

Changes in the Size Structure of Carabid Communities in Forest Ecosystems under Technogenic Transformation

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Abstract—The body size structure of carabid communities has been analyzed based on the 2009 and 2013 collections (with the use of pitfall traps) performed at 10 sites of a spruce–fir forest along the gradient of pollution with emissions from the Middle Ural Copper Smelter. A reduction in the unweighted mean body size of carabid individuals has been shown, as well as the heterogeneity of body sizes in the community (Gini coefficient) of the extremely polluted territory. It has been revealed that the weighted mean body size of individuals and the Lorentz asymmetry coefficient are not dependent on the level of pollution. Differences between the communities of carabids in the background and polluted territories are associated with the smaller number of large-sized species, while the similarity is explained by the dominance of medium- and small-sized species at all sites. The high interannual variability has been observed in the ratio of size groups of the analyzed communities at the background and moderate levels of pollution.

Keywords: Carabidae, community, size structure, forest ecosystems, industrial pollution, copper smelter

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Body size is an important functional feature of a living organism that determines its metabolic intensity and ability to adapt to certain conditions, as well as pattern of locomotion and migrations (Schmidt-Nielsen, 1987). The body size of insects determines egg production of females and depends on larval development conditions (Honěk, 1993; Chown and Gaston, 2010). The size structure of a community reflects how resources are distributed among various species, being related to the flow of matter and energy (Peters, 1983). According to the principle of competitive exclusion, the ratio of body size characteristics between closely related species using the same resource is a measure of similarity enabling coexistence of these species within a single community (Giller, 1988). The ratio of body sizes in carabid communities depends on their habitat conditions (Šustek, 1987). It has been demonstrated that the body size of carabid individuals decreases in territories affected by some adverse factors (urbanization, mowing of grass, grazing, soil treatment, application of fertilizers and pesticides) (Blake et al., 1994; Ribera et al., 2001; Magura et al., 2004).

Technogenic pollution can be considered to be a powerful ecological factor influencing all components of ecosystems. Industrial enterprises are surrounded by ecosystems transformed according to the pollution level. These impact regions are commonly regarded as a suitable test site to study reactions of biological sys-

tems of various levels to a strong external impact (Vorobeichik and Kozlov, 2012). However, the effect of pollution on the size structure of carabid communities has been insufficiently studied (Read et al., 1987, 1998). The territory around the Middle Ural Copper Smelter (MUCS) is one of the world's most investigated impact regions (Kozlov et al., 2009). Previously, a decrease in the dynamic density of carabids, rearrangement of the species and ecological structure of communities in the gradient of pollution have been shown (Ermakov, 2004; Belskaya and Zinov'ev, 2007), but changes in the size structure of communities have not been considered.

The aim of this study is to analyze changes in the distribution of body sizes of individuals in the community of carabids from a spruce–fir forest along the gradient of pollution with emissions from the MUCS. We test the hypothesis on negative correlation between the body size of an individual in the community and the level of load on the ecosystem (Szyszko, 1983; Blake et al., 1994), assuming that an increase of pollution leads to a reduction in the abundance of large-sized carabid species and, as a result, in the mean body size of individuals.

