

Does mixed diffused pollution decrease ground beetle diversity?

Tomasz Skalski, Krzysztof Gargas, Ryszard Laskowski

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The variation in species diversity pattern of over 120 ground beetles species in heavy metal pollution gradient (Zn, Cu, Cd, Pb and Ni) was investigated in Poland and Great Britain. The carabid beetles were collected on 124 sites in forest and meadow gradients. Forward selection of canonical correspondence analysis indicated that species composition seems to be influenced mostly by geographic region and land use history meanwhile heavy metals, however significantly, described smaller part of species variation. Indicator species of certain pollutant groups (zinc, nickel, copper) and certain concentration levels (high, medium, low) were identified using Indicator Species Analysis (IndVal). Most of them, characteristic for highly contaminated soils belong to small sized carnivores or granivores from genus *Amara* and *Harpalus*. We found a significant decrease in species diversity in more contaminated nickel soils, meanwhile zinc and copper gradients indicated highest values for the lowest and highest amounts of both stressors. We conclude that in most cases directional replacement of species can occur in contaminated sites. Species more competitive but less tolerant are replaced by less competitive but more flexible species.

Key words: Carabidae, diversity, heavy metals, CCA, IndVal

Tomasz Skalski. Department of Entomology, Institute of Zoology, Jagiellonian University, 6 Ingardena str. 30-360 Krakow, Poland, tomasz.skalski@uj.edu.pl

Krzysztof Gargas. Department of Entomology, Institute of Zoology, Jagiellonian University, 6 Ingardena str. 30-360 Krakow, Poland,

Ryszard Laskowski. Department of Ecotoxicology, Jagiellonian University, Gronostajowa 3, 30-387 Kraków, Poland

INTRODUCTION

Heavy metal pollution from industrial discharges has a pronounced effect on the environment (Clemetns & Newmann 2002). Most of the chemical concentration is deposited in contaminated soil taking living organisms into permanent exposition to stressors (press disturbance) and usually creates a new equilibrium (Wootton 1998).

Although most ecotoxicological tests study effects of toxicants on single organisms or populations (Jones & Hopkin 1996, Hopkin 1989, Kramarz & Laskowski 1997, Kramarz 1999) the pollution in nature affects a range of species (populations) inhabiting contaminated areas. In natural systems, community response is not a sum of individual species responses to

contamination. There are also some other factors like interspecific competition, niche space limitation, regional species pool richness or other factors which play also important role sometimes magnifying the effect of pollutants. On the other hand, more resistant species which usually are poorer competitors can replace dominated competitors which are more sensitive to pollution (eg. Connel 1978, Platt & Connel 2003).

At community level, negative effect of pollution on species richness diversity was usually presented (Hunter et al. 1987, Spurgeon & Hopkin, 1996a, b, Fountain & Hopkin 2004). Sometimes however, more resistant groups can replace more susceptible to pollutants (Nahmani et al 2006). In that case however usually functional diversity decrease is observed. Groups which benefit from higher contaminations are habitat and functional generalists with broad ecological range (food preferences, microhabitat limitation) (Ribeira et al 2001, Clements & Newman 2002, Skalski & Pospiech 2006). Their role as sufficient ecological engineers are mostly limited (decreased rates of such ecosystem processes as productivity, decomposition and biogeochemical cycling of nutrients) (Ives et al 1999, Robinson et al 2004, Pospiech & Skalski 2006).

Gross of recent data suggest that ground beetles should react directly to such kind of stress disturbance as heavy metal contamination. Laboratory tests indicate decreased tolerance of toxicant-resistant individuals to other stressing factors (Stone et al 2001). Beetles exposed to metal contaminated food have lower amount of energy available (Maryanski et al. 2001). Significantly increased mortality of larvae feeding zinc or cadmium contaminated food (Kramarz & Laskowski 1997, Lagisz et al 2002, Mozdzer et al. 2003).

Field test are less informative, showing results negating each other. Freitag et al. (1973) found significant negative effect of pollution on diversity of Carabidae. Similar results were reached by Bengtsson & Rundgren (1984), Gongalski & Butovski (1998), Skalski et al. (2006, 2010). Braun et al. (2004) showed decrease of

body size continuously after the contamination began. No effect of heavy metals on ground beetles communities however were described by Read et al. (1987), Read et al. (1998), Lock et al. (2001). So far, however we were not able to summarize all those results. Moreover, the effects of such changes on ecosystem function is unknown.

The objectives of the study were to assess the impact of heavy metals on species diversity and richness of ground beetle communities in different pollution systems, regarding geography, land use and different chronic stressors. We hypothesize that chronic concentration of heavy metals favors species with broad ecological range and eliminates more competitive specialists, depending of one source of habitat (eg. food). In our opinion species replacement of more resistant species which can replace those more susceptible to a particular pollutant but otherwise better fit in uncontaminated areas.

