Ant (Hymenoptera, Formicidae) *diversity along a pollution gradient near the Middle Ural Copper Smelter, Russia*

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RESEARCH ARTICLE

Ant (*Hymenoptera, Formicidae*) diversity along a pollution gradient near the Middle Ural Copper Smelter, Russia

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Abstract Ants are considered to be suitable indicators of ecological change and are widely used in land management and environmental monitoring. However, responses of ant communities to industrial pollution are less known so far. We studied pollution-related variations of ant diversity and abundance near the Middle Ural Copper Smelter (Russia) in 2009 and 2013, with pitfall traps set up at 10 sites in *Picea obovata* and *Abies sibirica* forest. This study provided evidences for humped pollution-induced dynamics of ant diversity and abundance. Species richness and diversity peaked in the habitat intermediate between slightly damaged and fully destroyed forest ecosystems. The total abundance of ants peaked in the middle of the pollution gradient and was determined mainly by the dominant species *Formica aquilonia*. The abundance of other species increased towards the smelter, but was less important for total abundance than that of red wood ants. Community dominants changed with increase of exposure; *F. aquilonia*, a typical species of mature forests, was replaced by species of open habitats, *Lasius niger* and *Myrmica ruginodis.* Habitat variables and competition between species seem to affect local ant communities more strongly than pollution exposure. Stand basal area and cover of the field layer were the main determinants of ant diversity and abundance of individual species.

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Introduction

Ant communities are widely used to monitor the state of ecosystems, their long-term changes and effects of anthropogenic stressors, including industrial pollution (Majer, 1983; Stary and Kubiznakova, 1987; Underwood and Fisher, 2006). Studies conducted near metallurgical factories have shown that ants are able to accumulate heavy metals more strongly than many other invertebrates (Bengtsson and Rundgren, 1984; Hunter et al., 1987; Rabitsch, 1995; Belskii and Belskaya, 2013). Heavy pollution results in decreased immune defence and body size of workers as well as lower colony size and density (Pętal, 1978; Eeva et al., 2004; Sorvari et al., 2007). Nevertheless, several ecological features of ants allow them to inhabit areas with high pollution exposure, such as social organisation, construction of nests protecting queens and workers from toxic exposure, division of individuals into castes with different abilities to accumulate pollutants, shifting activity to periods with least pollution exposure and so on (Pętal, 1978; Migula and Głowacka, 1996; Grześ, 2010a). Differences between species in ecological characteristics and abilities to regulate pollutant concentrations in the body (Grześ, 2009a, b, 2010b) determine the species specificity of responses to pollution and result in changes of ant community structure in polluted areas (Eeva et al., 2004). Many ant species prefer well-lightened and heated habitats, and anthropogenic deterioration of forest ecosystems may favour this group as a whole. For example, increases in ant diversity and evenness were observed along a pollution gradient near a zinc smelter in Poland (Grześ, 2009a). At the same time, many studies report negative effects of industrial pollution on ant communities (Pętal, 1978; Hoffman et al., 2000; Zvereva and Kozlov, 2010). According to the intermediate disturbance hypothesis (Connell, 1978), ant diversity can display a hump-backed response to stress factors. This has been observed for landscape disturbances such as military training and fire (Graham et al., 2009), but could not be shown for industrial pollution so far. Thus, the available data on ant responses to pollution are contradictory, and it is not clear which factors determine differences of responses between sources of emissions: exposure level, habitat characteristics or composition of ant communities.

Variations of ant communities near the Middle Ural Copper Smelter have been studied in the early 1990s (Vorobeichik et al., 1994). It was shown that species richness and density of colonies of soil-inhabiting species increased towards the smelter, with further decrease in the industrial barren. However, this study only considered a small number of sites and did not analyse the relationships between community indices and habitat variables.

The aim of the current study is to analyse variations of ant community structure along a pollution gradient near the Middle Ural Copper Smelter. We tested the intermediate disturbance hypothesis (Connell, 1978), expecting the highest ant diversity and abundance at intermediate pollution levels. Conducting censuses at 10 sites, we intended to study the pollution gradient in more detail, covering different stages of deterioration of the forest habitat typical of this region. By performing investigations over 2 years, we tested the repeatability of the results. Through analysis of the relationships of different species with habitat characteristics, we aimed to identify those variables which determine the responses of individual species and local ant communities.

Material and methods

Study area

The study was performed in 2009 and 2013 in the vicinity of the Middle Ural Copper Smelter (MUCS) located in Revda, Russia, 56°51′N, 59°53′E. Major pollutants are sulphur and nitrogen oxides, fluorine compounds and polymetallic dust containing Cu, Pb, Cd, Zn, Fe and As. Total emissions reached 150–225,000 tons per year in the 1980s (Vorobeichik et al., 2014; Kozlov et al., 2009) and steadily declined to 22,000 tons in 2009 and 3000 tons in 2013 (Alexandrov, 2010, 2014). However, the reduction of industrial emissions did not result in a decrease of soil metal concentrations; so far, vegetation has not recovered (Vorobeichik et al., 2014).