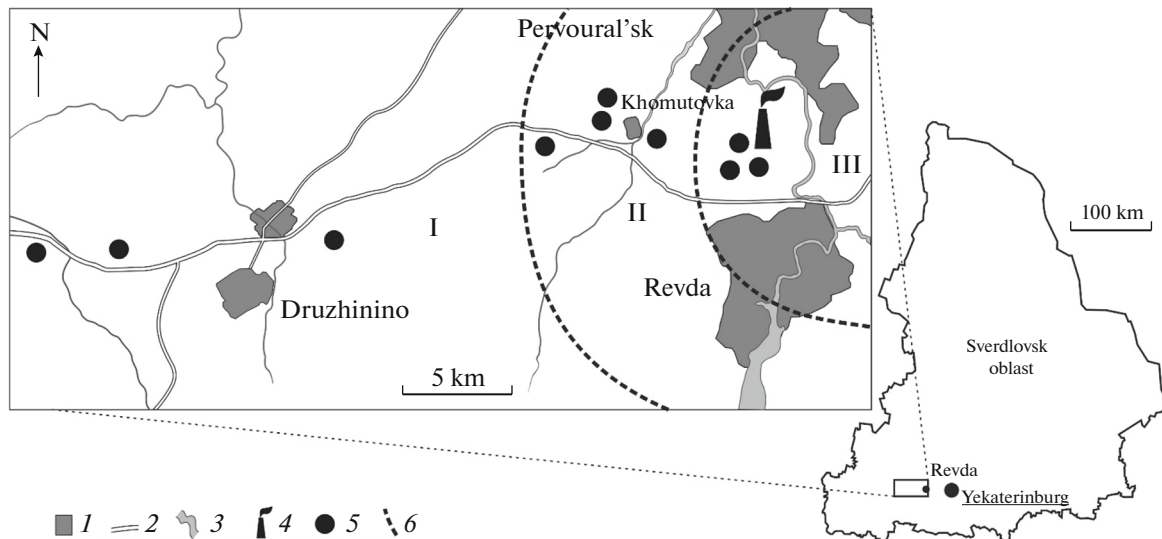


Fig. 1. The geographical location of the studied sites along the gradient of pollution with emissions from the MUCS: 1—human settlements; 2—roads; 3—water bodies; 4—pollution source; 5—study site; 6—borders between the pollution zones (I—background; II—buffer; III—impact).

OBJECTS AND METHODS

The study was performed in 2009 and 2013 near the MUCS (Revda, Sverdlovsk oblast). This enterprise operating since 1940 is one of the largest smelters in Russia. Its atmospheric emissions contain sulfur and nitrogen oxides, fluorine compounds, and polymetallic dust (Cu, Pb, Cd, Zn, Fe, etc.).

The material was collected at 10 stationary sites in the spruce-fir forest located to the west of the MUCS (Fig. 1): three sites with the regional background pollution level at 33, 30, and 20 km from the plant (background zone); four sites with the moderate pollution level at 10, 7, 6, and 4 km (buffer zone); and three sites with the high pollution level at 3, 2, and 1 km (impact zone). At each site, there were three sampling plots (SP, $10 \times 10 \text{ m}^2$) at 50–100 m from each other. In the studied spruce-fir forests, the toxic load increases closer to the source of pollution: the increase of concentrations along the gradient of pollution is most pronounced for copper (from 30.3 to 5530.4 $\mu\text{g/g}$ of litter); concentrations of Pb and Cd increase from 71.3 to 3069.0 $\mu\text{g/g}$ and from 2.5 to 38.7 $\mu\text{g/g}$, respectively. Simultaneously, soil acidity and litter thickness increase, plant associations change from nemoral-shamrock through herbgrass to moss-horsetail and dead-cover (Smorkalov and Vorobeichik, 2011). The forest stand at a distance of 1 km from the MUCS is sparse, being dominated by dry or extremely suppressed coniferous trees mixed with birch trees.

Carabid beetles were captured with pitfall traps (plastic cups 9 cm in diameter and 3% acetic acid as a fixer). In each SP, a line of five traps was set up. The distance between the traps was 3 m. In order to most completely identify the species composition, carabids

were collected during periods of increased activity of spring-summer and summer-autumn species: in 2009, June 10–15 and September 3–9; in 2013, June 14–19 and August 28–September 2. The collected individuals were counted in a laboratory and species were identified. The names of taxa are given according to K.V. Makarov et al. (2013).

The body size of an individual was a sum of its total pronotum length and mean elytra length (Ribera et al., 2001). The mean body size of each species was calculated based on five females and five males (by the smaller number of individuals for 10 rare and solitary species, see Table 1). Individuals for subsequent measurements were taken from our personal collections using the table of random numbers after numbering all males and females of the same species that were captured at all sites during two years. Possible intraspecific variation in the body size of individuals under the influence of pollution was neglected, because it is a priori less significant than differences between species. To determine the body size of rare species (fewer than 10 beetles in the collections), we used collections from the museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences with preference given to the samples from the Middle Urals. This approach to selection of individuals minimizes any possible bias in assessment of the size due to sexual dimorphism and geographical variability. Measurements were carried out using a micrometer of Leica EZ4 and Leica S6D (in the case of very large individuals) stereomicroscope. The pronotum length was determined along its median line. The elytra length was measured along the suture from the basal margin in the place of its junction with the scutellum

to the apex of elytra (from the shoulder angle in species with no basal margin). Magnification varied from $6.3\times$ to $30\times$, and measurement accuracy, from 0.08 to 0.02 mm. The size calculated by this procedure was assigned to all beetles of the species during subsequent analysis.

