover is formed by lithozems, rzhavozems, burozems, gray forest soils, and soddy-podzolic soils. There are spruce–fir or birch fragments of forest with species pour communities (*Equisetum sylvaticum*, *Deschampsia cespitosa*, *Tussilago farfara*, *Agrostis capillaris*, etc.) and a single-species moss cover (*Pohlia nutans*) adjacent to open areas covered by meadow vegetation near the smelter (Vorobeichik et al., 2014).

Mapping of the distribution of earthworm abundance. Mapping was carried out based on records from 179 temporary sampling plots (SPs) of 25 × 25 m, which were relatively regularly distributed over an area of 40 × 50 km with the smelter in the center. Each SP was surveyed once in July–September in 2013–2016 except for periods during droughts and after the first frosts. The abundance of worms (spec./m^2) was estimated by counting the number of individuals at ten sites with a size of 1 × 1 m that were randomly placed in each SP. The number of individuals was calculated in the upper 7- to 10-cm layer (the forest litter and upper layer of the humus horizon) by hand sorting of the substrate (without species identification and differentiation of earthworms by size and without taking into account cocoons). Therefore, the estimates cover the whole group of epigeic and epi-endogeic species. The map was constructed by spatial interpolations in Surfer 13 using the Kriging (exact interpolator, linear variogram, 0.2 km grid step).

CWD colonization by invertebrates. It was estimated in areas located 1–2 km west of the smelter, which were included in the "lumbricide desert" according to the mapping results (Fig. 1). We carried out two surveys: qualitative sampling of earthworms and mollusks on August 25, 2016, in six logs, located in the floodplain of a small forest river (Elchovka River) and in adjacent areas; quantitative sampling of invertebrates on August 29 and September 2, 5, and 15, 2016, in ten logs that were found outside the floodplain (Fig. 2).

In both cases, logs were randomly selected, taking into account the following criteria:

