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Changes in ground beetle (Coleoptera, Carabidae) assemblages along an industrial pollution gradient in the Southern Urals☆

Elena Belskaya *, Maxim Zolotarev, Artëm Sozontov **

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Eighth March Street 202, Yekaterinburg, 620144, Russia

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ABSTRACT

Industrial pollution can negatively affect ground beetles individuals and populations. At the same time, effects at the community level remain poorly understood and published data are inconsistent. The study analyzes changes in ground beetle assemblages (abundance, species composition, and diversity) along the pollution gradient caused by emissions from the Karabash Copper Smelter (KCS, Southern Urals, Russia). Sampling was conducted in 2009 and 2014 at 10 birch forest sites with different contaminant exposure and ecosystem disturbance. The abundance and diversity of ground beetles decreased in the heavily polluted area and the relationship with the distance to KCS was non-linear. Segmented regression provided the best fit to the data. The breakpoints after which the parameters decreased sharply differed among indices and were recorded at distances of 9–11 km to KCS for species richness, 7–10 km for diversity and 4–5 km for abundance. Heavy pollution affected species composition and ecological traits of dominant species. Spatial variations in all indices were consistent across years with differing weather conditions. Ground beetle larvae were recorded throughout the entire gradient, with the exception of the extremely disturbed industrial barren. The absence of larvae at the barren suggests that local reproduction is impossible; all individuals likely migrated from nearby areas.

1. Introduction

Airborne industrial pollution is one of the main forms of anthropogenic pressure on ecosystems. Worldwide, 72–123 million tons SO_2, 113–136 million tons NO_x, and 424–554 million tons CO were emitted into the atmosphere annually in 2000–2022 (Hoesly et al., 2024). Toxicants such as SO_2, fluorine compounds, and heavy metals found in industrial emissions negatively affect ecosystems (Sharifi et al., 2023; Shen et al., 2025). Non-ferrous metallurgy strongly affects natural ecosystems due to combination of SO_2 and heavy metals in atmospheric emissions. Surroundings of such factories provide good opportunities for studying responses of various ecosystem components to pollution (Vorobeichik and Kozlov, 2012). In the vicinities of such enterprises, sites can be selected with varying contamination and vegetation degradation, ranging up to industrial barrens — extreme examples of ecosystem destruction (Kozlov and Zvereva, 2007). Despite a long history of studying the biotic effects of industrial pollution, there are no firm conclusions about the impact of toxicants on biota until now (Kozlov et al., 2009). This concerns primarily changes in communities since most studies of ecological consequences of contaminant exposure have been focused mainly on effects at the organism and population levels (Sigmund et al., 2023). To bridge this gap, additional studies of groups of taxonomically related species that are known as bioindicators of industrial pollution (de Paula Gutiérrez and Agudelo, 2020; Comess et al., 2021; Pallottini et al., 2023) and can be used as model objects in ecotoxicology. Ground beetles are one of such model groups due to their high abundance and species diversity, well-studied life-history traits, close association with habitat conditions, and easy sampling (Rainio and Niemelä, 2003; Avgın and Luff, 2010). Their role as predators of other invertebrates provides a significant ecosystem service influencing the population dynamics of prey and nutrient cycling (Loreau, 1995; Woodcock et al., 2014). Consequently, evaluating the responses of ground beetles to anthropogenic impact is fundamental to understanding and predicting changes in ecosystem structure and function (Zvereva and Kozlov, 2010).

To provide an unbiased assessment of the biotic effects of pollution and the consequences of chronic contaminant exposure, investigations are needed in different regions and ecosystem types, taking into account

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* Corresponding author.
** Corresponding author.
E-mail addresses: belskaya@ipae.uran.ru (E. Belskaya), A.N.Sozontov@gmail.com (A. Sozontov).

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landscape and ecological specifics (Sigmund et al., 2023). However, studies of ground beetle responses to pollution from non-ferrous metallurgy have been conducted mainly in Western Europe and North America (Bengtsson and Tranvik, 1989; Skalski et al., 2011; Babin-Fenske and Anand, 2011). In contrast, central and eastern regions of Eurasia remain critically understudied. To date, only a few studies near the Middle Ural copper smelter located in the southern taiga subzone (Ermakov, 2004; Belskaya and Zinoviev, 2007; Zolotarev and Belskaya, 2012). A single point source of pollution is clearly insufficient to identify a general pattern across this vast region.

Moreover, the results from existing studies are inconsistent. While some researchers report decreased abundance and/or diversity of ground beetles in polluted areas (e.g., Bengtsson and Tranvik, 1989; Ermakov, 2004; Skalski et al., 2010), others have detected no significant effects (Read et al., 1987; Skalski et al., 2015). This ambiguity highlights two critical, unresolved issues: first, the shape of the dose-response relationship (i.e., the dynamics of abundance and diversity along pollution gradients) remains unclear, and second, there is only limited information regarding the specific pollution thresholds that trigger significant changes in ground beetle assemblages (Bengtsson & Tranvik, 1989). Such data are indispensable for a full understanding of biotic responses and for the effective management of industrially disturbed areas.

The Karabash Copper Smelter (KCS) is situated on the Europe-Asia border in the Southern Urals. The surroundings of this pollution source, recognized as one of the most polluted areas in the world (Kozlov et al., 2009), presents a prime opportunity to address these research needs. The KCS is among the most thoroughly studied emission sources in terms of the number of investigations and the range of biota components analyzed (Vorobeichik, 2004; Kozlov et al., 2009). However, data on ground-dwelling invertebrates, including ground beetles, are lacking. This study is designed to address this knowledge gap by providing the first quantitative assessment of changes in ground beetle assemblages (abundance, species composition, and diversity) along the pollution gradient from KCS, with a focus on the shape of a dose-effect relationship. This work supplies additional missing data for a central Eurasian region needed for a comparative analysis of general patterns and regional specifics in the response of this model group to non-ferrous metallurgy impact.

Three hypotheses were tested: 1) ground beetle abundance and diversity decrease towards the KCS; 2) the parameters change linearly along the pollution gradient; 3) the abundance and diversity of ground beetles change with the distance in a similar way.

