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Article in *Russian Journal of Ecology* · December 2024

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The Role of Coarse Woody Debris in the Survival of Soil Macrofauna in Metal-Contaminated Areas in the Middle Urals

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Received January 31, 2024; revised July 8, 2024; accepted July 8, 2024

Abstract—The soil macrofauna of three microsites in both 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 macrofauna composition was analyzed at two levels: supraspecific taxa and species, focusing on 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 vary depending on taxocene: the species composition within decaying trunks either closely resembles that of standard samples (mollusks), is more distinct (click beetles), is more diverse (centipedes, arachnids, and ground beetles), or is reduced due to the loss of a specific ecological group (earthworms). The ordination of microsites by the generalized list of species for the studied taxocenes aligns with the ordination based on macrofauna composition at the supraspecific taxa level. The total density and abundance of most soil macrofauna groups are higher in the decaying trunks than in the standard samples. This difference in the background area is particularly pronounced (2–6 times) for earthworms, harvestmen, lithobiids, herbivorous Heteroptera, ground beetles, and chironomid larvae. In the contaminated area, the difference is even more striking: 70 times higher 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 preferential habitation of soil macrofauna in decaying tree trunks within the contaminated area may be attributed to 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 trunks compared to standard soil samples.

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

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 within decaying tree trunks. However, zoologists surveying soil fauna often exclude CWD a priori, which can bias 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 inverte-

brates, at least for some taxa, have appeared relatively recently [2, 3]. Numerous studies have demonstrated that forest CWD is a biodiversity hotspot, and refuge 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 CWD as refuge, 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 defaunated substrate [22–24]. However, it would be wrong to consider industrial barrens 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 barrens [25]. In particular, earthworms and mollusks were found to live within CWD, 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, since (1) we did not compare the soil macrofauna of contaminated areas inhabiting CWD with background ones; (2) the invertebrate assemblage was analyzed only at the level of coarse supraspecific taxa; and (3) the metal concentrations in CWD were not examined. Due to these limitations, several questions remained unresolved: (1) How does the composition of the macrofauna within CWD change when transitioning from background areas to contaminated ones? (2) How unique is the species composition of the macrofauna in CWD compared to soil and forest litter? and (3) Does CWD differ from forest litter and soil in terms of the toxic load?

Objective—To address these questions. We tested the hypothesis that the substrate within decomposing tree trunks has significantly lower toxicity compared to the forest litter, enabling the survival of pollution-sensitive macrofauna groups (or species) that have disappeared from other microsites in the industrial barren.

MATERIALS AND METHODS

The study area is located in the southern taiga, at the boundary between the western and eastern macroslopes of the Urals. The climate, classified as the Dfb [26], is continental and humid, with warm summers, an average annual air temperature of +2.0°C, and total precipitation of 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 approximately 300 years ago. Currently, 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 MULL 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 nematocera, elaterids, and mollusks with the first two taxa being numerically predominant. The peculiarities of the soil macrofauna in the region, compared to areas located to the west and south, include a very low abundance of woodlice, diplopods, and forest cockroaches, as well as the absence of typical anecic earthworms [24, 28].

Our work focuses on analyzing 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 specific nature of the negative impact of its emissions, like that of other metallurgical plants engaged in primary smelting of non-ferrous metals, lies in the enhancement of the toxic effects 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 emissions of MUCS were maximal in the mid-1970s, reaching 350 000 t year, and then it gradually decreased: 225 000 t in 1980, 148 000 t in 1990, 63 000 t in 2000, 28 000 t in 2004, and only about 3 000–5 000 t/year after the radical reconstruction of the enterprise in 2010 and remaining at this level up to the present time [29]. Despite the decrease in emissions, high levels of soil pollution persist in areas located close to the plant [29, 30]. According to the 2016 data, 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 1 unit lower than the background level (5.9) [30].

The 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], a 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 total feeding activity of soil detritivores [33, 34], inhibition of microbial decomposition of organic matter [35, 36], disappearance of several taxa of macrofauna, primarily earthworms [22, 23], as well as the closely related earthworm-dependent 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 resulting from 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 also another consequence of environmental pollution [42, 43].

The recovery 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 recovery are also noted for the soil fauna: the distribution range of earthworms and mollusks [23], as well as moles [38], has shifted closer to the smelter. 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 mitigation 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 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. These trunks met specific criteria: (1) tree species – 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 point; and (7) there is no other CWD 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) and 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 placed in a plastic container to minimize mechanical damage during transportation. Then the samples were sorted layer by layer: first, the coarse bark was removed using a knife and tweezers, and then the wood fibers were sorted manually. If the core remained intact and uninhabited by soil invertebrates, it was excluded from sorting. In this case, only the volume of the sorted part was taken into account. This volume was calculated as the difference between the original volume of the fragment and the volume of the unsorted part, which was also calculated using the formula for a truncated cone.

Simultaneously, two standard soil monoliths measuring 20 × 20 cm and about 25–30 cm deep were collected: one directly beneath the trunk and the other 5–8 m away 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, with forest litter and organomineral horizon sampled separately, and then manually sorted in the laboratory. Before sorting, all samples were stored in an air-conditioned room maintained at 12°C for no more than 5 days.

Macrofauna (referred to as mesofauna according to Mercury Ghilarov) included invertebrates visible to the naked eye and manually extractable with tweezers, excluding microarthropods. In this study, we did not apply the standard size thresholds of 10 mm in body length or 2 mm in width, thus including enchytraeids, which occupy an intermediate position between the macro- and mesofauna. All collected invertebrates were fixed in 70% ethanol. We did not take into account invertebrate exuviae and clearly accidental finds, such as imagines of Lepidoptera.

The density of invertebrates was calculated based on the volume of the sorted trunk fragment and expressed as specimens/dm³. The density of macrofauna in standard soil monoliths was expressed in the same units. The depth of the monoliths was assumed to be 25 cm, i.e., the volume of the monolith is 10 dm³. The average volume of sorted trunk fragments was 8.86 ± 1.67 dm³ for the background and 8.76 ± 0.76 dm³ for the impact area (the difference between the two was statistically insignificant, the *t*-test = 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 excluded cocoon exuviae of earthworms (to avoid “double” counting of this group), as well as ants and dipteran imagines (since standard sampling is not suitable for accurately assessing the abundance of these groups).

A total of 75 samples were analyzed, including 25 fragments of decaying tree trunks (8 from the back-

ground area and 17 from the impact area) and 50 standard soil monoliths.