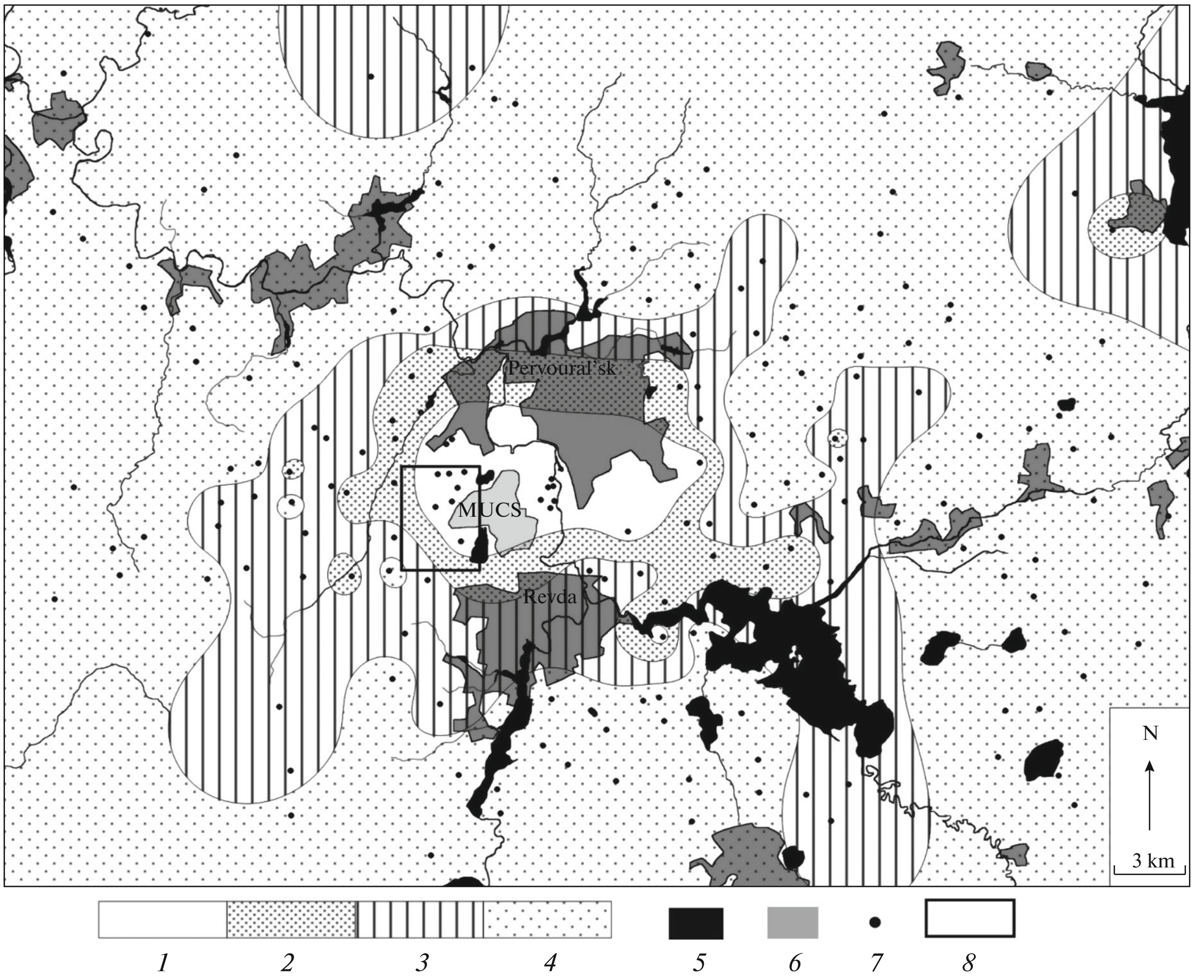

Fig. 1. Distribution of earthworms abundance in the impact region. Density: (*1*) 0, (*2*) 0.1–1.0, (*3*) 1.1–10.0, (*4*) over 10 spec./m^2. (*5*) water bodies, (*6*) human settlements, (*7*) temporary sampling plots, (*8*) plot where the degree of colonization of logs by soil macrofauna was estimated (Fig. 2).

the tree species: linden *Tilia cordata* Mill. or birch *Betula pendula* Roth or *B. pubescens* Ehrh.;

the diameter should be at least 20 cm in the butt-log portion and the length should be at least 3 m (the actual diameter was 31.4 ± 8.2 cm, mean ± SE, $n = 10$);

a log should be partially buried in the litter and mineral horizons of the soil, but not more than half of its diameter;

the fourth stage of decomposition according to the 5-point scale (Bergman and Vorobeichik, 2017), i.e., when the bark is partially preserved and the wood flakes off, changes its color, and can be easily penetrated with a knife and, at the same time, the core of the log is relatively strong;

the absence of visible traces of fire; and

the absence of total colonization of ants at least in an area with a length of not less than 2 m.

A log fragment with a length of about 1 m was carefully cut out for quantitative collections of pedobionts; its length and larger and smaller diameters were then measured (with an accuracy of 1 cm); the fragment volume was determined by the truncated cone formula. Samples were hand sorted in two stages: at the first stage, the flaking bark was removed with a knife and tweezers on a polyethylene sheet and wood fibers were then separated; at the second stage, the entire wood was put into a plastic bag and reexamined at the laboratory. The core of three logs was very strong and, therefore, was not sorted; in this case, we determined the volume only for the sorted part (as the difference between the initial volume of the fragment and the volume of the core).

At the same time, standard soil samples of 20 × 20 cm were taken to the depth at which macroinvertebrates occurred (as a rule, up to 25 cm). Some of them were collected directly in the "bed" of a log (three samples were collected for each of two logs and one sample was collected for each of the other logs) and some were collected at a distance of 3–5 m from a log (one sam-