The following parameters were used to analyze the size structure of carabid beetles: 1) the unweighted mean size of an individual in the community (without considering the abundance of each species); 2) the weighted mean size of an individual in the community (considering the abundance of each species). To analyze the frequency distributions of sizes, the Gini (G) and Lorentz (S) coefficients were used.

The Gini coefficient shows how diverse by size the community is:

$$G = \frac{\sum_{i=1}^N (2i - N - 1)x'_{[i]}}{N^2 \bar{x}} N(N - 1),$$

where N is the number of individuals; $x'_{[i]}$ is the size of i -th individual (beetles are ordered by increasing size); \bar{x} is the mean size of individuals in the community. This coefficient varies from 0 to 1, increasing as differences in the size of individuals grow. It has been widely used in economic and ecological works, for comparison of changes in the distribution of sizes in carabid communities under the effect of anthropogenic factors (Magura et al., 2006).

The distribution of sizes in the carabid community can be represented as a diagram where the cumulative percentage of individuals arranged in the order of increasing size of individuals is plotted on the x -axis and the cumulative percentage of body size is plotted on the y -axis (Lorentz diagram). In the case of equal sizes of all individuals, the diagram is the first coordinate angle bisector called the equality line. Otherwise, the Lorentz curve runs below the equality line. The Lorentz coefficient characterizes the asymmetry of the Lorentz diagram (Damgaard and Weiner, 2000):

$$S = \frac{m + \delta}{N} + \frac{L_m + \delta x'_{m+1}}{L_N},$$

where $\delta = \frac{\bar{x} - x'_m}{x'_{m+1} - x'_m}$; x' is the size of an individual in

the arranged series of $x'_1 \leq x'_2 \leq \dots \leq x'_N$; \bar{x} is the mean size of an individual in the community; m is the number of individuals with the body size smaller than \bar{x} ; L_m is the cumulative body size of individuals with the size less than \bar{x} ; L_N is the cumulative body size of all individuals. The Lorentz diagram is symmetrical at $S = 1$; the more S differs from 1, the greater asymmetry is.

When the size structure of local communities was described, four groups were distinguished based on the

classification of carabid body sizes proposed by Sharoova and Bulokhova (1995): I, $2 \leq x_i < 4$ mm (very small individuals); II, $4 \leq x_i < 8$ mm (small individuals); III, $8 \leq x_i < 10$ mm (medium-sized individuals); IV, $x_i \geq 10$ (large and very large individuals). Subsequently, the proportion of individuals of each size group from the total number of individuals was calculated.

To compare the average values and parameters of distribution of sizes in different years and different zones of pollution, analysis of variance was carried out. The calculations were based on nontransformed values of sizes and indices, because their distribution was close to normal. In case of the heterogeneity of variances, the White-Huber correction and HC3 algorithm were used (Long and Ervin, 2000). Multiple comparisons were performed with the Tukey HSD test. The experimental unit is the site (data summarized on three SP and two sampling periods). Statistical processing was performed with the R v.3.1.2 software (R Core Team, 2014).

The whole material used in this study is being stored in the collection of the Laboratory of Ecotoxicology of Populations and Communities, Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences.

RESULTS AND DISCUSSION

A total of 3570 individuals representing 54 carabid species were captured during two years (Table 1). Their body size varied from 2.06 to 24.18 mm. The most abundant carabids were *Trechus secalis*, *Pterostichus oblongopunctatus*, and *P. urengaicus*. These species determined the ratio of different size groups in the entire carabid community analyzed. For example, an increase in the abundance of *P. urengaicus* accompanied by a decrease in the number of *T. secalis* in 2013 explains a dramatic rise in the proportion of medium-sized carabids in the communities of the background sites and a reduction in the proportion of very small species (Fig. 2). The proportion of large-sized carabids found in the background territory was 5.6% (2009), 12.9% (2013) of all individuals. During the two-year period, ten species of large-sized carabids were registered. Among them, *Carabus aeruginosus*, *C. glabratus*, *Cychrus caraboides*, and *Pterostichus niger* were most abundant.

