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Changes in the Structure of Chortobiont Invertebrate Community Exposed to Emissions from a Copper Smelter

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Abstract—The aboveground phytomass of meadow plants and the density of chortobiont invertebrates in secondary upland meadows were estimated using a biocenometer in three areas differing in the level of pollution with emissions from the Middle Ural Copper Smelter (Revda, Sverdlovsk oblast) in 2006 and 2007. As the smelter is approached, the total amount of phytomass (dry weight) decreases by a factor of 1.3–1.9, with the proportion of grasses reaching 100%; the total abundance of invertebrates increases two- to threefold due to sucking phytophages, which account for up to 80% of the invertebrate community. The abundance of gnawing phytophages near the smelter is reduced, with some taxa entirely missing (e.g., mollusks and phalangiid harvestmen). Rearrangements in chortobiont community structure are attributable to changes in the physiological state of plants and in the species diversity and architecture of the herbaceous layer, with consequent modification of hydrothermal conditions in it, as well as by the direct toxic effect of heavy metals.

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Key words: chortobiont invertebrates, meadows, herbaceous layer, biocenometer, insects, Hemiptera, Cicadinea, trophic structure, phytophages, zoophages, density, industrial pollution, copper smelter, heavy metals, Middle Urals.

Beginning from the classic works of Valentin A. Dogel and Vladimir N. Beklemishev, invertebrates inhabiting the herbaceous layer have been traditionally regarded as an individual stratum of the terrestrial fauna (Chernov and Rudenskaya, 1975). The close association of chortobionts with plants leads one to expect their pronounced response to changes in the structure of the herbaceous layer caused by various adverse factors, including pollution. The functioning of chortobionts under the influence of industrial emissions is still poorly known, unlike the situation with other kinds of anthropogenic impact (livestock grazing, hay harvesting, irrigation, etc.). Only a few studies concern responses to pollution of the entire chortobiont community (Vorobeichik et al., 1994) or of a relatively wide set of its constituent groups (Perner et al., 2003). More attention has been paid to individual taxa: Orthoptera (Hoffman et al., 2002), Homoptera (Glowacka et al., 1997), Formicidae (Gilev, 1998), Aranei (Tarwid, 1987), and Mollusca (Rabitsch, 1996).

Meanwhile, the study of the entire invertebrate community inhabiting the herbaceous layer in the context of the classic biocenological approach is necessary for comparing the responses of different invertebrate groups within this community as well as for comparing chortobionts with other components of the biota. A comprehensive study of the chortobiont community is also important for characterizing its role in the biological cycle and for discussing issues concerning the structure and stability of trophic chains, the connection between production and biological diversity, and relationships within the plants–phytophages–zoophages system.

The purpose of this study was to reveal trends in the dynamics of abundance and structure of the meadow chortobiont community at the level of large taxa and trophic groups under conditions of long-term pollution with emissions from a copper smelter.

STUDY AREA

The study was carried out in the environs of the Middle Ural Copper Smelter located in the outskirts of Revda, Sverdlovsk oblast. The smelter has been in operation since 1940 and is placed among the largest sources of industrial pollution in Russia. The main components of its emissions are SO_2 and heavy metals (Cu, Zn, Cd, and Pb). The total amount of emissions exceeded 140000 t per year in the late 1980s but decreased to less than 30000 tons per year by the mid-first decade of the 21st century. The pattern of technogenic transformation of ecosystems was described in detail by Vorobeichik et al. (1994). Samples were taken in the impact, buffer, and background zones (1, 4, and

30 km west of the smelter, respectively) in depressed topographic areas occupied by secondary upland meadows with soddy podzolic soils. These meadows formed in glades (300–5000 m^2) resulting from forest clearcutting more than 50 years ago.

The floristic composition of the meadows changes considerably along the pollution gradient, with more sensitive herb species being replaced by pollution-tolerant grasses. Characteristic of the background zone are herb meadows dominated by *Cirsium heterophyllum* Hill., *Alchemilla* sp., *Filipendula* sp., *Leucanthemum vulgare* Lam., *Centaurea phrygia* L., and *Trollius europaeus* L. The plant cover is dense, multilayered, with a complex architecture formed by branching and intertwining herbaceous plants. The meadows of the buffer zone are herb–grass meadows dominated by *Agrostis tenuis* Sibtb., *Deschampsia caespitosa* Beauv., *Phleum pratense* L., *Cirsium heterophyllum*, and *Lathyrus pratensis* L. Characteristics of the plant cover are similar to those in the background meadows (relatively high density with well-developed stratification and architecture). The meadows of the impact zone are of a grass type, with absolute dominance of *Agrostis tenuis* and a minor proportion of *Deschampsia caespitosa* and *Coronaria flos-cuculi* A. Br. The plant cover is sparse, without distinct stratification.

All these meadows were regularly cut for hay in midsummer until withdrawn from agricultural use, first in the impact zone (in the mid-1980s), then in the buffer zone (in the mid-1990s), and finally in the background zone (in 2005). Neither hay harvesting nor livestock grazing took place in the study area in 2006 and 2007.

MATERIALS AND METHODS

The material was collected over two years, in three rounds, mostly at the end of summer months. The dates of the rounds were as follows: (I) June 21–July 1; (II) July 19–21, July 26–29, July 31–August 3; and (III) August 12–18, September 1–3 in 2006 and (I) June 22, June 24–July 2; (II) July 21–22, July 26–August 1; and (III) August 19–23, 26–29 in 2007. The breaks in the rounds were caused mostly by rains, during which sampling was suspended.

