ISSN 1067-4136, Russian Journal of Ecology, 2025, Vol. 56, No. 1, pp. 60–77. © Pleiades Publishing, Ltd., 2025.

Assemblages of Ground-Dwelling Arachnids and Carabids in Metal-Polluted Forests: Are There Any Signs of Recovery after Reductions of the Middle Ural Copper Smelter Emission?

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Received June 25, 2024; revised September 26, 2024; accepted November 3, 2024

Abstract—Information regarding the natural recovery of ground-dwelling invertebrate communities following reductions in industrial pollution remains fragmentary. Assemblages of epigeic arachnids (spiders and harvestmen) and ground beetles in the southern taiga spruce-fir forests have been analyzed in two sites: a background (control) site and a site polluted by long-term emissions from the Middle Ural Copper Smelter. Two periods were compared: one with relatively high emission rates (2005) and another after near-complete emission cessation beginning in 2010 (2018). The hypothesis that the differences between the sites diminished in the second period was tested. The total activity density, species richness, taxocene structure, and the abundance of groups identified by ecological traits (body size; moisture, stratum, and habitat preferences; hunting strategy for arachnids, and mobility and feeding preferences for ground beetles) have been assessed. The hypothesis has not been confirmed: differences persist between the studied areas in total abundance, species richness, and taxocene structure. However, some signs of recovery have been observed in arachnid assemblages, including a shift towards "linyphiidization" (i.e., replacement of Lycosidae with Linyphiidae), an increase in harvestmen abundance, and the appearance of species previously recorded only in the background forests. However, such signs were absent in the ground beetle assemblages: taxocene features characteristic of polluted areas remained unchanged, including an increased proportion of mixo-phytophages and the absence of large-sized species.

Keywords: Aranei, Opiliones, Carabidae, ground-dwelling arthropods, Middle Urals, southern taiga, industrial pollution, heavy metals, natural recovery, abundance, activity density, diversity, community structure, ecological traits of species

DOI: 10.1134/S1067413624602628

INTRODUCTION

In recent years, point polluter emissions have been decreasing in many countries, initiating natural recovery of previously industrially-damaged ecosystems. However, despite considerable interest in this issue and its obvious practical significance, recovery patterns remain understudied [1]. The situation is complicated by the fact that recovery trajectories and rates are likely to vary depending on the type of industrial facility and the duration of its impact, environmental conditions, and the tax a examined.

The arachnids and carabids (ground beetles) examined in this study, as well as ground-dwelling invertebrates in general, are among the least studied groups in terms of recovery successions after the cessation of industrial emissions [1]. Data for these groups are limited to single surveys of areas adjacent to metallurgical enterprises during periods of already reduced emissions, without direct comparison to the state before the reduction of emissions [2, 3]. Repeated studies (before and after emission reduction) at the same area were carried out only for one enterprise with a very localized (no more than 1 km) impact zone, a phosphorus fertilizer plant [4–6].

The interest of ecotoxicologists in predatory ground-dwelling arthropods, in particular arachnids and carabids, roots from their high abundance and diversity, and significant contribution to ecosystem functions [7]. These groups are sensitive to abiotic and biotic factors [8–10], including pollution [11–16]. The main factors include the soil chemistry and soil structure, moisture content and litter thickness, as well as the species composition and abundance of plants [17–21]. It is believed that changes in environmental parameters primarily affect the ratio of life-forms and ecological groups [22–25]. In addition to arachnids and ground beetles, our study area also supported high abundance and diversity of rove beetles (Staphylinidae). However, including this group in the analysis is challenging due to the difficulties of species identification and the lack of comprehensive data on species traits [26]. Other taxa, such as centipedes, are relatively uncommon in the study area.

The recovery of ecosystems after emission reduction has been studied very unevenly not only across different taxa, but also in terms of biota coverage within a specific area [1]. Among the most extensively studied sites is the area adjacent to the Middle Ural Copper Smelter (MUCS), which almost completely ceased emissions about 15 years ago. A comparison with the period of high emissions from the smelter (the late 1980s) showed a slow recovery of upper soil horizons [27]. Thus, in the most heavily polluted areas, there is no noticeable recovery of the ground-level vegetation [28, 29], mollusk population [30], soil macrofauna [31, 32], or small mammals [33]. At the same time, signs of recovery have been noted for epiphytic lichens [34], phyllophagous insects [35], hollow-nesting birds [36], moles [37], and many groups of organisms in moderately-polluted areas [28, 29, 31, 32, 38–40]. Moreover, shifts in soil pH toward the alkaline conditions following MUCS emission reduction [27] results in lower toxicity of metals despite their high total content. Consequently, some signs of soil macrofauna recovery have been observed even in severely polluted areas [31, 32, 39, 40]. These observations suggest that similar changes might occur in ground-dwelling communities as well.

Ground-dwelling invertebrates in the MUCS area have been studied since 1998 [41–45], though not in the context of post-industrial recovery. The presence of previously established permanent sample plots allows characterization of their assemblage dynamics after emission reduction. However, it is important to note that the sample plots used (nodes of a regular grid) were originally established to address a different problem — analyzing spatial distribution patterns of ground-dwelling organisms. At the scale of the entire pollution gradient, they enable some statistical conclusions about differences but not about pollution impact. On the other hand, repeated surveys at these "historical" plots allowed exclusion of spatial and temporal variability confounding effects as pitfall trap locations remained fixed during the compared periods. Given the extreme scarcity of information on post-industrial recovery of ground-dweller assemblages, comparison of sites remain valuable despite these limitations [46], particularly with the continued monitoring.

Objective—To compare the abundance, diversity, and assemblage structure of ground-dwelling arachnids and carabids between periods of relatively high (2005) and nearly ceased (2018) emissions from the MUCS. We expected to detect initial recovery patterns of the studied assemblages. In other words, we tested the hypothesis that the differences between polluted and background areas would become less pronounced following cessation of MUCS emissions.

MATERIALS AND METHODS

Study Area

The MUCS is located on the outskirts of Revda, Sverdlovsk oblast, 50 km west of Yekaterinburg. The smelter has been operating since 1940; its main emissions are gaseous compounds of sulfur, fluorine, and nitrogen, along with metals (Cu, Pb, Zn, Cd, Fe, Hg, etc.) and metalloids (As). In the 1980s, the plant's annual emissions reached 150000–225000 tons, making it one of Russia's largest industrial pollution sources. Since the early 1990s, emissions have progressively decreased: they amounted to 65000 tons in 1999, 27000 tons in 2005, and after a major plant reconstruction in 2010 stabilized at 3000–5000 tons per year [1, 27].

The study was conducted at two permanent monitoring sites, each approximately 0.4 hectares in area, during periods of relatively high MUCS emissions (2005) and 8 years after their reduction to minimal levels (2018). The sites were established in native spruce-fir forests typical of the region: the relatively unpolluted (background) site is located 20 km west of the smelter, while the heavily polluted (impacted) site, lies 2 km southwest. The spatial arrangement relative to the region's prevailing westerly winds minimized the pollution gradient length and prevented contamination of the background site from Yekaterinburg's emissions.

According to 2010 data, the concentrations of acid-soluble forms of metals in the forest litter at the impacted site exceeded the background levels for Cu, Pb, and Cd by 86.4, 35.2, and 10.6 times, respectively, while the pH values were one unit lower (more acidic) [47]. Compared to background conditions, the impacted area showed reduced stand height, stocking density, crown closure, and herbaceous layer projective cover (for details see [48]).