Laboratory processing included the grouping of invertebrates (a total of about 6.4 thousand specimens) into coarse supraspecific taxa, as well as species-level identification for several groups: earthworms, centipedes, millipedes, spiders, harvestmen, mollusks, click beetle imagines, and ground beetle imagines. Species identification of adult earthworms was carried out using the taxonomic key [54]. Given 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, and pattern of setae) and also features of the internal structure (shape of the nephridial bladders, presence and localization of diverticula) were used for identification. To identify spiders, the electronic resource “Spiders of Europe” (www.araneae.nmbe.ch) was used, and regional identification keys were employed for other invertebrates [55–57]. Species names were verified using the database GBIF Backbone Taxonomy (www.gbif.org).

Chemical Analysis. Samples of wood (without bark) from hand sorted fragments, forest litter, and mineral soil were ground in a laboratory mill (MF10, IKA, Germany) and sieved through a 2 mm mesh. The content of acid-soluble macroelements (Ca, Mg) and potentially toxic metals (Mn, Fe, Cu, Pb, Zn, and Cd) was determined using a 5% HNO₃ extract. Exchangeable metals (Cu, Pb, Zn, and Cd) were extracted with a 0.05 M CaCl₂ solution at a substrate-to-extractant ratio of 1:20. Concentrations of acid-soluble forms were measured on an AAS Vario 6 atomic absorption spectrometer (Analytik Jena, Germany), while exchangeable forms were analyzed using a contrAA 700 (Analytik Jena, Germany). pH (in water) was measured ionometrically at substrate-to-deionized water ratios of 1 : 25 for wood and litter and 1 : 5 for mineral soil.

Data Analysis. The content of elements and the abundance of macrofauna were compared between microsites (decaying trunk, beneath the trunk, and outside the trunk) and pollution areas (background and 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, defined as the natural logarithm of the ratio of the value in the impact area to the value in the background area or the ratio of the value in 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 ordinated based on the Bray–Curtis distance by absolute abundance using the prin-

cipal coordinate analysis (PCA) in the *ape v. 5.7* package [60]. Two ordination approaches 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, was challenging. Therefore, a generalized array of species was used in the second approach for earthworms, mollusks, arachnids, lithobiids, geophilids, ground beetles, and click beetles. This array also included single-species taxa (diplopods and several beetle families (Table 1)). The statistical significance of the differences in group and species composition between the areas and microsites was assessed using PERMANOVA (999 permutations) in the *vegan 2.6* package.

Calculations were performed in the R v. 4.3 software. The *tidyverse* package was employed for preliminary data transformation, and the *ggplot2* package was utilized 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 consistent difference between CWD and standard soil samples was observed for several families of Coleoptera: Curculionidae were absent from the trunks, while Ptiliidae, Lucanidae, Silphidae, Cerylonidae, and Scydmaenidae were absent from the standard samples.

This specificity of CWD, compared to standard soil samples, is quite understandable. The weevil larvae absent from CWD typically inhabit mineral soil horizons. Although this group includes xylophilic species, such as those from the genus *Magdalis*, their larvae prefer “fresh” wood over decaying wood at final stages of decomposition. The families of Coleoptera found exclusively 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 between the trunks of the background and impact areas: in the contaminated area, ectoparasitic nematodes (Mermithidae), enchytraeids (Enchytraeidae), wasp larvae (Hymenoptera, Parasitica), and several families of Diptera are absent from CWD. However, in the latter case, they are also absent in the impact area outside the trunks. The absence of diplopods in the trunks in the background area is most likely accidental.

Table 1. Macrofauna groups (density, specimens/dm³) in 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 (egg cocoons)	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 (cocoon exuviae)*	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
Opiliones	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 + 1	0.04 ± 0.04	0.04 ± 0.03	—	—	—	0.01 ± 0.01
Auchenorrhyncha, i + 1	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	—
Coccoidea, i + 1	0.08 ± 0.06	0.02 ± 0.02	0.05 ± 0.04	—	0.04 ± 0.03	0.01 ± 0.01
Heteroptera, i + 1***	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 + 1	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 + 1 (<i>Dictyoptera aurora</i>)	—	—	—	—	0.01 ± 0.01	0.01 ± 0.01
Silphidae, i (<i>Phosphuga atrata</i>)	—	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, 1 (<i>Orchesia duplicata</i>)	—	—	—	0.01 ± 0.01	—	—
Cerylonidae, 1 (<i>Cerylon histerooides</i>)	—	0.01 ± 0.01	—	—	0.01 ± 0.01	—
Lucanidae, 1 (<i>Ceruchus chrysomelinus</i>)	—	—	—	—	0.01 ± 0.01	—
other Coleoptera, 1 + 1	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, 1 + 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, 1	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, 1 + p	0.10 ± 0.04	0.07 ± 0.05	0.05 ± 0.03	0.08 ± 0.04	—	0.01 ± 0.01
Formicidae, 1 + 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, 1	0.05 ± 0.03	0.12 ± 0.11	0.01 ± 0.01	—	0.02 ± 0.01	—
Limoniidae, 1	0.08 ± 0.05	0.01 ± 0.01	0.14 ± 0.06	—	0.06 ± 0.03	—
Chironomidae, 1	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, 1	0.06 ± 0.06	—	—	—	—	—
Scatopsidae, 1	—	—	—	—	—	0.09 ± 0.09
Bibionidae, 1	0.50 ± 0.30	1.61 ± 1.41	1.89 ± 1.26	—	—	—
Sciariidae, 1	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, 1	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, 1	0.08 ± 0.04	0.07 ± 0.03	0.09 ± 0.04	—	—	—
Asilidae, 1	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	—	—	—
other Orthorrhapha, 1	0.05 ± 0.04	—	—	—	—	—
Diptera, Brachycera — Cyclorrhapha						
Syrphidae, 1	—	0.03 ± 0.02	0.01 ± 0.01	—	—	0.01 ± 0.01
Muscidae, 1	—	0.02 ± 0.02	—	—	—	—
other Cyclorrhapha, 1	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, 1 + 1 + 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 statistical unit is a sample (fragment of a trunk or 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 test ($p < 0.05$).

Stage of development: i—imago, l—larvae, p—pupa or cocoon.