Censuses of invertebrates were taken with a modified Konakov–Onisimova's biocenometer (Fasulati, 1971). This device consisted of a metal 50 × 50-cm frame with a hermetically attached cube-shaped cloth sack in which one side (screen) was made of mill gauze (mesh size 0.25 mm), and the other sides were made of tarpaulin. The side opposite to the screen had an access hole with a valve. The biocenometer was carefully placed on an even surface, and all plants inside it were carefully cut with scissors immediately above the ground surface and removed through the valve; insects attached to them were collected manually. After the removal of plants, invertebrates remaining in the biocenometer were collected with a specially modified vacuum cleaner with autonomous power supply. The screen was cleaned with particular care because of mass accumulation of invertebrates with positive phototaxis on its surface; the ground surface and bases of plant stems also received special attention. Vacuum cleaning was performed two to three times, until new invertebrates ceased to appear on the screen. After that, the biocenometer was turned upside down to examine its inner surface, including the seams, and the ground surface. All the collected invertebrates were sacrificed with ethyl acetate, and the sample was packed in a nylon gauze bag, labeled, and fixed in 70% ethanol.

Sampling plots 50 × 50 m in size, three plots per zone, were positioned at distances of 100–300 m from each other. All censuses were taken in the daylight period, after complete dew evaporation and before the descent of the sun below tree tops (approximately from 9–10 a.m. to 19–20 p.m. local time). To exclude possible displacement of estimations, all three plots in a certain zone were examined on the same day, with the same number of samples taken from each plot. The sequence of this procedure was adjusted so that the morning, midday, and evening samples from the same plot were available. Different zones were also visited consecutively during the same round. The points for installing the biocenometer were chosen randomly but at intervals of no less than 5 m. Ten samples per plot were taken during each round. Thus, a total of 540 samples (270 each year) were taken and more than 41 700 specimens of invertebrates were collected over the study period. The invertebrates were identified in the laboratory to the lowest possible taxonomic level, usually to families (Hemiptera were identified to species), and the number of specimens representing each taxon was counted. For each sample of plants, the total air-dry weight and the total weight of graminoids (grasses and sedges) were measured with 0.1-g accuracy.

RESULTS

The abundance and structure of meadow vegetation proved to change significantly depending on the level of industrial pollution (Fig. 1). The amount of aboveground phytomass (dry weight) in the impact zone was reduced by a factor of 1.3–1.9, compared to the background zone. The proportion of graminoids in the community increased from 20–30% in the background zone to 30–50% in the buffer zone and then to 99–100% in the impact zone. Both the total biomass and the proportion of graminoids in it differed from year to year, being markedly higher in 2006 than in 2007.

In the background zone, the bulk of chortobiont community in all censuses consisted of sucking phytophages from the orders Homoptera (suborders Aphidinea, Cicadinea, and Coccinea) and Hemiptera (families Tingidae, Miridae, Lygaeidae, Neididae, Coptosomatidae, Rhopalidae, Pentatomidae, Coreidae, and

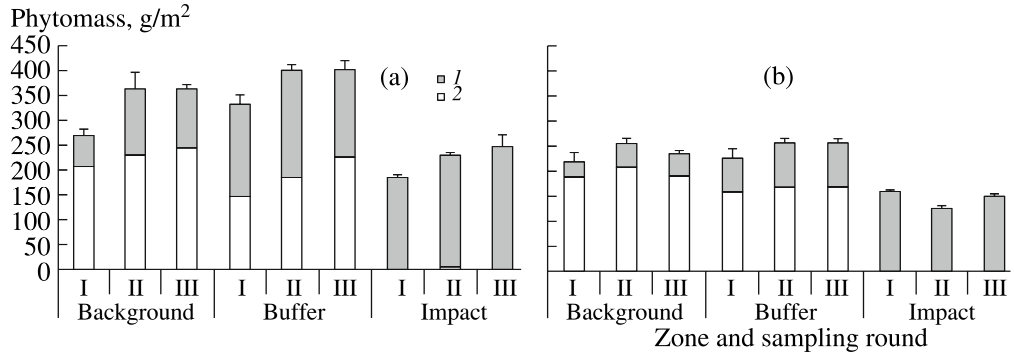

Fig. 1. Dynamics of aboveground phytomass of the herbaceous layer in zones with different pollution levels (a) in 2006 and (b) in 2007: (I–III) sampling rounds, (*1*, *2*) phytomass fractions (*1*, grasses and sedges; *2*, other species); vertical lines show standard deviation for total phytomass (census unit: sampling plot, $n = 3$).