2. Materials and methods

2.1. Study area

The study area is located in a subzone of pine-birch forests, a transitional zone between the southern taiga and forest-steppe, at the eastern slope of the Southern Urals. It consists of hilly elevations with an altitude of 250–650 m a.s.l. with rivers and lakes lying between them. The climate is continental. The mean temperature in January is −16 °C and in July +18 °C. The annual precipitation is 400–600 mm with a maximum in July–August. The growing season lasts 130–150 days.

The KCS, which has been operating since 1910, is located in Karabash (55°27′N, 60°13′E), an industrial town in Chelyabinsk region, Russia. The main pollutants include sulfur, carbon, and nitrogen oxides, along with polymetallic dust containing Cu, Pb, Cd, Zn, and As (Kozlov et al., 2009). Pollutants are dispersed predominantly to the northeast, following the prevailing wind direction (Purvis et al., 2006). In the immediate vicinity of KCS, concentrations of Zn in the soil exceed background values by 72 times, Cd by 233 times, Pb by 404 times (Shabanov and Strekulev, 2021). Metal concentrations in the soil decrease to background levels at distances of 30–40 km to KCS (Frontasyeva et al., 2004; Kozlov et al., 2009).

Airborne pollutant emissions peaked in the 1970s–1980s, up to 160–400 thousand tons annually (Kozlov et al., 2009). In 2009, emissions decreased to 16 thousand tons (Department of Rospotrebnadzor in Chelyabinsk oblast, 2010). Nevertheless, during the period of our study, soil contamination and vegetation degradation in the vicinity of KCS remained substantial (Mikryukov and Dulya, 2017; Smorkalov and Vorobeichik, 2022).

2.2. Site description

As part of an international project, in 2009, study sites were established at different distances to KCS to examine responses of different groups of plants and animals to industrial pollution. The methodology for selecting sites and sampling plots within the sites is described in detail earlier (Vorobeichik and Kozlov, 2012). The sites were selected in accordance with the basic principles of completeness, integrity, definiteness and homogeneity of the pollution gradient. Special attention was paid to selection of sites with similar tree stand, not subjected to grazing, logging, or fire and with least observable signs of recreation. To avoid pollution from motor vehicles sites were established at distances of 0.5–1.0 km of the asphalt road crossing the study area.

Two transects were established to the south and north of the KCS, with five sampling sites selected along each (Fig. 1). Except for the site nearest to the smelter, all were located in secondary deciduous forest areas, predominantly composed of *Betula pendula* Roth, which had replaced the pine forest. The site at a distance of 1 km to KCS is located within an industrial barren at the foot of Mount Zolotaya. Three sampling plots (SPs), 25 × 25 m each and spaced 50–300 m apart were established within each site. To avoid edge effects we positioned SPs at distances of ≥100 m from forest edges. At each SP, forest litter was sampled to analyze metal concentrations. The litter was chosen for chemical analyses because it is the main habitat of ground beetles. In addition, habitat variables were recorded as follows: number of trees per 1 ha, height of the top tree canopy and stand basal area; species richness and cover of the understory, field and moss layers; percentages of soil surface covered with woody debris (Table S1). Methods of measurement of habitat variables and parameter values were published earlier (Smorkalov and Vorobeichik, 2011; Usoltsev et al., 2012; Belskaya et al., 2019).

To group sites into pollution zones we calculated a pollution index for each site (PI). It is an analog of a Contamination Factor (dos Santos et al., 2022), but takes into account concentrations of several metals: $PI_j = 1/n \sum C_{ij}/F_i$ (1), where n – number of metals $(i = 1 \dots n)$; Cij – concentration of the metal i at the site j, F_i – minimal concentration of the metal i across sites (Vorobeichik et al., 1994).

Four distinct pollution zones were distinguished. Sites with *PI* in the range of 1–2 (at distances of 32, 27, and 26 km to KCS, Fig. S1a) were assigned to the background zone; sites with *PI* of 3–14 (at distances of 18, 12, 11, and 9 km to KCS, Fig. S1b) were assigned to the buffer zone; sites with *PI* of 89–99 (at distances of 5 and 4 km to KCS, Fig. S1c) were assigned to the impact zone; site with *PI* of 199 (at a distance of 1 km to KCS, Fig. S1d) was assigned to the industrial barren. The zoning of the area we use is the same as that given by Purvis et al. (2006). The background and buffer zones are characterized by a well-developed tree layer, the presence of undergrowth, neutral soil pH, and a litter layer thickness of 1–4 cm (Usoltsev et al., 2012; Belskaya et al., 2019; Smorkalov and Vorobeichik, 2022). As the distance to KCS decreases, plant communities change from forb-dominated associations in the background zone to forb-grass associations in the buffer zone accompanied by a slight decrease in phytomass, forest stand productivity, and projective cover of the herbaceous layer. In the impact zone, the acidity and thickness of the forest litter increase, while forest stand productivity decreases further; undergrowth and the herbaceous layer are nearly absent. At the industrial barren, litter layer is completely absent, and the soil is heavily eroded. Scattered low trees occur only in ravines, and sparse patches of grasses are confined to ravines and mountain slope. We