Data Collection

Invertebrates were sampled using pitfall traps consisting of plastic cups (8.5 cm opening diameter) containing 3% acetic acid as preservative. At each study site, a 60 × 60 m sampling plot was established with traps arranged in a regular 7 × 7 grid at 10 m intervals (49 traps per plot). Trap locations remained identical between sampling years (2005 and 2018).

Sampling was performed twice annually during peak activity periods (spring–summer and autumn): in 2005, on May 23–26 and August 1–4; in 2018, on May 24–29 and August 2–7. According to the data from the nearest weather station (Revda), the average daily air temperature were 13.1 and 15.4°C, and 8.9 and 14.9°C in May and August in 2005 and 2018, respectively. The temperature differences between surveyed dates within each year were more pronounced: 16.2°C (May) and 19.3°C (August) in 2005 versus 9.4°C (May) and 17.2°C (August) in 2018.

Table 1. Coding and trait gradations of ecological groups

Trait	Gradations
Size*	S, small-size individuals: <3 mm/<9 mm; M, middle-size individuals: 3–6 mm/9–11 mm; B, large-size individuals: >6 mm/>11 mm;
Moisture	hyg, hygrophilic; mes, mesophilic; xer, xerophilic;
Stratum	LS, forest litter, humus horizon of soil (stratobiont); SS, soil surface (epigeobiont); HSD, vegetation (horto-, tamno-, and dendrobiont);
Habitat	F, forest; E, eurytopic; Oh, open habitats (meadow and meadow-field for Arachnida and Carabidae, respectively);
Hunting**	H, ground-dwelling hunter; W, web builders; HW, ground-dwelling hunter-weavers; SH, scavenger-hunter;
Feeding***	Z, zoophages; Mx, mixo-phytophages;
Mobility***	lm, low mobility; mm, moderate mobility; hm, high mobility

*, the first size range is for Arachnida, the second, for Carabidae; **, only for Arachnida; ***, only for Carabidae.

In both years we visually assessed tree crown density (on a 5 × 5 m plot) and total herbaceous layer projective cover (on a 2 × 2 m plot) adjacent to each trap. Crown density showed minimal interannual variation (Mean ± SE, $n = 49$): at the background site, values were 55.1 ± 3.8 and 50.8 ± 3.1% in 2005 and 2018, respectively; at the impacted site, 45.2 ± 3.8 and 51.6 ± 3.5%, respectively. The projective cover of the herbaceous layer at the background site was 44.3 ± 4.6 and 50.2 ± 3.1% in 2005 and 2018, respectively; at the impacted site, 5.5 ± 2.0 and 5.6 ± 1.2%, respectively. All interannual differences proved statistically insignificant: Student's t-test values for the tree stand for the background and impacted sites are 0.9 ($p = 0.38$) and 1.2 ($p = 0.22$), respectively, and for the herbaceous layer, 1.1 ($p = 0.29$) and 0.02 ($p = 0.98$), respectively.

Across both sampling years, we collected 1223 sexually mature spiders, 243 harvestmen, and 2989 ground beetles. Laboratory identification used keys for spiders (https://araneae.nmbe.ch), harvestmen [49], ground beetles [50], and reference collections from the Museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences. The nomenclature of spider taxa follows the World Spider Catalogue (https://wsc.nmbe.ch), harvestmen nomenclature follows [51], and ground beetle nomenclature follows [52].

Ecological Traits of Arachnid Species

Ecological traits of arachnid species are detailed in Table 1. These data were compiled from faunal reports covering the Urals and adjacent territories [49, 53–55]. Body size measurements (separated by sex) were obtained from the taxonomic database at http://araneae.nmbe.ch. We classified arachnids into three functional groups based on vertical stratification: epigeobionts (soil surface dwellers), stratobionts (inhabit forest litter), and vegetation dwellers (occupying herb, shrub, and/or tree layers). By habitat preferences, species were grouped as forest specialists, eurytopic species (forest-meadow generalists), or open habitat specialists (meadow dwellers). According to the feeding mode, the species were divided into four groups: those that do not use webs (hunters and ambushers); web builders (weavers), i.e., those that use trapping nets (funnel-web spiders, orb-web spiders, sheet weavers, etc.); and scavenger-hunters (exclusively harvestmen). A separate group was established for the single species *Allomengea scopigera* (Grube, 1859), classified as "wandering weaver-hunters". This designation reflects its ontogenetic shift in foraging behavior: juveniles construct prey-capture nets while adults are active hunters [54]. The characteristics of all the species recorded are provided in the Supplementary Materials (Table S1).

Ecological Traits of Carabid Species

The data were extracted from the Ural fauna synopsis [56], with some categories consolidated into broader groups (Table 1). Individual size was determined as the sum of the pronotum length and the average length of both elytra. Species-specific mean size were obtained from previous study [44]. We distinguished three groups of species according to habitat preferences: forest (forest, deciduous-forest, and forest-bog), eurytopic (forest-meadow), and open habitat (meadow-field) groups. Based on feeding patterns, we identified obligate predators (zoophages) and herbivorous species at the imago stage (mixo-phytophages). Species locomotion characteristics were compiled from [57–59]. Following the classification in [60], we categorized species by mobility into three groups: those with low mobility (wingless and with undeveloped wing muscles, moving along the soil surface), moderate mobility (di- and polymorphic and long-winged species, some capable of flight), and high mobility (long-winged with functioning wing muscles, good flyers). The characteristics of all the species recorded are provided in the Supplementary Materials (Table S2).

Data Analysis

For all parameters, data from both seasonal sampling rounds were combined. To avoid artificially increasing replicate numbers, we used trap lines (7-trap averages) as statistical units. Since for a square grid averaging was possible both by rows and by columns, we used both grouping options. The results for both options almost completely coincided, which indicates the absence of pronounced anisotropy at the sites and can serve as a certain guarantee of the reliability of the conclusions. Main text presents the results for averaging by rows (i.e., by the trap lines); column-averaged data are provided in the Supplementary Materials (Figs. S1 and S2).

Unless otherwise stated, only statistically significant effects ($p < 0.05$) are discussed. Species with a proportion of 5% or more in the total abundance were classified as dominants. For the analysis of the species composition and ecological structures of taxocenes, both absolute (spec./100 trap-days) and relative (percentage of total abundance) density metrics were used.

Given significant abundance differences between sites, not only the observed number of species (Sp) but also the rarefied species richness standardized to 100 specimens (Sp’) [61] (calculated via the iNEXT v. 3.0 package [62]) were used as an indicator of species richness. Community data were ordinated using principal coordinate analysis (PCA) with the Bray–Curtis distance (ape v. 5.8 package [63]). Distances between sites and years and the statistical significance of differences in taxocene structure were estimated using the PERMANOVA [64] in the vegan 2.6 package. The effect size was calculated using the LRRi function of the SingleCaseES v. 0.7 package [65] as the log Response Ratio, i.e., the logarithm of the ratio of the value at the impacted site to the value at the background site. If the 95% confidence interval of the effect size did not include zero, its value was considered statistically significant.

The spider charts were constructed using original scripts (https://github.com/ANSozontov/SpiderCharts); other illustrations were created with ggplot2 v. 3.3.5. The functions of the tidyverse 1.3.1 package collection were utilized throughout all stages of data analysis. All calculations were performed in the R v. 4.3 software environment. The code and source data have been deposited in the repository (https://github.com/ANSozontov/Revda_2024).