*—not included in the total density;

**—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 *Liadopria serricornis*, *Agathidium* sp., and *Choleva* sp.

Abundance of Macrofauna

Absolute values of abundance for 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 pronounced (2–6 times) for earthworms (Lumbricidae), harvestmen (Opiliones), red velvet mites (Acari-formes, Trombididae), centipedes (Lithobiomorpha), herbivorous bugs (Heteroptera: Lygaeidae, Miridae, Tingidae), ground beetles (Carabidae), and lake fly larvae (Chironomidae). In the impact area, the difference in abundance between CWD and standard soil samples for many groups is even more contrasting compared to the background area. Specifically, 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, crane fly larvae (Tipulidae and Limoniidae).

Beneath the trunks, the overall abundance of macrofauna in both areas is lower compared to within the trunk and is similar to that of standard soil samples. In the background area, the abundance of most groups beneath the trunks is almost indistinguishable from that of standard samples. However, in the impact area, a preference of invertebrates for this microsite is evident. This is especially noticeable for crane fly larvae, whose density beneath the trunks is 17 times higher than in standard soil samples, as well as for mollusks (8 times), earthworms (7 times), and Heteroptera (3 times).

According to ANOVA results, the total macrofauna density (Table 1) varies statistically significantly between the areas ($F(1;69) = 164$, $p < 0.000001$) and microsites ($F(2;69) = 17.3$, $p = 0.000001$). However, the interaction of these factors is statistically insignificant ($p = 0.480$). In other words, the relative abundance of invertebrates across different microsites is similar in both areas.

In the contaminated area, the total macrofauna density in CWD is 3.1 times lower than in CWD in the background area, while the differences between the areas are even more pronounced for standard soil samples, with a 6.8-fold reduction in density. The differences for individual taxa are even more striking: pollution reduces the density of earthworms in CWD by 7.5 times and their cocoons by 5 times, whereas in standard soil samples, these reductions are 300-fold and 70-fold, respectively. Similarly, mollusk density decreases by 6 times in CWD and 150 times in standard samples, geophilids by 12 and 27 times, and Heteroptera by 3 and 6 times. For some groups (click beetles, spiders, and lepidopteran larvae), the effect of pollution is oppositely directed: a decrease in abundance in standard samples is accompanied by an increase in abundance in CWD.

The effect sizes clearly illustrate the mitigation of the negative impact of pollution. A more pronounced “concentration” of invertebrates within the trunks in the impact area (Fig. 1a) results in a less considerable suppression of their populations 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 than in standard samples. For several groups (spiders, Heteroptera, rove beetles, soldier 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 based on the group composition of macrofauna demonstrates weak differentiation among microsites in the background area (Fig. 2a). Standard soil samples and samples collected beneath 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 collected from within the trunks are distinctly separated from these microsites (0.25–0.27). In the impact area, the pattern is similar, but the differentiation is more pronounced (Fig. 3a). Samples collected outside and beneath the trunk form a single cluster (the distance between the centroids is 0.17), while samples from within the trunks are more distant (0.37–0.45). It is important to note that the separation of the macrofauna within the trunks reflects differences not only in the percentage of groups but also in their absolute density as the ordination metric accounted for the abundance of taxa. According to PERMANOVA results, the differences in group composition between microsites 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 areas clearly demonstrates a greater similarity in the group composition of trunk-associated 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 overlap and are widely separated (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 overlap, with smaller distances between their centroids (0.41–0.43). According to the results of PERMANOVA, the differences between the areas are less pronounced for trunk-associated macrofauna ($R^2 = 0.23$, $F(1;23) = 6.9$, $p = 0.001$) compared to the standard samples ($R^2 = 0.39$, $F(1;23) = 14.6$, $p = 0.001$).

