ISSN 1067-4136, Russian Journal of Ecology, 2024, Vol. 55, No. 6, pp. 562–581. © Pleiades Publishing, Ltd., 2024.
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The Role of Coarse Woody Debris in the Survival of Soil Macrofauna in Metal-Contaminated Territories of the Middle Urals

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Received

Abstract—The soil macrofauna of three microsites in the background and contaminated areas was compared: within decaying trunks of deciduous trees (linden and aspen) in the final stages of decomposition, beneath the trunks, and outside the influence of the trunks (standard soil samples). The composition of the macrofauna was analyzed at two levels: supraspecific taxa and species for several taxocenes (earthworms, centipedes, arachnids, ground beetles, click beetles, and mollusks). The study was conducted in the spruce-fir forests of the southern taiga, an area affected by emissions from the Middle Ural Copper Smelter. At the level of supraspecific taxa, the composition of the macrofauna differs little between decaying trunks and standard soil samples. At the species level, the difference between microsites depends on a specific taxocene: the species composition within decaying trunks either almost coincides with standard samples (mollusks), or is more specialized (click beetles), or is more diverse (centipedes, arachnids, ground beetles), or is reduced due to the loss of a certain ecological group (earthworms). The ordination of microsites by the generalized list of species for the studied taxocenes coincides with the ordination by the composition of macrofauna at the level of supraspecific taxa. The overall density and abundance of the majority of soil macrofauna groups are higher in the trunks than in the standard samples. The difference in the background area is especially contrasting (2–6 times) for earthworms, harvestmen, lithobiids, herbivorous Heteroptera, ground beetles, and chironomid larvae. The difference in contaminated areas is much more pronounced: 70 times for earthworms, 30 times for mollusks, 10 times for Heteroptera, 7 times for lepidopteran larvae, 5 times for spiders, and 4 times for diplopods. The predominant habitation of soil macrofauna in decaying tree trunks in the contaminated area may be caused by the significantly lower content of potentially toxic metals in decomposing wood compared to forest litter: the difference is 85 times for Pb, 77 times for Fe, 25 times for Cu, 2.6 times for Cd, and 1.7 times for Zn. Thus, the negative impact of pollution on soil macrofauna is less pronounced in decaying tree trunks compared to standard soil samples.

Keywords: heavy metals, copper smelter, industrial pollution, toxic load, decaying deadwood, soil invertebrates, biodiversity, sustainability

DOI: 10.1134/S106741362460304X

INTRODUCTION

From the point of view of soil zoologists, forest ecosystems differ from grass ecosystems, among other things, by the constant supply of a significant amount of dead organic matter to the soil surface in the form of coarse woody debris (CWD). During the process of decomposition, decaying tree trunks form a continuum between the distinguishable remains of wood and the structureless matter of the organic horizon of soils [1]. It is therefore not surprising that many typical soil inhabitants can be found inside decaying tree trunks. However, zoologists surveying soil fauna often a priori exclude CWD, which can lead to a bias in the estimates of the abundance and diversity of soil invertebrates in forests. Proposals to include CWD in the procedures for assessing the abundance and diversity of soil invertebrates, at least for some taxa, have appeared relatively recently [2, 3]. Numerous studies have demonstrated that forest CWDs are biodiversity hotspots, refuges from adverse conditions for many groups of organisms: fungi [4, 5], vascular plants [6], insects [4], amphibians [7], etc. High species diversity and abundance within this microsite have also been demonstrated for soil invertebrates: microarthropods [8, 9], mollusks [10, 11], centipedes [10, 12–15], woodlice [10, 12, 13, 15], and earthworms [3, 16–18]. It is believed that the functions of forest CWDs as refuges, compared to the surrounding areas, are caused by: (1) a more favorable microclimate smoothing out fluctuations in humidity and temperature [1, 7], although this is not always confirmed [19];

(2) increased concentration of trophic resources due to available organic matter [1]; and (3) more favorable acid-base properties due to the high content of exchangeable bases [20].

These observations suggest a significant role of CWD in preserving soil fauna in areas that have been heavily industrially polluted for a long time. Potentially toxic metals in high concentrations are detrimental to many groups of soil macrofauna [21], which is why the soil in the immediate vicinity of metallurgical plants turns into an almost completely defaunate substrate [22–24]. However, it would be wrong to consider technogenic wastelands as homogeneous in terms of the habitat conditions of soil animals. We found that decaying tree trunks can play the role of "safety islands" in wastelands [25]. In particular, earthworms and mollusks were found to live inside CWDs, although they were absent from standard soil samples in these areas. The present study continues the analysis of this phenomenon. The cited work was preliminary in nature, since: (1) we did not compare the soil macrofauna of contaminated areas living in CWDs with background ones; (2) the invertebrate population was analyzed only at the level of large supraspecific taxa; and (3) the metal content in the CWDs was not analyzed. Due to these circumstances, several questions remained open: (1) how does the composition of the macrofauna of the CWDs change when moving from background areas to contaminated ones? (2) How unique is the species composition of the macrofauna in the CWDs compared to the soil and forest litter? And (3) does the CWDs differ from the forest litter and soil in terms of the toxic load?

Objective—To find answers to these questions. We tested the hypothesis of a significantly lower toxicity of the substrate inside decomposing dead tree trunks compared to the forest litter, which makes it possible for relatively sensitive to pollution groups (species) of macrofauna to live in them, which have disappeared in other microstations of the technogenic wasteland.

MATERIALS AND METHODS

The study area is located in the southern taiga, on the border of the western and eastern macroslopes of the Urals. The climate corresponds to the Dfb category [26]: it is continental, humid, with warm summers; the average annual air temperature is +2.0°C, the total precipitation is 550 mm. The work was carried out on the western macroslope, where spruce-fir forests with the participation of nemoral flora species predominated before the start of industrial development of the territory about 300 years ago. Now, significant areas are also occupied by secondary birch and aspen forests. The ground cover is dominated by *Oxalis acetosella* L., *Dryopteris* spp., *Calamagrostis arundinacea* (L.) Roth, *Aegopodium podagraria* L., *Ajuga reptans* L., *Circaea alpina* L., *Maianthemum bifolium* (L.) F.W. Schmidt, and *Cerastium pauciflorum* Steven ex Ser. (Vorobeichik et al., 2014). The soil cover is composed of sod-podzolic soils, burozems, and grey forest soils (Albic Retisols, Stagnic Retisols, Leptic Retisols, Haplic Cambisols, Retic Phaeozems according to the World Reference Base) [27].

Three forms of the Müll humus system (Mesomull, Oligomull, and Dysmull) and two forms of the Moder humus system (Hemimoder and Eumoder) with Dysmull dominating are represented [27]. Such a spectrum indicates the high activity of large soil detritivores that actively process plant litter. This group (including phytosaprophages) in the study area includes earthworms, enchytraeids, larvae of long-horned dipterans, elaterids, and mollusks with the first two taxa being numerically predominant. The peculiarities of the soil macrofauna of the region, compared to the regions located to the west and south, include a very low abundance of woodlice, diplopods, and forest cockroaches, as well as the absence of typical burrowing earthworms among the earthworms [24, 28].

Our work is focused on the analysis of the consequences of environmental pollution by atmospheric emissions from the Middle Urals Copper Smelter (MUCS), located on the outskirts of Revda, Sverdlovsk oblast (50 km west of Yekaterinburg, 56°50′37″ N, 59°52′44″ E). The plant has been operating since 1940 and was one of the largest point sources of industrial pollution in Russia. The specificity of the negative impact of its emissions, like other metallurgical plants with primary smelting of non-ferrous metals, lies in the enhancement of the toxic effect of potentially toxic metals (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As) due to soil acidification caused by the emission of gaseous compounds of sulfur, nitrogen, and fluorine.

The gross emission of MUCS was maximal in the mid-1970s, reaching 350000 t year, and then it gradually decreased: 225000 t in 1980, 148000 t in 1990, 63000 t in 2000, 28000 t in 2004, and only about 3000–5000 t year after the radical reconstruction of the enterprise in 2010 and up to the present time [29]. Despite the decrease in emissions, high levels of soil pollution remain in areas located close to the plant [29, 30]. According to the data for 2016, the metal content in the forest litter 0.5–3 km west of the MUCS was 3484 mg kg^{-1} for Cu, 2462 mg kg^{-1} for Pb, 17 mg kg^{-1} for Cd, and 650 mg kg^{-1} for Zn, which exceeded the background values by 93, 37, 7, and 3 times, respectively; the pH of the litter was reduced compared to the background level (5.9) by 1 [30].

Long-term impact of MUCS emissions has radically changed the structure and functioning of forest ecosystems. Among the main changes in soils and soil biota, attention should be paid to the destruction of soil aggregates [31], increased acidity and decreased saturation of the exchange complex with calcium and magnesium [29], increased forest litter thickness [32], shift in the spectrum of humus forms from zoogenic to

non-zoogenic forms up to the transition to the extreme form in the series of biological activity Eumor [27, 30], a decrease in the general trophic activity of soil detritivores [33, 34], inhibition of microbial destruction of organic matter [35, 36], disappearance of several taxa of macrofauna, primarily earthworms [22, 23], as well as the closely related mole [37, 38], and a decrease in the abundance and diversity of soil microflora [39, 40]. These changes are caused by both the direct toxic effects of metals and the transformation of the habitat, primarily caused by the suppression of the tree and grass-shrub layers [41]. In the immediate vicinity of the plant, only 5–7 resistant species (*Deschampsia caespitosa* P.Beauv., *Brachypodium pinnatum* (L.) P.Beauv., *Equisetum sylvaticum* L., *Lathyrus vernus* (L.) Bernh., *Sanguisorba officinalis* L., *Vaccinium myrtillus* L., and *V. vitis-idaea* L.) out of 85 growing in the background area remain in the ground cover [41]. A decrease in the rate of decomposition of wood is another consequence of environmental pollution [42, 43].