As closer to the source of pollution, the number of large-sized carabids and their abundance reduced (Table 1, Fig. 2). In the buffer zone, six species (3.4–10.6% of the total abundance) were found, with only one individual of *Carabus cancellatus* in the impact territory over the period of investigation.

The distribution pattern of individuals according to their size is similar in all three zones of pollution (Fig. 3). The most even distribution was registered in 2009 and 2013 in the impact zone. The background and buffer zones were characterized by the higher diversity of

Table 1. The mean size (mean value \pm SE; n —number) of an individual and the total abundance of species over two years in different pollution zones

Species	n		Species size, mm	Total abundance by pollution zones		
	♂	♀		background	buffer	impact
Large and very large species						
<i>Carabus aeruginosus</i> Fisch.	5	5	22.71 \pm 0.32	36	67	0
<i>C. arcensis</i> Hbst.	5	5	16.14 \pm 0.44	1	0	0
<i>C. cancellatus</i> Ill	5	5	19.41 \pm 0.25	1	0	1
<i>C. glabratus</i> Payk.	5	5	22.27 \pm 0.27	13	6	0
<i>C. granulatus</i> L.	5	5	15.63 \pm 0.42	5	0	0
<i>C. henningi</i> Fisch.	5	5	17.91 \pm 0.19	2	1	0
<i>C. schoenherri</i> Fisch.	5	5	24.18 \pm 0.54	6	0	0
<i>Curtonotus gebleri</i> Dej.	5	5	10.14 \pm 0.14	0	1	0
<i>Cychrus caraboides</i> (L.)	5	5	13.21 \pm 0.16	15	4	0
<i>Pterostichus melanarius</i> (Ill.)	5	5	11.11 \pm 0.24	9	0	0
<i>P. niger</i> (Schall.)	5	5	14.00 \pm 0.29	64	14	0
Medium-sized species						
<i>Platynus assimilis</i> (Payk.)	5	5	8.33 \pm 0.09	1	0	0
<i>Poecilus cupreus</i> (L.)	5	5	9.75 \pm 0.18	0	0	1
<i>P. versicolor</i> (Sturm)	5	5	8.80 \pm 0.20	0	0	28
<i>Pterostichus aethiops</i> (Panz.)	5	5	9.42 \pm 0.14	93	5	0
<i>P. oblongopunctatus</i> (F.)	5	5	8.11 \pm 0.09	533	617	214
<i>P. quadrioveolatus</i> (Letz.)	5	5	8.15 \pm 0.10	0	0	4
<i>P. uralensis</i> Motsch.	5	5	8.86 \pm 0.20	0	1	0
<i>P. urengaicus</i> Jurec.	5	5	9.98 \pm 0.14	254	11	0
Small species						
<i>Agonum fuliginosum</i> (Panz.)	5	5	5.32 \pm 0.09	43	44	3
<i>A. gracilipes</i> (Duft.)	5	5	6.74 \pm 0.11	0	1	0
<i>A. sexpunctatum</i> (L.)	5	5	7.00 \pm 0.09	0	0	1
<i>Amara brunnea</i> (Gyll.)	5	5	5.17 \pm 0.07	0	10	26
<i>A. communis</i> (Panz.)	5	5	5.76 \pm 0.11	0	3	6
<i>A. lunicollis</i> Schioedte	5	5	6.73 \pm 0.06	0	0	5
<i>A. tibialis</i> (Payk.)	3	1	4.24 \pm 0.09	0	0	1
<i>Badister bullatus</i> (Schränk)	5	5	4.29 \pm 0.10	1	0	0
<i>B. dilatatus</i> (Chaud.)	0	1	4.50	0	0	1
<i>B. lacertosus</i> Sturm	5	5	4.93 \pm 0.07	7	5	1
<i>Calathus micropterus</i> (Duft.)	5	5	6.40 \pm 0.11	62	101	45
<i>Dicheirotichus discicollis</i> (Dej.)	1	1	4.72 \pm 0.18	0	0	1
<i>Harpalus laevipes</i> Zett.	5	5	7.91 \pm 0.13	0	3	1
<i>H. latus</i> (L.)	5	5	7.51 \pm 0.19	0	1	1
<i>Leistus ferrugineus</i> (L.)	4	4	5.80 \pm 0.04	0	0	1
<i>L. terminatus</i> (Hellw. in Panz.)	5	5	5.60 \pm 0.14	4	3	0
<i>Loricera pilicornis</i> (F.)	5	5	6.28 \pm 0.07	18	0	0
<i>Notiophilus aquaticus</i> (L.)	2	5	4.22 \pm 0.05	0	0	1
<i>N. palustris</i> (Duft.)	5	5	4.09 \pm 0.08	0	7	8
<i>N. reitteri</i> Spaeth	5	5	4.59 \pm 0.06	23	9	0