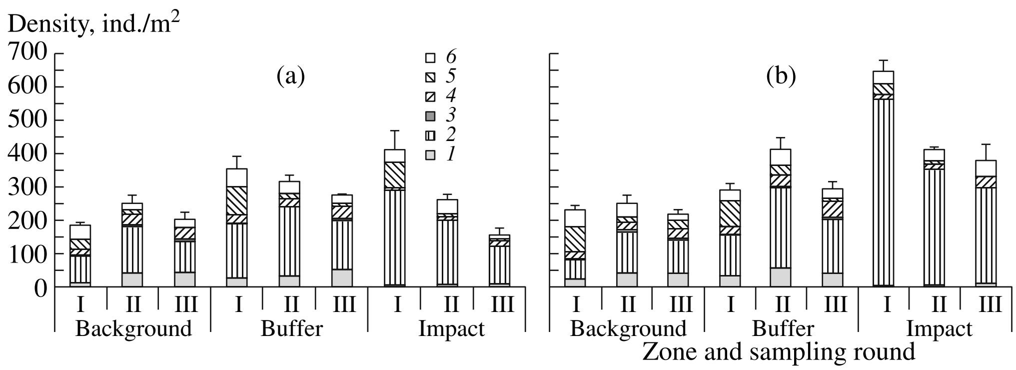

Fig. 2. Dynamics of invertebrate density in zones with different pollution levels (a) in 2006 and (b) in 2007: (I–III) sampling rounds; (*1–6*) trophic groups of chortobionts (*1*, gnawing phytophages; *2*, sucking phytophages; *3*, gnawing zoophages; *4*, sucking zoophages; *5*, bloodsuckers; *6*, other invertebrates); vertical lines show standard deviation for total density (census unit: sampling plot, $n = 3$).

Scutelleridae), anthophagous insects of the order Diptera (suborder Brachycera), and adults of the order Lepidoptera (Fig. 2, Table 1). Homopterans of the suborder Cicadinea and hemipterans of the family Miridae were especially abundant: their proportions were 41.8 and 4.4% in 2006 and 32.8 and 3.7% in 2007, respectively.

Second in abundance were gnawing phytophages of the orders Orthoptera (family Acrididae), Coleoptera (families Carabidae, Chrysomelidae, Curculionidae, Brentidae, Cerambycidae, Buprestidae, Byrrhidae, Elateridae, Malachiidae, Mordellidae, Nitidulidae, Oedemeridae, Lathridiidae, and Scarabaeidae), and Hymenoptera (suborder Symphyta and adults of the family Ichneumonidae, as well as the group Hymenoptera parasitica combining adults of numerous small parasitic hymenopterans), larvae of the order Lepidoptera, and mollusks. Especially great was the proportion of beetles of the family Chrysomelidae (up to 2.5% in 2006 and 1.9% in 2007), lepidopteran larvae (up to 2.8% in 2006 and 2.9% in 2007), and mollusks (up to 12.4% in 2006 and 11.1% in 2007).

Sucking zoophages were represented by the orders Hemiptera (families Saldidae, Nabidae, Anthocoridae, Reduviidae, and Pentatomidae), Diptera (family Asilidae), larvae of the order Neuroptera (family Chrysopidae), as well as by the order Aranei (families Araneidae, Clubionidae, Dictyonidae, Gnaphosidae, Liniphyidae, Lycosidae, Philodromidae, Pisauridae, Salticidae, Tetragnathidae, and Thomisidae). Especially great was the proportion of hemipterans of the family Nabidae (up to 1.6% in 2006 and 1.3% in 2007) and spiders of the family Salticidae (up to 1.6% in 2006 and 1.1% in 2007).

Relatively low was the abundance of gnawing zoophages of the orders Orthoptera (family Tettigoniidae), Coleoptera (families Carabidae, Pselaphidae, Staphylinidae, Silphidae, Colydiidae, Cantharidae, and Coccinellidae), Odonata, Chilopoda (family Lithobiidae), Opiliones (families Phalangiidae and Nematosto-

Table 1. Density (ind./m^2) of taxonomic and trophic groups of chortobiont invertebrates in zones with different pollution levels (average for all rounds ± standard deviation, with sampling plot (n = 9) taken as a census unit)