MATERIALS AND METHODS

Four study systems of air pollution in different geographic regions of Europe (Great Britain and Poland), various habitat types (forest-meadow) and main stressors (Table 1) were selected (Fig. 1). In Clydach area four meadow (CM) and forest localities (CF) were established in various distance to nickel smelter along single valley. Reference site was established in Eastern England at Monks Wood Research Station. In Avonmouth, highly contaminated by zinc and lead, only meadow gradient (A) was applied, because of lack of proper forest habitats. Reference site was located in the vicinity of Reading. Along a distance from former smelter, four localities were chosen. Near the one of the biggest copper smelter in Central Europe in Glogow, six meadow (GM) and five forest (GF) localities were established along the distance from the emitter of pollution. The localities in Olkusz zinc smelter were placed in forest (OF) and meadow (OM) ecosystems. At each locality five random replicates of ten pitfall trap rows were

arranged. The traps were collected weekly during the one high season (Duelli & Obrist 2001) in two spring months - May and June in 2004-2006.

The characteristic species of main stressors (Zinc, Copper and Nickel) were explored by the IndVal (Indicator Value) procedure (Dufr  ne & Legendre 1997). The statistical significance of the

Table 1. Average $\pm$ SD minimum and maximum concentrations (mg kg⁻¹) of major pollutants and other parameters in humus layer at the study system

	Mean	SD	min	max
Zn mg/kg dw	612.97	2053.70	6.69	12080.42
Cu mg/kg dw	366.87	624.48	9.51	3528.44
Pb mg/kg dw	944.68	3969.74	30.09	25582.94
Cd mg/kg dw	13.19	57.38	0.11	361.75
Fe [%]	1.47	1.27	0.23	4.38
Mg mg/kg dw	1313.43	1376.57	92.57	5643.74
Ni mg/kg dw	638.25	1725.70	0.95	6451.23
Mn mg/kg dw	313.30	175.48	52.53	781.09
Na mg/kg dw	199.02	122.41	22.85	411.74
Ca (mg/kg)	1303.18	1208.12	302.56	4808.94
K (mg/kg dw)	1779.98	1630.17	122.34	8203.70
N g/kg dw	9.10	5.66	2.21	25.30
C g/kg dw	137.17	120.82	9.15	343.35
S g/kg dw	1.35	1.51	0.02	7.30
C/N	12.21	7.61	2.91	26.27
pH (H ₂ O)	5.49	1.16	3.90	8.00
WHC (%)	105.53	67.10	32.11	279.31
org.matter (%)	25.29	21.88	2.22	62.45

species indicator values was evaluated using a randomisation procedure.

The diversity measures which were calculated for each sample point include richness (Species number) and its variance (Variance), alpha diversity indices: the Shannon-Wiener index (H), the Simpson index (Simpson), the Margalef index (Margalef), the Berger-Parker Dominance (Berger), the McIntosh index (McIntosh), the Brillouin index (Brillouin), the Fisher's alpha index (Fisher) and Q statistic (Q); and the evenness indices: Pielou index against maximum number of species (J sp max), Pielou index against maximum number of species in given sample (J sample), McIntosh E index (J McInsh) and Brillouin E (J Brillo) (Kempton 1979, Magurran 1988).

To determine the relative importance of independent variables (Table 1) responsible for

the variation of ground beetles in pollution gradients and its diversity, canonical correspondence analysis was applied (Teer Braak 1994, Teer Braak & Verschoft 1995). To reduce the number of environmental variables and to rank them on the basis of maximum extra fit, manual forward selection was adopted (CANOCO v.4.52, Ter Braak & Šmilauer 2003). We tested for significance of the variables using Monte Carlo permutation test, and retained the significant variables in the analyses at 0.05 significance level. All variables were then ranked in order of their importance in explaining beetles composition and relative abundance.

Three of the main pollution factors, concentration of Zn, Cu and Ni were classified using an optimal classification method, the Fisher-Jenks algorithm (Slocum 1999). The threshold value for the 'goodness of variance fit' used to select the optimal number of

classes was 0.9. Analysis of variance using a randomised block design was carried out to determine if there were any differences in the values of species diversity and its evenness between the derived classes of main pollutants. If a significant effect was detected, multiple comparisons among means was applied using the Newman-Keuls procedure.

RESULTS

During intensive field studies 30 000 of specimens belonging to 127 species of ground beetles were collected (Appendix 1). Table 2 shows the results of forward selection of canonical correspondence analysis. Zinc, cadmium, nickel and cooper exert a significant influence on the composition of ground beetles assemblages in the study systems. A biplot of canonical correspondence

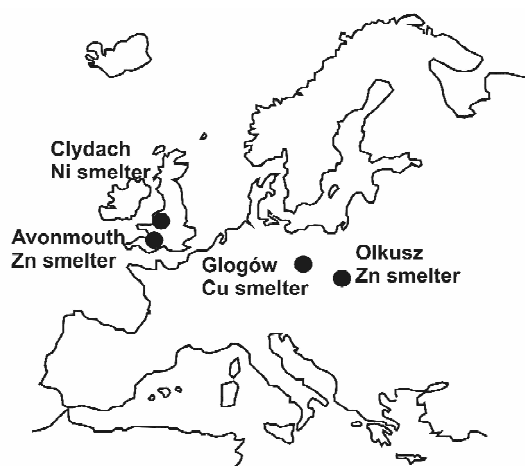


Fig. 1. Map of the study area and main pollution factors in Great Britain (Clydach and Avonmouth) and Poland (Olkusz and Glogow)