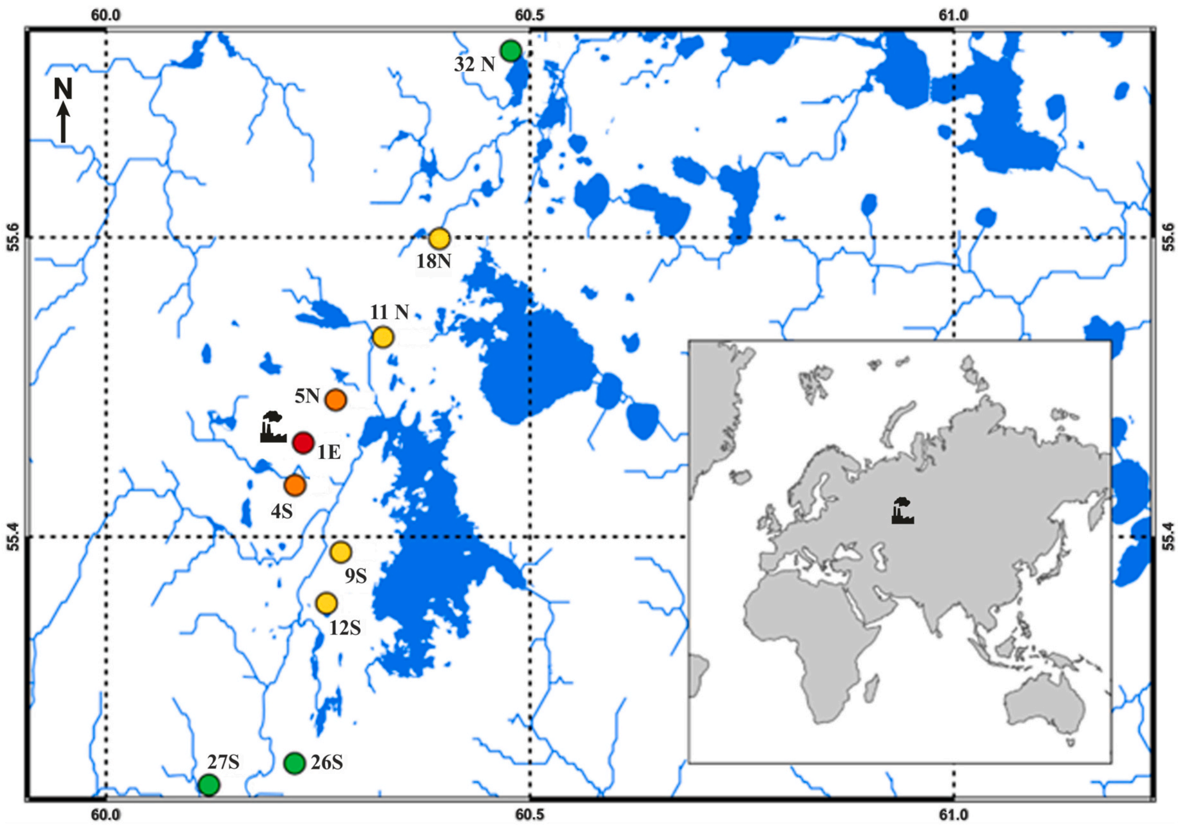

Fig. 1. Map of the study area. Dots represent sites; numbers in site names indicate distance to the smelter (km), letters denote direction (N—north, S—south, E—east). The black pictogram shows the location of KCS. Sites marked with green denote the background zone; yellow—buffer zone; orange—impact zone; red—industrial barren. Blue lines indicate the hydrographic network. The inset shows the location of the study area on the map of continents. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

used the division into zones when analyzing the composition and structure of ground beetle assemblages.

When analyzing effects of pollution on the abundance and diversity of ground beetles, various predictors are used: concentrations of metals in the soil or forest litter (Read et al., 1987; Skalski et al., 2011), principal components calculated on environmental parameters (Skalski et al., 2010; Zolotarev and Belskaya, 2012) or the distance to the pollution source (Babin-Fenske and Anand, 2011). Each approach has its pros and cons. As pointed out by Eeva et al. (2012), «litter metal levels in a particular year do not necessarily reflect a cumulative long-term effect of multiple pollutants on environment and biota». When selecting environmental variables for multivariate analysis, it is not always possible to take into account all the factors influencing ground beetles. Therefore, in this study, we use distance to the smelter as a measure of contaminant exposure. This makes sense, as it correlates strongly with metal concentrations and most habitat characteristics we considered (Belskaya et al., 2019).

2.3. Sampling

Ground beetles were sampled with pitfall traps consisting of plastic cups with a neck diameter of 9 cm filled with 3 % acetic acid as a preservative. This method is widely used in counting ground beetles since with the same sampling effort it allows for comparison of abundance and diversity among sites. At each SP, five traps were installed in a linear arrangement with 3 m intervals for five days exposure. Sampling was conducted twice per season (Table 1) to evaluate the activity of species with different phenology (spring–summer and autumn).

To test whether pollution effects differ between years, ground beetles were sampled in 2009 and 2014, years with similar emission levels but contrasting weather. Weather conditions, especially temperature, should be taken into account since temperature is the primary driver of changes in activity density (Kaspari et al., 2022). From May to August, air temperature in both study years was similar to the long-term (1984–2014) mean (Table 1); however, 2014 was notably more humid. Weather conditions during the sampling rounds varied between the years: 2009 was warmer in early summer, while 2014 was warmer in late summer. Precipitation levels in early summer were similar; however, in late summer of 2009, precipitation was five times higher compared to 2014.

Species identification was carried out in the laboratory using identification keys for adult beetles (Kryzhanovskii, 1965) and reference collections from the Museum of the Institute of Plant and Animal

Table 1
Weather conditions during the study years as recorded by the Zlatoust meteorological station, Russia (WMO_ID 28630).

Month, period		Mean temperature, °C		Total precipitation, mm	
		2009	2014	2009	2014
May		10.4	13.3	28.9	62.8
June		16.2	15.1	33.2	110
July		15.0	12.8	120.8	197.9
August		13.7	16.7	123.7	38.0
May–August		13.8	14.5	306.6	408.7
[a] May–August (1984–2014 mean)		14.3 (13.8–14.7)		336.7 (305.7–367.6)	
[b]Sampling round	Early summer	19.1	14.8	6.9	5.4
	Late summer	16.8	20.5	19.2	3.8

[a] Values in parentheses indicate the 95 % confidence interval.
[b] June 5–10, 2009; June 3–8, 2014 August 26–31, 2009; August 18–23, 2014.

Ecology, Ural Branch of the Russian Academy of Sciences. Larvae collected in 2009 were identified by Professor K.V. Makarov, PhD (Moscow Pedagogical State University).

2.4. Data processing and statistical analyses

Data processing and statistical analyses were conducted separately for each study year. The SPs served as replicates. Activity density per 100 trap-days was used as a measure of abundance and was summed across both sampling rounds. Sites located to the north and south of the KCS were combined into a single distance series, as the spatial distribution of pollutants in the forest litter was similar along both transects (Smorkalov and Vorobeichik, 2011).