Table 1. (Contd.)

Species	<i>n</i>		Species size, mm	Total abundance by pollution zones		
	♂	♀		background	buffer	impact
<i>Pterostichus diligens</i> (Sturm)	5	5	4.66 ± 0.05	7	30	78
<i>P. strenuus</i> (Panz.)	5	5	4.93 ± 0.09	1	0	16
<i>P. nigrita</i> (Payk.)	5	5	7.60 ± 0.04	1	0	0
<i>P. vernalis</i> (Panz.)	0	3	5.52 ± 0.18	0	0	3
<i>Synuchus vivalis</i> (Ill.)	5	5	5.59 ± 0.18	2	0	0
Very small species						
<i>Bembidion guttula</i> (F.)	2	2	2.65 ± 0.14	0	0	1
<i>B. humerale</i> Sturm	2	3	2.35 ± 0.04	0	0	7
<i>B. lampros</i> (Hbst.)	5	5	2.94 ± 0.06	0	0	2
<i>B. mannerheimii</i> C.Sahlb	5	5	2.45 ± 0.06	0	0	19
<i>B. properans</i> (Steph.)	1	2	3.41 ± 0.03	0	1	0
<i>Bradycellus caucasicus</i> (Chaud.)	5	5	3.13 ± 0.05	0	0	16
<i>Microlestes minutulus</i> (Gz.)	0	3	2.06 ± 0.13	1	0	3
<i>Notiophilus biguttatus</i> (F.)	5	5	3.91 ± 0.05	43	123	5
<i>Trechus rivularis</i> (Gyll.)	5	5	3.72 ± 0.05	1	0	0
<i>T. secalis</i> (Payk.)	5	5	2.86 ± 0.04	402	323	30
Total number of species				29	25	31
Total number of individuals				1649	1391	530

sizes of carabid individuals. The shape of the Lorentz diagram and the ratio of different size groups in the community vary between years, remaining most stable in the impact zone (see Fig. 2 and 3).

The unweighted mean size of a carabid individual in the community depended only on the type of pollution zone (Table 2) and decreased as the pollution

increased (Fig. 4a); effects of the year and the interaction zone×year were insignificant, as well as differences in the weighted mean size of a carabid individual between the pollution zones (Table 2, Fig. 4b). The Gini coefficient was influenced by the pollution zone and year (Table 2): the coefficient value decreased as the pollution level went up (Fig. 4c). The effect of a

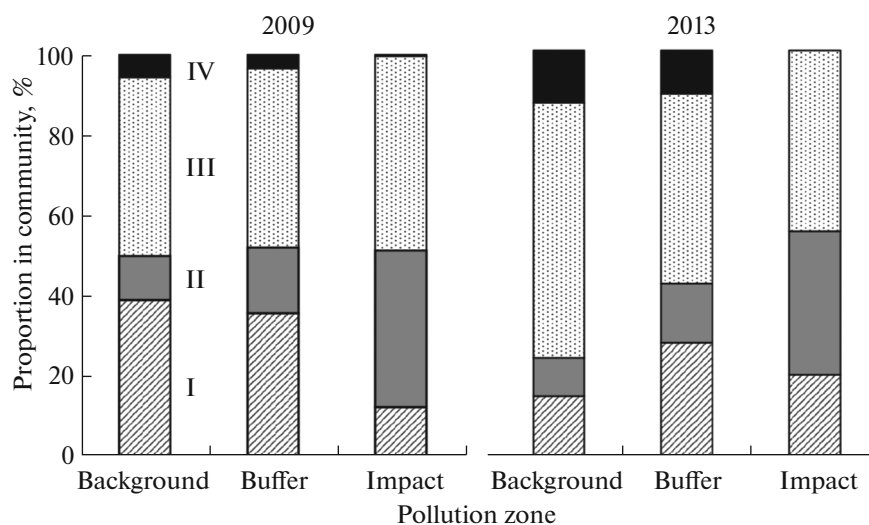


Fig. 2. The size structure of carabid community in different pollution zones. Data on the sites are summarized for each zone. Size interval, mm: I—2–3.99; II—4–7.99; III—8–9.99; IV—≥10.