RESULTS

Arachnids

A total of 83 arachnid species (78 spider species and 5 harvestmen species) were recorded over two years, with 54 species recorded at the background site and 60 at the impacted site. Arachnid abundance in 2018 was lower than in 2005 at both sites (Fig. 1, Table 2). In the vicinity of the smelter, abundance remained lower than at the background area in both years; moreover, the differences in 2018 were greater than in 2005 (57 and 38%, respectively). Despite these abundance difference, neither observed species richness (Sp) nor rarefied richness (Sp') differed significantly between sites in either period.

The structure of the assemblages differed significantly between the sites in both years with greater variability observed at the impacted site compared to the background site (Fig. 2, Table 3). At the background site, the composition of the dominant complex remained relatively stable over 13 years: it included spider (*A. scopigera*, *T. insecta*, and *A. paganus*) and harvestmen (*L. ephippiatus* and *N. lugubre*) species typical of spruce-fir forests (Table 4).

At the impacted site, the taxocene underwent radical changes: the distance between the years (in both absolute and relative abundance) is so great that it is comparable to the distance between the sites (Fig. 2; Table 3). In 2005, the impacted site was dominated by lycosids (*A. taeniata*, *P. lugubris*, *A. pulverulenta*) with minor representation of linyphiids (*A. affinis*, *T. insecta*, *D. bidentata*) (Table 4). In 2018, lycosids were completely displaced from the dominant complex by linyphiids (*C. brevis* and *T. mengei*) and the harvestman *L. ephippiatus*. All these species were recorded at the impacted site in earlier surveys, but in 2005 they together accounted for no more than 2% of total arachnid abundance.

In 2005, the abundance of many ecological groups was reduced at the impacted site relative to the background site. This negative effect was observed for stra-

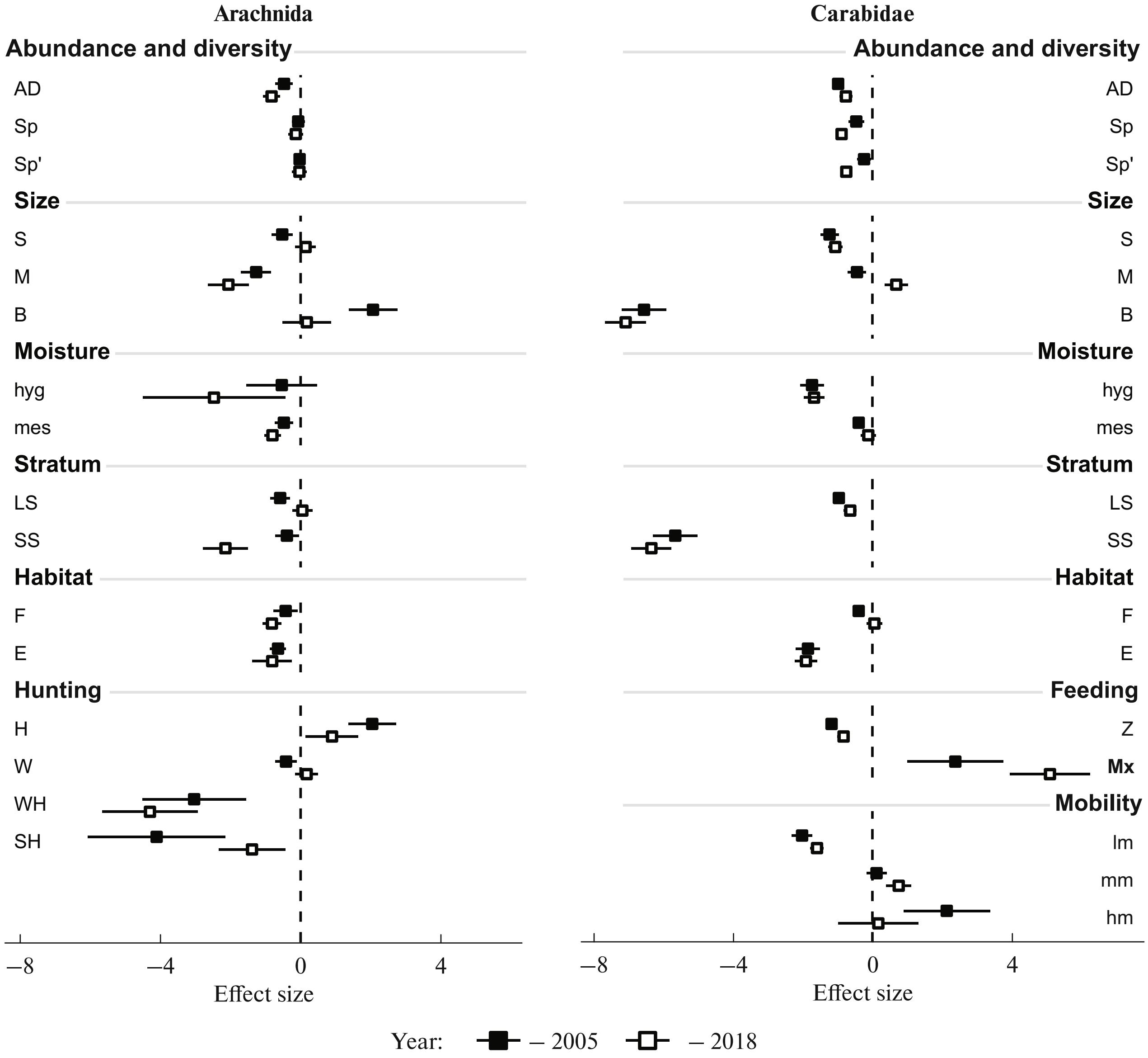

Fig. 1. The effect size and its 95% confidence interval for the compared periods (2005 and 2018). The designations of the ecological groups of arachnids (Arachnida) and ground beetles (Carabidae) are given in Table 1. Diversity and abundance parameters: AD, activity density; Sp, observed number of species; Sp', rarefied number of species (to 100 ind.).

tum-based groups (strato- and epigeobionts), habitat-based groups (forest and eurytopic), as well as mesophiles, small- and medium-sized species, web builders, hunter-weavers, and scavengers (Fig. 1). In contrast, hunters and large-sized species showed increased abundance, while hygrophiles exhibited no significant difference.

Following emission reduction, inter-site differences became less pronounced (Table 3). While most ecological groups remained less abundant at the impacted site, stratobionts, web-builders, and both small (previously negatively affected) and large-sized species (previously positively affected) showed abundance equalization. In contrast, hygrophile abundance became significantly reduced at the polluted site (Fig. 1).

The abundance of scavenger-hunters (i.e., harvestmen) requires special mention. Prior to emission reduction, only one specimen was captured at the impacted site (negative effect, Fig. 1). Following emission reduction, the negative effect persisted, though 25 specimens were recorded, including immature individuals.