Species richness was assessed using the number of species observed (S) and the interpolated number per 100 individuals (S') (Gotelli and Colwell, 2001; Chao et al., 2014; Hsieh et al., 2016), while species diversity was evaluated using the Shannon index (H'). Species accounting for at least 5 % of the total abundance were classified as dominant. Four models were considered to describe the relationship of abundance, species richness, and the diversity of ground beetles with the distance to KCS: linear, segmented, polynomial, and logarithmic. The model with the lowest Akaike Information Criterion (AIC) was selected and used for further analysis. The significance of differences between model parameters across years was evaluated based on the overlap of confidence intervals (CIs), with CI limits calculated as the standard error multiplied by 2. Differences were considered significant if the CIs did not overlap.

When analyzing species composition, assemblage structure, and rarefaction curves, the categorical predictor "zone" was used instead of the continuous predictor "distance to KCS". Ordination of assemblages based on the activity density of species was carried out using Bray-Curtis distance and principal coordinate analysis (PCoA) in the ape `v. 5.8` package (Paradis and Schliep, 2019). Bray-Curtis distance matrices were calculated using the vegan `v. 2.6` package (Oksanen et al., 2022). The significance of the effects of zone and year was assessed using PERMANOVA (999 iterations) (Anderson, 2001).

Data transformation and visualization were performed using the tidyverse `v. 2.0` package (Wickham et al., 2019). Calculations were conducted in the R v. 4.3.3 programming environment (R Core Team, 2024).

3. Results

A total of 6325 ground beetle specimens representing 58 different species were collected over the two-year study period (Tables S2 and S3).

3.1. Changes in the abundance and diversity of assemblages

The relationship of ground beetle abundance, species richness, and diversity with the distance to KCS was nonlinear (Fig. S1, Table S4). Among the four models considered, the segmented model provided the best fit for all indices, as indicated by the lowest AIC. The trajectories of change in abundance, species richness, and diversity followed a similar pattern: these metrics remained relatively stable in the background and

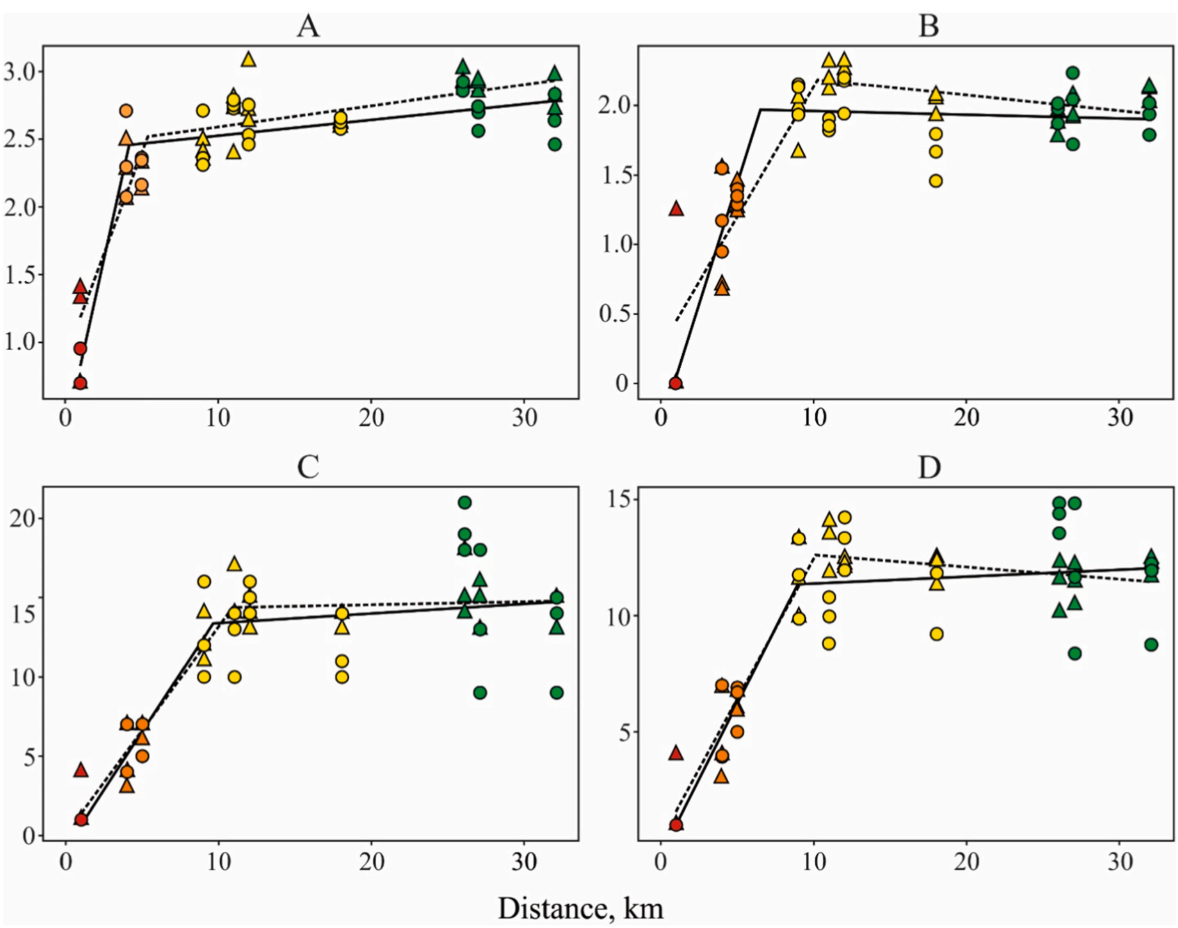

Fig. 2. Relationship of the ground beetle abundance (log_{10} individuals per 100 trap-days) (A), Shannon diversity (B), species richness observed (C) and interpolated per 100 individuals (D) with the distance to KCS. Parameter values are shown for each SP: circles and solid line correspond to 2009, triangles and dotted line to 2014. Pollution zones are marked as follows: background—green, buffer—yellow, impact—orange and industrial barren—red. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

buffer zones but decreased sharply in the polluted area compared to the background level (Fig. 2). The differences between the indices were associated with the position of the breakpoint relative to the distance to KCS (Table 2).