Site description

The data was collected at 10 sites established to the west and south-west of the smelter (Fig. 1) and comprising all stages of pollution-induced deterioration of forest ecosystems. The same spruce-fir (*Picea obovata* and *Abies sibirica*) forest, typical of the region, is presented at all sites, but ground vegetation changes with decreasing distance to the smelter. *Oxalis acetosella* and nemoral herbs (such as *Aegopodium podagraria, Gymnocarpium dryopteris, Asarum europaeum* and *Maianthemum bifolium*) dominate the field layer at sites with a distance of 33, 29 and 20 km from the smelter, out of range of industrial emissions. Herbs and grasses (such as *O. acetosella, M. bifolium, Carex montana, Calamagrostis obtusata, Rubus saxatilis* and *Linnaea borealis*) dominate at sites with a distance of 10, 7, 6 and 4 km (intermediate exposure level). Horsetails and grasses (such as *Equisetum sylvaticum, Deschampsia cespitosa, Agrostis capillaris, Calamagrostis arundinacea* and *Calamagrostis langsdorffii*) dominate at sites with a distance of 3, 2 and 1 km (high pollution) (Vorobeichik et al., 2014). The height of the top-canopy layer, stand basal area and field layer cover decrease at sites with a distance of 3 and 2 km compared to the unpolluted area (Table 1). The forest is sparse at the site with a distance of 1 km, and forest patches are interspersed with grassland areas. Here, the tree stand consists of dead or heavily damaged conifers with admixture of birches; the amount of woody debris is twice as much as in unpolluted sites (Bergman et al., 2015). Concentrations of mobile forms of metals (extracted with 5% HNO_3) in the forest litter, litter thickness and acidity increase as the distance to MUCS decreases. Litter metal concentrations at the most polluted sites of this area reach 3069 mg/kg for Pb, 5530 mg/kg for Cu and 38 mg/kg for Cd (Smorkalov and Vorobeichik, 2011). All sites are not isolated forest patches, but parts of a large forest area intersected with glades, cut-troughs and forest roads. At each site, basic habitat characteristics were measured in four points. Stand basal area was measured with a relascope at 1.3 m height. The height of the top tree canopy was estimated as a mean of five highest trees within 50 m from a point by the angle of elevation method with a Silva Clino Master height meter. Stand composition (rounded to the nearest 10%), cover of the tree canopy, understorey and field layer were determined visually. Site means of the variables were used in analyses.

Sampling

Ant numbers were evaluated using pitfall traps (plastic jars 9 cm in diameter, filled with 3% acetic acid). Pitfall trapping is widely used for counts of worker ants outside nests (Bestelmeyer et al., 2000; Underwood and Fisher, 2006; Tista and Fiedler, 2011); it provides a satisfactory estimate of species richness and abundance of ants foraging on ground and forest litter. The reason for the use of foraging workers in ant community studies is that namely the workers perform all interactions between species and affect other ecosystem components.

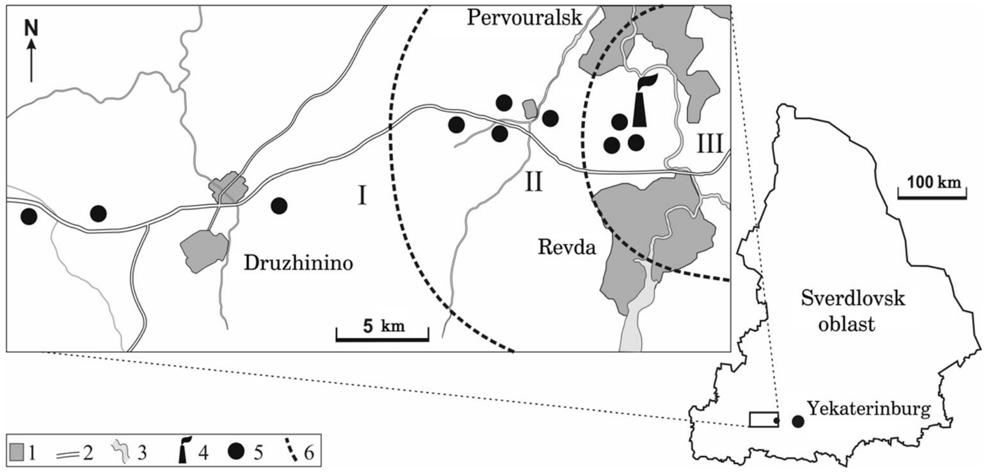


Fig. 1 Location of the study sites along the pollution gradient near the Middle Ural Copper Smelter. Symbols: *1* settlement, *2* highway, *3* river, *4* copper smelter, *5* study site, *6* presumable border between areas with different pollution levels (*I* background, *II* intermediate, *III* high)

In order to avoid possible seasonal variation, sampling was performed twice a season, at the beginning and at the end of summer, i.e. from 10 to 15th of June and 3rd to 9th of September in 2009, 14 to 19th of June and 28th of August to 2nd of September in 2013. At each site, three 10 × 10 m^2 plots were established at a distance of 50–100 m from each other. At each plot, five traps were placed along a line at a distance of 3 m from each other. Traps were located away from the ant trails, in the same points for all samplings. At each sampling event, traps were exposed for 5 days.