The restoration of ecosystems after the reduction of MUCS emissions in the last decade has not affected all components of the biota. First of all, it is expressed for groups not directly associated with the soil, in particular epiphytic lichens [44, 45], epixylic mosses [46]), phyllophagous insects [47], grass mollusks [48, 49], birds [50, 51], and small mammals [52]. The initial stages of restoration are also noted for the soil fauna: the distribution area of earthworms and mollusks [23], as well as moles [38], has shifted closer to the plant. In addition, humus forms have appeared in the contaminated area, indicating the recolonization of earlier defaunated soils by macrofauna [27, 53]. These changes coincide with the restoration of the original level of soil acidity, which leads to a decrease in the mobility, and, accordingly, the toxicity of metals [29].

Soil macrofauna was collected in June–August 2020 in two contaminated areas: background (two sites – 30 km and 11 km west of the MUCS) and impact (1–2 km), in spruce-fir forests. During a route survey of an area of about 2 × 2 km, decomposing decaying tree trunks were randomly selected that met the following criteria: (1) tree type – aspen (*Populus tremula* L.) or linden (*Tilia cordata* Mill.); (2) fragment diameter in the butt part – at least 10 cm, length – at least 3 m; (3) trunk is partially immersed in litter and mineral horizons of the soil, but not more than half the diameter; (4) fourth stage of decomposition on a 5-point scale [42], i.e., the bark is partially preserved, the wood is exfoliating, with a changed color, easily penetrated by a knife, but the core of the trunk is relatively strong; (5) there are no visible traces of fire; (6) there are no ant colonies at the sampling site; and (7) there are no other coarse wood remains on at least one side at a distance of at least 10 m.

The samples were collected as follows. A fragment of decaying wood approximately 0.4 m long was carefully cut out using a hand saw, its length (accuracy 1 cm), as well as the circumference of the larger and smaller ends (accuracy 1 cm) were measured with a tape. The fragment volume was calculated using the formula for a truncated cone. The sample was transferred to a plastic container, which ensured minimal mechanical damage during transportation. The samples were sorted in the laboratory layer by layer: first, the coarse bark was removed using a knife and tweezers, then the wood fibers were sorted manually. If the core remained very strong and, accordingly, not populated by soil invertebrates, it was not sorted. In this case, only the volume of the disassembled part was taken into account (as the difference between the original volume of the fragment and the volume of the undisassembled part, which was also calculated using the formula for a truncated cone).

At the same time, two standard soil monoliths measuring 20 × 20 cm and about 25–30 cm deep were collected: one directly beneath the trunk, the other at a distance of 5–8 m from the trunk. In the latter case, the location was chosen in a way that the monolith was not adjacent to other visible or buried in the soil CWD. Soil monoliths were collected in plastic bags, forest litter and organomineral horizon separately, then manually sorted in the laboratory. Before sorting, all samples were stored in an air-conditioned room at a temperature of 12°C for no more than 5 days.

Macrofauna (mesofauna according to M.S. Gilyarov) included invertebrates distinguishable with the naked eye, which could be manually selected with tweezers, with the exception of microarthropods. In this case, we did not use the "standard" size thresholds of 10 mm in body length or 2 mm in width, so we took into account enchytraeids, which occupy an intermediate position between the macro- and mesofauna. All invertebrates found were fixed in 70% alcohol. We did not take into account invertebrate exuviae and clearly random finds, such as imagines of Lepidoptera.

The density of invertebrates was calculated taking into account the volume of the disassembled trunk fragment and converted into specimens/dm^3. The density of macrofauna in standard soil monoliths is expressed in the same dimension (their depth is taken to be 25 cm, i.e., the volume of the monolith is 10 dm^3). The average volume of disassembled trunk fragments was 8.86 ± 1.67 dm^3 for the background and 8.76 ± 0.76 dm^3 for the impact area (the differences are statistically insignificant, the t-criterion is 0.06, $p = 0.951$). The abundance of invertebrates in different layers (bark and wood, litter, and organomineral horizon) was summarized within each sample. The total density of pedobionts did not include empty cocoons of earthworms (to avoid "double" counting of this group), as well as ants and dipteran adults (since man-

ual sampling does not allow for a correct assessment of the abundance of these groups).

A total of 25 fragments of decaying tree trunks were analyzed: 8 in the background area and 17 in the impact area; 75 samples taking into account standard soil monoliths were used.

Laboratory processing included the division of invertebrates (a total of about 6.4 thousand specimens) into large supraspecific taxa, as well as species diagnostics of several groups: earthworms, centipedes, spiders, harvestmen, mollusks, click beetles, and ground beetle imagines. Species identification of mature earthworms was carried out using the identification key [54]. With the known regional fauna, in most cases it was possible to identify juvenile (beltless) individuals to the species level. External features (coloration, shape of the prostomium, arrangement of setae) and also features of the internal structure (shape of the nephridial vesicles, presence and localization of diverticula) were used. To identify spiders, the electronic resource "Spiders of Europe" (www.araneae.nmbe.ch) was used, and regional identification keys were used for other invertebrates [55–57]. Species names were clarified using the database GBIF Backbone Taxonomy (www.gbif.org).

Chemical Analysis. Wood samples (without bark) from disassembled fragments, forest litter, and mineral horizon of soils were ground in a laboratory mill (MF10, IKA, Germany) and sifted through a sieve with a mesh diameter of 2 mm. The content of acid-soluble forms of macroelements (Ca, Mg) and potentially toxic metals (Mn, Fe, Cu, Pb, Zn, and Cd) was determined in an extract of 5% HNO_3, exchangeable forms of metals (Cu, Pb, Zn, and Cd) – in 0.05M $CaCl_2$ solution (the ratio of substrate : extractant is 1 : 20, the extraction time is 24 h after shaking on a rotator for 1 h). Concentrations of acid-soluble forms were measured on an AAS Vario 6 atomic absorption spectrometer (Analytik Jena, Germany), exchangeable forms were measured on contrAA 700 (Analytik Jena, Germany). pH (water) was measured ionometrically: the ratio substrate: deionized water is 1 : 25 for wood and litter and 1 : 5 for organomineral horizons.

Data Analysis. The content of elements and the abundance of macrofauna were compared between microsites (decaying trunk, beneath the trunk, outside the trunk) and pollution areas (background, impact) using ANOVA. The variables were pre-transformed: element concentrations were logarithmized, and density was taken as the square root. Tukey's test was used for multiple comparisons.

The effect size was calculated using the log response ratio as the natural logarithm of the ratio of the value in the impact zone to the value in the background zone or the ratio of the value in the CWD to the value in the standard soil sample. The confidence interval was estimated according to [58] using the LRR function of the SingleCaseES v. 0.7.2 package.

The diversity of taxocenes was characterized by Hill profiles [59] calculated in the vegan 2.6 package. The microsites were ordained based on the Bray–Curtis distance by absolute abundance using the principal coordinate analysis (PCA) in the ape v. 5.7 package [60]. Two ordination options were used: at the level of supraspecific taxa and by the species composition of the groups where it was determined. Due to the presence of a large number of zero samples in the impact area, ordination by species composition for individual taxocenes, especially those with few species, is difficult. Therefore, a generalized array of species was used in the second option for earthworms, mollusks, arachnids, lithobiids and geophilids, ground beetles, and click beetles. It also included single-species taxa (diplopods, a number of beetle families (Table 1)). The statistical significance of the differences in group and species composition between the pollution areas and microsites was assessed using PERMANOVA (999 permutations) in the vegan 2.6 package.

Calculations were implemented in the R v. 4.3 environment. The tidyverse package was used for preliminary data transformation, and the ggplot2 package was used for visualization.

RESULTS AND DISCUSSION

Structure of Macrofauna at the Level of Supraspecific Taxa

There are very few qualitative differences in the group composition of macrofauna between microsites (Table 1). The clearly non-random difference between the CWD and standard soil samples concerns several families of Coleoptera: Curculionidae are absent from the trunks, while Ptiliidae, Lucanidae, Silphidae, Cerylonidae, and Scydmaenidae are absent from the standard samples.

This specificity of the CWD, compared to standard soil samples, is quite understandable. The weevil larvae that are absent from the CWD usually live in mineral soil horizons. Although this group includes xylophilic species, such as the genus *Magdalis*, their larvae prefer "fresh" wood rather than decaying wood at late stages of decomposition. The families of Coleoptera found only in the trunks are characterized by a preference for accumulations of decomposing plant residues, including decaying wood.

There are also almost no differences in the group composition of the macrofauna of the trunks of the background and contaminated areas: in the contaminated areas, ectoparasitic nematodes (Mermithidae), enchytraeids (Enchytraeidae), wasp larvae (Hymenoptera, Parasitica), and several families of Diptera are absent from the CWD. However, in the latter case they are absent in the impact area and outside the trunks. The absence of diplopods in the trunks in the background area is most likely accidental.