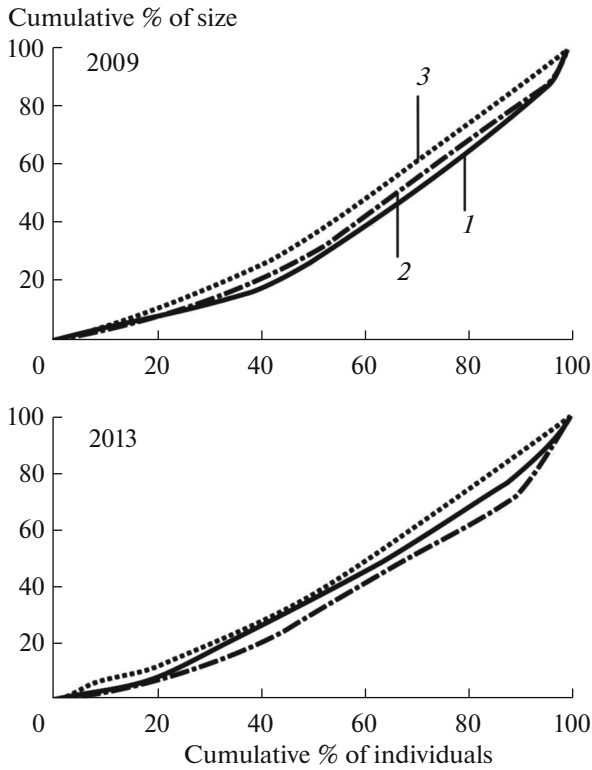


Fig. 3. The Lorenz curves of size distribution in the community in different pollution zones: 1—background; 2—buffer; 3—impact.

particular year is visible through the significantly ($p < 0.001$) lower coefficient value in the background zone observed in 2013 as compared to 2009. The asymmetry of the Lorenz diagram was dependent on neither the site nor the year of study (Table 2, Fig. 4d); the interaction of these factors was also insignificant.

The results of the study demonstrated that the size of carabids in forest communities of the background territory varied in a wide range. As the toxic load increased, the size diversity of individuals in the community decreased: the number of large-sized species and their abundance became lower. This conclusion

was based on the decrease in the unweighted mean size of a carabid individual and the Gini coefficient as closer to the source of pollution. The absence of significant differences in the weighted mean size of individuals and the Lorenz asymmetry coefficient between the pollution zones is explained by the high abundance of carabids from two size groups (medium- and small-sized) in all communities. At the same time, the abundance of large-sized species at the background sites was probably not high enough to influence significantly the distribution of sizes.

The long-term pollution with emissions from the copper smelter caused significant changes in the characteristics of the habitat of carabids near the MUCS: acidity and thickness of the litter, biomass and projective cover of the moss layer, crown density, and plant associations (Vorobeichik et al., 1994). Almost all these parameters determine the abundance and species richness of carabids (Guillemain et al., 1997; Poole et al., 2003; Magura et al., 2004; Vanbergen et al., 2005; Taboada et al., 2006). In the area of study, the abundance of most large-sized species correlates positively with the projective cover of the grass—dwarf shrub layer and pH values, but negatively with the forest litter moisture content (Zolotarev and Belskaya, 2012). However, it seems impossible to single out the key factor in reduction of the number and abundance of large-sized individuals owing to the close correlation between the environmental parameters and the pollution level.