Ground beetle abundance varied across the background, buffer, and impact zones. The highest numbers of individuals were recorded at the site 26S in both years, whereas the lowest numbers were sampled at the site 5N (Tables S1 and S2). At the site 4S, the number of individuals ranged from 152 to 206 across years. A sharp decrease in abundance occurred approximately at a distance of 1 km to KCS (Fig. 2A). The breakpoint of the fitted regression was located at a distance of 4–5 km to KCS (Table 2). There, pollution index was 89–99 times higher than in the background area (Table S1).

Species richness remained relatively stable at distances ranging from 32 to 11 km to KCS (Fig. 2C and D, Table 2). Closer to KCS ($PI > 8$) the number of species decreased from 18 to 1 in 2009 and from 15 to 4 in 2014 (Tables S1 and S2).

In 2009, ground beetle diversity remained stable along the gradient section from 32 to 6.5 km to KCS, followed by a sharp decrease closer to KCS (Fig. 2B–Table 2). In 2014, the breakpoint of the regression was at a distance of 10 km to KCS. As the distance to KCS decreased further ($PI > 13$), the diversity decreased to its lowest value at the site 1E.

Slope coefficients of the segmented regressions remained consistent across all years for all examined indices (Table 2). Significant variations between years were found only for the breakpoint after which the diversity decreased. This breakpoint was much closer to KCS in 2009 compared to 2014 (Fig. 2B–Table 2).

3.2. Changes in the species composition of assemblages

Over two years, 40 species were recorded in the background zone, 36 species in the buffer zone, 16 species in the impact zone, and 4 species at the industrial barren. The background and buffer zones showed similarity not only in observed but also in the interpolated number of species (Fig. 3). The species composition was also similar sharing 27 common species. Differences were mainly related to singleton and rare species. The ecological traits of dominant species also coincided (Table S5). These were exclusively zoophages of the genera *Pterostichus*, *Carabus*, and *Synuchus vivalis* (Table 3), with *Pterostichus oblongopunctatus* as the most abundant species. Larger species exhibited high relative abundance in both zones, while species typical of open habitats were absent.

Species richness in the impact zone was considerably lower compared to the background and buffer zones (Fig. 3). Species composition also changed in the impact zone. Near the KCS, only 8 species were shared with the background zone and 6 species were common with the buffer zone. The species lists differed not only by the number of single and rare species. In the impact zone, changes in the composition of dominant species and their ecological traits were observed (Table 3, Table S5).The abundance of *P. oblongopunctatus* near the KCS decreased by 4.3 times (in 2009) and 10.9 times (in 2014) compared to the background zone (Tables S2 and S3), leading it to become a subdominant species. The impact zone was dominated by smaller-sized species of the genus *Amara* that are mixo-phytophages. Large zoophages were absent, replaced by medium-sized (*Poecilus versicolor*) and small (*Calathus micropterus*) zoophages. *Poecilus versicolor*, favoring open habitats, appeared among the dominant species.

Only four species were recorded at the industrial barren: the small zoophages *Bembidion lampros* and *Microlestes minutulus*, and medium-sized ground beetles *Harpalus affinis* and *H. smaragdinus*, both belonging to the mixed-feeding guild (Table S5). The latter two species were found exclusively at the industrial barren (Tables S2 and S3). All species recorded at the barren had the ability to fly.

Table 2
Parameters of the segmented regression of the ground beetle diversity and abundance on the distance to KCS.

Model parameters	Coefficient±SE (95% confidence limits)	
	2009	2014
Abundance ($\log_{10}$ individuals per 100 trap-days)		
[a]Slope	0.511 ± 0.058 (0.395; 0.627)	0.303 ± 0.041 (0.221; 0.385)
breakpoint, km	4.192 ± 0.272 (3.648; 4.736)	5.409 ± 0.487 (4.435; 6.383)
Species richness (observed)		
Slope	1.475 ± 0.332 (0.811; 2.139)	1.313 ± 0.147 (1.019; 1.607)
breakpoint, km	9.588 ± 1.523 (6.542; 12.634)	10.867 ± 0.882 (9.104; 12.631)
Species richness (interpolated per 100 individuals)		
Slope	1.304 ± 0.442 (0.420; 2.188)	1.216 ± 0.115 (0.986; 1.446)
breakpoint, km	8.921 ± 1.991 (4.939; 12.903)	10.086 ± 0.656 (8.774; 11.398)
Shannon diversity		
Slope	0.348 ± 0.045 (0.258; 0.438)	0.187 ± 0.028 (0.131; 0.243)
breakpoint, km	6.518 ± 0.479 (5.56; 7.476)	10.266 ± 1.028[b] (8.21; 12.321)

[a] Slope coefficient of the segment from the breakpoint to KCS.
[b] Significant differences between years. Calculation methods are detailed in subsection 2.3.

3.3. Changes in the structure of assemblages

The structure of ground beetle assemblages varied with the pollution level. PERMANOVA showed that the effect of zone explained 52 % of the overall variation ($R^2 = 0.52$, $F = 21.2$, $p = 0.001$), while the effect of year accounted for only 2 % ($R^2 = 0.02$, $F = 2.1$, $p = 0.054$). Pollution-related changes in the assemblage structure differed between study years, as evidenced by a considerable interaction between zone and year ($R^2 = 0.05$, $F = 2.1$, $p = 0.008$). Assemblages in the background and buffer zones demonstrated the highest similarity. Ordination showed minimal distances between their centroids in both years, with substantial overlap of confidence ellipses (Fig. 4). Variations of assemblage structure across the zones were comparable to those observed among sites within zone (Table 4). Notably, ground beetle assemblages underwent considerable changes in the heavily polluted area. The centroids of the impact and background zones, as well as those of the impact and buffer zones, were markedly separated in both years, with no overlap of confidence ellipses (Fig. 4). Differences between the background and impact zones exceeded within-zone plot differences by factors of 1.4–2.2, while differences between the buffer and impact zones exceeded them by factors of 1.5–2.1 (Fig. 4). Variability among SPs within the impact zone was lower in 2014 compared to 2009 (Fig. 4).