The ecological profiles at the background and impacted sites differed significantly in both study years (Fig. 3). Prior to emission reduction, the background site exhibited higher proportions of ground-dwelling hunter-weavers, scavenger-hunters, and

Table 2. Diversity and activity density (Mean ± Standard Deviation) of ecological groups of arachnids, ground beetles, and other invertebrates at background and impacted sites

Group	Year and site			
	2005		2018	
	background	impacted	background	impacted
	Arachnida			
Diversity:				
Observed number of species (Sp)	17.3	16.1	17.3	15.0
Rarefied number of species (Sp')	16.4	16.0	15.5	14.9
Density, spec./100 trap-days:				
All Arachnida, adults	271 ± 61	168 ± 43	237 ± 37	102 ± 29
Aranei, juveniles	8 ± 7	33 ± 16	14 ± 7	48 ± 16
Opiliones, juveniles	51 ± 24	9 ± 6	43 ± 15	139 ± 59
Linyphiidae	184 ± 38	69 ± 17	177 ± 30	82 ± 25
Lycosidae	6 ± 7	79 ± 30	0 ± 1	5 ± 3
Size: B	7 ± 6	57 ± 18	4 ± 3	5 ± 3
Size: M	144 ± 37	39 ± 21	166 ± 40	20 ± 15
Size: S	120 ± 42	71 ± 15	67 ± 18	77 ± 23
Moisture: hyg	18 ± 6	10 ± 13	8 ± 6	–
Moisture: mes	252 ± 57	156 ± 43	229 ± 33	102 ± 29
Moisture: xer	–	2 ± 4	–	+
Stratum: SS	136 ± 34	91 ± 35	158 ± 42	17 ± 15
Stratum: HSD	5 ± 5	4 ± 4	5 ± 2	7 ± 6
Stratum: LS	129 ± 40	72 ± 16	75 ± 18	78 ± 24
Habitat: E	122 ± 34	64 ± 9	69 ± 25	30 ± 20
Habitat: F	147 ± 28	95 ± 41	161 ± 26	70 ± 23
Habitat: Oh	2 ± 4	7 ± 5	7 ± 3	2 ± 3
Hunting: H	11 ± 9	89 ± 29	3 ± 3	8 ± 5
Hunting: SH	69 ± 24	1 ± 2	47 ± 28	11 ± 13
Hunting: W	114 ± 40	76 ± 17	69 ± 22	82 ± 26
Hunting: WH	76 ± 23	3 ± 5	117 ± 27	1 ± 2
	Carabidae			
Diversity:				
Observed number of species (Sp)	12.3	7.7	13.9	5.7
Rarefied number of species (Sp')	9.3	7.3	11.8	5.6
Density, spec./100 trap-days:				
All Carabidae, imagos	847 ± 143	317 ± 34	359 ± 58	168 ± 31
Carabidae, larvae	13 ± 6	15 ± 8	32 ± 18	33 ± 9
Size: B	52 ± 22	+	89 ± 20	+
Size: M	245 ± 38	156 ± 49	45 ± 16	90 ± 23
Size: S	550 ± 123	161 ± 44	226 ± 49	78 ± 13
Moisture: hyg	499 ± 122	88 ± 34	209 ± 50	39 ± 12
Moisture: mes	334 ± 42	225 ± 42	145 ± 24	128 ± 31
Moisture: xer	14 ± 10	4 ± 6	6 ± 4	+
Stratum: SS	21 ± 9	–	42 ± 7	–
Stratum: HSD	–	1 ± 2	–	–
Stratum: LS	826 ± 141	316 ± 32	317 ± 54	168 ± 31

Table 2. (Contd.)

Group	Year and site			
	2005		2018	
	background	impacted	background	impacted
Habitat: E	496 ± 129	78 ± 30	233 ± 63	34 ± 12
Habitat: F	348 ± 44	235 ± 44	126 ± 27	133 ± 29
Habitat: Oh	3 ± 3	3 ± 5	–	–
Mobility: hm	5 ± 9	55 ± 21	10 ± 7	11 ± 15
Mobility: mm	152 ± 41	171 ± 49	44 ± 19	95 ± 23
Mobility: lm	690 ± 141	91 ± 31	305 ± 58	62 ± 11
Feeding: Mx	4 ± 7	56 ± 18	–	11 ± 15
Feeding: Z	843 ± 140	261 ± 33	359 ± 58	157 ± 28
	Other invertebrates			
Density, spec./100 trap-days:				
Staphylinidae, imagos	807 ± 81	103 ± 26	249 ± 65	164 ± 56
Coleoptera others, imagos	47 ± 14	26 ± 14	31 ± 7	16 ± 6
Formicidae	120 ± 57	434 ± 94	91 ± 45	245 ± 106
Hemiptera	16 ± 13	17 ± 15	5 ± 4	26 ± 17
Lithobiomorpha, adults	15 ± 7	–	34 ± 11	6 ± 5
Lithobiomorpha, juvenils	9 ± 3	–	5 ± 4	0.8 ± 1
Geophilomorpha	–	–	0.4 ± 1	–
Diplopoda	6 ± 5	–	3 ± 3	–
Lumbricidae	5 ± 4	–	9 ± 6	–
Mollusca	1 ± 2	–	19 ± 8	0.4 ± 1
Others, imagos*	441 ± 97	210 ± 54	147 ± 24	246 ± 80
Others, larvae*	42 ± 24	22 ± 14	36 ± 11	23 ± 9

Ecological group designations are provided in Table 1. "–", absence of a group; "+", occasional captures do not allow a reliable density estimation; *, Diptera, Lepidoptera, Hymenoptera, Homoptera, Neuroptera, Thysanoptera, and Mecoptera.

medium-sized species, whereas the impacted site had greater representation of large-sized and ground-dwelling hunters. The reduction in emissions resulted in decreases of the proportion of epigeobionts (became lower than in the background site) and large-sized species (became comparable to that in the background site in 2005) at the polluted site. By 2018, web-builders dominated the assemblage at the polluted site. Although hunter proportions decreased, they remained higher than at the background site. Increases were also observed in stratobionts and small-size species.

Ground Beetles

A total of 32 species were recorded over two years, with 24 species recorded at the background site and 16 at the impacted site. Similar to arachnids, the ground beetle abundance in the vicinity of the smelter was reduced by factors of 2.1–2.6 in both years (Fig. 1; Table 2). Prior to emission reduction, both observed and rarefied species richness were statistically significantly lower at the impacted site compared to the background site; by 2018, the differences between the sites increased.

The taxocene structure differed significantly between the sites in both years (Fig. 2). At the background site, the interannual dissimilarity was significantly greater when ordinated by absolute abundance compared to species proportions (Table 3). Analyses of proportional data revealed higher interannual variability in the taxocene structure at the impacted site, whereas ordination based on absolute values showed comparable variability between sites (Fig. 2). The dominant complex at both sites comprised two species, *Trechus secalis* and *Pterostichus oblongopunctatus* (Table 4); however, the former predominated at the background site, and the latter, at the impacted site.