The large-sized carabids prefer undisturbed habitats and disappear under anthropogenic pressure, which is a common phenomenon (Ribera et al., 2001; Kotze, O’Hara, 2003). High sensitivity of large-sized species to the habitat conditions may be due to low abundance of populations, low egg production, and longer development of larvae, which makes them vulnerable to violations of the soil cover (Kotze, O’Hara, 2003). Important factors may be also their high requirements to habitat conditions (specialized species suffer more from habitat changes than nonspecialized species) and the limited ability to dispersal, which impede maintenance of the population abundance

Table 2. The results of the two-way ANOVA of differences between the years and zones of pollution by the size characteristics of carabids in the spruce—fir forest studied

Parameter	Source of variation		
	Year (<i>df</i> = 1)	Pollution zone (<i>df</i> = 2)	Year × pollution zone (<i>df</i> = 2)
Unweighted mean size	0.5 (0.475)	20.5 (<0.001)	0.5 (0.613)
Weighted mean size	3.9 (0.068)	1.9 (0.190)	1.3 (0.304)
Gini coefficient	49.7 (<0.001)	6.3 (0.011)	1.5 (0.254)
Lorenz asymmetry coefficient	0.01 (0.933)	0.22 (0.808)	0.02 (0.977)

The F-test is given, in brackets—the achieved level of significance. The experimental unit—site (background and impact zones— $n = 3$; buffer zone— $n = 4$).

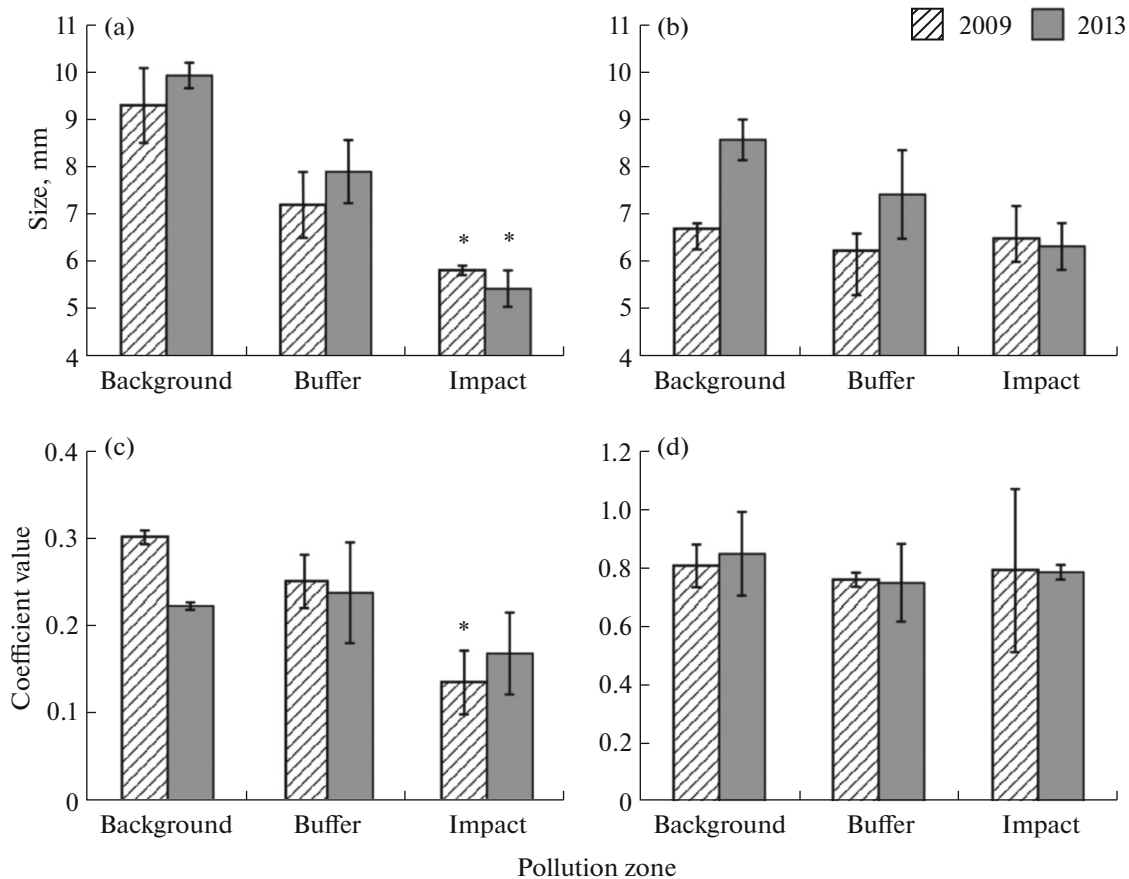


Fig. 4. Characteristics of the size structure of carabid community in different pollution zones: a—unweighted mean size of an individual, mm; b—weighted mean size of an individual, mm; c—Gini coefficient; d—Lorenz coefficient. Error bars—standard error; experimental unit—site (background and impact zones— $n = 3$; buffer zone— $n = 4$); *—significant ($0.01 < p < 0.05$) differences from the background zone (Tukey HSD test).