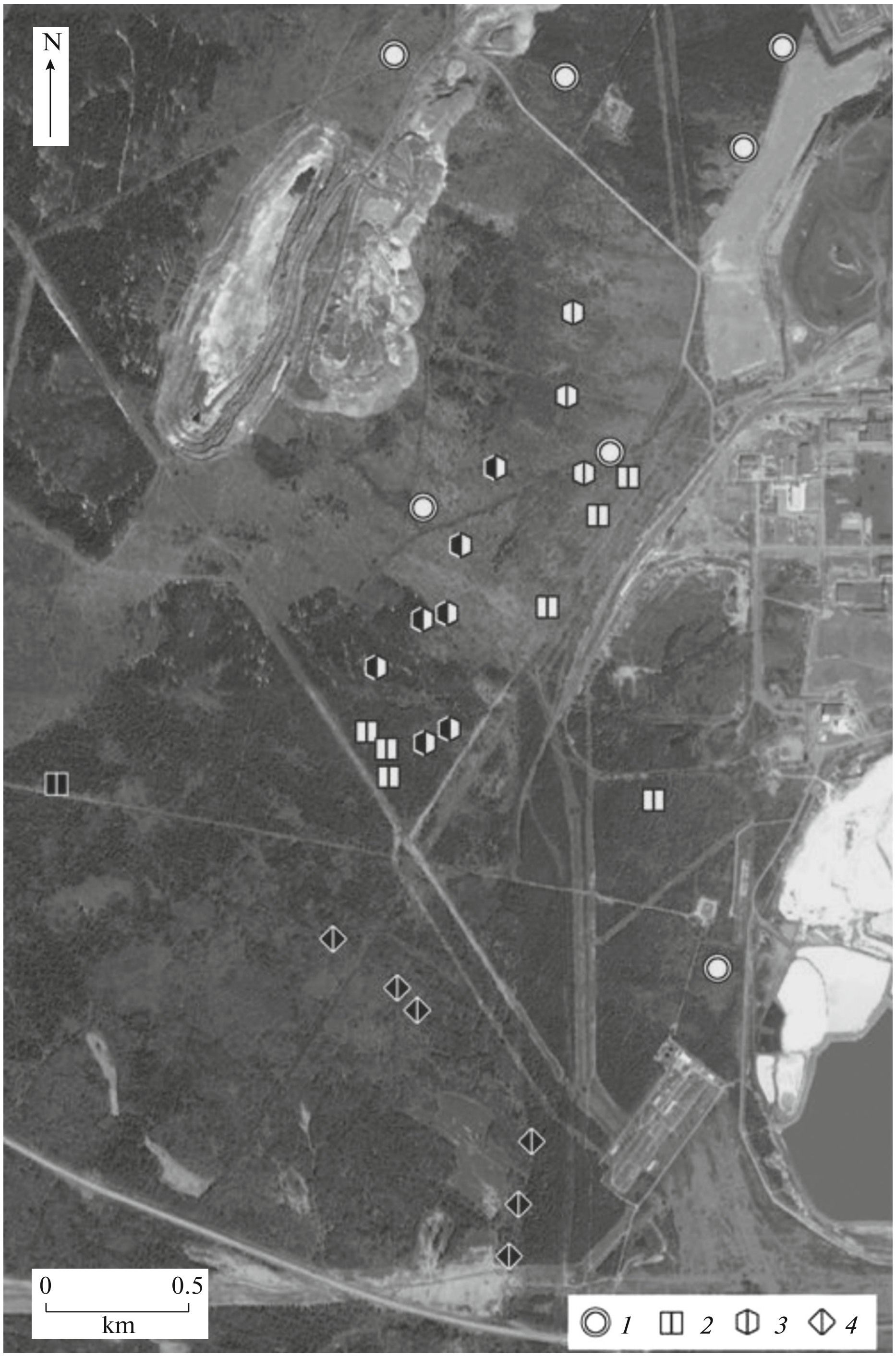

Fig. 2. Occurrence of earthworms and mollusks near the current boundary of the "lumbricide desert." The position of a plot in the impact region is shown in Fig. 1. Markers: (*1*) temporary sampling plots (SPs) where the abundance of earthworms was estimated (the plots correspond to the points in Fig. 1), (*2*) permanent SPs for recording soil macrofauna; (*3*) logs where invertebrates were quantitatively collected; (*4*) logs where invertebrates were qualitatively collected. Marker shading: the presence (black) or absence (white) of earthworms (left half) and terrestrial mollusks (right half). The scheme is based on Google Earth satellite imagery.

ple per log). These samples were collected into plastic bags and hand sorted in the laboratory.

All identified invertebrates with a length of over 2 mm were fixed in 70% ethanol (ants, empty cocoons of worms, and exuvia were not taken into account). The abundance of invertebrates was calculated taking into account the volume of the sorted fragment of the log and expressed in spec./dm^3; the same unit was used to express the abundance of invertebrates when they were recorded in soil samples (the sample depth was assumed to be 25 cm).