Similar to arachnids, during the period of high emissions, the abundance of many ecological groups of ground beetles was reduced at the impacted site compared to the background site. This pattern was observed for all groups identified by size (small-,

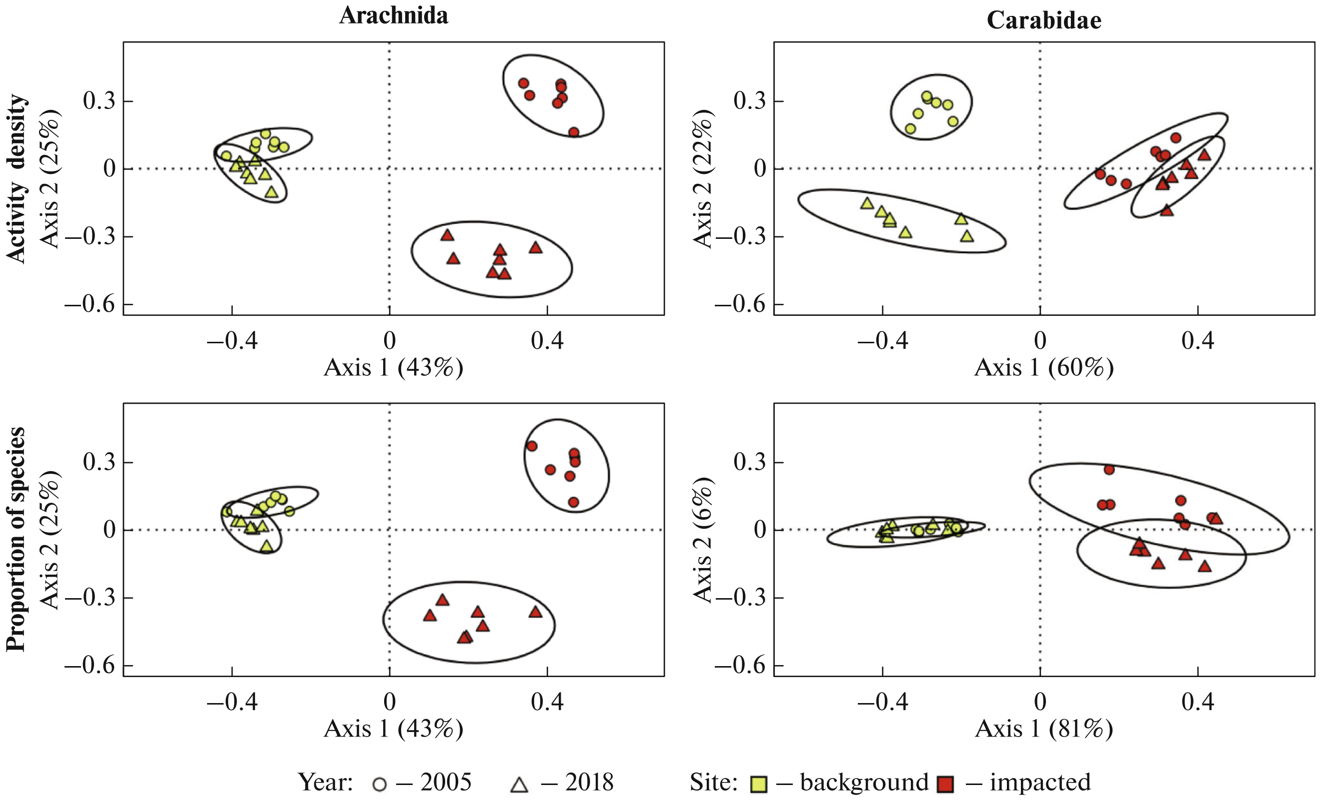

Fig. 2. Ordination (based on the Bray–Curtis distance) of arachnid (Arachnida) and ground beetle (Carabidae) assemblages across study sites and periods by absolute (activity density) and relative (proportion of species) abundance metrics. 95% ellipses are shown; percentage of explained variance is given in parentheses.

Table 3. Intra- and intergroup distances between compared sites (background and impacted) and periods (2005 and 2018)

Site (year)	Arachnida		Carabidae	
	AD	Fr	AD	Fr
	Average intragroup distance			
Background (2005)	0.37	0.36	0.20	0.15
Background (2018)	0.32	0.29	0.22	0.18
Impacted (2005)	0.49	0.48	0.26	0.25
Impacted (2018)	0.51	0.50	0.22	0.18
	Average intergroup distance*			
Background (2005)–background (2018)	0.47 (0.36)	0.47 (0.43)	0.54 (0.76)	0.29 (0.53)
Impacted (2005)–impacted (2018)	0.87 (0.55)	0.86 (0.56)	0.39 (0.51)	0.29 (0.33)
Background (2005)–impacted (2005)	0.89 (0.65)	0.89 (0.67)	0.66 (0.80)	0.60 (0.81)
Background (2018)–impacted (2018)	0.83 (0.63)	0.81 (0.64)	0.75 (0.85)	0.71 (0.89)

AD, ordination based on absolute values of activity density; Fr, ordination based on species proportions; *, R^2 values are given in parantheses (proportion of variance explained by ordination according to PERMANOVA results, all differences between intra- and intergroup distances are statistically significant, at least $p < 0.003$).

Table 4. Activity density (spec./100 trap-days, Mean ± Standard Deviation; in parentheses—% of total number) of arachnid and ground beetle species at background and impacted sites

Group	Year and site			
	2005		2018	
	background	impacted	background	impacted
	Arachnida			
	Dominant complex			
Allomengea scopigera	38 ± 17 (28.1)	1 ± 3 (1.6)	58 ± 31 (49.4)	1 ± 2 (1.2)
Lacinius ephippiatus	20 ± 9 (14.6)	+ (0.4)	16 ± 12 (13.8)	5 ± 6 (10.1)
Alopecosa taeniata	–	16 ± 17 (19.4)	–	+ (0.8)
Ceratinella brevis	+ (0.3)	1 ± 2 (0.8)	2 ± 4 (1.9)	16 ± 20 (31.0)
Asthenargus paganus	9 ± 9 (6.5)	–	1 ± 2 (0.5)	–
Nemastoma lugubre	9 ± 8 (6.5)	–	4 ± 4 (3.3)	–
Pardosa lugubris	2 ± 4 (1.3)	9 ± 9 (10.1)	+ (0.2)	–
Tapinocyba insecta	9 ± 7 (6.3)	5 ± 8 (5.7)	+ (0.3)	+ (0.4)
Tenuiphantes mengei	–	1 ± 3 (1.2)	+ (0.2)	7 ± 7 (12.9)
Agyneta affinis	–	6 ± 7 (7.3)	–	–
Alopecosa pulverulenta	–	6 ± 7 (7.3)	–	–
Diplocentria bidentata	+ (0.3)	5 ± 5 (6.1)	–	2 ± 3 (4)
	Other species			
Agroeca brunnea	+ (0.3)	–	–	–
Agyneta conigera	–	3 ± 4 (3.6)	+ (0.2)	–
Agyneta olivacea	2 ± 4 (1.8)	+ (0.4)	+ (0.3)	–
Alopecosa aculeata	–	+ (0.4)	–	–
Alopecosa pinetorum	1 ± 2 (0.5)	+ (0.4)	–	–
Anguliphantes angulipalpis	–	–	–	1 ± 1 (2.0)
Antistea elegans	–	+ (0.4)	–	–
Araneus sturmi	–	+ (0.4)	–	–
Bathyphantes nigrinus	+ (0.3)	–	–	–
Bathyphantes parvulus	1 ± 3 (0.8)	–	–	–
Bolyphantes alticeps	–	–	1 ± 1 (0.9)	+ (0.4)
Centromerus arcanus	9 ± 10 (6.8)	–	1 ± 1 (0.7)	–
Centromerus clarus	2 ± 5 (1.8)	–	4 ± 7 (3.3)	1 ± 2 (2.4)
Centromerus incilium	–	–	–	+ (0.4)
Centromerus sylvaticus	+ (0.3)	–	2 ± 2 (1.4)	–
Cercidia prominens	–	+ (0.4)	–	–
Clubiona caerulescens	+ (0.3)	+ (0.4)	–	–
Cnephalocotes obscurus	+ (0.3)	+ (0.4)	–	–
Cryphoeca silvicola	+ (0.3)	–	+ (0.2)	+ (0.4)
Decipiphantes decipiens	–	–	1 ± 1 (0.5)	–
Diplocephalus picinus	2 ± 4 (1.8)	+ (0.4)	–	–
Diplostyla concolor	1 ± 2 (0.8)	–	+ (0.3)	–
Drapetisca socialis	–	+ (0.4)	–	+ (0.4)
Erigonella hiemalis	–	+ (0.4)	1 ± 2 (0.7)	1 ± 1 (1.2)
Ero furcata	–	–	+ (0.3)	–
Euophrys frontalis	–	–	–	+ (0.4)
Evarcha falcata	–	+ (0.4)	–	+ (0.4)

Table 4. (Contd.)