Ant species were identified by A.V. Gilev according to Dlussky (1967), Radchenko (1994, 1995, 1996), Seifert (1992) and Czechowski et al. (2002). Because *Lasius niger* and *Lasius platythorax* are difficult to distinguish we consider them as *Lasius* cf. *niger*.

Table 1 Characteristics of the study sites near the Middle Ural Copper Smelter

Distance to smelter, km	Litter Pb concentration, mg/kg dry mass[a]	Top-canopy height, m	Stand basal area, m^2/ha		Cover, %			Proportion of conifers, %	Woody debris, pieces/ha[b]
			Live trees	Dead standing trees	Tree canopy	Understorey	Field layer		
33	73.1 (4.1)	26.5 (1.1)	44.8 (14.1)	0.0	72.5 (9.6)	62.5 (9.6)	35.0 (5.8)	77.5 (9.6)	331 (51)
29	71.3 (7.0)	25.2 (1.6)	36.8 (7.9)	0.0	70.0 (8.2)	55.0 (17.3)	32.5 (9.6)	80 (0)	317 (71)
20	76.0 (14.6)	25.1 (1.0)	42.3 (6.7)	0.8 (1.0)	75.0 (5.8)	52.5 (20.6)	72.5 (9.6)	75 (5.8)	–
10	345.2 (20.4)	24.4 (2.2)	36.0 (9.6)	1.8 (1.7)	60.0 (8.2)	67.5 (17.1)	80.0 (8.2)	82.5 (5.0)	458 (201)
7	527.9 (62.5)	25.0 (1.3)	33.8 (7.6)	3.3 (2.2)	62.5 (9.6)	72.5 (15.0)	82.5 (9.6)	80 (8.2)	683 (82)
6	819.2 (44.7)	26.0 (1.1)	36.5 (9.5)	0.8 (1.0)	70.0 (11.5)	56.3 (14.9)	30.0 (18.3)	82.5 (5.0)	–
4	1135.7 (203.1)	25.5 (1.3)	34.0 (9.7)	2.5 (1.7)	70.0 (8.2)	75.0 (17.3)	22.5 (5.0)	82.5 (9.6)	551 (74)
3	2677.8 (210.5)	23.4 (1.0)	23.0 (7.7)	2.0 (1.4)	52.5 (12.6)	60.0 (14.1)	12.5 (6.5)	85 (10)	–
2	2780.9 (263.8)	21.7 (2.1)	15.3 (5.6)	0.8 (1.0)	37.5 (12.6)	56.3 (24.3)	10.0 (7.1)	82.5 (9.6)	–
1	3069.0 (281.3)	11.9 (1.5)	0.3 (0.5)	8.8 (4.9)	8.8 (2.5)	32.5 (9.6)	67.5 (9.6)	30 (34.6)	682 (126)

Values represent site mean and SD in parentheses [a] Pb concentrations (mobile forms) from Smorkalov and Vorobeichik (2011), n = 3 samples per site [b] Woody debris from Bergman et al. (2015), n = 3 plots per site; other data are original, n = 4 points per site. Dash means no data available

Data processing

For each plot and year, we determined the (1) number of individuals as a measure of ant abundance (although this also depends on activity), (2) species richness (S), (3) two diversity indices: Shannon (H) and α log-series and (4) Pielou's index of evenness $E = \frac{H}{\ln S}$.

Interannual repeatability of the indices was examined with a dependent t test for paired samples if differences between the years 2009 and 2013 were normally distributed or with a Wilcoxon matched pairs test if distribution of differences was not normal (abundance). Normality of differences was evaluated using the Kolmogorov-Smirnov test (n = 30 plots).

The differences in community structure between years and sites were tested with two-way ANOSIM (http://nhm2.uio.no/norlex/past) with plot as a measurement unit. The number of permutations equalled 10,000. In further analyses of diversity, the sum of all individuals per site for 2 years was used in order to increase the sample size and validity of estimates. In addition, for each site, the abovementioned indices were calculated as well as number of species per minimal sample (n = 126 individuals) by using individual rarefaction procedure. Calculations were performed in PAST v.1.92 (Hammer et al., 2001). In order to explore associations of community indices with distance to the pollution source, Pearson correlations between species richness, diversity, evenness and logarithmic ($\log_e$) distance were calculated. Associations of species abundances with toxic load and distance to smelter were assessed with Spearman rank correlation.

Because different habitat variables are intercorrelated, we used principal components analysis to produce uncorrelated principal components (PCs). Top-canopy height, stand basal area of live and dead trees, proportion of conifers, cover of understorey, field layer and pollution exposure were analysed, with site means as replicates (n = 10). Logarithmic ($\log_{10}$) Pb concentration in the forest litter was used as pollution exposure index due to the strong correlation with logarithmic concentrations of other metals: Pb–Cu r = 0.996, Pb–Cd r = 0.988. Principal components analysis allowed reduction of habitat variable sets to three PCs (Table 2). The first PC (eigenvalue 4.5) explained 64% of variation in the data and was related mainly to top-canopy height, stand basal area of live trees, proportion of conifers and basal area of dead trees (factor loadings equalled −0.99, −0.92, −0.91 and 0.91, respectively). The PC2 (eigenvalue 1.5) explained 21% of variation and was related mainly to cover of field layer (0.87). The PC3 (eigenvalue 0.8) explained 11% of variation and was related mainly to cover of understorey (0.60). Pollution exposure (litter Pb concentrations) contributed both to PC1 and PC2 (factor loadings equalled 0.62 and −0.68, respectively). For further analyses, one variable of each PC1–PC3 was selected: stand basal area (live trees only), cover of field layer and cover of understorey. Association between these variables was weak in all cases, with Spearman correlation $r_s < 0.26$.