Censuses at permanent sampling plots. These censuses were performed from July 11, 2014 to August 20, 2014 (Vorobeichik et al., 2019) and compared with the abundance of invertebrates in CWD. The analysis included materials on seven permanent SPs with an area of 10 × 10 m in the "lumbricide desert" (Fig. 2) and five plots in the background zone (20–30 km west of the MUCS). Ten samples were taken at each SP and randomly placed under the forest canopy; the sample size was 20 × 20 × 20–30 cm. The samples were delivered in plastic bags to laboratory, where invertebrates (>2 mm) were hand sorted. To increase the censuses accuracy, we divided the samples into two layers, the forest litter and the mineral horizon, during their sampling and sorting and then pooled the data on the layers (indicated as "soil" in the text). The abundance of invertebrates is also expressed in spec./dm^3 (the depth was assumed to be 25 cm).

The ordination was performed by analysis of the principal coordinates for the absolute abundance of taxonomic groups using the Bray–Curtis dissimilarity in vegan v. 2.4-5 with R v. 3.4.3.

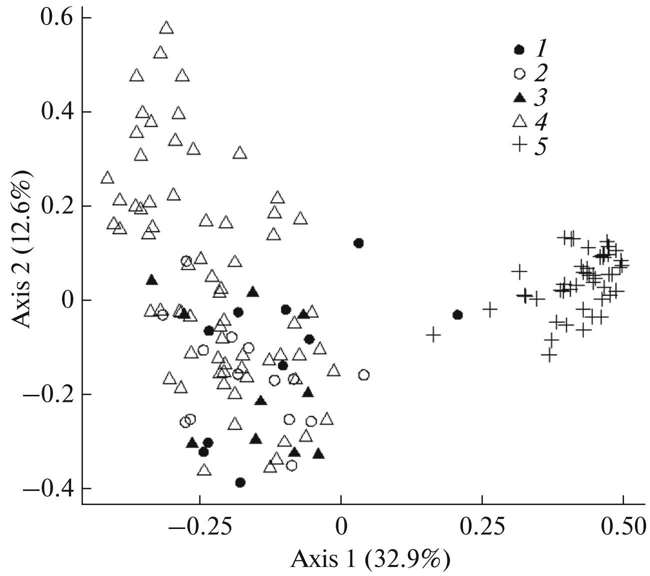

Fig. 3. Ordination of samples in the space of the first and second principal coordinates (the proportion of explained variance is given in parentheses). Plots and microhabitats: (*1*) in logs, (*2*) soil under logs, (*3*) soil near logs, (*4*) soil in permanent sampling plots in the "lumbricide desert," and (*5*) soil in the background area.

RESULTS

The boundary of the earthworm distribution in the study area is 3–5 km (maximum 10 km) from the source of emissions and outlines the area of the "lumbricide desert" (Fig. 1). Its area is currently about 65 km^2.

During the qualitative sampling, all logs in the floodplain of the small forest river on the external periphery of the "lumbricide desert" proved to be inhabited by earthworms (adult individuals and cocoons) and gastropods (Fig. 2). The worms were represented by *Dendrodrilus rubidus tenuis* (Eisen, 1874), mollusks *Nesovitrea hammonis* (Strøm, 1765), *Discus ruderatus* (W. Hartmann, 1821), *Euconulus fulvus* (O.F. Müller, 1774), *Zonitoides nitidus* (O.F. Müller, 1774), and *Arion subfuscus* (O.F. Müller, 1774).

During quantitative surveys, mollusks were not found in the logs outside the floodplain; however, some of the logs were inhabited by earthworms (also only by *D. rubidus tenuis*). Both mature adult and juvenile individuals (60%) and cocoons were found. The abundance of earthworms reached high values in the logs, being only two times lower than that in the soil of the background zone (Table 1). Earthworms (only mature adult) and cocoons were also found in the soil under the logs; however, their abundance and occurrence were very low. There were no earthworms or mollusks in the soil near the logs and at permanent SPs in the "lumbricide desert" (the closest place of their detection was 1 km away from the smelter (Fig. 2)).