under unfavorable conditions by means of migrations. However, these features fail to explain fully decreased abundance of large species in polluted territories around the MUCS, because specialized forest dwellers (*C. aeruginosus*, *C. glabratus*, *C. schoenherri*, *C. caraboides*) disappear along with nonspecialized forest–meadow species (*C. granulatus*, *P. melanarius*, *P. niger*). The main type of locomotion of all above-mentioned species is movement on the soil surface (Sharova, 1981). Nevertheless, some individuals in the populations of *P. niger*, *P. melanarius*, and *C. granulatus* may have well-developed wings and active wing muscles and, thus, are capable of flying (Matalin, 2003).

In our opinion, the assumption about the leading role of food supply reduction in the impact territory is the most likely. The large body size determines high energy requirements to ensure the life activity of an individual (Grüm, 1980). Thus, large beetles must consume significantly more prey than small- and medium-sized beetles or their prey should also be large. The dietary spectrum of large carabids is wide (Dennison and Hodkinson, 1983). It mostly includes

earthworms and slugs, especially in females (Sergeeva and Gryuntal', 1990). Along the gradient of pollution with emissions from the MUCS, the abundance of most invertebrates in the litter and soil layers (centipedes, spiders, harvestmen, nematodes, potworms, dipteran and elaterid larvae) significantly decreases, and the largest potential prey of carabids (earthworms and mollusks) were not found in the heavily polluted territory (Vorobeichik et al., 2012; Nesterkov, 2013). In the case of food shortage, the activity of beetles increases (Lenski, 1984), which should result in a more energy-consuming search for food objects. As the number of prey decreases, the fertility of females decreases and the mortality of larvae increases due to starvation and cannibalism (Heessen, 1980; Heessen and Brunsting, 1981). In this situation, it is more difficult for large-sized individuals to provide themselves with a sufficient amount of food to maintain their activity and reproduction than for smaller individuals. The dietary spectrum of *P. oblongopunctatus*, a medium-sized species dominating in all zones, coincides with the spectrum of large-sized species of the genus *Pterostichus*, but the demand for food resources

in *P. oblongopunctatus* should be significantly lower owing to the summer diapause and a lower proportion of active beetles than in *P. niger* and *P. melanarius* (Sergeeva and Gryuntal', 1990). These features may contribute to maintenance of the high abundance of *P. oblongopunctatus* in the impact zone.

The registered interannual differences in the size structure of the community of carabids that were most pronounced in the background territory are related to the abundance dynamics of some dominant species.

CONCLUSIONS

Each considered parameter describes only a particular aspect of the size structure of the carabid community. The use of different parameters results in opposite conclusions on the effect of industrial pollution on the size structure of carabid communities. For example, a decrease in the unweighted mean size of an individual in the heavily polluted territory compared to the background zone supports the hypothesis on reduction in the mean size of an individual in the community of carabids as the pollution increases. At the same time, the weighted mean size of an individual does not depend on pollution, thereby disproving this hypothesis. A decrease in the Gini coefficient along the gradient of pollution indicates a reduction in the size diversity of the community. The absence of significant differences in the Lorentz coefficient points to small differences in the patterns of size distribution. Only simultaneous analysis of several indices allows the understanding of what changes take place in the community of carabids under the effect of pollution and to assess their significance.

In our case, differences between the communities of carabids in the background and polluted sites are associated with the decrease in the number of large-sized species, while their similarity is explained by the dominance of medium- and small-sized species in all sites. We believe that the disappearance of large carabid species at the high pollution level is related to the dramatic decrease in the abundance of their prey. The significant interannual variability in the ratio of size groups in the communities of the areas with background and moderate pollution levels may be a result of the temporal populations dynamics of particular species.

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