Group	Year and site			
	2005		2018	
	background	impacted	background	impacted
Hahnia ononidum	+ (0.3)	4 ± 5 (4.5)	–	–
Hahnia pusilla	+ (0.3)	–	2 ± 3 (1.6)	–
Haplodrassus soerenseni	–	+ (0.4)	–	–
Hypselistes jacksoni	–	–	–	+ (0.4)
Macrargus multesimus	–	–	–	+ (0.8)
Macrargus rufus	+ (0.3)	1 ± 2 (0.8)	1 ± 2 (0.5)	+ (0.8)
Maro pansibiricus	–	2 ± 3 (2.8)	+ (0.2)	1 ± 1 (1.2)
Micrargus herbigradus	1 ± 2 (0.5)	–	–	+ (0.4)
Microneta viaria	4 ± 5 (3.0)	3 ± 5 (4.0)	5 ± 6 (4.4)	2 ± 3 (3.6)
Minyriolus pusillus	+ (0.3)	–	+ (0.3)	1 ± 2 (2.4)
Mitopus morio	3 ± 4 (2.0)	–	3 ± 2 (2.6)	–
Neriene emphana	1 ± 3 (1.0)	+ (0.4)	–	1 ± 3 (2.0)
Oligolophus tridens	3 ± 4 (2.3)	–	–	–
Oryphantes geminus	2 ± 3 (1.3)	–	1 ± 2 (0.9)	–
Ozyptila trux	+ (0.3)	–	+ (0.2)	–
Pachygnatha listeri	+ (0.3)	–	+ (0.2)	–
Palliduphantes alutacius	–	–	1 ± 2 (0.5)	–
Piratula hygrophila	+ (0.3)	4 ± 7 (4.5)	–	–
Pocadicnemis pumila	–	+ (0.4)	–	–
Rilaena triangularis	+ (0.3)	–	+ (0.3)	–
Robertus lividus	2 ± 4 (1.8)	–	1 ± 2 (1.0)	–
Semljicola faustus	–	–	+ (0.2)	–
Tenuiphantes cristatus	–	+ (0.4)	–	+ (0.4)
Tenuiphantes nigriventris	1 ± 2 (1.0)	+ (0.4)	5 ± 5 (4)	1 ± 2 (2.0)
Tenuiphantes tenebricola	5 ± 6 (3.5)	1 ± 2 (1.6)	4 ± 4 (3.3)	2 ± 2 (3.6)
Tetragnatha pinicola	–	–	–	+ (0.4)
Tibioplus diversus	+ (0.3)	+ (0.4)	+ (0.3)	1 ± 2 (1.6)
Trochosa ruricola	–	+ (0.4)	–	–
Trochosa spinipalpis	–	1 ± 2 (0.8)	–	+ (0.4)
Trochosa terricola	+ (0.3)	2 ± 4 (2.4)	–	2 ± 2 (3.6)
Walckenaeria alticeps	–	–	–	1 ± 2 (1.2)
Walckenaeria antica	–	1 ± 2 (0.8)	–	1 ± 2 (2.4)
Walckenaeria atrotibialis	+ (0.3)	–	–	+ (0.4)
Walckenaeria cucullata	–	–	–	+ (0.8)
Walckenaeria lepida	–	–	–	+ (0.4)
Walckenaeria obtusa	1 ± 3 (0.8)	–	0 ± 1 (0.3)	–
Xerolycosa nemoralis	–	1 ± 3 (1.2)	–	–
Xysticus audax	+ (0.3)	–	–	–
Xysticus cristatus	+ (0.3)	–	1 ± 1 (0.5)	1 ± 2 (2.0)
Xysticus luctuosus	–	+ (0.4)	–	–
Zelotes subterraneus	–	3 ± 4 (4.0)	–	+ (0.4)
Zora spinimana	+ (0.3)	+ (0.4)	–	–

Table 4. (Contd.)

Group	Year and site			
	2005		2018	
	background	impacted	background	impacted
Carabidae				
Dominant complex				
Trechus secalis	490 ± 124 (57.8)	71 ± 32 (22.3)	190 ± 53 (53.6)	33 ± 13 (19.6)
Pterostichus oblongopunctatus	119 ± 37 (14.1)	152 ± 50 (47.9)	24 ± 15 (6.7)	89 ± 23 (53.4)
Pterostichus urengaicus	125 ± 40 (14.8)	–	21 ± 8 (6.0)	–
Amara brunnea	4 ± 7 (0.5)	54 ± 19 (17.2)	–	11 ± 15 (6.4)
Pterostichus niger	6 ± 6 (0.7)	–	36 ± 14 (10.2)	–
Cychrus caraboides	4 ± 6 (0.5)	–	33 ± 7 (9.4)	–
Calathus micropterus	17 ± 12 (2.0)	14 ± 8 (4.5)	6 ± 7 (1.6)	27 ± 7 (16.4)
Other species				
Agonum fuliginosum	1 ± 2 (0.1)	1 ± 2 (0.4)	+ (0.1)	3 ± 2 (2)
Agonum gracilipes	–	1 ± 2 (0.2)	–	–
Amara ovata	–	1 ± 2 (0.2)	–	–
Badister lacertosus	6 ± 8 (0.7)	–	1 ± 1 (0.2)	–
Bembidion guttula	–	1 ± 2 (0.4)	–	–
Bembidion mannerheimi	–	3 ± 5 (0.9)	–	–
Carabus aeruginosus	–	–	+ (0.1)	–
Carabus glabratus	3 ± 5 (0.4)	–	3 ± 2 (0.8)	–
Carabus granulatus	–	–	+ (0.1)	–
Carabus schoenherri	14 ± 9 (1.6)	–	4 ± 4 (1.3)	–
Harpalus laevipes	–	1 ± 2 (0.2)	–	–
Leistus terminatus	3 ± 4 (0.3)	–	1 ± 2 (0.3)	–
Loricera pilicornis	1 ± 2 (0.2)	–	10 ± 8 (2.8)	–
Notiophilus biguttatus	14 ± 10 (1.6)	3 ± 5 (1.1)	5 ± 4 (1.5)	+ (0.2)
Notiophilus palustris	–	3 ± 4 (1.1)	–	1 ± 3 (0.7)
Notiophilus reitteri	8 ± 7 (1.0)	–	4 ± 3 (1.3)	–
Platynus assimile	–	–	0 ± 1 (0.1)	–
Platynus mannerheimi	1 ± 2 (0.1)	–	–	–
Poecilus versicolor	–	3 ± 4 (0.9)	–	–
Pterostichus aethiops	24 ± 19 (2.9)	–	5 ± 3 (1.5)	–
Pterostichus diligens	1 ± 2 (0.1)	5 ± 5 (1.5)	–	1 ± 1 (0.5)
Pterostichus melanarius	–	–	4 ± 4 (1.0)	–
Pterostichus quadrifoveolatus	–	1 ± 2 (0.2)	–	1 ± 1 (0.5)
Pterostichus strenuus	3 ± 7 (0.4)	3 ± 5 (1.1)	4 ± 5 (1.3)	+ (0.2)
Synuchus vivalis	3 ± 3 (0.3)	–	–	–

"–“, absence of a species; "+", occasional captures do not allow a reliable density estimation.

medium-, and large-sized species), stratum (stratobionts and epigeobionts), habitat (forest and eurytopic), and moisture preferences (mesophiles and hygrophiles) (Fig. 1). A negative effect was also recorded for zoophages and wingless species. The abundance of moderately mobile species showed no differences between sites, while mixo-phytophages and highly mobile species were more abundant at the impacted site.