Ground beetle larvae were found in both years at all sites of the background, buffer, and impact zones. Larvae of the 1st to 3rd instars of *A. brunnea, A. praetermissa, Carabus glabratus, C. granulatus, Curtonotus aulicus,* and *P. niger* were recorded in the background zone; larvae of *Amara* sp., *C. granulatus, Poecilus* sp., and *P. niger* were found in the buffer zone; while only *A. brunnea* larvae were sampled in the impact zone (Table S2). No larvae of ground beetles were recorded at the industrial barren.

4. Discussion

4.1. Changes in the abundance and diversity of assemblages

A segmented model was selected to describe and analyze changes in abundance and diversity of ground beetles along the pollution gradient. This model yielded the lowest AIC among the four models considered. In addition, the segmented model enables the incorporation of nonlinear relationship and facilitates determining position of a breakpoint in a trend that reflects parameter variation. This model showed non-linear

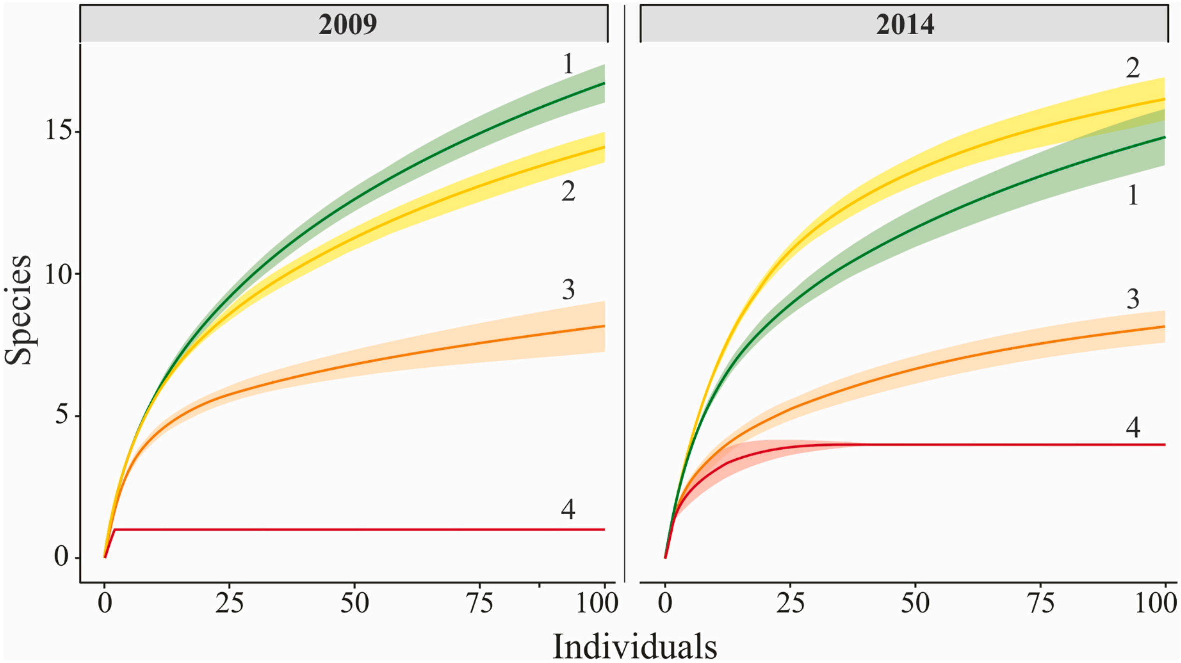

Fig. 3. Dependence of the number of ground beetle species on the sample size in different pollution zones, calculated using the rarefaction method. Pollution zones are marked as follows: background—1, green; buffer—2, yellow; impact—3, orange; and industrial barren—4, red.

Table 3
Composition of dominants (proportion of individuals in total abundance, %) across pollution zones and years (industrial barren is excluded due to exceedingly low species richness and abundance of ground beetles).

Species	Pollution zone					
	background		buffer		impact	
	2009	2014	2009	2014	2009	2014
Pterostichus oblongopunctatus	34.3	25.7	21.7	23.2	27.4	13.9
Pterostichus melanarius	11.7	14.4	26.9	11.2	0	0
Carabus granulatus	14.4	7.7	12.6	5.5	0	0
Pterostichus uralensis	12.9	17.8	5.0	5.0	0	0
Pterostichus niger	3.3	11.9	1.1	6.2	0	0
Pterostichus magus	3.4	6.2	10.8	6.7	0	0
Carabus cancellatus	0.4	1.0	8.7	10.7	0	0
Pterostichus mannerheimi	3.1	3.9	1.9	7.7	0	0
Synuchus vivalis	0.2	1.4	0.2	6.0	0	0
Amara brunnea	1.2	0.4	0.2	0.4	35.8	54.1
Amara communis	2.9	0.3	2.1	2.5	7.1	17.2
Calathus micropterus	0.8	1.6	1.9	6.9	9.0	3.0
Poecilus versicolor	0	0	0	0	15.4	1.7

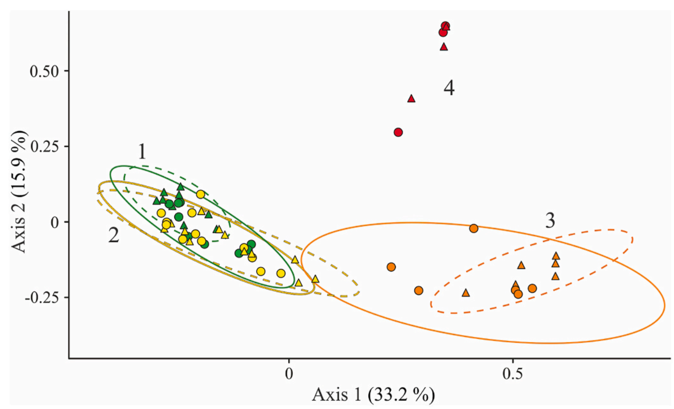

Fig. 4. Ordination of ground beetle assemblages across pollution zones (marked as in Fig. 3). Ellipses represent confidence intervals (solid lines and circles—2009, and dotted lines and triangles—2014). Calculation methods are detailed in subsection 2.3.

dynamics in the abundance and diversity along the pollution gradient.