Taxon (group)	Zone					
	2006			2007		
	background	buffer	impact	background	buffer	impact
Taxon:						
Tettigoniidae	0.6 ± 0.2	0.4 ± 0.1	0.2 ± 0.1	0.4 ± 0.3	0.9 ± 0.3	0.3 ± 0.1
Acrididae	0.8 ± 0.3	1.2 ± 0.4	1.3 ± 0.4	0.3 ± 0.1	0.6 ± 0.2	1.9 ± 0.6
Cicadinea	72.7 ± 12.9	140.5 ± 13.8	151.5 ± 20.0	63.0 ± 9.3	120.8 ± 15.2	346.8 ± 50.3
Aphidinea	1.0 ± 0.2	1.5 ± 0.4	3.6 ± 1.8	3.4 ± 0.7	12.1 ± 4.2	17.4 ± 6.1
Nabiidae	3.1 ± 0.6	5.4 ± 1.0	1.2 ± 0.4	1.1 ± 0.4	2.7 ± 1.0	1.5 ± 0.7
Miridae	6.4 ± 1.5	11.6 ± 2.6	25.7 ± 5.9	6.0 ± 1.3	14.6 ± 4.1	19.3 ± 3.5
Coccinellidae	0.3 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.4 ± 0.2	0.4 ± 0.2	0.2 ± 0.1
Chrysomelidae	3.9 ± 0.5	2.7 ± 1.0	0.2 ± 0.1	3.2 ± 0.6	6.6 ± 2.2	0.1 ± 0.1
Lepidoptera larvae	3.6 ± 0.9	6.7 ± 1.2	0.5 ± 0.1	4.2 ± 1.2	14.2 ± 4.2	3.1 ± 1.0
Symphyta larvae	3.2 ± 0.6	2.5 ± 0.5	–	5.2 ± 1.4	2.7 ± 0.6	–
Hymenoptera parasitica	4.9 ± 1.0	10.3 ± 2.4	11.3 ± 2.6	6.0 ± 0.8	13.5 ± 2.2	23.6 ± 4.1
Diptera, Brachycera (anthophagous)	14.1 ± 2.7	14.8 ± 2.4	10.9 ± 2.0	11.5 ± 0.9	23.0 ± 4.8	15.2 ± 2.8
Diptera (bloodsucking)	13.8 ± 4.2	35.9 ± 13.3	30.3 ± 17.6	40.1 ± 11.7	38.2 ± 11.5	15.0 ± 5.8
Diptera, Nematocera	7.7 ± 2.3	10.1 ± 2.0	6.0 ± 2.8	15.2 ± 3.1	11.3 ± 1.6	5.6 ± 0.9
Salticidae	2.2 ± 0.3	2.1 ± 0.4	1.8 ± 0.4	2.1 ± 0.4	1.4 ± 0.3	2.6 ± 0.2
Phalangiidae	3.9 ± 1.3	1.0 ± 0.4	–	4.0 ± 1.2	1.9 ± 0.8	–
Mollusca	18.0 ± 4.2	18.4 ± 2.2	–	21.9 ± 1.6	13.9 ± 1.8	–
Other invertebrates	52.6 ± 4.5	50.7 ± 4.1	30.2 ± 1.4	48.5 ± 2.8	57.5 ± 4.8	32.7 ± 2.0
All invertebrates	212.6 ± 14.5	314.4 ± 17.7	274.8 ± 40.8	236.6 ± 11.6	336.4 ± 24.8	485.3 ± 45.6
Trophic group:						
gnawing phytophages	33.2 ± 5.6	36.8 ± 4.4	7.4 ± 1.1	37.0 ± 3.7	43.6 ± 4.1	6.5 ± 0.9
sucking phytophages	103.2 ± 14.9	171.3 ± 14.9	194.3 ± 25.3	92.6 ± 11.5	177.0 ± 20.8	402.8 ± 44.9
gnawing zoophages	6.8 ± 1.4	3.9 ± 1.1	0.6 ± 0.2	7.2 ± 1.7	5.1 ± 0.8	0.8 ± 0.3
sucking zoophages	27.2 ± 2.6	28.0 ± 2.9	11.4 ± 1.5	23.4 ± 1.9	35.5 ± 5.8	20.3 ± 3.2
bloodsuckers	13.8 ± 4.2	35.9 ± 13.3	30.3 ± 17.6	40.1 ± 11.7	38.2 ± 11.5	15.0 ± 5.8
others	28.5 ± 4.2	38.4 ± 4.8	30.8 ± 4.6	36.3 ± 5.3	36.9 ± 4.0	39.8 ± 3.3

matidae), as well as adults of the order Neuroptera (family Chrysopidae). Among them, phalangiid harvestmen were the most abundant group (up to 3.2% in 2006 and 2.6% in 2007).

The abundance of bloodsucking insects (families Simuliidae and Tabanidae) was high (up to 33.6%), but they were obviously attracted by the person who collected the samples. The group designated "other invertebrates" comprised poorly represented taxa with trophic specialization other than listed above—insects of the families Hydrophilidae, Catopidae, and Trogidae (Coleoptera) and of the superfamily Apoidea and families Eumenidae, Pompilidae and Formicidae (Hymenoptera), as well as earthworms and cockroaches—and a number of taxa not identified accurately enough to estimate their trophic specialization, such as dipterans of suborder Nematocera, ticks and mites (Acari), and coleopteran and hymenopteran larvae.

The total abundance of invertebrates increased considerably closer to the smelter. In 2006, their density in the impact zone was 2.2 times that in the background zone and 1.9 times that in the buffer zone; in 2007, the respective ratios were 2.8 and 1.3.

Different groups of invertebrates differed in their response to pollution, which accounted for certain trends of changes in the community structure. The relative abundance of sucking phytophages increased considerably closer to the smelter: in 2006, the proportions of Cicadinea and Miridae in the buffer zone were 53.2 and 5.8%, reaching 53.3 and 12.0% in the impact zone; in 2007, they were 42.0 and 6.4% vs. 80.8 and 1.2%, respectively. Conversely, the abundance of gnawing phytophages was considerably lower near the smelter. The proportions of chrysomelid beetles and larval lepidopterans in the buffer zone reached the highest values (up to 2.0 and 3.6% in 2006 and up to 4.3 and 7.4% in 2007), whereas those in the impact zone did not exceed 0.2 and 1.9%, respectively, in both years; mollusks were totally lacking in the impact zone. In general, the abundance of sucking carnivores decreased closer to the smelter, although in some taxa (e.g., Salticidae spiders) no trend was observed. Gnawing zoophages, the least numerous group, showed a distinct decrease in abundance closer to the smelter. Phalangiid harvestmen were common at background sites, but their abundance dropped sharply in the buffer zone (down to 0.8% in 2006 and to 1.5% in 2007), and they were not found at all in the herbaceous layer of the impact zone.