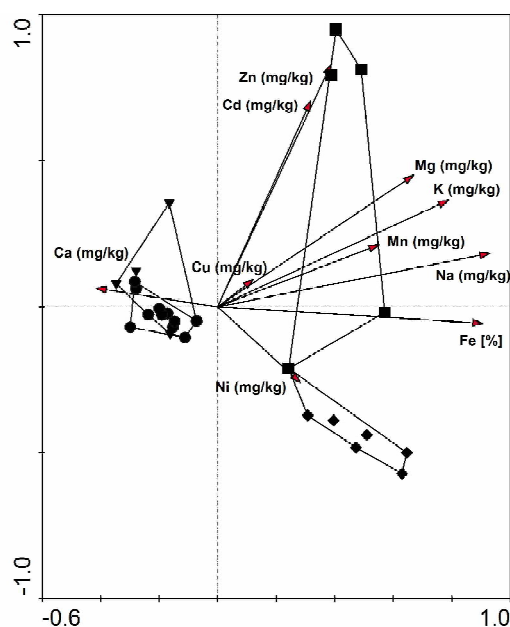


Fig. 2. Biplot of canonical correspondence analysis for the ground beetles communities. Independent variables are reduced by forward selection (assemblages: diamonds - Clydach - nickel, squares - Avonmouth - zinc, triangle - Olkusz - zinc, circles - Glogow - copper)

analysis for ground beetles assemblages (Fig 2) shows that regional variation is the most important factor. The assemblages from each region creates separate groups and don't overlap. The only ranking concerns assemblages from Poland.

The first two axes of CCA described 86.2% of species-environment relations. The organization of ground beetles communities along first canonical axis indicates strong dissimilarity between Polish and British communities along iron and calcium gradient. Weighed correlations of these two factors with the first ordination axis is high (0.91 and -0.41 respectively). Second canonical axis corresponds mostly to zinc and cadmium concentrations ($R_{Zn}=0.83$, $R_{Cd}=0.70$).

Fig. 3 shows the presence of three groups of species related to different factors. In group A, positively correlated to Nickel concentration, there are species which are characteristic for Welsh sites. In group B related to zinc and cadmium, species which were characteristic for English meadows are included. Group C however, the most numerous consists of species which were more abundant in Poland. This analysis indicates the importance of regional variation in species composition and shows difficulties in generalization concerning sensitiveness of species to pollution.

Table 2. Rank of the independent variables after evaluation of forward selection of canonical correspondence analysis for 124 assemblages in study system

Name	Extra fit lambda	Monte Carlo permutation test
Cu	0.11	P-value 0.0080; F-ratio= 2.15
Ca	0.24	P-value 0.0080; F-ratio= 3.16
Ni	0.28	P-value 0.0020; F-ratio= 3.29
Mn	0.33	P-value 0.0040; F-ratio= 2.77
Cd	0.35	P-value 0.0020; F-ratio= 2.90
Mg	0.49	P-value 0.0120; F-ratio= 2.67
Zn	0.49	P-value 0.0020; F-ratio= 6.57
K	0.58	P-value 0.0020; F-ratio= 5.76
Fe	0.62	P-value 0.0020; F-ratio= 4.59
Na	0.65	P-value 0.0020; F-ratio= 9.48

Possible indicator species of certain pollutant groups (zinc, nickel, copper) and certain concentration levels (high, medium, low) were identified using Indicator Species Analysis (IndVal). The method combines information on the abundance and faithfulness of occurrence of species abundance in particular groups. IndVal analysis revealed some species which seems to be statistically linked to the kind of pollution (Table 3). In zinc gradient communities, strong indicator species are represented for low, medium and high concentration. Most of the high concentration indicators belong to genus *Amara* and *Harpalus*, which are herbivores as adults. There are also some omnivorous *Poecilus* and *Pterostichus* species mostly with broad ecological range occurring in high density on disturbed areas.

In copper polluted ground beetles communities most of the strong indicators were linked with low and medium concentrations. Surprisingly, most of them belong to high concentrations of zinc (eg. *Poecilus versicolor*, *Harpalus* sp.). Lack of copper high concentration species indicators suggests that concentration over 1000 mg/kg of dry humus mass creates conditions for accidentally occurring species only. Among nickel indicators, there is high number of species avoiding higher concentrations. They occurred only on uncontaminated sites. Most of them (eg. *Pterostichus oblongopunctatus*, *Pt. niger* or *Notiophilus aquaticus*) are characteristic for forest habitats.

The variation of ground beetle species diversity along a gradient of heavy metal pollution was analyzed using forward selection of canonical correspondence analysis (CCA). The first two partial CCA axes accounted respectively for 56.7% (eigenvalue=0.254) and 29.5% (eigenvalue = 0.118) of the extracted variance in the indices–environment relationship. Therefore, the first two canonical axes explain about 86% of the indices variance.