Table 2 Factor loadings according to principal components analysis

Variable	Principal Components		
	1	2	3
$\log_{10}$ Pb concentrations in the forest litter	0.616	−0.677	0.363
Top-canopy height	−0.992	−0.015	0.048
Stand basal area, live trees	−0.917	0.348	−0.035
Basal area of dead standing trees	0.912	0.145	0.322
Proportion of conifers	−0.908	−0.339	0.133
Cover of understorey	−0.759	−0.162	0.600
Cover of field layer	0.182	0.870	0.406

Proportion of the total variance explained by PC1 equalled 0.638, PC2 0.214 and PC3 0.112

The relationship between the abundance of each species, site and habitat variables was examined with canonical correspondence analysis, using XLSTAT Version 2016.05.34059 ©Addinsoft 1995–2016 (https://www.xlstat.com/en/). Relationships between ant community indices and stand basal area, cover of field layer and cover of understorey were analysed with generalised linear models with normal distribution and logarithmic link function. Normality of variable distribution was tested using the Kolmogorov-Smirnov test. Insignificant predictors (Wald statistic, $p > 0.1$) were excluded from the model. Calculations were performed with the Statistica v10 software.

Results

Habitat transformation

Deterioration of the forest ecosystem progressed with decreasing distance to the smelter. Detrimental effect of pollution was highest at the site with a distance of 1 km. Here, top-canopy height, understorey cover and proportion of conifers were lowest among sites (Table 1). In contrast, basal area of dead trees and cover of field layer at a distance of 1 km were highest among sites indicating more open and lightened habitat. Impairment of the tree stand was visible at a distance of 2 km as well, where basal area of live trees and tree canopy cover were lower than at sites with distances of 4–33 km from the smelter. In addition, tree stand indices tended to be lower at a distance of 3 km compared to sites that are more distant.

Species composition

In total, 14 species belonging to 5 genera were registered in the study area. The most abundant species (>1% of individuals, all sites combined) were *Formica aquilonia* (79.6%), *Myrmica ruginodis* (7.1%), *Formica lugubris* (6.8%), *Lasius* cf. *niger* (2.6%) and *Myrmica scabrinodis* (1.1%). The most widespread species were *M. ruginodis* (registered at all 10 sites), *Camponotus herculeanus* (9 sites), *F. aquilonia* and *M. rubra* (8 sites), *L.* cf. *niger* (7 sites), *Leptothorax acervorum* (6 sites) and *M. scabrinodis* (5 sites).

Differences between sampling years

Interannual differences in ant community indices were insignificant. The dependent t test for paired samples for species richness equalled $t = 0.60$, $p = 0.56$, $n = 30$ plots; for Shannon index $t = 1.25$, $p = 0.22$; for α log-series $t = 0.48$, $p = 0.63$; and for evenness $t = 1.04$, $p = 0.31$. Only the number of individuals differed between years (Wilcoxon Test $z = 2.39$, $p = 0.017$), with higher abundance in 2013. The two-way ANOSIM showed that structure of local communities depended only on site ($R = 0.56$, $p < 0.0001$), and effect of the year was insignificant ($R = -0.09$, $p = 0.86$).

Community response

Species richness increased towards the smelter, from 5 species at distances 20–33 km to 11 species at distances 4–10 km and 13 species at distances 1–3 km (Table 3). The number of species per minimal sample near the smelter (sites 1–3 km) was 1.5–3 times greater than in the unpolluted area (sites 20–33 km). Diversity and evenness indices increased towards the smelter as well (Fig. 2). There were significant negative linear correlations between Shannon index, α log-series and logarithmic (ln) distance to MUCS: $r = -0.69$, $n = 10$, $p = 0.027$; $r = -0.67$, $p = 0.033$, respectively. Correlation between the number of species per minimal sample, evenness and logarithmic distance was marginally significant: $r = -0.61$, $p = 0.063$; $r = -0.59$, $p = 0.071$, respectively. Despite general increase of diversity towards the smelter, all indices peaked at the site with a distance of 2 km and then decreased, being 1.5–2 times less at the site with a distance of 1 km than at a distance of 2 km.

Total abundance showed a humped relationship with distance to smelter. It reached maximum values at sites with a distance of 6 and 7 km and decreased towards heavily polluted sites (1 and 2 km) and unpolluted sites (20 and 29 km). Different species responded differently to pollution. The abundance of red wood ants *F. aquilonia* and *F. lugubris*, which prefer old forests, peaked in the middle of the gradient and did not depend on pollution. At the same time, abundance of other species, which prefer open habitats, forest edges and young stands, increased with pollution exposure: Spearman correlation with litter Pb concentration $r_s = 0.88$, $n = 10$, $p < 0.001$ (Fig. 3).