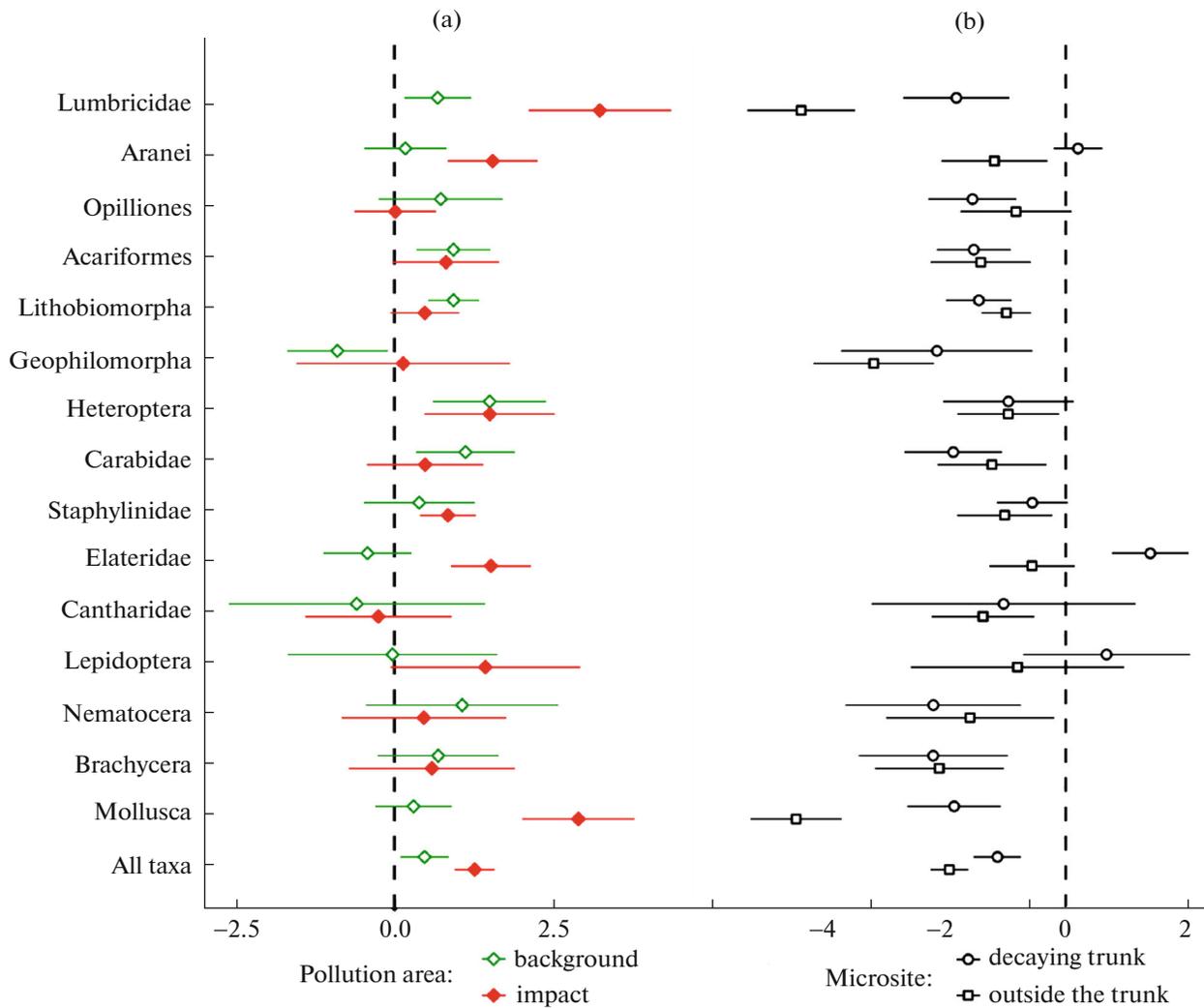


Fig. 1. Effect size and 95% confidence intervals for several taxa: (a) ratio of abundance in a decaying trunk to abundance outside the trunk in the background and impact areas, (b) ratio of abundance in the impact area to abundance in the background area in a decaying trunk and outside the trunk.

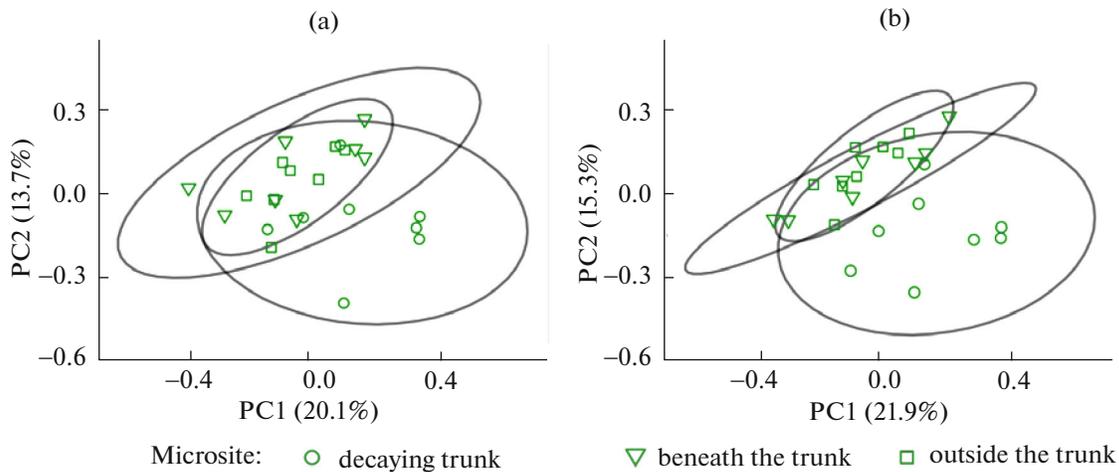


Fig. 2. Ordination of three microsites (decaying trunk, beneath the trunk, and outside the trunk) in the background area: (a) by group composition of macrofauna, (b) by species composition of several taxa (earthworms, mollusks, spiders, harvestmen, centipedes, millipedes, ground beetles, and click beetles).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

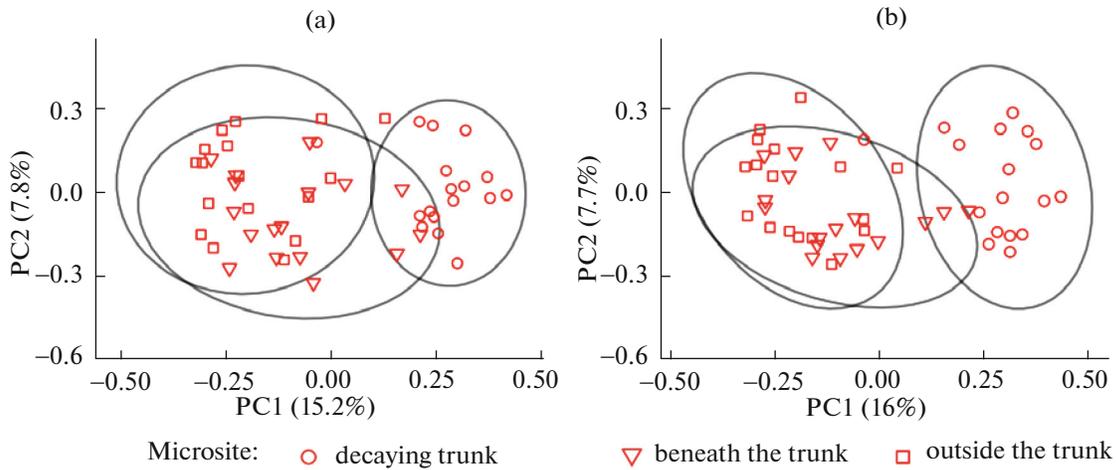


Fig. 3. Ordination of three microsites (decaying trunk, beneath the trunk, and outside the trunk) in the impact area: (a) by group composition of macrofauna, (b) by species composition of several taxa (earthworms, mollusks, spiders, harvestmen, centipedes, millipedes, ground beetles, and click beetles).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

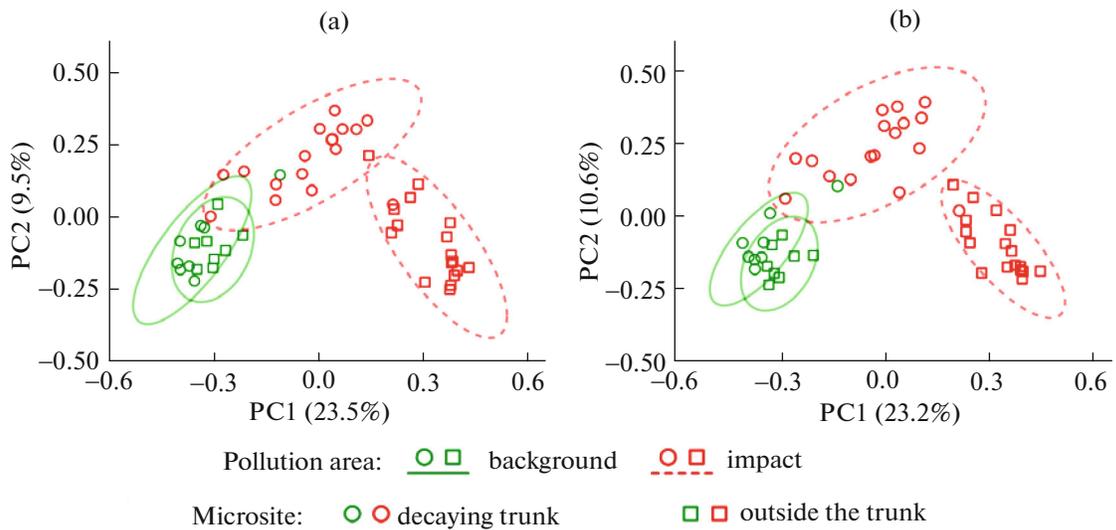


Fig. 4. Ordination of two microsites (decaying trunk and outside the trunk) in the background and impact areas: (a) by group composition of macrofauna, (b) by species composition of several taxa (earthworms, mollusks, spiders, harvestmen, centipedes, millipedes, ground beetles, and click beetles). The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