Forward selection of canonical correspondence analysis (Table 3) derived significant factors responsible for description of diversity indices

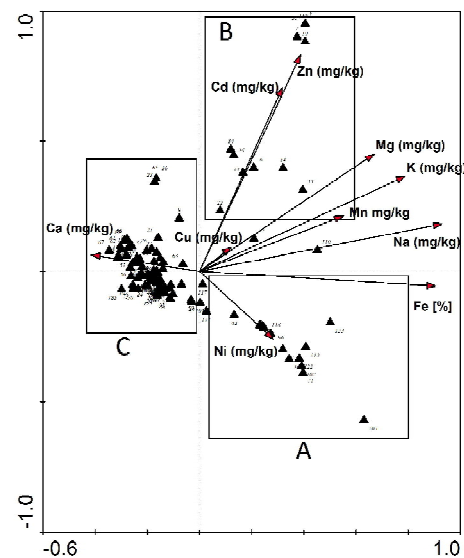


Fig. 3. Biplot of canonical correspondence analysis for the ground beetle species (numbers see appendix 1)

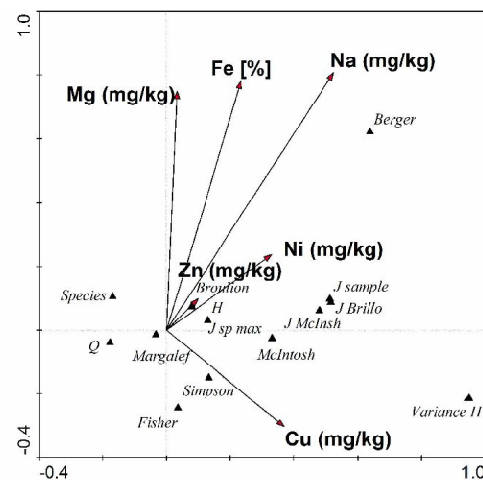


Fig. 4. Ordination biplot depicting the first and second axes of the partial canonical correspondence analysis of the species assemblage diversity indices. Number of variables reduced by forward selection.

Table 3. Indicator species in contaminated soils for Zn, Cu and Ni concentrations in three classes (low, medium and high concentrations).

variation. As it was mentioned in former section concerning species composition, variables significantly describing variation are three microelements: Na, Fe and Mg and three heavy metals (Cu, Ni and Zn).

The biplot of the first two axes and diversity indices shows a positive relationship between evenness of diversity (J) and Zinc and Nickel concentrations (Fig. 4). Also Shannon and Brillouin indices which are sensitive to rare and singleton species were affected by those metals. Surprisingly also Berger-Parker index which reflects proportion of dominant species was highly positively affected by pollutants. On the other way Simpson index and Fisher alpha increased with higher amounts of copper. The only index which was negatively correlated with heavy metals was species richness and Q statistics reflecting parametric structure of investigated

Species	Ind Value	Class	Mean	Std	t	p<0.01
Zinc indicators						
C_horten	16.86	Low concentration	5.86	2.91	3.784	**
A_curs	20.69	Low concentration	4.79	2.57	6.182	**
D_globo	13.79	Low concentration	4.12	2.19	4.409	**
H_pici	18.26	Low concentration	7.07	2.98	3.761	**
H_tard	49.91	Low concentration	15.99	4.21	8.054	**
L_pice	23.52	Low concentration	8	2.85	5.441	**
M_minut	17.24	Low concentration	4.32	2.36	5.48	**
M_plag	50.89	Low concentration	12.73	4.18	9.131	**
A_com	64.98	High concentration	22.62	6.04	7.017	**
A_fame	22.38	High concentration	7.02	2.99	5.136	**
A_luni	54.91	High concentration	12.6	4.92	8.593	**
A_pleb	20.69	High concentration	5.01	2.6	6.035	**
H_rufip	51.2	High concentration	21.36	5.86	5.089	**
P_cupr	62.87	High concentration	26.38	6.89	5.296	**
P_versi	75.73	High concentration	28.59	5.84	8.075	**
Pt_stren	40.03	High concentration	11.26	3.87	7.44	**
Pt_ver	34.48	High concentration	6.43	2.95	9.521	**
Copper indicators						
H_affin	40.07	Low concentration	17.08	5.31	4.332	**
H_tard	36.98	Low concentration	16.78	5.13	3.936	**
P_lepid	31.93	Low concentration	12.37	4.54	4.305	**
P_versi	47.63	Low concentration	28.99	5.75	3.243	**
Ab_par	72.94	Medium concentration	18.32	4.87	11.23	**
D_globo	26.67	Medium concentration	4.41	2.61	8.536	**
Pt_stren	35.05	Medium concentration	11.62	3.9	6.014	**
Pt_ver	21.5	Medium concentration	6.68	3.32	4.465	**
Nickel indicators						
C_arcen	52.65	Low concentration	19.21	5.02	6.662	**
N_aqua	26.47	Low concentration	10.5	3.79	4.214	**
H_lutei	22.06	Low concentration	8.68	3.53	3.787	**
H_pumil	20.59	Low concentration	8.23	3.18	3.886	**
H_rubri	51.81	Low concentration	16.42	4.28	8.26	**
H_tard	40	Low concentration	16.12	4.67	5.109	**
L_pice	22.06	Low concentration	7.97	2.75	5.118	**
M_plag	38.24	Low concentration	12.74	4.07	6.26	**
P_lepid	26.11	Low concentration	11.59	4.06	3.577	**
Pt_niger	35.11	Low concentration	15.07	4.88	4.107	**
Pt_obl	52.89	Low concentration	17.69	5.1	6.902	**
A_luni	30.76	Medium concentration	12.61	4.6	3.945	**
A_pleb	14.19	Medium concentration	4.67	2.17	4.385	**
P_cupr	72.71	Medium concentration	26.28	6.79	6.841	**
P_versi	52.14	Medium concentration	29.06	5.78	3.991	**
Pl_ass	15.99	Medium concentration	4.9	2.45	4.525	**
Pt_mad	28.62	Medium concentration	8.52	3.52	5.704	**
Ab_par	70.6	High concentration	18.27	4.67	11.21	**
N_brev	61.82	High concentration	22.1	6.07	6.543	**
Pt_stren	26.38	High concentration	11.25	3.57	4.245	**
Pt_ver	17.1	High concentration	6.54	2.61	4.043	**