Table 1. Group composition of macrofauna (density, specimens/dm^3) in different microsites in background and impact areas

Group	Background area			Impact area		
	outside the trunk	CWD	beneath the trunk	outside the trunk	CWD	beneath the trunk
Nematoda (Mermithidae)	0.10 ± 0.03	0.02 ± 0.01	0.13 ± 0.06	0.01 ± 0.01	–	–
Lumbricidae, worms	1.78 ± 0.17	3.25 ± 0.84	1.16 ± 0.19	0.01 ± 0.01	0.43 ± 0.17	0.04 ± 0.03
Lumbricidae, p (filled)	0.81 ± 0.25	1.79 ± 0.41	1.10 ± 0.24	0.01 ± 0.01	0.36 ± 0.16	0.08 ± 0.04
Lumbricidae, p (empty)*	4.53 ± 0.33	4.88 ± 1.62	6.25 ± 1.34	–	0.62 ± 0.26	0.24 ± 0.17
Enchytraeidae	0.66 ± 0.22	0.50 ± 0.12	1.05 ± 0.32	0.01 ± 0.01	–	0.02 ± 0.01
Arachnida						
Aranei	0.71 ± 0.21	0.89 ± 0.09	0.21 ± 0.08	0.22 ± 0.07	1.07 ± 0.18	0.17 ± 0.04
Opilliones	0.05 ± 0.03	0.14 ± 0.03	0.05 ± 0.03	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
Acariformes	0.46 ± 0.07	1.16 ± 0.28	0.29 ± 0.09	0.11 ± 0.04	0.26 ± 0.04	0.05 ± 0.02
Myriapoda						
Lithobiomorpha	0.76 ± 0.09	1.93 ± 0.31	0.51 ± 0.10	0.28 ± 0.05	0.45 ± 0.10	0.35 ± 0.08
Geophilomorpha	0.79 ± 0.12	0.30 ± 0.11	0.40 ± 0.07	0.03 ± 0.01	0.03 ± 0.02	0.07 ± 0.02
Diplopoda**	0.01 ± 0.01	–	0.05 ± 0.03	0.03 ± 0.02	0.11 ± 0.06	0.12 ± 0.04
Hemiptera						
Aphidoidea, i + l	0.04 ± 0.04	0.04 ± 0.03	–	–	–	0.01 ± 0.01
Auchenorhyncha, i + l	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	–
Coccoidea, i + l	0.08 ± 0.06	0.02 ± 0.02	0.05 ± 0.04	–	0.04 ± 0.03	0.01 ± 0.01
Heteroptera, i + l***	0.08 ± 0.02	0.34 ± 0.10	0.01 ± 0.01	0.01 ± 0.01	0.13 ± 0.06	0.04 ± 0.01
Coleoptera						
Carabidae, i	0.09 ± 0.03	0.27 ± 0.08	0.05 ± 0.02	0.02 ± 0.01	0.04 ± 0.02	0.01 ± 0.01
Carabidae, l	0.01 ± 0.01	0.04 ± 0.03	0.04 ± 0.02	–	0.01 ± 0.01	0.02 ± 0.01
Staphylinidae, i	0.76 ± 0.30	1.13 ± 0.31	0.60 ± 0.18	0.29 ± 0.04	0.66 ± 0.10	0.36 ± 0.06
Staphylinidae, l + p	0.06 ± 0.02	0.14 ± 0.06	0.11 ± 0.05	0.02 ± 0.01	0.09 ± 0.04	0.02 ± 0.01
Elateridae, i	–	–	–	–	0.09 ± 0.03	–
Elateridae, l + p	0.36 ± 0.10	0.24 ± 0.05	0.14 ± 0.03	0.21 ± 0.04	0.88 ± 0.23	0.48 ± 0.08
Curculionidae, i	0.03 ± 0.02	–	0.03 ± 0.02	0.02 ± 0.01	–	–
Curculionidae, l + p	0.11 ± 0.05	–	0.03 ± 0.02	0.02 ± 0.02	–	0.02 ± 0.01
Cantharidae, i + l	0.19 ± 0.05	0.07 ± 0.06	0.10 ± 0.04	0.05 ± 0.01	0.03 ± 0.02	0.06 ± 0.02
Ptiliidae, imago	–	0.62 ± 0.20	–	–	0.45 ± 0.22	–
Chrysomelidae, l	0.03 ± 0.02	–	0.01 ± 0.01	–	–	–
Cryptophagidae, i	–	–	–	0.03 ± 0.01	0.03 ± 0.02	–
Scydmaenidae, i	–	–	–	–	0.02 ± 0.01	–
Leiodidae, i****	0.01 ± 0.01	0.01 ± 0.01	–	–	0.03 ± 0.01	–
Lycidae, i + l (*Dictyoptera aurora*)	–	–	–	–	0.01 ± 0.01	0.01 ± 0.01
Silphidae, i (*Phosphuga atrata*)	–	0.02 ± 0.02	–	–	–	–

Table 1. (Contd.)

Group	Background area			Impact area		
	outside the trunk	CWD	beneath the trunk	outside the trunk	CWD	beneath the trunk
Melandryidae, i (*Orchesia duplicata*)	–	–	–	0.01 ± 0.01	–	–
Cerylonidae, i (*Cerylon histeroides*)	–	0.01 ± 0.01	–	–	0.01 ± 0.01	–
Lucanidae, l (*Ceruchus chrysomelinus*)	–	–	–	–	0.01 ± 0.01	–
other Coleoptera, i + l	0.10 ± 0.04	0.13 ± 0.06	0.13 ± 0.03	0.04 ± 0.01	0.03 ± 0.01	0.05 ± 0.02
Lepidoptera, l + p	0.06 ± 0.04	0.07 ± 0.03	0.04 ± 0.04	0.02 ± 0.02	0.13 ± 0.06	0.01 ± 0.01
Hymenoptera						
Parasitica, i	0.35 ± 0.12	0.39 ± 0.11	0.25 ± 0.04	0.07 ± 0.02	0.13 ± 0.04	0.05 ± 0.03
Parasitica, l + p	0.10 ± 0.04	0.07 ± 0.05	0.05 ± 0.03	0.08 ± 0.04	–	0.01 ± 0.01
Formicidae, i + p*	0.13 ± 0.08	0.10 ± 0.06	0.06 ± 0.03	0.05 ± 0.02	0.25 ± 0.11	0.17 ± 0.07
Diptera, Nematocera						
Tipulidae, l	0.05 ± 0.03	0.12 ± 0.11	0.01 ± 0.01	–	0.02 ± 0.01	–
Limoniidae, l	0.08 ± 0.05	0.01 ± 0.01	0.14 ± 0.06	–	0.06 ± 0.03	–
Chironomidae, l	0.01 ± 0.01	0.07 ± 0.05	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.02	0.20 ± 0.07
Ceratopogonidae, l	0.06 ± 0.06	–	–	–	–	–
Scatopsidae, l	–	–	–	–	–	0.09 ± 0.09
Bibionidae, l	0.50 ± 0.30	1.61 ± 1.41	1.89 ± 1.26	–	–	–
Sciaridae, l	0.08 ± 0.05	0.21 ± 0.13	0.06 ± 0.02	0.01 ± 0.01	0.07 ± 0.04	0.04 ± 0.02
other Nematocera, l	0.10 ± 0.04	0.06 ± 0.02	0.08 ± 0.03	0.13 ± 0.09	0.10 ± 0.04	0.21 ± 0.06
Diptera, Brachycera – Orthorrhapha						
Rhagionidae, l	0.08 ± 0.04	0.07 ± 0.03	0.09 ± 0.04	–	–	–
Asilidae, l	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	–	–	–
other Orthorrhapha, l	0.05 ± 0.04	–	–	–	–	–
Diptera, Brachycera – Cyclorrhapha						
Syrphidae, l	–	0.03 ± 0.02	0.01 ± 0.01	–	–	0.01 ± 0.01
Muscidae, l	–	0.02 ± 0.02	–	–	–	–
other Cyclorrhapha, l	0.11 ± 0.04	0.36 ± 0.18	0.13 ± 0.05	0.02 ± 0.01	0.05 ± 0.02	0.11 ± 0.07
Diptera, i *	0.05 ± 0.03	0.29 ± 0.15	0.06 ± 0.02	0.02 ± 0.01	0.06 ± 0.03	0.04 ± 0.01
other Insecta, i + l + p	–	0.01 ± 0.01	0.06 ± 0.02	0.03 ± 0.02	0.02 ± 0.01	0.02 ± 0.01
Mollusca	2.65 ± 0.52	3.57 ± 0.77	3.75 ± 1.21	0.02 ± 0.01	0.55 ± 0.17	0.15 ± 0.06
TOTAL	12.38 ± 1.01 a	19.76 ± 3.27 a	12.83 ± 2.3 a	1.82 ± 0.24 b	6.44 ± 0.59 c	2.87 ± 0.36 b

Here and in Tables 2 and 3 the mean ± standard error is given, the unit of account is a sample (fragment of a trunk, soil monolith), $n = 8$ for the background area and $n = 17$ for the impact area. For the total abundance, the same letters mean the absence of statistically significant differences within the row according to the Tukey criterion ($p < 0.05$).
Stage of development: i—imago, l—larvae, p—pupa or cocoon.