In the background zone, the abundance of all invertebrates, including sucking phytophages, was maximal in July and slightly lower in August. The abundance of gnawing phytophages and zoophages increased during summer, reaching a peak in August. Closer to the smelter, the seasonal dynamics of abundance had a somewhat different pattern. In the buffer zone, the total abundance of invertebrates reached a peak in early summer (2006) or in midsummer (2007); in the impact zone, the greatest values in both years were observed in June. Thus, differences between the zones were more distinct in early summer and leveled off by the end of summer.

Since the assumptions of standard ANOVA did not hold for our data, we used its nonparametric counterpart, the Scheirer–Ray–Hare test (Table 2). The abundance of most invertebrate groups (with the exception of Tettigoniidae, Coccinellidae, anthophagous Brachycera, and Salticidae) differed considerably between the zones. Differences between the rounds (i.e., seasonal dynamics) at the level of individual taxa were weakly manifested (they were observed in only half of the cases), and those at the level of trophic groups were distinct only in sucking zoophages and bloodsuckers. Differences dependent on the year of sampling were significant in only three taxa (Aphidinea, Nabidae, and Hymenoptera parasitica). The effect of pairwise interactions between the above sources of variance was significant only at the level of particular taxonomic, but not trophic, groups: "zone × round," only for anthophagous Brachycera; "round × year," for Miridae and Hymenoptera parasitica; and "zone × year," for none of the taxa.

DISCUSSION

The structure and dynamics of chortobiont communities have been well studied in natural meadows. In terms of composition and proportions of taxonomic and trophic invertebrate groups, the territory we used as control was generally similar to undisturbed territories of the Urals, such as the Il'men Nature Reserve (Lagunov, 1994; Chashchina, 2000) and Visim Nature Reserve (Fedyunin et al., 2008).

The pattern of meadow vegetation changes drastically as the source of pollution is approached: the total aboveground phytomass decreases by half, with herbs disappearing almost completely and grasses gaining absolute dominance. According to Khantemirova (2004), the species richness of meadow plants between 1999 and 2002 was 63–69 species in the background zone (20–30 km from the smelter), 30–54 species in the buffer zone (4–7 km), and only 3–5 species in the impact zone (1–2 km), with the respective amounts of phytomass (air-dry weight) being 150–270, 110–200, and 70–130 g/m^2. However, an opposite pattern was observed in July 1989, when the phytomass in the impact zone was twice as great as in the background zone (Vorobeichik et al., 1994). The fourfold difference in the amount of aboveground phytomass may be explained by the well-known effect observed upon cessation of hay harvesting: a thick litter layer accumulated over many years interferes with plant growth. An additional factor contributing to litter formation is the retardation of decay processes, well documented for this territory (Vorobeichik, 2007). The apparent consequences of decrease in the abundance and diversity of meadow plants include changes both in the spectrum of food objects for phytophages and in local hydrothermal conditions (lower air humidity and increasing amplitude of daily temperatures).

Considerable changes dependent on pollution level also take place in the chortobiont community. The total abundance of these invertebrates near the smelter increases two- to threefold, mainly on account of sucking phytophages dominated by Cicadinea and Miridae. Gnawing phytophages and zoophages become scarce in this zone or disappear completely (mollusks and Phalangiidae harvestmen). Some taxa (Chrysomelidae, Nabidae) are most abundant in the zone with an intermediate pollution level.

According to Kozlov (1990), changes in the abundance of invertebrates under anthropogenic influences (in our case, industrial pollution) may be accounted for four types of responses. The first type, with abundance increasing in the zone of strong pollution, is characteristic mainly of sucking phytophages. We observed it in Cicadinea, Aphidinea, herbivorous Hemiptera, as well as in gnawing zoophages (Tettigoniidae and adult Hymenoptera parasitica). The second type, with a peak abundance at a certain distance from the source of emissions, was observed in many gnawing phytophages (larval Lepidoptera and Brachycera dipterans), as

Table 2. Results of three-way ANOVA for differences in chortobiont invertebrate density between zones, years, and sampling rounds