assemblages. Whole diagram however shows that concentration of heavy metals don't affect negatively the diversity of ground beetles. And what is more important there is no clear relationship between species diversity and pollution levels.

There were significant differences in the mean values of diversity indices among the classes of the concentrations of main pollutants (Table 5). The high concentration of Zinc and Copper produce various patterns of species diversity among sites. In most cases the assemblages of the highest and the lowest concentrations of these metals are the most diverse. Only in nickel gradient show similar pattern of distribution of species diversity. Generally higher amount of Ni reduces species diversity values and increases evenness of the assemblages.

DISCUSSION

The data obtained in our study revealed toxic effect of heavy metals on structure and diversity of ground beetles. Other factors, however, such as regional species pool or land use history is much more important. In natural environment many methodological problems can appear, because other environmental disturbances such as fires, agriculture practices or land use changes as well as microhabitat conditions (pH, temperature, rate of decomposition) can be also responsible for results of the estimation and overall effect. It is therefore difficult to deduce reliability whether between communities differences are due to metal levels or habitat variation. So the impact of pollution on community and ecosystem level must be provided in different ecosystems and in various regions to show more universal conclusions. Our results suggest that ground beetles are quite resistant to heavy metal contamination. More important is regional variation. One of the requirement of good indicator is broad geographic distribution (Noss 1990). Most of the widely distributed

species are habitat generalists with high dispersal power. Such species are usually less sensitive to habitat changes and also contamination level. The canonical correspondence analysis (Fig. 2 and 3) showed that if we want to find good indicators we must consider them in each region separately.

There was however possible to find some species which preferred less or more contaminated soils (Table 3). Among species living in highly polluted areas are small sized species such as *Pterostichus strenuous* and *Pt. vernalis* and some species feeding on plants such as *Amara* spp. and *Harpalus* spp. Szyszko (1983) and later Blake et al. (1994) assumed that high level of human disturbance alter the distribution of body sizes towards a prevalence of smaller species. Such a decreasing body size pattern has subsequently been reported for several ground beetle assemblages (Alarukka et al. 2002; Magura et al. 2002, 2003).

The causes of this pattern are still not well explained. Lövei & Sunderland (1996) showed that less mobile larvae are more affected by changing conditions in disturbed habitats, whereas Thorbek & Bilde (2004) argued that lower total abundances under unfavorable conditions reflects increased extinction rates of larger and therefore often less abundant species. Skalski et al. (2008) explains that frequency and intensity of disturbance negatively impacts the amount of energy conversion into offspring. Smaller species have faster rate of energy conversion meanwhile

Table 4. Ranking of independent variables significantly describing diversity variation of ground beetle communities using unrestricted Monte Carlo significance test

Name	Extra fit lambda	Monte Carlo permutation test
Zn	0.001	P-value 0.0320; F-ratio= 3.01
Ni	0.001	P-value 0.0480; F-ratio= 2.76
Cu	0.001	P-value 0.0360; F-ratio= 3.38
Mg	0.01	P-value 0.0020; F-ratio= 6.31
Fe	0.01	P-value 0.0020; F-ratio= 8.02
Na	0.01	P-value 0.0020; F-ratio= 11.42

Table 5. ANOVA of Zn, Cu and Ni concentration variable classes and ground beetle species diversity and evenness