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

The arrangement of points by species composition (Figs. 2b–4b) closely resembles that by group composition (Figs. 2a–4a). However, the distances between the centroids of the trunk microsite and those of the other microsites are slightly greater at the species level than those observed for supraspecific taxa. In the background area, these distances range from 0.31 to 0.33, while in the impact area, they range from 0.40 to 0.48. The distances between microsites beneath the

trunk and those outside it remain nearly identical to those observed in the group composition analysis.

Considering the known effect of taxonomic resolution on the analysis of the community response to environmental factors [61], we expected to find differences in the nature of the variations between microsites at the supraspecific and species levels. The absence of such differences is likely due to the fact that we analyzed a generalized list of species across multiple taxocenes rather than individual taxocene list. It should be noted that taxa identified to the species level constitute approximately half of the soil macrofauna

(46–65% of the total abundance). The minimal impact of taxonomic resolution on the conclusions regarding microsite similarity is methodologically significant, as it suggests that species-level identification may not be necessary in initial analyses, and supraspecific taxa can be used instead.

Structure of Taxocenes

The species composition of the studied taxocenes 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. Endogeic species (*Aporrectodea rosea*, *Perelia tuberosa*, and *Octolasion lacteum*) are absent in the trunks.

The higher abundance of earthworms in the trunks is attributed to a single dominant species in this microsite: *D. rubidus*, whose 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 dominant *D. rubidus*, and *D. octaedra*, which was found in low abundance. In the contaminated area, the earthworm taxocene associated with trunks represents a reduced version of the taxocene found in the background CWD, with several common species absent. This suggests that the two remaining species (*D. rubidus* and *D. octaedra*) exhibit greater resistance to pollution compared to those that disappeared. Previously, we documented only the first of these species in CWD in contaminated areas [25]. The pollution tolerance of these species aligns with numerous reports of other authors, highlighting their relatively high resistance to toxic load [62–66].

Centipedes. *Lithobius curtipes* dominates among lithobiids in both CWD and standard soil samples at both sites, and *Arctogeophilus macrocephalus* dominates among geophilids; other species are present in low number. Centipedes exhibit greater diversity in CWD compared to the standard samples due to the presence of low-abundance species.

Spiders. The spider assemblage is dominated by representatives of the Linyphiidae family, with *Maro pansibiricus*, *Porrhomma pallidum*, and *Tapinocyba insecta* being relatively abundant. Unfortunately, immature individuals of this family cannot be identified even to the genus level, resulting in incomplete information on species composition differences. Nevertheless, it is possible to note the association of the aforementioned species, as well as several others (*Tibioplus diversus*, *Thyreosthenius parasiticus*, and *Robertus lividus*) with CWD in the impact area. The higher abundance and diversity of spiders in the

decaying trunks within the impact area can be attributed to both web-weaving and non-web-weaving forms, likely due to the availability of a wide range of shelters and a high abundance of potential prey. In the impact area, the microclimate also likely plays a significant role: the high density of spiders within and beneath the trunks is largely driven by immature Linyphiidae, which are sensitive to desiccation.

Harvestmen. In CWD of the background area, harvestmen are more diverse and abundant compared to the standard samples, primarily due to the presence of relatively numerous *Nemastoma lugubre* and several rare species. In the contaminated area, harvestmen are rare in all microsites. The discovery of the hygrophilous *N. lugubre* in the impact area is noteworthy, as this species had not been previously recorded here through standard soil samples, soil traps, or surveys of grass-dwelling invertebrates [22, 24, 67, 68]. Although only a single individual of this species was found, its presence in the contaminated area—beneath a tree trunk, where humidity is elevated—is significant.

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

Click beetles. The taxocene of click beetles is more diverse in CWD compared to standard soil samples, primarily due to the presence of several species associated with decaying wood (*Ampedus* spp., *Melanotus villosus*, *Denticollis linearis*, and *Mosotalesus impressus*). Additionally, the taxocene of click beetles in CWD is more distinct, as it lacks species dominant in litter and soil (*Athous subfuscus* and *Dalopius marginatus*). This specificity of CWD is observed in both the background and impact areas, and it is even more pronounced in the latter, where the highest number of wood-associated species was recorded.

The higher species richness and abundance of click beetles in the impact area compared to the background area may be attributed to the pronounced microbiodiversity of this territory, resulting from the lower density of the tree canopy, combined with the well-known resistance of this group to metal pollution [22, 23]. In other words, decaying trunks should be regarded not as survival microsites, but as microsites of preferred habitats for a specific set of species in the case of click beetles.

Mollusks. In the background area, the species composition of gastropods in CWD differs slightly from that of standard soil samples, except for the absence of several low-abundance species. The higher density in CWD compared to standard samples is primarily driven by a single species, *Discus ruderratus*; in addition, two other species, *Perpolita hammonis* and *Euconulus fulva*, are also abundant in CWD. All three species are typical inhabitants of litter in the study area.