Taxon (group)	Source of variance											
	Zone		Round		Year		Zone × round		Zone × year		Round × year	
	H	*p*	*H*	*p*	*H*	*p*	*H*	*p*	*H*	*p*	*H*	*p*
Taxon:												
Tettigoniidae	2.08	0.3537	13.98	0.0009	0.08	0.7812	2.56	0.6338	4.04	0.1327	1.73	0.4214
Acrididae	6.05	0.0485	5.59	0.0610	0.36	0.5477	5.24	0.2633	1.01	0.6046	1.30	0.5211
Cicadinea	27.62	<0.0001	3.96	0.1382	0.46	0.4999	5.96	0.2018	4.38	0.1122	0.79	0.6743
Aphidinea	3.42	0.1807	0.82	0.6643	20.99	<0.0001	4.01	0.4048	0.55	0.7582	1.45	0.4843
Nabiidae	7.01	0.0300	19.55	0.0001	6.28	0.0122	0.79	0.9393	3.06	0.2165	5.55	0.0623
Miridae	16.52	0.0003	11.05	0.0040	0.01	0.9310	3.27	0.5143	0.16	0.9249	6.90	0.0317
Coccinellidae	2.26	0.3238	0.79	0.6739	0.22	0.6377	6.51	0.1644	0.71	0.6996	0.53	0.7687
Chrysomelidae	31.17	<0.0001	2.36	0.3078	0.40	0.5293	4.06	0.3974	2.81	0.2456	0.19	0.9079
Lepidoptera larvae	21.62	<0.0001	11.17	0.0038	2.94	0.0862	3.04	0.5508	1.17	0.5563	0.65	0.7210
Symphyta larvae	37.52	<0.0001	3.89	0.1427	0.10	0.7507	3.17	0.5293	0.09	0.9547	0.27	0.8734
Hymenoptera parasitica	16.41	0.0003	6.67	0.0356	4.76	0.0292	1.85	0.7638	1.73	0.4206	13.25	0.0013
Diptera, Brachycera (anthophagous)	2.98	0.2253	3.94	0.1395	0.97	0.3239	16.04	0.0030	1.81	0.4054	5.95	0.0511
Diptera (bloodsucking)	30.12	<0.0001	3.95	0.1389	1.97	0.1609	1.13	0.8901	0.46	0.7937	3.11	0.2116
Diptera, Nematocera	15.26	0.0005	8.94	0.0114	2.97	0.0849	7.70	0.1031	0.02	0.9893	1.08	0.5839
Salticidae	2.05	0.3587	3.45	0.1779	0.08	0.7804	3.23	0.5209	4.98	0.0831	0.30	0.8599
Phalangiidae	25.55	<0.0001	8.49	0.0144	0.19	0.6637	4.76	0.3128	0.10	0.9516	1.21	0.5473
Mollusca	37.93	<0.0001	2.62	0.2694	0.02	0.8878	3.09	0.5428	1.18	0.5555	1.58	0.4537
Other invertebrates	2.64	0.2675	30.86	<0.0001	0.32	0.5738	0.52	0.9718	1.46	0.4815	0.42	0.8096
All invertebrates	19.15	0.0001	6.17	0.0458	4.94	0.0262	5.83	0.2125	4.48	0.1063	1.12	0.5723
Trophic group:												
gnawing phytophages	34.17	<0.0001	7.49	0.0237	0.37	0.5448	1.49	0.8291	0.60	0.7418	0.46	0.7964
sucking phytophages	26.99	<0.0001	4.29	0.1173	1.30	0.2535	5.91	0.2058	1.30	0.5217	3.80	0.1492
gnawing zoophages	31.52	<0.0001	0.73	0.6940	0.53	0.4665	2.56	0.6348	1.25	0.5353	0.65	0.7223
sucking zoophages	18.91	0.0001	15.87	0.0004	1.27	0.2606	0.74	0.9468	0.31	0.8558	3.57	0.1681
bloodsuckers	3.95	0.1389	30.12	<0.0001	1.97	0.1609	1.13	0.8901	0.46	0.7937	3.11	0.2116
others	0.65	0.7232	14.58	0.0007	0.99	0.3197	3.33	0.5043	3.04	0.2189	1.00	0.6079

Note: *H*, Scheirer–Ray–Hare test; *p*, significance level.

well as in carnivorous Hemiptera. The third type of response, with abundance decreasing closer to the source of emissions, was observed in most gnawing invertebrates, both phyllophagous (Coleoptera, larval Symphyta hymenopterans, and mollusks) and zoophagous (Coleoptera and Opiliones). The fourth type, with abundance remaining unchanged, is characteristic of only a few invertebrate taxa, including some families of spiders. Thus, we may conclude that sucking phytophages are the group of chortobionts most tolerant to pollution with emissions from the copper smelter, gnawing zoophages are the group most sensitive to this factor, while gnawing phytophages and sucking zoophages occupy an intermediate position.

The results of a single census of chortobionts taken in the environs of the same smelter in July 1989 (Vorobeichik et al., 1994) differ slightly from those described above: general trends in total invertebrate abundance and trophic structure were the same, but the proportion of sucking phytophages in the buffer zone almost equal to that in the impact zone due to the absence of mollusks and dominance of Cicadinea in the former. This fact can be explained by considerable interannual variation in the abundance of Cicadinea (Table 1) and a mosaic distribution of mollusks. Another possible explanation is the absence of hay harvesting and almost fivefold decrease in the amount of emissions over the past 20 years.

We are unaware of any other comprehensive studies on the influence of copper smelter emissions on chortobiont communities. However, data on invertebrates inhabiting the tree and shrub layers are indicative of a broad range of their responses to this factor. On the Kola Peninsula, for example, the abundance of insects near the source of emission, compared to that in the background zone, is increased in mining Lepidoptera (Zvereva and Kozlov, 2006) and *Chrysomela lapponica* (Zvereva and Kozlov, 2000) but decreased in Noctuidae moths (Kozlov et al., 1996a), butterflies (Kozlov et al., 1996b), and bloodsucking insects (Kozlov et al., 2005).

Diverse responses of invertebrates have also been observed near other types of industrial pollution sources. It means that the direction and degree of changes in invertebrate communities are determined not only by individual responses of their constituent groups but also by the type and level of pollution. For instance, alkalinization of upper soil horizons near a phosphate fertilizer plant in Germany, with soil pH increasing from 7 to 9, resulted in a reduced species richness of both herbaceous plants and gnawing phytophages most closely associated with them; the response of sucking zoophages was less distinct, while gnawing zoophages were indifferent to the change in plant species richness (Perner et al., 2003). In another example, alkalinization of acid forest soil (with pH increasing from 4 to 6) near a source of SO_2 and calcium compound emissions in central Germany provided for a considerable increase in the species richness of plants and phytophagous Hemiptera against the background of decrease in the total abundance of these insects (both phytophagous and zoophagous) (Brandle et al., 2001). In young birch forests exposed to SO_2 pollution in Silesia, the abundance of Aphidinea and Hemiptera in the zone of strong pollution was increased, while that of Formicidae and Attelabidae was decreased; Cicadinea, free-living larval Lepidoptera, some Coleoptera (Curculionidae, Chrysomelidae, and Elateridae) and zoophages of several orders (larval Neuroptera and Syrphidae and adult Coccinellidae) were most abundant in the zone of moderate pollution (Chlodny and Styfi-Bartkiewicz, 1982).