*—not included in the overall density estimate;

**—are represented by a single species, *Polyzonium germanicum*, with the exception of one individual of *Altajosoma golovatchi*;

***—mainly represented by the families Lygaeidae, Miridae, Tingidae;

****—represented by *Liodopria serricornis*, *Agathidium* sp., and *Choleva* sp.

Abundance of Macrofauna

Absolute values of abundance of most groups of soil macrofauna in both areas were higher in trunks compared to standard soil samples (Table 1). In the background area, the differences are especially contrasting (2–6 times) for earthworms (Lumbricidae), harvestmen (Opilliones), chigger mites (Acariformes, Trombidiidae), drupes (Lithobiomorpha), herbivorous bugs (Heteroptera: Lygaeidae, Miridae, Tingidae), ground beetles (Carabidae), and midge larvae (Chironomidae). In the impact area, the difference in abundance between the CWD and standard soil samples for many groups is even more contrasting compared to the background area. Thus, it reaches 70 times for earthworms, 30 times for mollusks, 10 times for Heteroptera, 7 times for lepidopteran larvae, 5 times for spiders, and 4 times for diplopods. Only the trunks in the impact area contained scale insects (Coccoidea), ground beetle larvae, long-legged mosquitoes (Tipulidae), and marsh beetles (Limoniidae).

Beneath the trunks, the overall abundance of macrofauna in both areas is lower compared to the trunk and is comparable with standard soil samples. Although in the background territory the abundance of most groups beneath the trunks is practically no different from standard samples, it is possible to note the preference of invertebrates for this particular microsite in the impact area. This is especially noticeable for mosquito larvae (their density beneath tree trunks is 17 times higher than in standard soil samples), mollusks (8 times), earthworms (7 times), and Heteroptera (3 times).

According to the ANOVA results, the total macrofauna density (Table 1) differs statistically significantly between the contaminated zones ($F(1;69) = 164$, $p < 0.000001$) and microsites ($F(2;69) = 17.3$, $p = 0.000001$), but the interaction of these factors is statistically insignificant ($p = 0.480$). In other words, the ratio of different microsites by invertebrate abundance is similar in both zones.

In the contaminated area, the total macrofauna density in the CWD is 3.1 times lower than in the CWD in the background area, while the differences between the zones according to standard soil samples are more contrasting – 6.8 times. The differences for individual groups are even more impressive: pollution reduces the density of earthworms in the CWD by 7.5 times, their cocoons, by 5 times, while in standard soil samples they are reduced by 300 and 70 times, respectively. For mollusks, the decrease in density is 6 times in the CWD and 150 times in standard samples, 12 and 27 times for geophilids, and 3 and 6 times for Heteroptera. For some groups (click beetles, spiders, and lepidopteran larvae) the effect of pollution is multidirectional: a decrease in abundance in standard samples is accompanied by an increase in abundance in the CWD.

The effect sizes clearly visualize the leveling of the negative impact of pollution. A more pronounced "concentration" of invertebrates in the trunks in the impact area (Fig. 1a) leads to their less significant suppression in this microsite compared to standard soil samples (Fig. 1b). The negative effect of pollution is statistically significant for earthworms, mollusks, and geophilids (i.e., the confidence interval of the effect size does not include zero) in both microsites, but it is less pronounced in the trunks compared to standard samples. For several groups (spiders, Heteroptera, rove beetles, soft-bodied beetles, and click beetles), the negative effect of pollution is statistically significant in standard samples, but absent or even positive in the trunks.

Ordination of Microsites

The ordination of samples by the group composition of macrofauna demonstrates weak differentiation of microsites in the background area (Fig. 2a). Standard soil samples and samples under the trunk form a single cloud of points (the distance between the centroids in the space of the first two coordinates is 0.03). Samples in the trunks are distanced from these microsites (0.25–0.27). The situation in the impact area is similar, but the differentiation is more pronounced (Fig. 3a): samples outside the trunk and beneath the trunk form a single cloud (the distance between the centroids is 0.17), from which the cluster of samples in the trunks is distant (0.37–0.45). It should be noted that the distance of the macrofauna of the trunks reflects differences not only in the relative proportion of groups, but also in their absolute density, since a metric taking into account the number of taxa was used for ordination. According to the results of PERMANOVA, the differences between microsites in terms of group composition are statistically significant: $F(2;21) = 2.5$ ($p = 0.004$), $R^2 = 0.19$ for the background area and $F(2;48) = 6.5$ ($p = 0.004$), $R^2 = 0.22$ for the impact area.

The ordination of microsites on a single scale for both zones clearly visualizes a greater similarity in the group composition of the stem macrofauna of the background and impact areas compared to the standard soil samples (Fig. 4a). The point clouds for the standard soil samples of the background and impact areas do not intersect and are distant from each other (the distance between the centroids is 0.63). In contrast, the point clouds for the trunks in the impact area and both microsites of the background area partially intersect, and the distance between the centroids is smaller (0.41–0.43). According to the results of PERMANOVA, the differences between the areas are less pronounced for the trunks' macrofauna ($R^2 = 0.23$, $F(1;23) = 6.9$, $p = 0.001$) compared to the standard samples ($R^2 = 0.39$, $F(1;23) = 14.6$, $p = 0.001$) and the

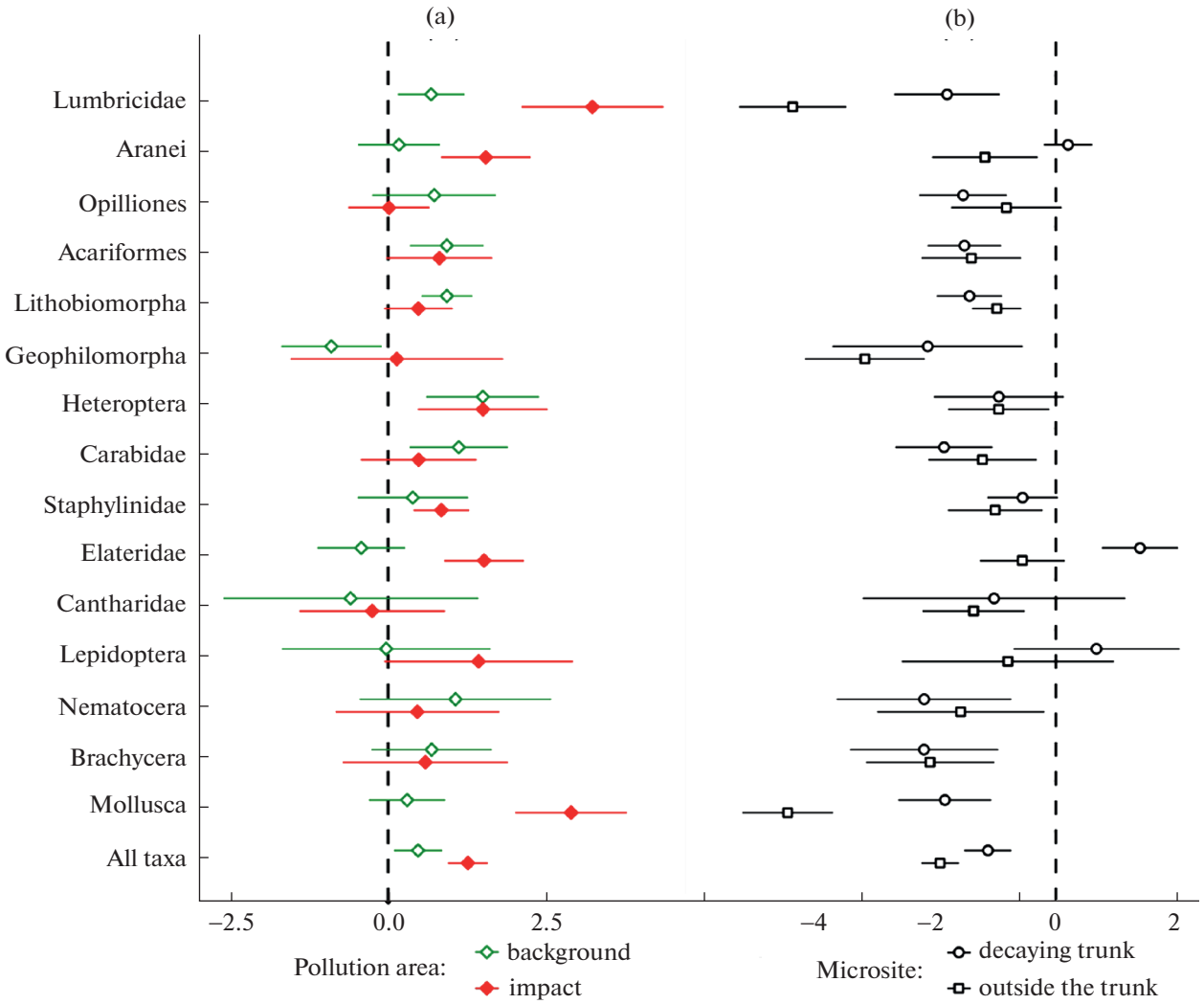

Fig. 1. Effect size and 95% confidence intervals for several taxa: (a) – ratio of abundance in a decaying trunk to abundance outside the trunk in the background and impact pollution areas, (b) – ratio of abundance in the impact area to abundance in the background area in a decaying trunk and outside the trunk.