Species-specific responses

Of the seven species analysed, the abundance of three species showed a significant relationship with the distance to the pollution source. Spearman correlation between the number of individuals and the distance to MUCS in *L. acervorum* equalled $r_s = -0.92$, $n = 10$, $p < 0.001$; in *M. rubra*, $r_s = -0.77$, $p = 0.009$; and in *M. scabrinodis*, $r_s = -0.85$, $p = 0.002$. Therefore, the abundance of these species increased towards the smelter. Species dominating local ant communities changed along the pollution gradient. *F. aquilonia* prevailed in ant communities at sites with low and moderate pollution levels, amounting to 47–98% of total abundance; *L.* cf. *niger* prevailed at the site with a distance of 2 km (43%) and *M. ruginodis* at sites with distances of 1 km (69%), 20 km (81%) and 29 km (95%).

Associations of diversity with habitat variables

The canonical correspondence analysis positioned species and sites along two axes (Fig. 4). The first axis accounted for 87.2% of total inertia and was determined by stand basal area (regression coefficient equalled 0.83). The second axis accounted for 12.7% of total inertia and was most closely related to the cover of the field layer (1.13) and understorey (−0.94). Sites with high exposure level (1–3 km) segregated from other sites mainly by stand basal area and were located in the left part of the triplot, indicating high damage of the tree stand. The site with a distance of 33 km was characterised by high stand basal area, the sites 1 and 20 km by high cover of the field layer and the site 4 km by high understorey cover.

The ordination showed species-specific relationships with habitat variables. The abundance of *F. aquilonia* peaked at higher stand basal area compared to other species (Fig. 4). While *C. herculeanus* and *L. acervorum* preferred habitats with denser field layers, species of the genus *Myrmica* were more abundant in habitats with sparse field layers. *Lasius* cf. *niger* showed a negative relationship with all vegetation layers.

Of the habitat variables, only stand basal area and cover of the field layer significantly affected the diversity indices; all coefficients were negative (Table 4). Slopes of regressions on these explanatory variables were similar for different indices.

Discussion

In a previous study, 12 ant species have been registered in the surroundings of MUCS (Vorobeichik et al., 1994). Our study has added 4 new species to this list, which now includes 16 species. The most abundant species is *F. aquilonia*; it

Table 3 Number of individuals and species of ants in the spruce-fir forest at different distances to the Middle Ural Copper Smelter (years 2009 and 2013 combined)

Species	Distance to smelter, km									
	33	29	20	10	7	6	4	3	2	1
Camponotus herculeanus (L.)	13	1	15	26	0	26	3	6	68	80
Formica aquilonia Yarrow	1657	0	1	2432	6317	4754	1748	3301	42	0
F. fusca L.	0	0	0	0	0	0	1	75	34	1
F. lugubris Zetterstedt	0	0	0	0	0	0	1722	0	0	0
F. pratensis Retzius.	0	0	0	0	0	6	0	0	41	1
F. sanguinea Latreille	0	0	0	0	0	0	0	0	1	1
Lasius cf. *niger* (L.)	4	3	19	0	0	8	0	320	242	77
Leptothorax acervorum (Fabricius)	0	0	0	0	2	1	1	39	26	50
L. muscorum (Nylander)	0	0	0	0	0	0	0	0	5	0
Myrmica lobicornis Nylander	0	0	0	0	0	3	0	0	5	9
M. rubra (L.)	0	2	1	0	1	3	59	41	37	13
M. ruginodis Nylander	93	120	155	219	120	310	207	23	28	527
M. rugulosa Nylander	0	0	0	0	0	0	0	0	8	0
M. scabrinodis Nylander	0	0	0	0	0	3	1	243	27	3
N	1767	126	191	2677	6440	5114	3742	4048	564	762
S	4	4	5	3	5	9	8	8	13	10
S′	2.9/0.7	4/0	4.3/0.7	2.7/0.4	2.0/0.4	3.0/0.9	4.1/0.5	6.0/0.9	11.5/0.8	6.0/0.9

N total number of individuals, *S* number of species, *S′* number of species per minimal sample 126 individuals (number of species above the line, SD below the line)

determined the humped pattern of the total ant abundance along the pollution gradient. Moderately polluted sites provide optimal conditions for *F. aquilonia* with established large colonies consisting of dozens and hundreds of nests (Gilev, 2010). *F. aquilonia* is a behaviourally dominant species within such areas and affects all other ant species by decreasing their occurrence and abundance and changing their foraging behaviour, i.e. performing interspecies social control (Reznikova, 1999, 2003). This species prefers mature forests (Zakharov, 2015), and its decreased abundance at two most heavily polluted sites is in line with pollution-induced tree damage. The absence of this species in pitfalls at sites with a distance of 20 and 29 km may be due to local conditions. According to our visual evaluation, the site with a distance of 29 km is characterised by high