	SS	df	MS	SS	df	MS	F	p	Newmann Kelus test			
	Zn classes			Error								
H	7.14	2	3.57	38.21	121	0.32	11.31	0.000031	H	=	L	> M
J sp max	0.30	2	0.15	1.63	121	0.01	11.31	0.000031	H	=	L	> M
Broulion	5.42	2	2.71	31.29	121	0.26	10.48	0.000063	H	=	L	> M
Fisher	129.70	2	64.85	865.64	121	7.15	9.06	0.000215	H	=	L	> M
Margalef	19.43	2	9.71	133.47	121	1.10	8.81	0.000269	H	=	L	> M
Berger	0.56	2	0.28	4.57	121	0.04	7.43	0.000907	H	=	L	< M
McIntosh	0.56	2	0.28	4.60	121	0.04	7.34	0.000984	H	=	L	> M
Q	60.10	2	30.05	517.32	121	4.28	7.03	0.001294	H	=	L	> M
Simpson D	97.56	2	48.78	1115.26	121	9.22	5.29	0.006261	H	=	L	> M
Species No.	336.87	2	168.43	5563.93	121	45.98	3.66	0.028542	H	=	L	> M
J McInsh	0.24	2	0.12	6.19	121	0.05	2.32	0.102407				
J Brillouin	0.14	2	0.07	5.78	121	0.05	1.49	0.229596				
J sample	0.13	2	0.06	5.45	121	0.05	1.43	0.242608				
Variance H	0.00	2	0.00	0.04	121	0.00	0.61	0.546732				

	SS	df	MS	SS	df	MS	F	p	Newmann Kelus test			
	Cu classes			Error								
Variance H	0.00	2	0.00	0.03	121	0.00	9.05	0.000217	H	>	M	> L
Species No.	530.88	2	265.44	5369.92	121	44.38	5.98	0.003334	H	=	M	< L
Q	45.21	2	22.60	532.21	121	4.40	5.14	0.007209	H	=	L	> M
J Brillouin	0.46	2	0.23	5.47	121	0.05	5.04	0.007882	H	=	M	> L
J sample	0.43	2	0.21	5.16	121	0.04	5.02	0.00808	H	=	M	> L
J McInsh	0.46	2	0.23	5.97	121	0.05	4.64	0.011471	H	=	M	> L
Margalef	7.12	2	3.56	145.77	121	1.20	2.96	0.055799				
McIntosh	0.14	2	0.07	5.02	121	0.04	1.68	0.190951				
Berger	0.10	2	0.05	5.04	121	0.04	1.18	0.310865				
Broulion	0.68	2	0.34	36.03	121	0.30	1.14	0.323301				
H	0.28	2	0.14	45.07	121	0.37	0.38	0.684917				
J sp max	0.01	2	0.01	1.92	121	0.02	0.38	0.685272				
Simpson D	6.84	2	3.42	1205.97	121	9.97	0.34	0.710064				
Fisher	0.49	2	0.24	994.85	121	8.22	0.03	0.970729				

	SS	df	MS	SS	df	MS	F	p	Newmann Kelus test			
	Ni classes			Error								
Margalef	38.61	2	19.31	114.28	121	0.94	20.44	0	H	=	M	< L
H	9.14	2	4.57	36.21	121	0.30	15.27	0.000001	H	=	M	< L
J sp max	0.39	2	0.19	1.54	121	0.01	15.27	0.000001	H	=	M	< L
Q	117.05	2	58.52	460.37	121	3.80	15.38	0.000001	H	=	M	< L
Broulion	7.22	2	3.61	29.49	121	0.24	14.82	0.000002	H	=	M	< L
Fisher	195.49	2	97.75	799.85	121	6.61	14.79	0.000002	H	=	M	< L
Species No.	1053.65	2	526.82	4847.15	121	40.06	13.15	0.000007	H	=	M	< L
McIntosh	0.66	2	0.33	4.49	121	0.04	8.94	0.00024	H	=	M	< L
Simpson D	146.31	2	73.15	1066.51	121	8.81	8.30	0.000419	H	=	M	< L
Berger	0.57	2	0.28	4.57	121	0.04	7.51	0.000842	H	=	M	> L
J sample	0.56	2	0.28	5.02	121	0.04	6.77	0.001634	H	=	M	> L
J Brillouin	0.58	2	0.29	5.34	121	0.04	6.61	0.00189	H	=	M	> L
J McInsh	0.62	2	0.31	5.81	121	0.05	6.41	0.002251	H	=	M	> L
Variance H	0.00	2	0.00	0.03	121	0.00	4.10	0.018991	H	=	M	> L

the bigger ones should accumulate the energy into biomass for longer time. Ground beetles females should accumulate high enough volume of biomass which is necessary for high fecundity (Walin et al. 1992). High rate of dry weight production was observed by Chaabane et al. (1994). Two first months of dry weight production of female *Abax ater* was almost twice the production during the seven months of larva life. In highly press-disturbed habitats contaminated by heavy metals, a significant decrease in average ground beetle body size was recorded in moving from the pollution to the post-pollution period (Braun et al. 2004).