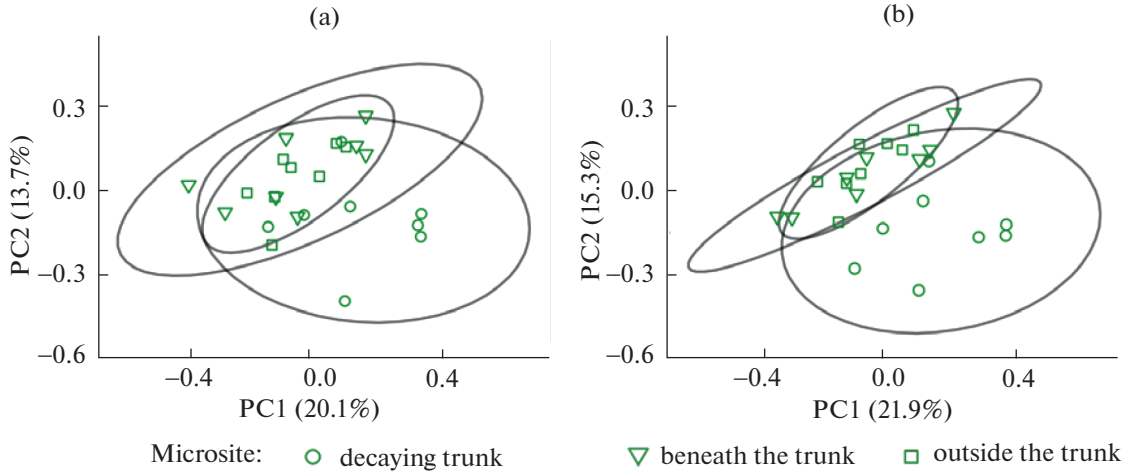

Fig. 2. Ordination of three microsites (decaying trunk, beneath the trunk, and outside the trunk) in the background zone: (a) – by group composition of macrofauna, (b) – by species composition of several taxa (earthworms, mollusks, spiders, harvestmen, centipedes, ground beetles, and click beetles). The proportion of explained variance is in the brackets, the line denotes 95% ellipses.

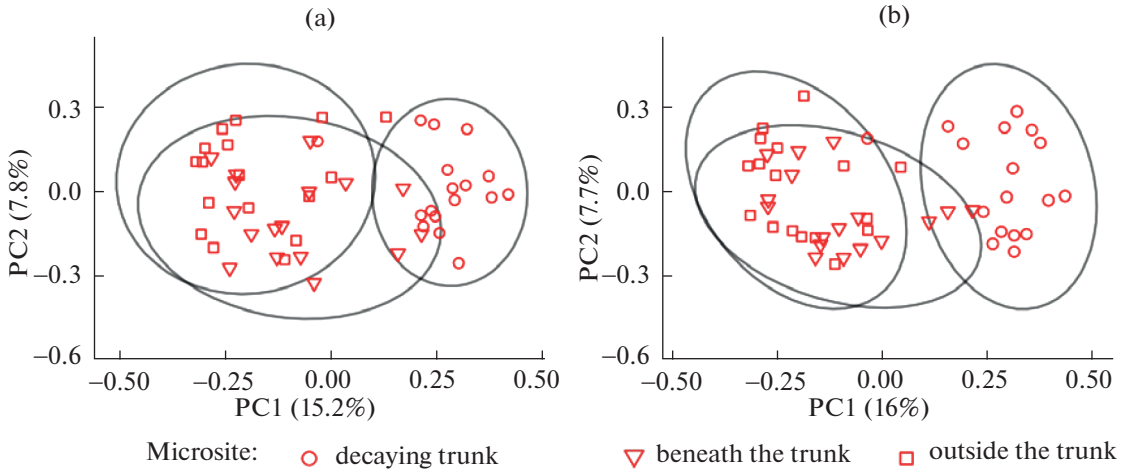

Fig. 3. Ordination of three microsites (decaying trunk, beneath the trunk, and outside the trunk) in the impact area: (a) – by group composition of macrofauna, (b) – by species composition of several taxa (earthworms, mollusks, spiders, harvestmen, centipedes, ground beetles, and click beetles). The proportion of explained variance is in the brackets, the line denotes 95% ellipses.

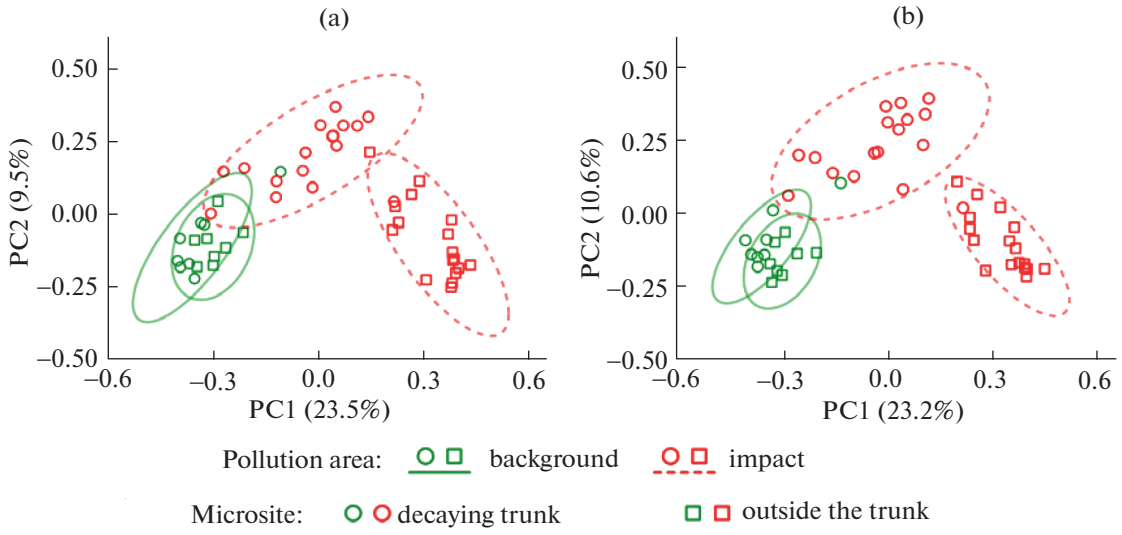

Fig. 4. Ordination of two microsites (decaying trunk and outside the trunk) in the background and impact areas: (a) – by group composition of macrofauna, (b) – by species composition of several taxa (earthworms, mollusks, spiders, harvestmen, centipedes, ground beetles, and click beetles). The proportion of explained variance is in the brackets, the line denotes 95% ellipses.

samples beneath the stem ($R^2 = 0.31$, F(1;23) = 10.3, $p = 0.001$).

The configuration of points by species composition (Figs. 2b–4b) is very close to the configuration by group composition (Figs. 2a–4a). The distances between the centroids of the trunks and other microsites at the species level are somewhat larger compared to the corresponding distances at the level of supraspecific taxa. Thus, the distance between the centroids of the trunks and two other microsites is 0.31–0.33 in the background area and 0.40–0.48 in the impact area (the distances between the microsites beneath the stem and outside the stem are almost the same as for the group composition).

Taking into account the known effect of taxonomic resolution on the results of the analysis of the community response to any factor [61], we expected to reveal a different nature of the differences between the compared microsites for the level of supraspecific taxa and for the species level. The absence of differences is probably explained by the fact that we analyzed a generalized list of species for several taxocenes, and not lists for individual taxocenes. It should be noted that the taxa for which species definitions have been made make up approximately half of the soil macrofauna

(46–65% of the total number). The weak influence of taxonomic resolution on the conclusions about the similarity of different microsites that has been discovered is important from a methodological point of view, since it allows one to do without species definitions in the first approximation, operating with large supraspecific taxa.

Structure of Taxocenes

The species composition of the taxocenes considered is presented in Table 2.

Earthworms. In the background area, only two ecological groups are present in decaying trunks: epigeic (*Dendrobaena octaedra*) and epi-endogeic (*Rhiphaeodrilus diplotetratheca*, *Dendrodrilus rubidus*, *Eisenia atlavinyteae*, and *Lumbricus rubellus*). Within these ecological groups, the species composition does not differ between the trunks and standard soil samples. Endogean species (*Aporrectodea rosea*, *Perelia tuberosa*, and *Octolasion lacteum*) are absent in the trunks.

The higher abundance of worms in the trunks is caused by the only species that dominates in this microsite: *D. rubidus*, and its abundance is 15 times higher in the trunks compared to standard samples. In the impact area, only two species were found in the trunks: the same *D. rubidus* dominated, and *D. octaedra* was also found singly. In the contaminated area, the taxocene of trunk earthworms is a reduced version of the taxocene of background CWD, in which several common species are missing. It is logical to assume a more pronounced resistance to pollution of the two remaining species (*D. rubidus* and *D. octaedra*) compared to the ones that disappeared. Earlier, we noted only the first of them in CWD in contaminated areas [25]. The resistance of these species to pollution is consistent with numerous testimonies of other authors regarding their relatively high tolerance to toxic load [62–66].

Centipedes. *Lithobius curtipes* dominates among lithobiids in both the CWD and standard soil samples at both sites, and *Arctogeophilus macrocephalus* dominates among geophilids, other species are few in number. Predatory centipedes are more diverse in the CWD compared to the standard samples due to the presence of low-abundance species.

Spiders. The spider complex is based on the representatives of the Linyphiidae family, among which *Maro pansibiricus, Porrhomma pallidum,* and *Tapinocyba insecta* are relatively abundant. Unfortunately, immature individuals of this family cannot be identified even to the genus level, so information on the differences in species composition of spiders is incomplete. Nevertheless, it is possible to note the confinement of the above-mentioned and several other species (*Tibioplus diversus*, *Thyreosthenius parasiticus*, and *Robertus lividus*) to the CWD in the impact area. The higher abundance and diversity of spiders in the decaying trunks of the impact area is caused by both web-weaving and non-web-weaving forms, which may be explained by the presence of a wide range of shelters and a large number of potential victims. In the impact zone, the role of microclimate is most likely also important: it is due to immature Linyphiidae, which are sensitive to drying, that a high density of spiders is achieved in the trunks and beneath them.