Table 2. Species composition of taxocenes (density, specimens/dm³) in 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
<i>Dendrobaena octaedra</i>	0.08 ± 0.03	0.10 ± 0.05	0.09 ± 0.04	—	0.02 ± 0.01	—
<i>Rhiphaodrilus diplotetratheca</i>	1.24 ± 0.14	1.23 ± 0.62	0.79 ± 0.19	—	—	—
<i>Dendrodriulus rubidus*</i>	0.11 ± 0.06	1.64 ± 0.65	0.15 ± 0.04	0.01 ± 0.01	0.41 ± 0.16	0.04 ± 0.03
<i>Eisenia ailavinyteae</i>	—	0.10 ± 0.07	0.03 ± 0.02	—	—	—
<i>Lumbricus rubellus</i>	0.18 ± 0.07	0.15 ± 0.08	0.03 ± 0.02	—	—	—
<i>Aporrectodea rosea</i>	0.01 ± 0.01	—	0.01 ± 0.01	—	—	—
<i>Octolasion lacteum</i>	0.03 ± 0.02	—	0.01 ± 0.01	—	—	—
<i>Perelia tuberosa</i>	0.13 ± 0.04	—	0.05 ± 0.03	—	—	—
				Lumbricidae		
<i>Hypsosinga</i> sp.	—	—	—	—	0.01 ± 0.01	—
<i>Araneus</i> sp.	—	—	0.01 ± 0.01	0.01 ± 0.01	—	—
<i>Clubiona subsultans</i>	0.01 ± 0.01	—	—	—	—	—
<i>Clubiona</i> sp.	0.03 ± 0.02	—	—	—	—	—
<i>Dictyna</i> sp.	—	—	—	—	—	0.01 ± 0.01
<i>Micaria subopaca</i>	—	—	0.01 ± 0.01	—	—	—
<i>Phrurolithus festivus</i>	—	—	—	—	0.01 ± 0.01	—
<i>Hahnia pusilla</i>	—	—	—	0.01 ± 0.01	—	—
<i>Hahnia sibirica</i>	—	—	—	0.01 ± 0.01	—	—
<i>Agyneta subtilis-allosubtilis</i>	—	—	—	—	—	—
<i>Allomengea scopigera</i>	—	0.04 ± 0.03	—	—	—	—
<i>Asthenargus paganus</i>	0.04 ± 0.02	—	—	—	0.01 ± 0.01	—
<i>Bolyphantes alticeps</i>	0.01 ± 0.01	—	—	—	—	—
<i>Centromerus sylvaticus</i>	—	0.05 ± 0.03	—	—	—	0.01 ± 0.01
<i>Ceratinella brevipes</i>	—	—	—	—	0.01 ± 0.01	—
<i>Ceratinella scabrosa</i>	—	—	0.01 ± 0.01	—	—	—
<i>Ceratinella</i> sp.	—	0.02 ± 0.02	—	—	—	—
<i>Decipiphantes decipiens</i>	—	—	—	—	0.01 ± 0.01	—
<i>Drapetisca socialis</i>	—	0.02 ± 0.02	—	—	—	0.01 ± 0.01
<i>Erigonella</i> sp.	—	—	—	—	—	0.01 ± 0.01
<i>Macrargus rufus</i>	0.01 ± 0.01	—	—	—	—	—
<i>Maro pansibiricus</i>	0.01 ± 0.01	0.02 ± 0.02	0.03 ± 0.02	0.04 ± 0.03	0.34 ± 0.15	0.04 ± 0.02
<i>Micrargus herbigradus</i>	0.01 ± 0.01	—	—	—	—	—
<i>Microneta viaria</i>	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
<i>Minyriolus pusillus</i>	—	—	—	0.02 ± 0.02	0.04 ± 0.03	—
<i>Porrhomma pallidum</i>	—	—	—	—	0.14 ± 0.04	0.01 ± 0.01
<i>Tapinocyba insecta</i>	0.08 ± 0.03	0.04 ± 0.04	0.03 ± 0.02	0.05 ± 0.03	0.03 ± 0.02	0.02 ± 0.01
<i>Tenuiphantes nigriventris</i>	—	—	0.01 ± 0.01	—	—	—
<i>Thyreosthenius parasiticus</i>	—	0.05 ± 0.05	—	—	0.04 ± 0.01	0.01 ± 0.01
<i>Tibioplus diversus</i>	—	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
<i>Trochosa</i> sp.	—	0.02 ± 0.02	—	—	—	—
<i>Ero furcata</i>	0.01 ± 0.01	—	—	—	—	—
<i>Metellina</i> sp.	—	—	—	—	—	0.01 ± 0.01
<i>Pachignatha</i> sp.	0.01 ± 0.01	—	—	—	—	—
<i>Robertus lividus</i>	0.11 ± 0.05	0.27 ± 0.07	—	—	0.03 ± 0.01	—
				Opiliones		
<i>Nemastoma lugubre</i>	0.03 ± 0.02	0.1 ± 0.04	0.01 ± 0.01	—	—	0.01 ± 0.01
<i>Lacinius ephippiatus</i>	0.03 ± 0.02	—	—	0.01 ± 0.01	—	—
<i>Lophopilo palpinalis</i>	—	0.01 ± 0.01	0.03 ± 0.02	—	—	—
<i>Oligolophus tridens</i>	—	0.02 ± 0.02	0.01 ± 0.01	—	0.01 ± 0.01	0.01 ± 0.01
<i>Rilaena triangularis</i>	—	0.01 ± 0.01	—	—	—	—
				Lithobiomorpha and Geophilomorpha		
<i>Lithobius curtipes</i>	0.75 ± 0.09	1.84 ± 0.28	0.51 ± 0.10	0.27 ± 0.04	0.41 ± 0.10	0.34 ± 0.08
<i>Lithobius proximus</i>	—	0.07 ± 0.05	—	—	—	—
<i>Lithobius</i> sp.	—	0.01 ± 0.01	—	—	0.01 ± 0.01	—
<i>Chinobius uralensis</i>	0.01 ± 0.01	0.01 ± 0.01	—	0.01 ± 0.01	0.03 ± 0.02	0.01 ± 0.01
<i>Arctogeophilus macrocephalus</i>	0.64 ± 0.11	0.28 ± 0.11	0.28 ± 0.06	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
<i>Escaryus japonicus</i>	0.15 ± 0.03	—	0.13 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	0.06 ± 0.02
<i>Sirigamia pusilla</i>	—	0.02 ± 0.02	—	—	—	—
				Carabidae**		
<i>Pterostichus oblongopunctatus</i>	—	0.18 ± 0.09	0.03 ± 0.02	—	—	0.01 ± 0.01
<i>Pterostichus aethiops</i>	—	0.01 ± 0.01	—	—	—	—
<i>Pterostichus melanarius</i>	—	0.01 ± 0.01	—	—	—	—
<i>Trechus secalis</i>	0.06 ± 0.02	0.03 ± 0.03	0.01 ± 0.01	0.01 ± 0.01	—	—
<i>Calathus micropterus</i>	—	—	—	—	0.02 ± 0.01	—
<i>Calathus melanocephalus</i>	0.01 ± 0.01	—	—	—	—	—
<i>Nothophilus biguttatus</i>	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		outside the trunk	CWD	
		beneath the trunk	Elateridae***		beneath the trunk	outside the trunk
<i>Loricera pilicornis</i>	—	0.01 ± 0.01	—	—	—	—
<i>Carabus granulatus</i>	—	0.01 ± 0.01	—	—	—	—
<i>Agonum gracile</i>	—	—	—	—	0.02 ± 0.01	0.01 ± 0.01
<i>Athous subfuscus</i>	0.30 ± 0.11	—	0.11 ± 0.03	0.11 ± 0.03	0.01 ± 0.01	0.25 ± 0.07
<i>Dalopius marginatus</i>	0.06 ± 0.03	—	0.03 ± 0.02	0.06 ± 0.03	—	0.08 ± 0.03
<i>Ampedus</i> sp.	—	0.10 ± 0.05	—	—	0.82 ± 0.22	—
<i>Ampedus balteatus</i>	—	—	—	0.01 ± 0.01	—	0.01 ± 0.01
<i>Ampedus nigerrimus</i>	—	—	—	—	0.01 ± 0.01	—
<i>Ampedus nigrinus</i>	—	—	—	—	0.04 ± 0.02	0.02 ± 0.02
<i>Ampedus pomotae</i>	—	0.01 ± 0.01	—	—	—	—
<i>Ampedus pomorum</i>	—	—	—	—	0.04 ± 0.02	—
<i>Melanotus villosus</i>	—	0.08 ± 0.03	—	—	0.03 ± 0.01	0.01 ± 0.01
<i>Denticollis linearis</i>	—	0.04 ± 0.03	—	—	0.01 ± 0.01	—
<i>Mosotalesus impressus</i>	—	—	—	0.04 ± 0.02	0.01 ± 0.01	0.11 ± 0.04
				Mollusca		
<i>Perpolita hammonis</i>	1.34 ± 0.32	0.51 ± 0.13	0.85 ± 0.18	—	0.004 ± 0.004	—
<i>Cochlicopa</i> sp.	0.44 ± 0.10	0.15 ± 0.08	0.31 ± 0.09	—	—	—
<i>Discus ruderatus</i>	0.24 ± 0.12	2.04 ± 0.57	1.86 ± 0.72	0.01 ± 0.01	0.34 ± 0.10	0.11 ± 0.05
<i>Euconulus fulva</i>	0.06 ± 0.02	0.36 ± 0.13	0.31 ± 0.07	0.01 ± 0.01	0.19 ± 0.12	0.04 ± 0.02
<i>Carychium</i> sp.	0.04 ± 0.04	—	0.03 ± 0.02	—	—	—
<i>Fruiticola fruticum</i>	0.06 ± 0.03	0.02 ± 0.01	0.05 ± 0.04	—	—	—
<i>Punctum pygmaeum</i>	0.04 ± 0.02	0.15 ± 0.05	0.01 ± 0.01	—	—	—
<i>Columella</i> sp.	0.11 ± 0.04	—	—	—	—	—
<i>Vallonia costata</i>	0.25 ± 0.17	0.20 ± 0.16	0.29 ± 0.18	—	—	—
<i>Acanthinula aculeata</i>	0.01 ± 0.01	—	—	—	—	—
<i>Arion subfuscus</i>	0.01 ± 0.01	0.04 ± 0.03	—	—	0.02 ± 0.02	—
<i>Vitrina pellucida</i>	0.05 ± 0.04	0.04 ± 0.04	0.01 ± 0.01	—	—	—
<i>Vertigo</i> 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 identification are impossible based on immature individuals.