The colonization of CWD by earthworms was highly uneven: although they were recorded only in half of the logs, their maximum abundance is comparable to that in the soil of the background zone. The picture is even more impressive for cocoons: they were found only in two of the ten logs investigated; however, their abundance in one of them was three times higher than the maximum value in the soil of the background area. Unlike the polluted sites, worms and cocoons occur in almost every sample from the soil of the background zone.

Some typical pedobionts (pot worms, geofilids, diplopods, and scale insects) are absent in logs in the "lumricide desert," although their minimum abundance was recorded in the soil of permanent SPs. The abundance of other groups in the logs is comparable to that in the soil of permanent SPs; however, it is considerably lower than the background values.

The first two principal coordinates explain about half of the variability in the composition of the macrofauna at the level of supraspecific taxa (Fig. 3). In most cases, CWD and soil communities in polluted area are similar to each other; however, the axes values for two logs are close to those in the soil of the background zone. In the "lumbricide desert," soil samples under the logs, next to them, and in the SP form a single cloud, which is clearly separated from the background zone.

DISCUSSION

Although our approach to mapping does not take into account the seasonal and interannual variability in the earthworm abundance, the roughness of the

Table 1. Abundance (spec./dm^3) and occurrence (%) of invertebrates in different microhabitats in polluted and background areas

Group (development stage)	Area (distance from the source of emissions, km), microhabitat									
	"lumbricide desert" (1–2)								background area (20–30)	
	decaying wood (SP = 1, n =10)		soil under the log (SP = 1, n = 14)		soil near the log (SP = 1, n = 10)		soil in permanent sampling plots (SP = 7, n = 70)		soil in permanent sampling sites (SP = 5, n = 50)	
	X ± SE* [max]	F	X ± SE* [max]	F	X ± SE* [max]	F	X ± SE** [max]	F	X ± SE** [max]	F
Lumbricidae (worms)	0.50 ± 0.37 [3.5]	60	0.01 ± 0.01 [0.1]	14	–	–	–	–	1.10 ± 0.16 [3.2]	100
Lumbricidae (p)	0.75 ± 0.79 [7.5]	20	0.04 ± 0.03 [0.3]	21	–	–	–	–	0.60 ± 0.08 [2.3]	98
Enchytraeidae	–	–	–	–	–	–	0.01 ± 0.003 [0.1]	6	4.93 ± 0.63 [21.5]	100
Aranei	0.20 ± 0.10 [0.9]	80	0.45 ± 0.14 [2.0]	93	0.49 ± 0.16 [1.5]	80	0.17 ± 0.04 [1.3]	63	1.05 ± 0.19 [3.8]	100
Opiliones	–	–	–	–	–	–	0.003 ± 0.002 [0.1]	3	0.05 ± 0.01 [0.3]	30
Lithobiidae	0.10 ± 0.05 [0.4]	70	0.11 ± 0.05 [0.5]	50	0.06 ± 0.04 [0.4]	30	0.15 ± 0.08 [1.0]	44	1.09 ± 0.26 [3.3]	98
Geophilidae	–	–	0.02 ± 0.02 [0.2]	14	0.01 ± 0.01 [0.1]	10	0.02 ± 0.01 [0.2]	16	0.46 ± 0.11 [2.8]	98
Diplopoda	–	–	–	–	0.01 ± 0.01 [0.1]	10	0.01 ± 0.01 [0.4]	6	0.07 ± 0.04 [2.2]	16
Heteroptera (im + l)	0.04 ± 0.02 [0.2]	50	0.06 ± 0.03 [0.3]	35	0.02 ± 0.02 [0.2]	10	0.01 ± 0.01 [0.1]	11	0.03 ± 0.01 [0.2]	24
Coccodea (im + l)	–	–	–	–	–	–	0.09 ± 0.05 [1.6]	13	0.13 ± 0.06 [2.0]	40
Lepidoptera (l + p)	0.02 ± 0.02 [0.2]	10	0.03 ± 0.01 [0.1]	29	0.04 ± 0.04 [0.4]	10	0.02 ± 0.01 [0.2]	17	0.04 ± 0.01 [0.4]	28
Diptera (l + p)	0.08 ± 0.04 [0.3]	70	0.11 ± 0.05 [0.6]	46	0.04 ± 0.02 [0.2]	30	0.22 ± 0.07 [1.2]	60	1.34 ± 0.25 [8.0]	100
Carabidae (im + l)	0.01 ± 0.01 [0.1]	20	0.04 ± 0.02 [0.2]	36	0.11 ± 0.04 [0.4]	60	0.02 ± 0.01 [0.2]	14	0.11 ± 0.05 [0.8]	48
Staphylinidae (im + l)	0.43 ± 0.16 [1.3]	90	0.50 ± 0.09 [1.0]	100	0.40 ± 0.14 [1.3]	80	0.2 ± 0.06 [0.8]	69	0.85 ± 0.07 [1.9]	100
Elateridae (l + p)	0.10 ± 0.05 [0.3]	40	0.16 ± 0.05 [0.5]	57	0.05 ± 0.02 [0.2]	40	0.34 ± 0.1 [2.5]	83	0.29 ± 0.04 [1.6]	88
Other Coleoptera (im + l)	0.16 ± 0.08 [0.7]	80	0.32 ± 0.18 [1.9]	50	0.11 ± 0.07 [0.7]	40	0.16 ± 0.03 [2.0]	57	0.56 ± 0.04 [1.3]	100
Other Insecta	0.004 ± 0.004 [0.04]	10	0.09 ± 0.03 [0.4]	43	0.02 ± 0.01 [0.1]	20	0.01 ± 0.003 [0.1]	9	0.13 ± 0.05 [0.7]	62
Mollusca	–	–	–	–	–	–	0.001 ± 0.002 [0.1]	1	1.34 ± 0.08 [5.1]	100
Total	2.39 ± 1.45 [14.5]	100	1.94 ± 0.32 [4.6]	100	1.36 ± 0.32 [3.0]	100	1.43 ± 0.23 [3.5]	100	14.17 ± 0.83 [29.8]	100