Why heavy polluted communities are usually smaller? Maryanski et al. (2002) showed that ground beetles exposed to metal contaminated food have lower energy available, which may be reflected in lower energetic reserves in their body. Kozłowski 1991 suggested that energetic budget of every organism is limited. The energy taken by organisms must be distributed to all processes, also detoxication. It explains why at population level overall body mass decreases with increasing heavy metal accumulation (Spurgeon & Hopkin 1999, Maryanski et al. 2002). Why in disturbed multispecies system smaller species are preferred? In classic ecological works, competition and equilibrium is regarded as a main force for formation of multispecies systems (Pielou 1969, McArthur 1972). Resource competition seems to be the only important biological interaction (Chesson & Case 1986). Smaller species are then regarded as worse competitors in equilibrium conditions. When disturbance limiting food availability and increasing energetic expenses for detoxication appears bigger species are more sensitive and eliminated. Then replacement of smaller species into the communities may be observed. (Plat & Connell 2003).

It explains why many species diversity indices are insensitive to high pollution. There are basically three different anticipated kinds of pollution effects on communities: (1) decrease in species richness (i.e., number of species

inhabiting an area); (2) species replacement (for example, more resistant species can replace those more susceptible to a particular pollutant but otherwise better fit in uncontaminated areas); and (3) changes in community structure (even with no changes in species composition, a distribution pattern of species within a community may be affected). A decrease of species population is certainly one of the most dramatic effects of pollution (Hopkin & Hames 1994, Spurgeon & Hopkin 1996a). Ground beetles however are poor accumulators of heavy metals (Kramarz 1999) which may result from elevated mechanisms of detoxication and excretion. There are also evidence that beetles residing in highly contaminated sites have incurred physiological or genetic costs and living on more polluted sites they are able to tolerate higher concentration of heavy metals (Stone et al. 2001, Lagisz & Laskowski 2008). In each gradient of pollution directional replacement of species can occur. As a result overall number of species or its species diversity will not change at all. That is probably why in zinc and copper gradients the mean values of species diversity are not significant between the highest and lowest class of concentration (Table 5). Only in nickel gradient the mean species diversity significantly decreased when the concentration reached medium and high values. On the other hand mean evenness indices showed significant increase on more polluted sites. It indicates that in nickel gradient high species turnover may occur resulting higher mortality and higher recolonization rate.

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Appendix 1 List of species collected in polluted and reference sites

	Species	Abreviation	Body size (mm)	biomass (mg)	Total abundance
1	Amara sp.1	A_1	6.8	4.83	46
2	Amara sp.2	A_2	6.8	4.83	1
3	Amara (s. str.) aenea (De Geer , 1774).	A_aen	7.5	6.25	156
4	Amara (Curtonotus) aulica (Panzer , 1796).	A_aul	12.5	24.08	282
5	Amara (Celia) bifrons (Gyllenhal , 1810).	A_bifro	6.3	3.95	4
6	Amara (s. str.) communis (Panzer , 1797).	A_com	6.6	4.46	714
7	Amara (s. str.) convexior Stephens , 1828.	A_conv	7.7	6.70	43
8	Amara (Celia) cursitans C. Zimmermann , 1832.	A_curs	7.7	6.70	10
9	Amara (s. str.) curta Dejean , 1828.	A_curta	7.7	6.70	40
10	Amara (Percosia) equestris equestris (Duftschmid , 1812).	A_eque	8.9	9.82	63
11	Amara (Celia) erratica (Duftschmid , 1812).	A_erra	7.2	5.62	8
12	Amara (s. str.) eyrinota (Panzer , 1797).	A_eyri	10.4	14.82	17
13	Amara (s. str.) famelica C. Zimmermann , 1832.	A_fame	7.8	6.94	34
14	Amara familiaris (Duftschmidt, 1812)	A_fami	6.4	4.12	8
15	Amara (Bradytus) fulva (O. F. Müller , 1776).	A_fulv	8.9	9.82	32
16	Amara (Celia) infima (Duftschmid , 1812).	A_infi	4.9	2.03	1
17	Amara (Celia) ingenua (Duftschmid , 1812).	A_inge	9.6	12.00	75
18	Amara (s. str.) littorea C. G. Thomson , 1857.	A_lit	7.7	6.70	10
19	Amara (s. str.) lunicollis Schiodte , 1837.	A_luni	7.7	6.70	702
20	Amara (s. str.) montivaga Sturm , 1825.	A_mont	8.2	7.91	188
21	Amara (s. str.) ovata (Fabricius , 1792).	A_ovata	9	10.12	48
22	Amara plebeja (Gyllenhal, 1810)	A_pleb	6.8	4.83	13
23	Amara (Paracelia) quenseli silvicola C. Zimmermann , 1832.	A_quen	7.3	5.82	71
24	Amara (s. str.) schimperi Wencker , 1866.	A_schi	7.7	6.70	5
25	Amara (s. str.) similata (Gyllenhal , 1810).	A_simil	8.7	9.25	18
26	Amara (s. str.) sprete Dejean , 1831.	A_sprete	7.8	6.94	11
27	Amara (s. str.) tibialis (Paykull , 1798).	A_tibia	5.1	2.26	46
28	Abax (Abacopercus) carinatus carinatus (Duftschmid , 1812).	Ab_car	14.1	33.08	89
29	Abax (s. str.) ovalis (Duftschmid , 1812).	Ab_ova	14.3	34.34	195
30	Abax (s. str.) parallelepipedus (Piller et Mitterpacher , 1783).	Ab_par	18.6	68.71	287
31	Agonum (s. str.) sexpunctatum (Linné , 1758).	Ag_sex	8.7	9.25	2
32	Anisodactylus (s. str.) binotatus (Fabricius , 1787).	Ani_binot	11.2	18.02	5
33	Anisodactylus poeciloides (Stephens, 1828)	Ani_poe	12.5	24.08	1
34	Asaphidion flavipes (Linné , 1761).	Asa_flavi	4.4	1.53	36
35	Asaphidion pallipes (Schrank , 1781).	Asa_palli	4.7	1.82	2
36	Bembidion (Philochthus) aeneum aeneum (Germar , 1824).	B_aen	3.8	1.04	2
37	Bembidion guttula (Fabricius, 1792)	B_gut	3.3	0.72	2
38	Bembidion (Metallina) lampros (Herbst , 1784).	B_lamp	3.6	0.90	6
39	Bembidion (Metallina) properans (Stephens , 1828).	B_prop	4	1.19	5
40	Bembidion (s. str.) quadrimaculatum (Linné , 1761).	B_quadri	4	1.19	1
41	Badister bullatus (Schrank 1828)	Ba_bull	5.4	2.63	1
42	Badister (Baudia) dilatatus Chaudoir , 1837.	Ba_dila	5.4	2.63	2
43	Badister sodalis (Duftshmidt, 1812)	Ba_sol	4.3	1.44	1
44	Broscus cephalotes (Linné , 1758).	Br_ceph	20.3	86.55	3
45	Bradycellus harpalinus (Serville, 1821)	Bra_ha	4.3	1.44	1
46	Carabus (s. str.) arcensis arcensis Herbst , 1784.	C_arcen	23	120.34	2529
47	Carabus (Chrysocarabus) auronitens auronitens Fabricius , 1792.	C_aur	23	120.34	86
48	Carabus (Tachypus) cancellatus cancellatus Illiger , 1798.	C_cance	30	242.60	66