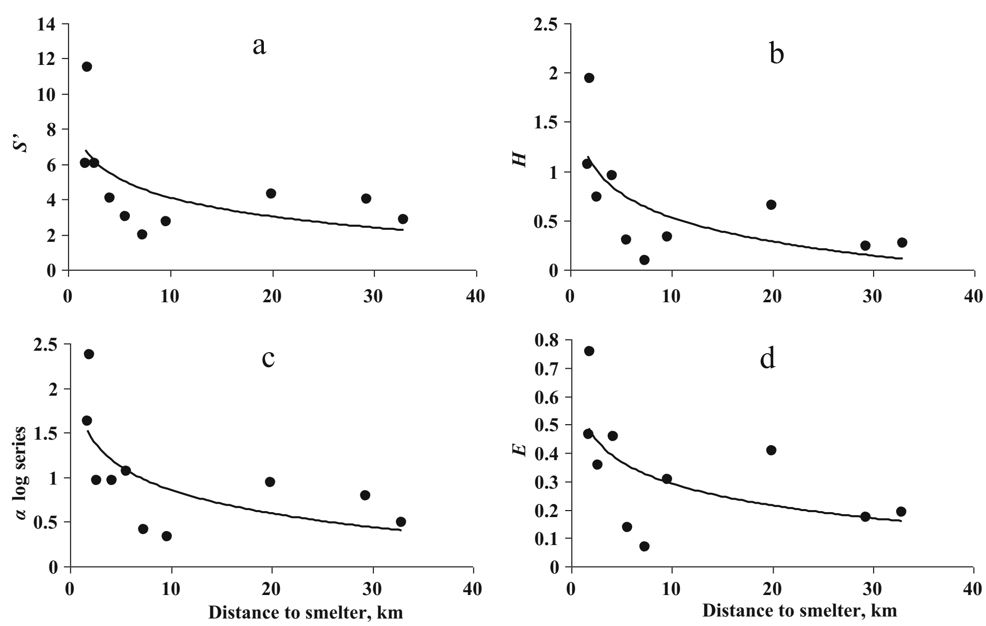
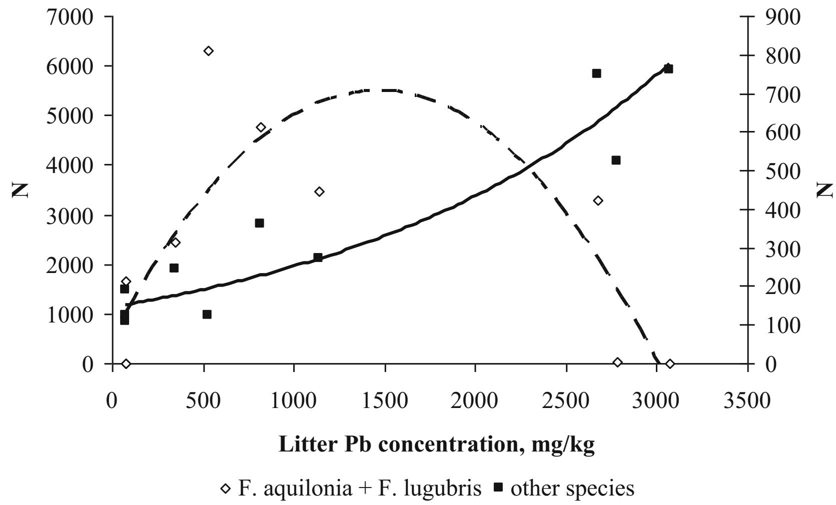


Fig. 2 Dependence of ant diversity on the distance to the Middle Ural Copper Smelter. **a** Number of species per minimal sample, $R^2 = 0.37$, $p = 0.06$; **b** Shannon diversity, $R^2 = 0.48$, $p = 0.03$; **c** α log-series, $R^2 = 0.45$, $p = 0.03$; **d** evenness, $R^2 = 0.35$, $p = 0.07$.

Fig. 3 Relationship between abundance of red wood ants (*Formica aquilonia* and *F. lugubris*, left Y-axis, $R^2 = 0.62$, $p = 0.035$), other species (right Y-axis, $R^2 = 0.83$, $p < 0.001$) and toxic exposure near the Middle Ural Copper Smelter



soil moisture, which likely results in low total ant abundance. At the site with a distance of 20 km, the forest is shady (*F. aquilonia* inhabits only forest edges at this site).