Stage of development: im, imago; l, larvae; p, cocoons or pupae; SP, number of sampling plots (SPs); n, number of samples; X, arithmetic mean; SE, standard error; max, maximum value in a sample; F, occurrence (proportion of nonempty samples, %); sample unit: *, sample, **, SP; the dash indicates the absence of a group.

scale that we used significantly mitigates the effect of these factors on the final pattern of the distribution of the group under consideration in the area affected by the MUCS. Figure 1 clearly shows the gradient decrease in the abundance of earthworms towards the smelter: sites with high abundance on the periphery of the area are followed by sites with a medium and low abundance, and then by the "lumbricide desert." This pattern of the earthworm distribution actually visualizes the main cause of their disappearance in the study area: the transformation of the environment under the impact of emissions from the copper smelter, in particular, due to the accumulation of high toxicity in substrates. The decrease in the abundance of earthworms is typical of polluted areas; however, they do not always completely disappear there (Bengtsson et al., 1983; Spurgeon and Hopkin, 1996). The formation of the vast "lumbricide desert" near the MUCS is most probably due to the combined effect of the long-term pollution of the soil with heavy metals and its acidification (Vorobeichik, 1998).

The issue of recolonization mechanisms is one of the key problems in analysis of ecosystem stability (Bengtsson, 2002). The idea that a disturbed area is colonized not only from the adjacent undisturbed sites but also from microsites within this area has been discussed many times in different research fields. According to metapopulation theory, the system of microhabitats connected by donor–acceptor bonds stabilizes the population due to rapid reparation processes (Hanski, 1999). In paleoecology and biogeography, the concept of microrefugia explains the "instantaneous" (on a historical scale) colonization of species in vast areas that previously disappeared there during glaciations (Rull, 2009). The similar concept of perfugia (biotope fragments that accidentally remained undamaged after forest fires) is proposed as a mechanism of rapid postpyrogenic recovery of soil fauna (Gongalskii, 2014). By analogy with these views, we assumed the existence of "survival microsites" in the area defaunated by pollution, which may lead to its recolonization after the decrease of substrate toxicity. The specific feature of such microsites (in particular, compared to perfugia) is determined by the nonrandom pattern of microsites and the considerable duration of their existence.