Harvestmen in the CWD of the background area are more diverse and abundant compared to the standard samples due to the presence of relatively numerous *Nemastoma lugubre* and several rare species. In the contaminated area, harvestmen are single in all microsites. Finding of a hygrophilous *N. lugubre* in the impact area, which had not been recorded here either by standard soil samples, or soil traps, or in the surveys of grass invertebrates, is of interest [22, 24, 67, 68]. Although we found only one individual of this species, the very fact of its habitation in the contaminated area and beneath a tree trunk in a microsite with increased humidity, is important.

Ground beetles in the background area are more diverse in CWD compared to the standard soil samples, both due to the relatively abundant *Pterostichus oblongopunctatus* and the rare species. The imagines of ground beetles are single in all microsites of the contaminated area.

Click beetles. The taxocene of click beetles is more diverse in the CWD compared to standard soil samples, which is explained by the presence of several species specific to decaying wood (*Ampedus* spp., *Melanotus villosus*, *Denticollis linearis*, and *Mosotalesus impressus*). In addition, the taxocene of click beetles in the CWD is more distinctive: it does not contain species dominant in the litter and soil (*Athous subfuscus* and *Dalopius marginatus*). The noted specificity of the CWD is expressed both for the background and for the impact areas, even to a greater extent in the latter case, since the largest number of "woody" species was identified here.

The higher species abundance and abundance of click beetles in the impact area compared to the background area may be associated with the pronounced microbiotopic diversity of this territory caused by the lower density of the tree canopy in combination with the well-known resistance of this group to metal pollution [22, 23]. In other words, decaying trunks should be considered not as survival microsites, but as microsites of predominant habitation of a specific set of species in the case of click beetles.

Mollusks. In the background area, the species composition of gastropods in the CWD differs little from standard soil samples, with the exception of the absence of several low-abundance species. The higher density in the CWD, compared to standard samples, is mainly caused by a single species, *Discus ruderatus*; in addition to it, two more species, *Perpolita hammonis*

Table 2. Species composition of taxocenes (density, specimens/dm^3) in different microsites in background and impact areas

Species	Background area			Impact area		
	outside the trunk	CWD	beneath the trunk	outside the trunk	CWD	beneath the trunk
			Lumbricidae			
Dendrobaena octaedra	0.08 ± 0.03	0.10 ± 0.05	0.09 ± 0.04	–	0.02 ± 0.01	–
Rhiphaeodrilus diplotetratheca	1.24 ± 0.14	1.23 ± 0.62	0.79 ± 0.19	–	–	–
*Dendrodrilus rubidus**	0.11 ± 0.06	1.64 ± 0.65	0.15 ± 0.04	0.01 ± 0.01	0.41 ± 0.16	0.04 ± 0.03
Eisenia atlavinyteae	–	0.10 ± 0.07	0.03 ± 0.02	–	–	–
Lumbricus rubellus	0.18 ± 0.07	0.15 ± 0.08	0.03 ± 0.02	–	–	–
Aporrectodea rosea	0.01 ± 0.01	–	0.01 ± 0.01	–	–	–
Octolasion lacteum	0.03 ± 0.02	–	0.01 ± 0.01	–	–	–
Perelia tuberosa	0.13 ± 0.04	–	0.05 ± 0.03	–	–	–
			Aranei			
Hypsosinga sp.	–	–	–	–	0.01 ± 0.01	–
Araneus sp.	–	–	0.01 ± 0.01	0.01 ± 0.01	–	–
Clubiona subsultans	0.01 ± 0.01	–	–	–	–	–
Clubiona sp.	0.03 ± 0.02	–	–	–	–	–
Dictyna sp.	–	–	–	–	–	0.01 ± 0.01
Micaria subopaca	–	–	0.01 ± 0.01	–	–	–
Phrurolithus festivus	–	–	–	–	0.01 ± 0.01	–
Hahnia pusilla	–	–	–	0.01 ± 0.01	–	–
Hahnia sibirica	–	–	–	0.01 ± 0.01	–	–
Agyneta subtilis-allosubtilis	–	–	–	0.01 ± 0.01	–	–
Allomengea scopigera	–	0.04 ± 0.03	–	–	–	–
Asthenargus paganus	0.04 ± 0.02	–	–	–	0.01 ± 0.01	–
Bolyphantes alticeps	0.01 ± 0.01	–	–	–	–	–
Centromerus sylvaticus	–	0.05 ± 0.03	–	–	–	0.01 ± 0.01
Ceratinella brevipes	–	–	–	–	0.01 ± 0.01	–
Ceratinella scabrosa	–	–	0.01 ± 0.01	–	–	–
Ceratinella sp.	–	0.02 ± 0.02	–	–	–	–
Decipiphantes decipiens	–	–	–	–	0.01 ± 0.01	–
Drapetisca socialis	–	0.02 ± 0.02	–	–	–	0.01 ± 0.01
Erigonella sp.	–	–	–	–	–	0.01 ± 0.01
Macrargus rufus	0.01 ± 0.01	–	–	–	–	–
Maro pansibiricus	0.01 ± 0.01	0.02 ± 0.02	0.03 ± 0.02	0.04 ± 0.03	0.34 ± 0.15	0.04 ± 0.02
Micrargus herbigradus	0.01 ± 0.01	–	–	–	–	–
Microneta viaria	0.01 ± 0.01	–	0.01 ± 0.01	0.01 ± 0.01	–	–

Table 2. (Contd.)

Species	Background area			Impact area		
	outside the trunk	CWD	beneath the trunk	outside the trunk	CWD	beneath the trunk
Minyriolus pusillus	–	–	–	0.02 ± 0.02	0.04 ± 0.03	–
Porrhomma pallidum	–	–	–	–	0.14 ± 0.04	0.01 ± 0.01
Tapinocyba insecta	0.08 ± 0.03	0.04 ± 0.04	0.03 ± 0.02	0.05 ± 0.03	0.03 ± 0.02	0.02 ± 0.01
Tenuiphantes nigriventris	–	–	0.01 ± 0.01	–	–	–
Thyreosthenius parasiticus	–	0.05 ± 0.05	–	–	0.04 ± 0.01	0.01 ± 0.01
Tibioplus diversus	–	0.01 ± 0.01	–	–	0.07 ± 0.03	0.04 ± 0.01
Linyphiidae spp. (indet.)	0.36 ± 0.10	0.32 ± 0.08	0.10 ± 0.04	0.07 ± 0.03	0.35 ± 0.05	0.03 ± 0.01
Trochosa sp.	–	0.02 ± 0.02	–	–	–	–
Ero furcata	0.01 ± 0.01	–	–	–	–	–
Metellina sp.	–	–	–	–	–	0.01 ± 0.01
Pachignatha sp.	0.01 ± 0.01	–	–	–	–	–
Robertus lividus	0.11 ± 0.05	0.27 ± 0.07	–	–	0.03 ± 0.01	–
Opilliones						
Nemastoma lugubre	0.03 ± 0.02	0.1 ± 0.04	0.01 ± 0.01	–	–	0.01 ± 0.01
Lacinius ephippiatus	0.03 ± 0.02	–	–	0.01 ± 0.01	–	–
Lophopilio palpinalis	–	0.01 ± 0.01	0.03 ± 0.02	–	–	–
Oligolophus tridens	–	0.02 ± 0.02	0.01 ± 0.01	–	0.01 ± 0.01	0.01 ± 0.01
Rilaena triangularis	–	0.01 ± 0.01	–	–	–	–
Lithobiomorpha and Geophilomorpha						
Lithobius curtipes	0.75 ± 0.09	1.84 ± 0.28	0.51 ± 0.10	0.27 ± 0.04	0.41 ± 0.10	0.34 ± 0.08
Lithobius proximus	–	0.07 ± 0.05	–	–	–	–
Lithobius sp.	–	0.01 ± 0.01	–	–	0.01 ± 0.01	–
Chinobius uralensis	0.01 ± 0.01	0.01 ± 0.01	–	0.01 ± 0.01	0.03 ± 0.02	0.01 ± 0.01
Arctogeophilus macrocephalus	0.64 ± 0.11	0.28 ± 0.11	0.28 ± 0.06	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
Escaryus japonicus	0.15 ± 0.03	–	0.13 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	0.06 ± 0.02
Strigamia pusilla	–	0.02 ± 0.02	–	–	–	–
Carabidae**						
Pterostichus oblongopunctatus	–	0.18 ± 0.09	0.03 ± 0.02	–	–	0.01 ± 0.01
Pterostichus aethiops	–	0.01 ± 0.01	–	–	–	–
Pterostichus melanarius	–	0.01 ± 0.01	–	–	–	–
Trechus secalis	0.06 ± 0.02	0.03 ± 0.03	0.01 ± 0.01	0.01 ± 0.01	–	–
Calathus micropterus	–	–	–	–	0.02 ± 0.01	–
Calathus melanocephalus	0.01 ± 0.01	–	–	–	–	–
Notiophilus biguttatus	0.01 ± 0.01	0.03 ± 0.03	0.01 ± 0.01	0.01 ± 0.01	–	–

Table 2. (Contd.)