**—only imago.

***—the total abundance for all stages of development is given (larvae make up about 90%).

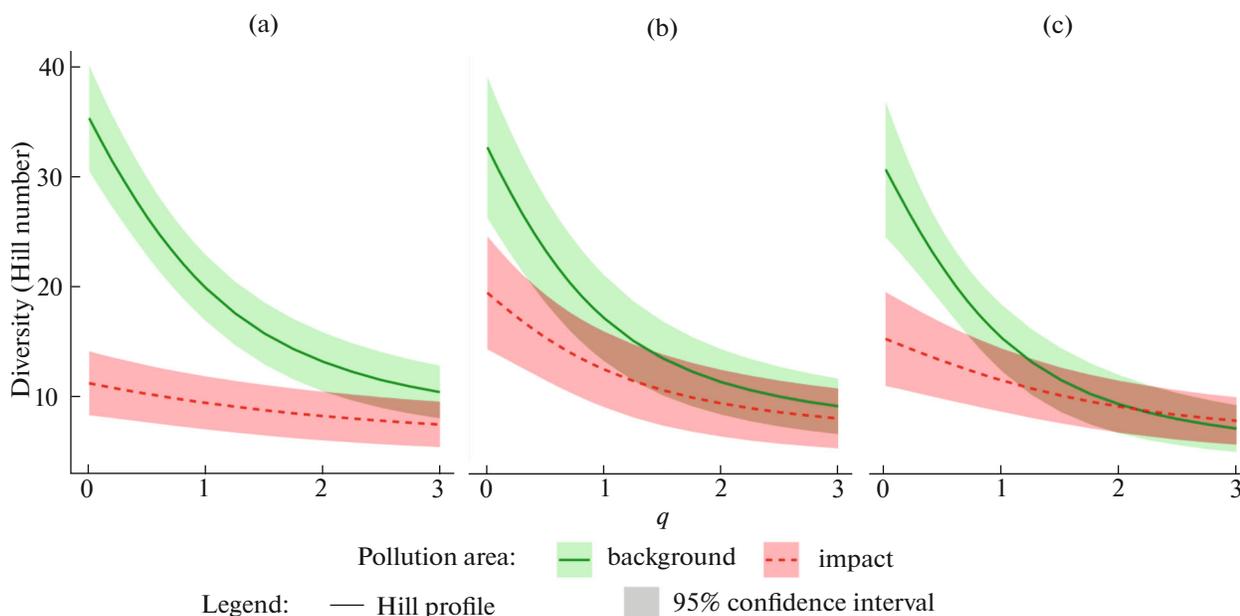


Fig. 5. Hill profiles for a generalized list of species: (a) outside the trunk, (b) CWD, (c) beneath the trunk.