To the best of our knowledge, the colonization of CWD by soil invertebrates has never been studied specifically in areas exposed to industrial emissions. Undoubtedly, our research is reconnaissance and largely qualitative, rather than quantitative. Nevertheless, its results are important, since for the first time they indicate that the most pollution sensitive invertebrates (at least at the supraspecific level) can exist far beyond the technogenic boundary of their distribution, in areas with extremely high concentrations of heavy metals. The general possibility of the discussed mechanism of recolonization is shown by the records (albeit single ones) of earthworms and cocoons not only in logs but also in the soil under them.

On the one hand, the results of our research are unexpected, since earthworms were found in an area that had always been included in the "lumbricide desert" according to the results of standard soil-zoological surveys (Vorobeichik, 1998; Vorobeichik et al., 2012, 2019). On the other hand, soil invertebrates dwelling within decaying tree trunks is well known (Harmon et al., 1986; Goncharov et al., 2015; Geras'kina, 2016). CWD is colonized by typical pedobionts both due to the greater availability of trophic resources, determined by the development of fungal mycelium, and due to the more stable temperature and moisture regime than in the upper soil layers (Harmon et al., 1986). The latter is particularly important in heavily polluted areas, where the microclimate has great contrasts (Kozlov and Zvereva, 2007).

The prevailing colonization of CWD by pedobionts in polluted areas may also be due to specific causes. The low concentrations of heavy metals in living wood even in contaminated environments (Koptsik et al., 2008), as well as the shielding effect of bark and the high content of disintegrated organic matter, suggest a lower concentration of metals in CWD or at least a lower toxicity than those in the forest litter or mineral soil horizons. Unfortunately, there are no direct comparisons of the metal content in CWD and soil for heavily polluted areas. Although metal concentrations in CWD can be slightly higher under pollution conditions than the background values (Esenin and Ma, 2000), their content is clearly much lower in CWD than in the litter.

The earthworm species, *D. rubidus tenuis*, recorded in the logs is a typical inhabitant of dead wood, which is indicated even by its Latin generic name and one of the English trivial names (tree worm). Its abundance is equally high both in CWD and in soil in the northern taiga in the Urals (Geras'kina, 2016); in our area, it rarely occurs in soil (Vorobeichik et al., 2012). It is so far unclear whether or not CWD in polluted sites can be colonized by other local species that tend to inhabit dead wood, in particular, by *Dendrobaena octaedra* (Savigny, 1826) and *Lumbricus rubellus* Hoffmeister, 1843. The same uncertainty is characteristic of the dominant epi-endogeic species in our area, namely, *Perelia diplotetratheca* (Perel, 1976), which has also been recorded in dead wood in the northern taiga (Geras'kina, 2016).

It is known that *D. rubidus tenuis* is relatively tolerant to the impact of metals and metalloids: this has been determined for Cu (Arnold et al., 2008), As (Langdon et al., 2003), Ni (Płytycz et al., 2010), and Pb (Terhivuo et al., 1994). It should be noted that the tolerable concentrations that were recorded by other authors for *D. rubidus tenuis*, e.g., 790 μg/g of soil for Cu (Arnold et al., 2008), are significantly lower than those recorded near the study source of emissions. A relatively quick development of metal resistance has been demonstrated for this species (Arnold et al., 2008; Płytycz et al., 2010). Other properties of *D. rubidus tenuis* that may explain their successful colonization of CWD in the polluted area are its capability for parthenogenetic reproduction, the wide range of its biotopes and microhabitats, and its cosmopolitan distribution (Geras'kina, 2016). This species can even live in domed anthills, where it is protected from ant consumption by the repellent action of its mucus (Laakso and Setälä, 1997); therefore, it can be assumed that this mechanism also allows this species to cohabitate with ants in CWD. It should be noted that everything that concerns the tolerance of *D. rubidus tenuis* to toxicants and its ecological plasticity is also characteristic of the species *D. octaedra* and *L. rubellus*, which we, however, did not find in the logs in the "lumbricide desert." Therefore, it is so far unclear why successful existence is observed exactly and only for *D. rubidus tenuis*.