Pollution-related variations of ant communities near MUCS differ from those of other invertebrates, which show mainly negative effects. Decreases of taxonomic, functional group diversity and/or abundance towards MUCS have been documented for ground beetles (Belskaya and Zinoviev, 2007), arachnids inhabiting soil surface and herbaceous layer (Zolotarev, 2009; Zolotarev and Nesterkov, 2015), gnawing phyto- and zoophages inhabiting meadow herbage (Nesterkov and Vorobeichik, 2009), soil dwelling (Vorobeichik et al., 2012; Korkina and Vorobeichik, 2016) and necrophilous invertebrates (Ermakov, 2013). Trophic activities of leaf-chewing insects and miners decreased near this polluter (Belskaya and Vorobeichik, 2015). Only sucking phytophages benefited from pollution (Nesterkov and Vorobeichik, 2009). Ants, unlike other invertebrates, showed a humped relationship with distance from pollution source in our area. The lack of a definite "dose-effect" relationship and the tolerance of ants to high concentrations of heavy metals (Grześ, 2010a) suggest that ant community structure depends on factors other than pollution intensity. The key role of habitat characteristics and competition between species in shaping ant communities in polluted areas has been confirmed by studies in Karkonosze Mountains, Poland (Pętal, 1994), near the Cu–Zn smelter in Finland (Eeva et al., 2004) and in an As-contaminated area in Brazil (Ribas et al., 2011). Grześ (2009a) hypothesised that spiders and ground beetles as potential ant predators and competitors for food can affect ant diversity and abundance. This is not the case for red wood ants, which force other litter predators (carabids) out of their territory (Reznikova and Dorosheva, 2004;

Fig. 4 CCA triplot with sites (numerals mean distance to smelter, km), most common species (*hollow rectangles*) and explanatory variables (*arrows*; *FL* cover of the field layer, *SBA* stand basal area, *U* cover of understorey). Species abbreviations: *C_h Camponotus herculeanus*, *F_aq Formica aquilonia*, *L_ac Leptothorax acervorum*, *L_ni Lasius* cf. *niger*, *M_ru Myrmica rubra*, *M_sc M. scabrinodis*

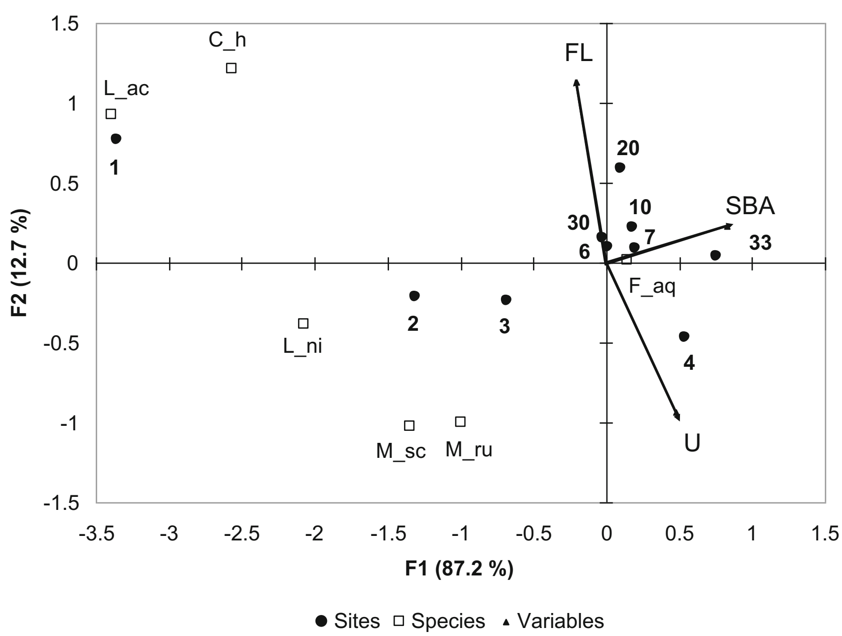


Table 4 Relationship between diversity indices and habitat variables according to GLZ analysis

Habitat variable	Stand basal area		Cover of field layer	
Index	Estimate ± SE	p	Estimate ± SE	p
Number of species per minimal sample	−0.029 ± 0.006	<0.001	−0.014 ± 0.003	<0.001
Shannon diversity	−0.044 ± 0.010	<0.001	−0.019 ± 0.005	<0.001
α log-series	−0.031 ± 0.007	<0.001	−0.011 ± 0.003	0.001
Evenness	−0.026 ± 0.009	0.004	−0.010 ± 0.005	0.034

Cover of understorey is not included in the table due to its insignificant effect

Dorosheva and Reznikova, 2006). However, this hypothesis cannot be rejected a priori for small ant species, which have rather many enemies, e.g. ant-eating spiders (Pekar, 2004, 2005) and ant lions.

Our results agree with the intermediate disturbance hypothesis predicting maximum biodiversity at intermediate frequencies and/or intensities of disturbances (Connell, 1978). Two mechanisms may underlie this phenomenon. The first one is increased environmental heterogeneity that allows coexistence of species with different habitat preferences. The second one is decreased abundance of dominant species and weakened competition, facilitating the existence of subordinate species. Both mechanisms are likely to act in our study area.