Following emission reduction, the negative impact of pollution persisted for most ecological groups. However, some negative effects disappeared (for

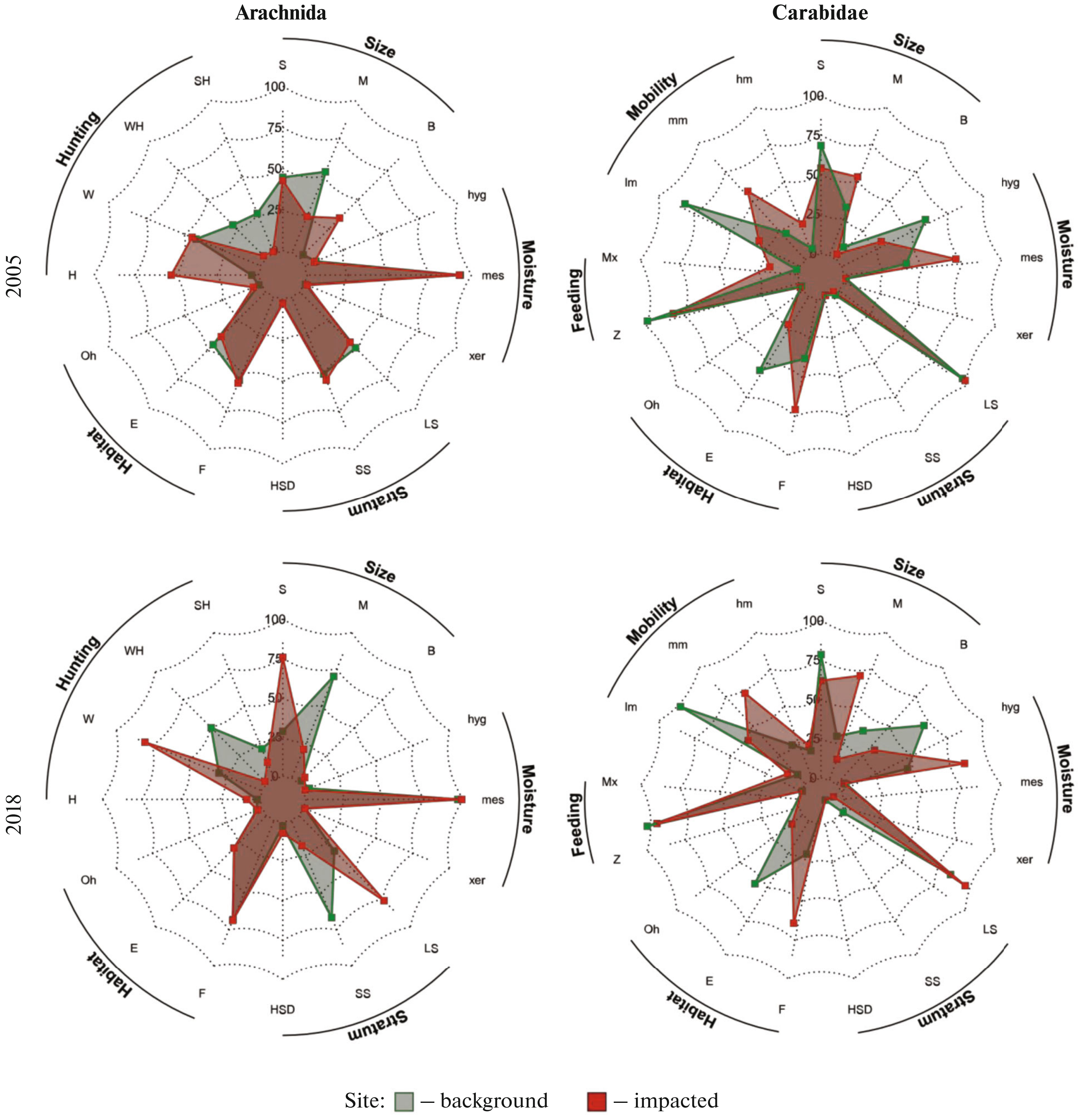

Fig. 3. Ecological profiles (group proportion, %) of arachnid (Arachnida) and ground beetle (Carabidae) assemblages across compared sites and periods. Ecological group designations are provided in Table 1.

mesophilic and forest species) or even reversed (for low- and medium-mobility species). In contrast, the abundance of highly mobile species at the impacted site decreased to the background level (Fig. 1).

The ecological profiles of the taxocene differed between the sites (Fig. 3). In 2005, the background site was dominated by eurytopic, hygrophilous, wingless, small-sized species, with occasional occurrence of large-size individuals. The proportions of epigeobionts and stratobionts were comparable at both sites. Although the taxocene consisted primarily of zoophages at both locations, their proportion was higher at the background site. The impacted site exhibited higher proportion of forest-associated, moderately and highly mobile, mesophilic and medium-sized species, while large-sized species were absent.

The ecological profiles at both studied sites showed minimal interannual variation. Observed differences between years were primarily limited to groups categorized by size, mobility, and stratum. Thus, at the background site, the proportion of large-sized species and stratobionts showed a slight increase in 2018 compared to 2005, whereas the proportion of medium-sized species and epigeobionts, on the contrary, decreased (Fig. 3). This shift amplified between-site differences. Conversely, a minor reduction in highly mobile species and mixo-phytophages at the impacted site partially mitigated these inter-site disparities.

DISCUSSION

Abundance and Diversity

Contrary to expectations, no significant increase in the abundance of arachnids and ground beetles was found near the MUCS following emission reduction: in both study years, the activity density at the impacted site remained lower than at the background site. The negative pollution effects on these taxa have been well-documented in other contaminated regions. For instance, in the subarctic pine forests near Pechenganickel and spruce forests near Monchegorsk (Kola Peninsula), spider activity density near metallurgical plants was 6–10 times lower than at the control sites [66, 67]. Similarly, reduced ground beetle density at polluted versus background sites has been reported near metallurgical plants in the vicinities of Olkusz (Poland) [68] and Tula [69].

It is important to emphasize that the decrease in activity density of arachnids and ground beetles in 2018 compared to 2005 was observed at both the impacted and background sites. One of potential explanation for this pattern could be colder weather during the 2018 survey period, which may have reduced arthropod locomotor activity [10] and consequently affected trap captures. During the surveys in May 2018, the average daily temperatures were lower than in 2005 by 6.8°C, and in August, by 2.1°C. Unfortunately, the inherent limitation of the pitfall trap method—which measures activity density rather than true density—prevents complete accounting for weather-related effects when analyzing taxocene recovery.