The variety of mollusks in CWD (five species, including one slug species) was more than we had previously recorded in standard soil samples at a distance of 4 km from the smelter (three species); however, it was lower than that found at a distance of 7 km (six species) and 20–30 km (11 species) from the smelter (Vorobeichik et al., 2012). Most of the species living in logs were also previously recorded in soil samples: 4 km (*N. hammonis*, *D. ruderatus*, and *E. fulvus*) or 7 km (slug *A. subfuscus*) from the smelter (Vorobeichik et al., 2012). Only *Z. nitidus*, which prefers humid habitats, was not found previously in soil samples; however, it was recorded in grass stand 4 km from the smelter (Nesterkov, 2013).

The very uneven colonization of CWD by earthworms, as well as the general heterogeneity in the composition of log macrofauna, may be due to many factors. Possible sources of their variability may be the position of logs in the microrelief and the pattern of the biotic environment of logs, as well as the age of logs, the degree of their fragmentation, their physical and chemical properties, including acidity and toxicity, the presence of other wood-destroying agents, etc. A high spatial heterogeneity is typical of polluted areas. In particular, it is recorded for soil microflora (Vorobeichik, 2007; Mikryukov et al., 2015), herbaceous plants (Trubina and Vorobeichik, 2012), and small mammals (Mukhacheva et al., 2012). However, it is still unclear what factors exactly determine the abundance of pedobionts in CWD.

The issue of possible ways of CWD colonization by earthworms is also open, which can be currently discussed only speculatively. Although the rate of dead wood decomposition varies greatly (Harmon et al., 1986), large logs partially buried in the soil can be preserved for several centuries at the last stages of their decomposition (McFee and Stone, 1966). Our indirect data indicate inhibition of wood destruction in polluted areas (Bergman and Vorobeichik, 2017). Therefore, the assumption that CWD had been colonized by earthworms before the smelter started its active operation (i.e., over 75 years ago) is not so fantastic. Another possible scenario is the relatively recent repeated colonization of the area, determined by active or passive migration of earthworms from less polluted sites. It is known that soil invertebrates, including earthworms, can actively avoid sites with a locally increased degree of pollution (Lukkari and Haimi, 2005; Gongalskii et al., 2009), which even serves as a basis for ecotoxicological tests (Kim et al., 2017). In this case, CWD can be peculiar "safety islands," which aggregate invertebrates from adjacent areas. In addition, earthworms and mollusks may be passively dispersed by water flows during wet periods. One should also admit the possibility of bird phoresia; its significant role in the distribution of soil invertebrates has been demonstrated not only for microarthropods (Lebedeva and Krivolutskii, 2003) but also for some macrofaunal groups (Matyukhin, 2004).

CONCLUSIONS

Earthworms and mollusks can colonize logs of late stages of decomposition in heavily polluted areas near the smelter, although they are absent in forest litter and mineral soil horizons under these conditions. This confirms our hypothesis about the existence of "survival microsites" in the "lumbricide desert," which can be considered as one of the possible mechanisms of recolonization of polluted areas after the reduction of emissions, followed by a decrease in the soil toxicity.

Soil zoologists usually ignore atypical pedobiont microhabitats. When the range of explored microhabitats is expanded, the ideas about the diversity and structure of soil invertebrate communities are also significantly extended. It is even truer for soil zoological studies in polluted areas, moreover the expansion of the range of the studied microhabitats also greatly changes the established knowledge of soil fauna functioning in extreme habitats.

The results of our research are largely of qualitative rather than quantitative value, and we had more questions than answers during its implementation. Nevertheless, we consider the results important, since they show the possibility of pollution-sensitive pedobionts dwelling in areas with extremely high concentrations of pollutants. The prospects for the further study of the patterns of the microhabitat distribution of soil invertebrates in polluted areas are evident.

ACKNOWLEDGMENTS

We are grateful to A.V. Nesterkov for assistance in field studies, as well as to E.V. Golovanova for earthworms identifying and V.S. Mikryukov, O.V. Dulya, M.R. Trubina, and K.B. Gongalskii for discussion and comments on the text of the manuscript.

FUNDING

The material was collected as part of the state assignment of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences; the data analysis and manuscript preparation were supported by the Russian Foundation for Basic Research, project no. 18-04-00160.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

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

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Translated by D. Zabolotny