Species	Background area			Impact area		
	outside the trunk	CWD	beneath the trunk	outside the trunk	CWD	beneath the trunk
Loricera pilicornis	–	0.01 ± 0.01	–	–	–	–
Carabus granulatus	–	0.01 ± 0.01	–	–	–	–
Agonum gracile	–	–	–	–	0.02 ± 0.01	0.01 ± 0.01
Elateridae***						
Athous subfuscus	0.30 ± 0.11	–	0.11 ± 0.03	0.11 ± 0.03	0.01 ± 0.01	0.25 ± 0.07
Dalopius marginatus	0.06 ± 0.03	–	0.03 ± 0.02	0.06 ± 0.03	–	0.08 ± 0.03
Ampedus sp.	–	0.10 ± 0.05	–	–	0.82 ± 0.22	–
Ampedus balteatus	–	–	–	0.01 ± 0.01	–	0.01 ± 0.01
Ampedus nigerrimus	–	–	–	–	0.01 ± 0.01	–
Ampedus nigrinus	–	–	–	–	0.04 ± 0.02	0.02 ± 0.02
Ampedus pomonae	–	0.01 ± 0.01	–	–	–	–
Ampedus pomorum	–	–	–	–	0.04 ± 0.02	–
Melanotus villosus	–	0.08 ± 0.03	–	–	0.03 ± 0.01	0.01 ± 0.01
Denticollis linearis	–	0.04 ± 0.03	–	–	0.01 ± 0.01	–
Mosotalesus impressus	–	–	–	0.04 ± 0.02	0.01 ± 0.01	0.11 ± 0.04
Mollusca						
Perpolita hammonis	1.34 ± 0.32	0.51 ± 0.13	0.85 ± 0.18	–	0.004 ± 0.004	–
Cochlicopa sp.	0.44 ± 0.10	0.15 ± 0.08	0.31 ± 0.09	–	–	–
Discus ruderatus	0.24 ± 0.12	2.04 ± 0.57	1.86 ± 0.72	0.01 ± 0.01	0.34 ± 0.10	0.11 ± 0.05
Euconulus fulva	0.06 ± 0.02	0.36 ± 0.13	0.31 ± 0.07	0.01 ± 0.01	0.19 ± 0.12	0.04 ± 0.02
Carychium sp.	0.04 ± 0.04	–	0.03 ± 0.02	–	–	–
Fruticicola fruticum	0.06 ± 0.03	0.02 ± 0.01	0.05 ± 0.04	–	–	–
Punctum pygmaeum	0.04 ± 0.02	0.15 ± 0.05	0.01 ± 0.01	–	–	–
Columella sp.	0.11 ± 0.04	–	–	–	–	–
Vallonia costata	0.25 ± 0.17	0.20 ± 0.16	0.29 ± 0.18	–	–	–
Acanthinula aculeata	0.01 ± 0.01	–	–	–	–	–
Arion subfuscus	0.01 ± 0.01	0.04 ± 0.03	–	–	0.02 ± 0.02	–
Vitrina pellucida	0.05 ± 0.04	0.04 ± 0.04	0.01 ± 0.01	–	–	–
Vertigo sp.	–	0.07 ± 0.06	0.03 ± 0.02	–	–	–

A dash indicates the absence of a species.
*—the total number for two subspecies *D. rubidus subrubicundus* and *D. rubidus tenuis* is given, since subspecies diagnostics are impossible based on immature individuals.
**—only imago.
***—the total abundance for all stages of development is given (larvae make up about 90%).

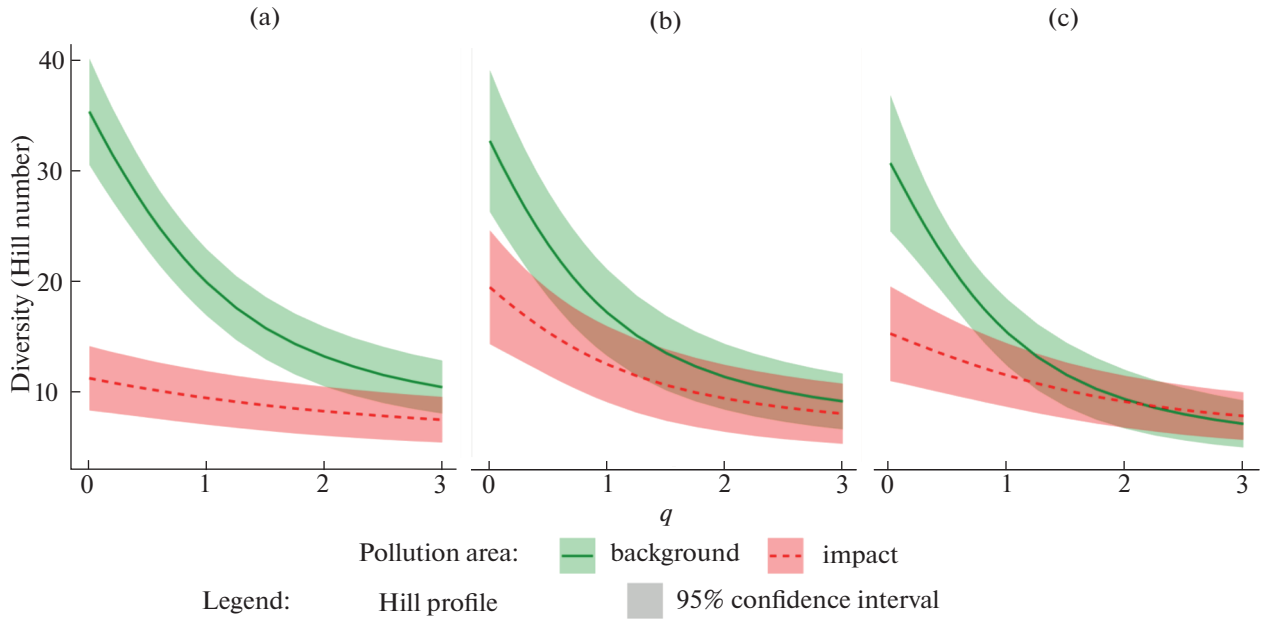

Fig. 5. Hill profiles for a generalized list of species: (a) – standard soil samples, (b) – trunk, (c) – beneath the trunk.

and *Euconulus fulva*, are abundant in the CWD. All three species are typical inhabitants of the litter in the study area. They, as well as *Arion subfuscus*, are preserved in the trunks of the contaminated area. Outside the trunks in the impact area, only two species were encountered individually (*D. ruderatus* and *E. fulva*)

Thus, it is possible to note a certain specificity of the considered taxocenes in relation to the differences between decaying trunks and standard soil samples. Different options are possible: the species composition of decaying trunks of the background area either almost completely coincides with standard soil samples (mollusks), or is more diverse (centipedes, spiders, harvestmen, and ground beetles), or is specific (click beetles), or it is reduced due to the loss of a certain ecological group (earthworms).

In the impact area, all taxocenes, with the exception of click beetles, can be considered as a reduced version of the taxocene of background trunks. In these cases, one can assume "hidden" inhabitation in the litter of those species that are not found in it but inhabit the trunks. Probably, their inhabitation in the litter can be revealed only with very large sampling efforts, significantly exceeding the usual level. The survey of decomposing CWDs actually imitates such an increase in sampling efforts, since it is applied to places of concentration of macrofauna.

Species Diversity of Macrofauna

There is no pattern of differences in species abundance and species saturation between the microsites in the background area that is common to different taxocenes (Table 3). In some cases, species abundance is higher in standard soil samples (earthworms, spiders, and mollusks), in others cases, in trunks (centipedes, harvestmen, ground beetles, and click beetles). In the impact area, species abundance is in most cases higher in trunks compared to standard samples. For all groups, with the exception of click beetles, the species abundance common to all microsites decreases when moving from the background to the impact area. The Hill profiles for the list of species generalized for all taxocenes differ sharply between the background and impact areas in the region $q < 1$ and are closer in the region $q > 2$ (Fig. 5). This means that differences between zones concern relatively low-abundance species that make the main contribution to species abundance, while differences in dominant species are almost not expressed.

It is important to note that the greatest differences in Hill profiles between the areas are observed in standard soil samples, and the smallest differences are observed in decaying trunks. In other words, the differences between the areas in the structure of soil macrofauna diversity in trunks are greatly smoothed out compared to standard soil samples.

Toxic Load

In all substrates, acidity is higher in the impact area (by more than one pH unit) compared to the background area, but it does not differ between the CWD and the litter within the area (Table 4). In both zones, the content of Ca is higher in the CWD compared to the litter (by 1.2–1.4 times) and even higher in the mineral horizon (by 4.1–7.3 times).