No increase in arachnid and ground beetle diversity was observed near the MUCS following emissions reduction. The persistent differences observed between the background and impacted sites align with prior studies of these taxa in the MUCS area [41–44, 70]. Spider species richness showed no interannual variation between sites, while ground beetle species richness at the impacted site not only failed to increase, but even declined post-reduction, contrasting with stable levels at the background site. Long-term studies near non-ferrous metallurgy plants reveal similar patterns: neither arachnid assemblages (Santo Amaro, Brazil) [3] nor ground beetles (Sudbury, Canada) [2] exhibited recovery decades after major emission reductions, with both abundance and diversity remaining significantly depressed at polluted areas. The sole documented case of post-industrial recovery in the abundance and species richness of ground beetles occurred near a phosphate fertilizer plant (Steudenitz, Germany) [5, 6]. However, the soil retention time of such pollutants is markedly shorter than that of metals emitted by metallurgical plants.

Arachnid Taxocene Structure

In contrast to activity density and species richness, changes in the arachnid taxocene structure may represent recovery signals. This interpretation is partially supported by the reduced dissimilarity between impacted and background sites in the second period compared to the first one (Table 3), suggesting a tentative convergence of ecological conditions. However, abundance dynamics of indicator groups provide more conclusive evidence.

First of all, this concerns a clearly expressed change of the dominant species composition, particularly, the “linyphiidization” of the arachnid assemblages—that is, the replacement of Lycosidae species by Linyphiidae species. It was previously established for the MUCS area that increasing pollution leads to a higher proportion of hunters from the families Lycosidae and Gnaphosidae [43, 45]. The dominance of Lycosidae representatives in a heavily polluted area was also documented near the copper-nickel plant in Harjavalta [71], while the prevalence of Linyphiidae is considered an indicator of the undisturbed habitats [72].

Representatives of the Lycosidae and Gnaphosidae families show a preference for open habitats: their proportion in meadow vegetation is significantly higher than in forest habitats [54, 55]. Changes in vegetation structure were previously considered to influence the species composition of arachnid assemblages in polluted areas [45, 71]. The suppression of tree and herbaceous layers caused by pollution appears neutral or even beneficial for hunting spiders, while negatively affecting web-building species that typically utilize vegetation for trap construction.

Theoretically, the described linyphiidization could be explained by vegetation recovery following emission reduction. However, as of 2013, forest vegetation in the area of severe MUCS pollution remained in a depressed state, which was attributed to persistently high soil toxicity, the considerable thickness of the forest litter, and insufficient diaspore availability [27–29]. Our data on herbaceous layer projective cover and tree crown density also demonstrated no signs of recovery (see the “Materials and Methods” section). Therefore, the mechanisms underlying these changes in functional and taxonomic group ratios among arachnids remain unclear.

Beyond linyphiidization, other signs of recovery deserve mention. These include the appearance of the spider *C. clarus*, a species previously recorded only in unpolluted areas (unpublished data by M.P. Zolotarev), at the impacted site in 2018. Also significant is the high abundance of the harvestman *L. ephippiatus*, a typical background species, near the smelter in 2018, along with a tenfold increase in total harvestmen abundance at the impacted site. This increase was observed in both adults and juveniles (Table 2).

A detailed discussion of the reasons for the differing response of spiders and harvestmen to pollution falls outside the scope of our study. However, it should be noted that these differences may be linked to the biological characteristics of these groups. Unlike spiders, harvestmen lack complete external digestion [73], allowing them to ingest soil particles containing potentially toxic metals along with their food. Furthermore, harvestmen deposit their eggs directly in the soil and litter [73], where the eggs remain less protected from environmental stressors (e.g., desiccation) compared to spider sacs, which are encased in protective cocoon and avoid substrate contact even in sedentary species. The observed increase in harvestmen abundance at the impacted site may reflect improved environmental conditions for this group.

Ground Beetle Taxocene Structure

Unlike arachnids, the ground beetle assemblage shows no signs of recovery, both in integral parameters (total abundance and diversity) and structural characteristics. No reduction in between-site differences was detected: the dissimilarity between background and impacted site assemblages not only failed to decrease by 2018 compared to 2005, but showed a further increased (Table 3).

The phenomenon of an increase in the average body size of predatory ground beetle communities during post-industrial succession has been previously documented [6]. By analogy, the appearance of large-sized species at the impacted site following emission reduction could be expected, particularly given the recovery of soil macrofauna—especially the reappearance of earthworms near the MUCS [31, 39, 40], which constitute a major dietary component for large ground beetles [74]. However, the anticipated changes in size structure were not observed at the impacted site. Furthermore, between-site differences in large-sized ground beetle abundance actually intensified due to increased numbers at the background site in 2018.

The absence of large-sized ground beetles at the impacted site may be linked not only with the insufficient prey abundance, but also to low prey availability. In floodplain, earthworms can inhabit decaying fallen logs and spaces beneath them [32]. However, the abundance of other potential prey invertebrates suitable for large-sized ground beetles remains significantly reduced compared to the background site [31, 75].

Following emission reduction, the ground beetle taxocene at the impacted site maintained the previously identified pollution-associated characteristics. In addition to the above-mentioned almost complete absence of large-sized species [44], these features included a reduced abundance of zoophages and, correspondingly, an increased abundance of mixo-phytophages [41, 42]. While some positive trends in functional group ratios were observed at the impacted site in 2018 relative to 2005 (notably decreased proportion of mixo-phytophages and highly mobile species), these changes remained negligible compared to the substantial restructuring observed in the arachnid assemblages.

CONCLUSIONS

No recovery of arachnid and ground beetle abundance was detected near the Middle Ural Copper Smelter eight years after nearly complete cessation of emissions. In 2018 compared to 2005, activity density declines were observed at both the impacted and background sites. Given the parallel decrease, the pattern may be attributed to the lower temperatures recorded in 2018. Unfortunately, the inherent limitations of the pitfall trap method, which simultaneously measure the number of arthropods and their mobility (the latter being directly temperature-dependent) necessitate significantly longer observation periods to distinguish true recovery from weather-induced fluctuations. These methodological constraints warrant caution when using activity density to analyze recovery processes in ground-dweller assemblages. Structural indicators, particularly shifts in ecological group ratios and reappearance of previously absent indicator taxa, prove are more informative. Notably, conclusions about assemblage recovery differed substantially for two arthropod groups studied.

The ground beetle taxocene at the impacted site retained pollution-associated characteristics, including reduced abundance of zoophages and the absence of large-sized species. Moreover, the ratio of ecological groups at this site showed minimal change between periods of high and reduced emissions. These observations indicate that ground beetle assemblages have not yet demonstrated post-industrial recovery. This conclusion aligns with the absence of significant improvement in tree and herbaceous layer conditions near the smelter.

In contrast to ground beetles, the arachnid assemblage structure at the impacted site exhibited significant changes following emission reduction. Several observed shifts—including linyphiidization, increased harvestmen abundance, and the appearance of species previously restricted to unpolluted areas—may represent initial recovery signals. This interpretation is further supported by reduced structural dissimilarity between the impacted and background sites in the later period compared to earlier observations. Continued monitoring will be required to verify the validity of these recovery patterns.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1134/S1067413624602628.

ACKNOWLEDGEMENTS

The authors are grateful to two anonymous reviewers for constructive comments on the initial version of the article.

FUNDING

Data analysis and the manuscript preparation were carried out within the the State Order of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences (Project No. 122021000076-9).

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Collection and analysis of invertebrates was carried out with the approval of 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 declare that they have no conflicts of interest.

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Translated by T. Kuznetsova