Responses of abundance and diversity of ground beetles to industrial pollution can either coincide (Skalski et al., 2010) or differ (Read et al., 1987; Babin-Fenske and Anand, 2011). In this study, all examined parameters varied slightly in the background and buffer zones but decreased sharply closer to KCS. According to published data, the maximum no adverse effect metal concentrations for species number of carabids equal 172 mg/kg soil or litter Cu, 971 mg/kg Pb, 256 mg/kg Cd (Bengtsson and Tranvik, 1989). Unfortunately, the authors did not report to what forms (total or mobile) of metals this applies. In our study, the diversity started to decrease when concentrations of the mobile forms of metals in the litter exceeded 235 mg/kg dry mass Cu, 402 mg/kg Pb, and nearly 6 mg/kg Cd. The abundance of carabids decreased at higher pollution: >3934 mg/kg dry mass Cu, 1908 mg/kg Pb, and 23 mg/kg Cd.

Our conclusion that the diversity and abundance of ground beetles change at different rates under the pollution is consistent with the published data. Experimental studies have shown that a reduction in species diversity leads to a decrease in the abundance or biomass of different trophic groups including predators (Cardinale et al., 2006). However, minor losses of biodiversity do not noticeably affect ecosystem functions, whereas larger losses accelerate the rate of changes (Cardinale et al., 2012). In other words, reduction of biodiversity precedes a decrease in abundance.

In our study, pollution-related changes in biodiversity and abundance of ground beetles were consistent across both years, despite differences in weather conditions. This indicates the stability of the pollution effect over time and suggests that this effect can exceed that of the weather.

4.2. Changes in the species composition and structure of assemblages

It was found that the composition and ratio of dominant ground beetle species changed in the impact zone compared to background and

Table 4
Within-group (gray cells) and between-group (uncolored cells) Bray-Curtis average distances. Within-group distances represent differences among sampling plots within a zone, whereas between-group distances reflect differences between zones and years. Calculation methods are detailed in subsection 2.3.

Pollution zone	year	industrial barren		impact		buffer		background	
		2014	2009	2014	2009	2014	2009	2014	2009
background	2009	1	1	0.86	0.81	0.57	0.53	0.47	0.45
	2014	1	1	0.92	0.87	0.6	0.57	0.43	
buffer	2009	1	1	0.87	0.83	0.52	0.46		
	2014	1	1	0.86	0.81	0.52			
impact	2009	1	1	0.5	0.56				
	2014	0.98	0.98	0.41					
industrial barren	2009	0.76	0.78						
	2014	0.72							

buffer zones. The decreased abundance of *P. oblongopunctatus* in the impact zone may be attributed to reduced reproduction of it's local population like that recorded in another polluted area. Thus, the proportion of reproductive females of *P. oblongopunctatus*, as well as the number of eggs per reproductive female near the Middle Ural copper smelter (Revda, Russia), were lower than in the background area (Belskaya, 2008). Decreased reproduction could result from the direct toxic effect of pollutants. Reduction in the number of eggs laid by females of *P. oblongopunctatus* and a decrease in the number of F_1 imagoes produced per female of the parental generation were associated with elevated concentrations of heavy metals in the soil (Łagisz et al., 2002). Furthermore, heavy metals in the food delayed development of *P. oblongopunctatus* larvae and increased mortality (Mozdzer et al., 2003). Other potential causes of larval mortality of this species include limited food availability and, consequently, increased cannibalism (Heessen and Brunsting, 1981). Earlier studies reported the absence of worm families *Lumbricidae* and *Enchytraeidae* in the soil contaminated by KCS, along with decreased abundance and biomass of millipedes and insects that are key food resources for ground beetles (Sadykov et al., 1992). We are not aware of more recent studies on soil invertebrates in this region. At the same time, high heavy metal litter concentrations near the KCS that have been documented at the time of this study (Mikryukov and Dulya, 2017) indicate persistent toxicity for soil invertebrates.

The reduction in food availability could also affect other ground beetles, particularly larger species. Their vital functions require a substantial amount of energy (Grüm, 1980). Therefore, it is crucial for larger species to obtain food with lower energy costs, which is partly achieved by feeding on larger prey (Wheater, 1988). This may explain why annelids and mollusks constitute a substantial part of the diet of large ground beetles, particularly females (Sergeeva and Gryuntal, 1990; Symondson et al., 1996; Jelaska et al., 2014). A notable decrease in the abundance of annelids and mollusks, resulting in their complete disappearance near non-ferrous metallurgy plants (Sadykov et al., 1992; Koneva, 1995; Nahmani et al., 2003; Nesterkov, 2013; Vorobeichik et al., 2019), is one potential cause of the notable decline in the abundance of large ground beetles. Other factors contributing to the decline of large-bodied species in harsh environments include their high sensitivity to changes in habitat conditions due to small population sizes, low fecundity, and prolonged larval development (Kotze and O'Hara, 2003).