They, along with *Arion subfuscus*, persist in the trunks of the contaminated area. Outside the trunks in the impact area, only two species were found sporadically (*D. ruderatus* and *E. fulva*)

Thus, a certain specificity of the studied taxocenes can be noted in relation to the differences between decaying trunks and standard soil samples. Several patterns are observed: the species composition of decaying trunks in the background area either almost entirely overlaps with standard soil samples (mollusks), is more diverse (centipedes, spiders, harvestmen, and ground beetles), is distinct (click beetles), or 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 reduced version of their counterparts in background trunks. In these cases, it is possible to hypothesize “hidden” inhabitation in litter by species that are not detected there but are found in the trunks. Their presence in litter may only be revealed through significantly increased sampling efforts, far exceeding standard levels. The examination of decomposing CWD effectively simulates such an increase in sampling efforts, as it targets areas of macrofauna concentration.

Species Diversity of Macrofauna

There is no consistent pattern of differences in species richness and species density between the microsites in the background area that applies uniformly across different taxocenes (Table 3). In some cases, species richness is higher in standard soil samples (earthworms, spiders, and mollusks), while in others,

it is higher within the trunks (centipedes, harvestmen, ground beetles, and click beetles). In the impact area, species richness is generally higher in trunks compared to standard samples. For all groups except click beetles, the overall species richness across all microsites decreases when transitioning from the background to the impact area. The Hill diversity profiles for the species lists aggregated across all taxocenes show sharp differences between the background and impact areas in the region $q < 1$ but are more similar in the region $q > 2$ (Fig. 5). This indicates that differences between areas concern relatively low-abundance species which contribute significantly to species richness, while differences in dominant species are minimal.

It is noteworthy that the greatest differences in Hill profiles between the areas are observed in standard soil samples, while the smallest differences occur within decaying trunks. In other words, the differences between the areas in the structure of soil macrofauna diversity are significantly less pronounced within the trunks 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 CWD and litter within the same area (Table 4). In both areas, the content of Ca is higher in CWD compared to litter (by 1.2–1.4 times) and even higher in the mineral horizon (by 4.1–7.3 times).

In the background area, the concentrations of acid-soluble forms of potentially toxic metals are lower in CWD compared to litter: by 45 times for Fe, 32 times

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

Element	Outside the trunk		CWD	Beneath the trunk	
	litter	soil		litter	soil
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:			Background area		
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:			Impact area		
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
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:			10940 (4960) a	8770 (1920) a	2980 (680) b
Ca	7890 (2240) a	2660 (600) b	720 (250) b	840 (160) a	810 (90) ab
Mg	860 (150) a	780 (70) ab	170 (90) b	760 (530) a	630 (300) a
Mn	600 (360) a	590 (180) a	70 (90) b	6080 (3120) a	5350 (1220) a
Fe	5400 (2740) a	5880 (1320) a	68.6 (61.9) c	2070 (578) a	443 (155) b
Cu	1710 (502) a	285 (101) b	9.1 (10.5) c	972 (317) a	55.3 (24.6) b
Pb	773 (301) a	47.5 (32.4) b	316 (139) c	511 (127) a	237 (31.6) bc
Zn	527 (170) a	224.2 (26.0) b	2.81 (2.45) b	7.20 (3.05) a	2.25 (0.7) b
Cd	7.35 (3.55) a	1.95 (0.46) b			
Exchangeable forms, µg/g:			2.78 (5.68) c	49.9 (19.1) a	19.9 (12.3) b
Cu	42.2 (14.3) a	9.76 (5.16) b	0.26 (0.21) c	4.67 (2.44) a	0.58 (0.35) b
Pb	4.35 (2.84) a	0.94 (1.98) bc	38.0 (34.0) b	120.5 (28.2) a	42.7 (13.1) b
Zn	122 (41) a	34.9 (10.3) b	1.16 (1.00) c	4.22 (1.16) a	1.98 (0.62) b
Cd	4.65 (1.30) a	1.63 (0.35) 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 test ($p < 0.05$).

for Pb, and by 2–7 times for other metals. In the impact area, the differences between CWD and litter are even more pronounced: 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 metals are less pronounced compared to acid-soluble ones, but they also reach sixfold in the background area (for Zn) and 17-fold in the impact area (for Pb). Concentrations in CWD are comparable (Zn and Cd) or even lower (other metals) compared to the mineral soil horizon. According to ANOVA results, all the observed differences in element content between 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 Pb and Cd.

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

Lower metal content in decaying wood compared to forest litter has been previously demonstrated for coniferous CWD [5]. To the best of our knowledge, the cited study and our work are the first direct to directly compare metal content in decaying wood (coniferous and deciduous trees) and forest litter under conditions of industrial pollution. Another relevant study on metal content in decaying wood [69] focused on regional pollution and did not include comparisons with other substrates.

CONCLUSIONS

The analysis of the composition and abundance of soil macrofauna confirmed our hypothesis that decaying tree trunks are not only as “concentrators” of pedobionts in background forests, but also as microsites of their survival in heavily contaminated areas. We leave aside the question of possible ways of soil invertebrates colonize 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 are present in both microsites. At the species level, the difference between microsites depends on the specific taxocene: the species composition of decaying trunks either closely resembles that of standard samples (mollusks), is distinct (click beetles), or is more diverse (centipedes, arachnids, and ground beetles), or is reduced due to the loss of a specific ecological

group (earthworms). The result of the ordination of microsites are noteworthy: the configuration at the species level closely matches that at the level of supra-specific taxa. This indicates that in this case, taxonomic resolution had little influence on the conclusions regarding the similarity of macrofauna across different microsites.

The findings regarding the potential reasons for the preferential habitation of soil macrofauna areas within decaying trunks in contaminated areas are also important. Given the huge difference in metal content between decaying wood and forest litter, reaching almost two orders of magnitude, it is reasonable to hypothesize that the phenomenon under discussion may be linked to the lower toxicity of the trunk substrate. This suggests that the “standard” function of CWD as a favorable habitat for soil invertebrates, due to the microclimate and provision of trophic resources, pollution conditions by a specific function: serving as “safety islands” amidst highly toxic surrounding litter. In the context of the predicted increase in the drought frequency due to climate change, the combination of these functions becomes particularly crucial for the preservation of soil fauna. Furthermore, it can be hypothesized that after the cessation of emissions from industrial enterprises, decaying trunks may act as sources of invertebrate dispersal to adjacent areas. This which should be taken into account when analyzing post-technogenic successional recovery.

ACKNOWLEDGMENTS

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

FUNDING

The material collection was financially supported by the Russian Foundation for Basic Research (project no. 2018-04-00160). Data analysis and manuscript preparation 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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