Discussing the possible cause-and-effect relationships between industrial pollution and changes in chortobiont communities, it is worth noting that the observed effects are the resultants of several differently directed processes. First, components of industrial emissions, ingested or inhaled, have a direct toxic effect on invertebrates, which leads to suppression of more sensitive groups. Numerous toxicological experiments provide evidence that insect mortality increases while fecundity decreases at high concentrations of toxic agents in the environment (Vickerman and Trumble, 2003; Cervera et al., 2004). Second, the species composition, diversity, and architecture of plant communities change in a polluted environment, and these changes, in turn, result in modification of both microclimatic conditions and food spectrum for phytophages. Observations made in nature (Schaffers et al., 2008) and experimental data (Koricheva et al., 2000) show that the species composition and diversity of plants are the main factors determining the structure and diversity of the invertebrate community. Third, the functional state of plants exposed to pollution can change in the direction favorable for the development of phytophages. A nonspecific response of plants to various stress factors, including heavy metals, sometimes involves an increase in the concentration of free amino acid nitrogen in leaves, which improves their quality as food for phytophages (White, 1984) and, consequently, provides conditions for an increase in the abundance of these insects.

Moreover, changes in pollution-affected plants that may be important for phytophages include disturbances in water balance, hormonal status, and composition of secondary metabolites, as well as modifications of the leaf surface (Manning and Keane, 1988). The results of numerous experiments confirm an indirect stimulating effects of pollutants on sucking phytophages in general (Koricheva and Larsson, 1998) and on their individual groups, such as Aphidinea (Dohmen et al., 1984), Coleoptera (Hughes and Laurence, 1984), and larval Lepidoptera (Jeffords and Endress, 1984).

Fourth, the pressure of predators on other invertebrates in anthropogenic communities is often weakened: compared to other trophic groups, predators are more susceptible to toxicants, because these agents (e.g., heavy metals) accumulate in food chains or are consumed by predators in more toxic forms. This factor probably accounts for the increased abundance of *Chrysomela lapponica* near the Severonikel Combined Works (Zvereva and Kozlov, 2000). There is experimental evidence for a negative correlation between the accumulation of nickel in the bodies of Miridae bugs and the survival rate of spiders feeding on them (Boyd and Wall, 2001). Other elements, e.g. selenium (Vickerman and Trumble, 2003), arsenic, cadmium, and lead (Mackay et al., 1997), were not found to accumulate in the food chain, but their toxic effect on higher-level consumers was stronger due to chemical transformations of their compounds. Thus, selenium is most toxic in the organic form, into which most of it is transformed in phytophage bodies and, therefore, is available to predators, whereas phytophages themselves consume low-toxic selenates contained in plant tissues (Vickerman and Trumble, 2003).

The pattern of changes in the abundance of each functional group of invertebrates in a polluted environment depends on the balance between stimulation and suppression. In the study area, this balance is positive for phytophages and negative for zoophages. The main factors accounting for this situation are changes in the species composition and physiological state of plants in the former case and direct toxic effects in the latter case.

This explanation can be accepted on assumption that the invertebrate groups whose abundance increases near the smelter are indeed relatively tolerant to the direct action of pollutants. This assumption is indirectly supported by the results of many studies. For instance, some Miridae (Boyd et al., 2006a; Jnee et al., 2005), Cicadinea (Jnee et al., 2005), and Brachycera (Boyd et al., 2006a) feeding on plants with artificially increased concentration of heavy metals proved to accumulate these pollutants in their tissues without any distinct toxic symptoms. The same follows from studies on the communities of invertebrates associated with plants that hyperaccumulate metals from serpentinite soils (Boyd et al., 2006b). These studies supplemented the list of phytophages highly tolerant to toxins with two more groups, Pentatomidae bugs and Tephritidae flies. Evidence for high tolerance to large doses of heavy metals in zoophages is scarce: for example, some spiders, Mantodea, and Neuroptera are capable of feeding on prey with a high nickel content, accumulating this metal without any distinct adverse consequences (Boyd and Wall, 2001).

The disappearance of mollusks in the impact zone of the smelter is apparently explained mainly by changes in hydrothermal conditions, namely, by aridization of meadows, especially in midsummer. Direct toxic influence of pollutants is less likely to be the cause, because terrestrial mollusks are regarded as concentrators of some metals (cadmium, zinc, copper) that can accumulate them in large amounts even in relatively clean areas (Rabitsch, 1996).

Gnawing phytophages in the course of feeding damage subepidermal vacuoles, cuticle, and cell walls in which plants concentrate heavy metals, whereas sucking phytophages escape the influence of these pollutants (Jnee et al., 2005). Moreover, gnawing phytophages can ingest dust particles with absorbed metals directly from the plant surface. The increased consumption of toxicants by these invertebrates may well account for the observed differences in the trends of changes in abundance between sucking and gnawing phytophages.