Ground beetles inhabiting the soil surface and litter layer are strongly dependent on environmental parameters such as vegetation composition and structure, soil composition and moisture, litter layer thickness, and the extent of moss cover on the soil (Rainio and Niemelä, 2003). This relationship is evident regardless of the study scale, whether regional (Jukes et al., 2001; Yanahan and Taylor, 2014) or local (Koivula et al., 1999; Antvogel and Bonn, 2001). Approaching the KCS, changes were observed in the habitat characteristics of ground beetles. Along with the increasing concentrations of heavy metals, the acidity, thickness, and moisture of the forest litter increased, whereas the height and density of the forest stand, species richness, and projective cover of the field layer decreased (Smorkalov and Vorobeichik, 2011; Usoltsev et al., 2012; Mikryukov and Dulya, 2017). The emergence of ground beetle species with mixed diet and a species preferring open habitats among the dominants in the impact zone likely reflects an indirect effect of pollution reflecting in the habitat change. The presence of *Amara* larvae at a distance of 4–5 km from KCS indicates that these ground beetles are capable of successful reproduction even in heavily polluted areas and, consequently, can sustain populations under such conditions. Ground beetles of the genus *Amara* are justifiably recognized as indicators of severely contaminated soils (Skalski et al., 2011). Nearly all species disappeared from the industrial barren, with the exception of a few well-flying ones of small to medium size. An increased proportion of ecologically flexible, highly mobile species with smaller individuals is also a common feature under other forms of anthropogenic impact on ecosystems, such as urbanization, land use type (Hahs et al., 2023; Martínez-Núñez et al., 2024), and recreation (Grandchamp et al., 2000).

To accurately characterize the structure of ground beetle assemblages, it is essential to evaluate the ratio of resident and migratory species, distinguished based on their demographic spectra (Matalin and Makarov, 2011). At this stage, it is not possible to determine the exact number of such species across areas with varying levels of pollution. However, the presence of larvae at different developmental stages confirms that at least six species are capable of reproduction in the background zone, four species in the buffer zone, and one species in the impact zone. Extremely low abundance of ground beetles and the absence of larvae at the industrial barren suggest that the species recorded in this area are sporadic (Matalin and Makarov, 2011). The bare, eroded, and acidified soil at the industrial barren is hardly suitable for reproduction of ground beetles. Nevertheless, the very presence of imagoes, even single ones, indicates the presence of nearby places that provide temporary stay of beetles during migration. In such patches called "stepping stones" (Saura et al., 2014) that provide shelter and food for imagoes, ground beetles don't complete a full developmental cycle judging by the incomplete demographic spectra (Matalin and Makarov, 2011). Presence of such patches at the barren and in the impact zone is due to high heterogeneity of environment around strong pollution sources (Vorobeichik and Pozolotina, 2003; Trubina and Vorobeichik, 2012). Such patches include fragments of tree and herb vegetation as well as woody debris (stumps, fallen trunks) (Fig S3) that serve as refugia maintaining biodiversity (Raymond-Léonard et al., 2020; Mikryukov et al., 2021; Vorobeichik et al., 2024). On the ground covered with fallen leaves under trees (Fig S3b), beetles can spend part of their life cycle searching for food and partner for mating. These microhabitats can facilitate the colonization of the disturbed territory by ground beetles at the initial stages of ecosystem recovery. It has been established that small patches and scattered trees have a positive effect on dispersal (Rocha et al., 2021a).

4.3. The recommendations for environmental restoration

The state of the environment around the KCS is critical and calls for immediate action. Chronic pollution from the led to significant changes in all ecosystem components including soil microbiota (Mikryukov and Dulya, 2017), invertebrates (Belskaya et al., 2019; Nesterkov and Nesterkova, 2023), birds (Eeva et al., 2012; Belskii and Belskaya, 2013), and mammals (Mukhacheva et al., 2010; Nesterkova, 2014). The reduction of pollutant emissions after a radical technological modernization in 2001–2005 led to reduced pollutant fallout creating conditions for the natural recovery of degraded landscapes and vegetation. This process can be accelerated through active restoration measures, including land reclamation and agrotechnical methods for soil and vegetation restoration. However, such measures don't guarantee the reestablishment of a functioning and stable ecosystem (Skalski et al., 2015; Parkhurst et al., 2021). Successful ecosystem restoration requires the preservation of existing ecological heterogeneity, particularly fragments of natural herbaceous and woody vegetation that act as stepping stones for species dispersal into depopulated areas (Rocha et al., 2021b). Special attention in conservation efforts within this region should be given to the area within a 9–11 km radius of the KCS, where significant alterations in plant and animal assemblages have been recorded. The number of study sites should be increased by including stepping stones along with permanent habitats of ground beetles.

To evaluate the effectiveness of conservation measures, it is essential to implement comprehensive environmental monitoring in the polluted area. Ground beetle assemblages are a promising tool for assessing the direction and success of ecosystem recovery (Kędzior et al., 2020). Valuable insights can be gained from analyzing the species diversity, assemblage structure, and life-history traits of ground beetles (Kosewska et al., 2023). An important criterion of the assemblage recovery could be a shift in the breakpoint in the dose-effect relationship of parameters towards the pollution source. Further research should also include an analysis of the demographic spectra of ground beetle populations (Matalin and Makarov, 2011) and the manual counting of larvae from soil samples. A full demographic spectrum or the presence of larvae indicates suitability of a habitat for reproduction and sustainable existence of ground beetle populations.

5. Conclusion

This study quantified the response of ground beetle assemblages to industrial pollution in the Southern Urals. The analysis revealed a conspicuous non-linear dose-effect relationship between the distance to a copper smelter and multiple parameters of ground beetle assemblages. As the distance to the smelter decreased, assemblages exhibited significant restructuring and marked decline in abundance, species richness, and diversity. The thresholds for these changes differed among parameters: species richness decreased sharply within 9–11 km to the smelter, diversity within 7–10 km, and abundance within 4–5 km. These distance-dependent relationships remained consistent across years with varying weather conditions.

Given the ongoing reduction in industrial emissions, these findings provide a baseline for monitoring the long-term recovery of ground beetle assemblages in this polluted region.

CRediT authorship contribution statement

Elena Belskaya: Writing – review & editing, Writing – original draft, Supervision, Investigation, Formal analysis, Data curation, Conceptualization. **Maxim Zolotarev:** Writing – review & editing, Visualization, Investigation. **Artëm Sozontov:** Writing – review & editing, Visualization, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Elena A. Belskaya reports financial support and administrative support were provided by Russian Foundation for Basic Research. Maxim Zolotarev reports financial support and administrative support were provided by Russian Foundation for Basic Research. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2025.127340.

Data availability

The code and raw data are available in a public repository at: https://github.com/ANSozontov/Karabash_2025.

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