Table 3. Diversity of taxocenes in different microsites in background and impact areas

Species	Background area			Background area		
	outside the trunk	CWD	beneath the trunk	outside the trunk	CWD	beneath the trunk
			Lumbricidae			
Species abundance, species per sample*	3.38 ± 0.35	2.75 ± 0.34	3.25 ± 0.39	0.06 ± 0.06	0.71 ± 0.16	0.12 ± 0.08
Total number of species for microsite	7	5	8	1	2	1
Total number of species per site		8			2	
			Lithobiomorpha and Geophilomorpha			
Species abundance, species per sample*	3.00 ± 0.18	2.38 ± 0.17	2.88 ± 0.12	1.24 ± 0.13	1.35 ± 0.18	1.47 ± 0.19
Total number of species for microsite	4	6	3	4	5	4
Total number of species per site		7			5	
			Aranei			
Species abundance, species per sample	2.25 ± 0.82	2.13 ± 0.41	1.00 ± 0.35	0.76 ± 0.23	2.59 ± 0.36	1.18 ± 0.28
Total number of species for microsite	12	10	7	8	12	10
Total number of species per site		23			22	
			Opilliones			
Species abundance, species per sample	0.50 ± 0.25	0.88 ± 0.21	0.50 ± 0.31	0.06 ± 0.06	0.06 ± 0.06	0.12 ± 0.08
Total number of species for microsite	2	4	3	1	1	2
Total number of species per site		5			3	
			Carabidae			
Species abundance, species per sample	0.75 ± 0.23	1.38 ± 0.3	0.50 ± 0.18	0.18 ± 0.09	0.29 ± 0.11	0.12 ± 0.08
Total number of species for microsite	3	7	3	2	2	2
Total number of species per site		8			5	
			Elateridae			
Species abundance, species per sample	1.38 ± 0.17	1.5 ± 0.35	1.00 ± 0.25	1.12 ± 0.18	2.00 ± 0.36	1.82 ± 0.19
Total number of species for microsite	2	4	2	4	9	6
Total number of species per site		6			10	
			Mollusca			
Species abundance, species per sample	5.13 ± 0.84	4.5 ± 0.68	4.88 ± 0.69	0.18 ± 0.09	1.24 ± 0.24	0.65 ± 0.17
Total number of species for microsite	12	10	10	2	4	2
Total number of species per site		13			4	

*—taking into account zero values if the species is not present in the sample.

Table 4. The content of elements in different microsites and soil horizons in the background and impact areas

Element	Outside the trunk		CWD	Beneath the trunk	
	litter	soil		litter	soil
			Background area		
pH	5.4 (0.2) a	4.6 (0.1) b	5.0 (0.9) ab	5.3 (0.3) a	4.7 (0.2) b
Acid-soluble forms, μg/g:					
Ca	12920 (4450) a	2080 (460) b	15110 (8440) a	12550 (3170) a	2660 (690) b
Mg	1340 (110) a	550 (140) b	1330 (870) a	1130 (180) a	640 (200) b
Mn	1690 (590) a	1090 (300) a	250 (120) b	1700 (520) a	1180 (190) a
Fe	1670 (450) a	3190 (1040) b	40 (20) c	1790 (810) a	3080 (1570) b
Cu	80.4 (44.2) a	46.6 (18.7) a	17.7 (18.8) b	91.8 (49.5) a	50.3 (19.6) a
Pb	54.6 (25) a	18.3 (4.7) b	1.7 (0.7) c	75 (44.8) a	19.3 (5.4) b
Zn	383.8 (74.6) a	157.7 (9.1) b	190.1 (56.3) b	352.7 (56.5) a	162.2 (6.1) b
Cd	2.38 (0.78) a	0.46 (0.24) b	0.88 (0.72) b	2.69 (1.09) a	0.52 (0.26) b
Exchangeable forms, μg/g:					
Cu	0.92 (0.58) ab	0.27 (0.15) a	1.24 (1.22) b	0.84 (0.45) ab	0.77 (1.26) ab
Pb	0.54 (0.27) a	0.43 (0.21) a	0.39 (0.20) a	0.29 (0.10) a	0.34 (0.15) a
Zn	26.1 (13.5) a	8.8 (4.3) ab	4.2 (2.9) b	19.6 (11.7) a	8.3 (4.2) ab
Cd	0.61 (0.44) a	0.31 (0.13) ab	0.16 (0.09) b	0.61 (0.36) a	0.35 (0.21) ab
			Импактная зона		
pH	4.3 (0.2) a	4.2 (0.7) a	4.3 (0.5) a	4.3 (0.2) a	4.3 (0.1) a
Acid-soluble forms, μg/g:					
Ca	7890 (2240) a	2660 (600) b	10940 (4960) a	8770 (1920) a	2980 (680) b
Mg	860 (150) a	780 (70) ab	720 (250) b	840 (160) a	810 (90) ab
Mn	600 (360) a	590 (180) a	170 (90) b	760 (530) a	630 (300) a
Fe	5400 (2740) a	5880 (1320) a	70 (90) b	6080 (3120) a	5350 (1220) a
Cu	1710 (502) a	285 (101) b	68.6 (61.9) c	2070 (578) a	443 (155) b
Pb	773 (301) a	47.5 (32.4) b	9.1 (10.5) c	972 (317) a	55.3 (24.6) b
Zn	527 (170) a	224.2 (26.0) b	316 (139) c	511 (127) a	237 (31.6) bc
Cd	7.35 (3.55) a	1.95 (0.46) b	2.81 (2.45) b	7.20 (3.05) a	2.25 (0.7) b
Exchangeable forms, μg/g:					
Cu	42.2 (14.3) a	9.76 (5.16) b	2.78 (5.68) c	49.9 (19.1) a	19.9 (12.3) b
Pb	4.35 (2.84) a	0.94 (1.98) bc	0.26 (0.21) c	4.67 (2.44) a	0.58 (0.35) b
Zn	122 (41) a	34.9 (10.3) b	38.0 (34.0) b	120.5 (28.2) a	42.7 (13.1) b
Cd	4.65 (1.30) a	1.63 (0.35) b	1.16 (1.00) c	4.22 (1.16) a	1.98 (0.62) b

The arithmetic mean is given, the standard deviation is in brackets, $n = 8$ for the background area, $n = 17$ for the impact area. The same letters mean the absence of statistically significant differences within the row according to the Tukey criterion ($p < 0.05$).

In the background area, the concentrations of acid-soluble forms of potentially toxic metals are lower in the CWD compared to the litter: by 45 times for Fe, 32 times for Pb, and by 2–7 times for other metals. In the impact area, the differences between the CWD and the litter are even more contrasting: by 85 times for Pb, 77 times for Fe, 25 times for Cu, and by 1.7–3.6 times for other metals. The differences in exchangeable forms of metals are less pronounced compared to acid-soluble ones, but they also reach six times in the background area (for Zn) and 17 times in the impact area (for Pb). Concentrations in the CWD are comparable (Zn and Cd) or even lower (other metals) compared to the mineral soil horizon. According to the ANOVA results, all the indicated differences between the content of elements in different substrates are statistically significant in the impact area ($p < 0.00001$) and for all elements in the background area (at least, $p < 0.015$), with the exception of exchangeable forms of Pb and Cd.

Thus, our assumption about a significantly lower content of potentially toxic metals in decomposing wood compared to the forest litter and the mineral soil horizon is confirmed. This is combined with a higher content of calcium in the trunks, which reduces the mobility of metals. Low toxicity, either alone or in combination with a favorable microclimate, may explain the survival of soil invertebrates in the CWD while they are eliminated in other microsites of the impact area.

Lower metal content in decaying wood compared to forest litter has been shown earlier for coniferous CWDs [5]. To our knowledge, the cited work and our study are the first direct comparisons of metal content in decaying wood (coniferous and deciduous trees) and forest litter under conditions of industrial pollution. Another work known to us on metal content in decaying wood [69] concerned regional pollution and did not include comparisons with other substrates.

CONCLUSIONS

The analysis of the composition and abundance of soil macrofauna confirmed our assumption that decaying tree trunks are not only "concentrators" of pedobionts in background forests, but also microsites of their survival in heavily contaminated areas. We leave aside the question of possible ways of soil invertebrates getting into decaying tree trunks in contaminated areas, since it requires special study.

In the present work, no fundamental differences in macrofauna were found between tree trunks and standard soil samples at the level of supraspecific taxa. With minor exceptions concerning several families of Coleoptera, the same groups of invertebrates can be found in both microsites. At the species level, the difference between microsites depends on the specific taxocene: the species composition of decaying trunks either almost coincides with standard samples (mollusks), or is specific (click beetles), or is more diverse (centipedes, arachnids, and ground beetles), or is reduced due to the loss of a certain ecological group (earthworms). The result of the ordination of microsites seems important: the configuration at the species level almost completely coincides with the configuration at the level of supraspecific taxa. This means that in this case, taxonomic resolution had little effect on the conclusion about the similarity of the macrofauna of different microsites.

The result concerning the possible reasons for the preferential habitation of soil macrofauna in contaminated areas in fallen trunks is also important. Considering the huge difference in metal content in decaying wood compared to forest litter, reaching almost two orders of magnitude, it is logical to assume that the phenomenon under discussion may be associated with the lower toxicity of the trunk substrate. This means that the "standard" function of decaying trees as a favorable site for soil invertebrates due to the microclimate and provision of trophic resources for pollution conditions is supplemented by a specific function: "safety islands" among the surrounding areas of highly toxic litter. In the context of the predicted increase in the frequency of droughts due to climate change, the combination of these functions becomes especially important for the preservation of soil fauna. It can also be assumed that after the cessation of emissions from industrial enterprises, decaying trunks can be sources of invertebrate dispersal to adjacent territories, which should be taken into account when analyzing post-technogenic restorative successions.

ACKNOWLEDGMENTS

The authors are grateful to E.Kh. Akhunova, T.N. Orekhov, A.D. Loginova, K.G. Khorosh, and O.A. Mezhevikina for sample preparation and chemical analysis.

FUNDING

The material was collected with the financial support of the Russian Foundation for Basic Research (project no. 2018-04-00160), data analysis and preparation of the article were supported by the state assignment of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (project no. 122021000076-9).

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The protocols for collecting invertebrates were approved by the Bioethics Commission of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences (protocol No. 13 dated November 1, 2022).

CONFLICT OF INTEREST

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

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Translated by M. Shulskaya

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