Mechanisms of invertebrate adaptations to naturally increased concentrations of toxic agents were discussed in detail in relation to the concept of plant defense from phytophages via hyperaccumulation of metals (Boyd and Wall, 2001; Jnee et al., 2005; Boyd et al., 2006b). These mechanisms may operate in the contexts of three different strategies (Boyd et al., 2006b). The first strategy implies selective consumption exclusively of substrates poor in metals; the second, the consumption of substrates either rich or poor in metals in proportions allowing the maintenance of their concentrations in the body at tolerable levels; the third, the presence of specific physiological mechanisms of detoxification allowing the consumption of substrates rich in metals without negative consequences. Implementation of the first two strategies in the impact zone is unlikely, considering the dramatically decreased plant diversity, but the range of possible physiological detoxification mechanisms is extremely broad. In holometabolic insects, for instance, large proportions of metals accumulated by larvae are lost in the course of metamorphosis, both with integuments they shed and due to the development of previously metabolically inactive and, consequently, unpolluted tissues from imaginal discs (Davison et al., 1999). Dipteran larvae accumulate metals in gut epithelium cells, thereby excluding them from metabolism and periodically removing their excess with excrements (Boyd et al., 2006b). Hemimetabolic insects employ still different mechanisms: for instance, larval Aphrophoridae excrete metals while producing their protective cocoons (Jnee et al., 2005).

However, it may well be that specific physiological detoxification mechanisms play no principal role in the case considered in this study. Meadow plants, which are both food and home for chortobionts, are represented in the impact zone almost exclusively by grasses, *Agrostis tenuis* and *Deschampsia caespitosa*, which accumulate metals rather poorly. These species belong to pseudometallophytes, i.e., plants with stable genotypes that dominate in herbaceous communities with the highest levels of heavy metal pollution. Unlike true metallophytes (hyperaccumulators of metals), pseudometallophytes have an efficient root barrier preventing the accumulation of metals in leaves and stems (Dahmani-Muller et al., 2000). The abnormally high abundance of sucking phytophages near the smelter is probably explained not only by their high tolerance to toxic agents but also by relatively low concentrations of metals in food plants they prefer.

CONCLUSIONS

In studying trends in the functioning of invertebrate community in the herbaceous layer exposed to industrial pollution, we concentrated on the analysis of chortobiont assemblage as a whole in order to correctly evaluate the observed changes in its taxonomic and trophic structure.

Differently directed responses to pollution were observed in different functional groups of chortobionts: the abundance of sucking phytophages (Cicadinea, Aphidinea, Miridae) increased in the impact zone, whereas that of gnawing phytophages (Chrysomelidae, Lepidoptera and Symphyta larvae, mollusks) and zoophages (Cantharidae, Aranei, Opiliones, and Nabidae) decreased. Thus, the community structure of chortobionts changes and their abundance increases as the source of emissions is approached. In this respect, chortobionts are no different from inhabitants of the tree layer, in which a general response to pollution is considered to involve an increase in the abundance of sucking phytophages and a decrease in that of gnawing phytophages (Koricheva and Larsson, 1998).

A number of methodological aspects should be considered for interpreting these results correctly. First, chortobionts are understood in this study in the broadest sense, as invertebrates occurring in the herbaceous layer. Not all of them, however, can be considered chortobionts in the strict sense, since inhabitants of other layers—aerobionts, herpetobionts, and pedobionts—also occur periodically in the herbaceous layer. On the other hand, many of the species common in the herbaceous layer are actually associated with it only at certain stages of their life cycles, and it appears more correct to classify these forms with “tourists,” or chortophiles, rather than with typical chortobionts (Lagunov, 1994). At the same time, their a priori exclusion from the category of chortobionts may lead to biased conclusions about the structure and diversity of invertebrate community in the herbaceous layer. Second, attention should be paid to limitations of the method of census with a biocenometer, which underestimates the abundance of large, active invertebrates such as orthopterans. These insects are collected only occasionally, since they can notice the researcher from a distance and escape from the census site in advance. The biocenometer method is also imperfect for taking census of ants and bloodsucking insects, because the former easily enter and leave the biocenometer through tunnels in the soil and the latter are attracted to the researcher. Although members of these groups are sometimes abundant in samples, the data relating to them cannot be interpreted unambiguously but, at the same time, should not be ignored. Third, the experiment was designed so as to reveal the most general pattern of the chortobiont community and to minimize the influence of circadian dynamics, which needs a separate study.

An important methodological conclusion drawn from this study concerns the absence of significant interaction of factors in pairs “zone × year” and “zone × round.” This means that, regardless of interseasonal and interannual differences in the absolute abundance of individual groups, the general trend in the response of chortobionts to pollution is reproduced from year to year and remains relatively stable during the season. This stability of response in time simplifies its analysis in a certain sense, at least as concerns a conservative property of the community such as its structure at the level of large taxa and trophic groups. Interestingly, the trophic structure of the chortobiont community near the smelter has not changed significantly over the past 20 years, irrespective of a considerable decrease in toxic pressure, cessation of agricultural land use, and the consequent fourfold difference in the amount of phytomass. At the same time, the community of the buffer zone has become more similar to the community of the background zone and less similar to that of the impact zone, which it resembled previously.

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