Species richness of ants changed most strongly between sites with a distance of 3 and 2 km, with the latter gaining five additional species. This change of species composition can be linked to habitat transformation. The decreases of top-canopy height, stand basal area and cover of field layer due to long-term pollution are most expressed within this section of the pollution gradient. In contrast to less polluted sites, the habitat at the site with a distance of 2 km represents forest fragments interspersed with open spaces. Such patchiness creates an edge effect which usually allows for greater biodiversity. It is well known that ant diversity increases at borders between contrasting habitats (Punttila et al., 1994; Zakharov, 2015). According to this, ant diversity peaks at the site with a distance of 2 km, at which habitat represents an intermediate stage between a slightly damaged and fully destroyed forest ecosystem. Deterioration of the forest ecosystem was accompanied by increased abundance of *F. pratensis* inhabiting young tree stands and forest edges, *C. herculeanus*, which settles in weakened and dead trees, *M. scabrinodis* and *L. niger*, which are open habitat specialists. Further increase in exposure level and forest deterioration resulted in decreased ant diversity at the site with a distance of 1 km. At the extreme pollution near the border of the smelter (~0.5 km from the smokestack), where only the stress-tolerant moss species *Pohlia nutans* exists, the ant community consisted of a single species, *L. niger* (Vorobeichik et al., 1994). This Cd-tolerant species (Grześ and Okrutniak, 2016), along with some *Myrmica* species, can survive under conditions unfavourable for other ants, even in heavily polluted areas with very sparse vegetation (Pętal, 1978).

Interspecies hierarchy along with habitat characteristics is an important factor in shaping ant communities (Reznikova, 1980; Savolainen et al., 1989; Punttila et al., 1994; Zakharov, 2015). Among species presented in our area, red wood ants *F. aquilonia* dominate the community and affect occurrence and abundance of other species. A sharp decrease in the abundance of *F. aquilonia* at the heavily polluted site with a distance of 2 km facilitated the incorporation of subordinate species, resulting in a more even community. Large species (e.g. *C. herculeanus*), which suffer more strongly from competition with *F. aquilonia*, benefit from the disappearance of red wood ants (Savolainen et al., 1989; Gilev et al., 2007). The blood-red ant *F. sanguinea* was registered only at two sites closest to the smelter because *F. aquilonia* displaces it at other sites. The absence of red wood ants along with plenty of open sun-exposed spaces and high abundance of woody debris at heavily polluted sites favours the occurrence of *Myrmica* species, which take a subordinate position in multispecies ant communities (Savolainen et al., 1989; Zakharov, 2015).

The total abundance of ant communities is hump-shaped, similar to species diversity, but with a maximum in the middle of the pollution gradient. Spatial mismatch of diversity and abundance peaks is a result of different mechanisms behind these characteristics. Total abundance of ants depends mainly on the abundance of the dominating species *F. aquilonia* (and *F. lugubris* at the site 4 km), which found optimal conditions at sites with distances of 6 and 7 km. The density of other species increased steadily towards the site with a distance of 1 km, but this effect was small compared to that of red wood ants. In contrast to abundance, ant diversity depends mainly on a complex of subordinate species. Decline of the dominant species at the site with a distance of 2 km favours to subordinates, resulting in higher community diversity. Therefore, total abundance of ants and species diversity provide different information on the community.

The hump-shaped diversity dynamics along gradients of environmental stress or disturbance is typical for ants because of the high role of competition in ant community dynamics (Andersen, 1997). According to this model, ant diversity declines at extremely high stress/disturbance levels and at the other end of the stress/disturbance gradient due to exclusion of subordinate species by dominants. Such hump-shaped dynamics can explain the inconsistency in conclusions of different researchers studying responses of ants to industrial pollution. It is likely that these researchers examined limited parts of stress gradients where humped diversity pattern was not expressed. Therefore, the steady increase in ant diversity towards the Zn smelter near Olkusz, Poland (Grześ, 2009a), may be explained with the fact that the pollution at this area was not high enough to decrease diversity. The highest soil Pb concentration near Olkusz equalled to that of our site at a distance of 3 km, where ant diversity had not decreased yet. Furthermore, pollution did not affect habitat characteristics near Olkusz, confirming that exposure was not very strong. In contrast, ant diversity decreased along the pollution gradient near a Cu–Pb smelter at Mount Isa, Australia (Hoffmann et al., 2000). Such an effect may be due to the very high industrial emissions, which equal 700,000 t/year and are dozens and hundreds of times greater than in our study area. Nevertheless, data presented by these authors (Figs. 3 and 5 in Hoffmann et al., 2000) show that ant diversity and abundance peak at low (but not lowest) exposure levels, indicating hump-shaped dynamics.

The comparison between 2 years showed that ant abundance and diversity did not differ between years within each study plot in our area. Community indices showed similar variation along the pollution gradient in both years. Small interannual variability is due to the residency of ants and longevity of their colonies. Stability in time increases the reliability of results and provides methodological advantage because it allows the comparisons of ant communities studied in different areas and different years.

Conclusion

This study provided evidences for hump-shaped dynamics of ant diversity and abundance along a pollution gradient in the Middle Urals, Russia. At the same time, diversity and abundance of local ant communities did not coincide in space due to different habitat requirements of dominant red wood ants which determine total abundance and habitat preferences of subordinate species whose variety determines diversity. To test the intermediate disturbance hypothesis for ants in polluted areas, further studies are needed. In order to precisely determine key factors shaping ant communities, variables should be analysed including exposure level, habitat characteristics and interactions between ants, their predators and competitors. The use of ants to assess the state of natural ecosystems subjected to anthropogenic disturbances requires consideration of community composition and characteristics of species because of species-specific responses to a complex of ecological factors.

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