	Species	Abreviation	Body size (mm)	biomass (mg)	Total abundance
49	Cychrus caraboides (Linné , 1758).	C_carabo	15	38.95	4
50	Carabus (Procrustes) coriaceus coriaceus Linné , 1758.	C_coria	40	518.31	19
51	Carabus (Tomocarabus) convexus convexus Fabricius , 1775.	C_cov	17	54.20	43
52	Clivina fossor fossor (Linné , 1758).	C_fossor	6.2	3.78	3
53	Carabus (Oreocarabus) glabratus glabratus Paykull , 1790.	C_glab	28	202.22	393
54	Carabus (s. str.) granulatus granulatus Linné , 1758.	C_granul	19.5	77.84	18
55	Carabus (Oreocarabus) hortensis hortensis Linné , 1758.	C_horten	30	242.60	41
56	Carabus (Chaetocarabus) intricatus intricatus Linné , 1761.	C_intri	36	392.51	8
57	Carabus linnei Duft.	C_linn	18	63.02	39
58	Carabus (Archicarabus) nemoralis nemoralis O. F. Müller , 1764.	C_nemo	24	134.64	295
59	Carabus problematius Herbst, 1876	C_prob	24	134.64	40
60	Carabus (Megodontus) violaceus violaceus Linné , 1787.	C_viola	35	364.39	1688
61	Calathus (Neocalathus) erratus erratus (C. R. Sahlberg , 1827).	Ca_errat	9.7	12.33	554
62	Calathus fuscipes (Goeze, 1777)	Ca_fus	11.7	20.22	1008
63	Calathus (Neocalathus) melanocephalus (Linné , 1758).	Ca_melano	7.2	5.62	93
64	Calathus (Neocalathus) micropterus (Duftschmid , 1812).	Ca_mic	7.9	7.17	177
65	Cicindela (s. str.) campestris campestris Linné , 1758.	Ci_cam	12	21.62	1
66	Cicindela (s. str.) hybrida hybrida Linné , 1758.	Ci_hyb	13.5	29.50	1
67	Cymindis (s. str.) humeralis (Geoffroy , 1785).	Cim_hu	9.4	11.35	1
68	Curtonotus convexuscula (Marsham, 1802)	Cu_con	11.4	18.88	3
69	Dyschirius (Eudyschirius) globosus (Herbst , 1784).	D_globo	2.5	0.34	11
70	Dromius quadrimaculatus (Linnaeus, 1758)	Dr_qua	5.2	2.38	1
71	Elaphrus cupreus Duftshmidt, 1812	El_cup	6.7	4.64	1
72	Harpalus (s. str.) affinis (Schrank , 1781).	H_affin	10.2	14.08	174
73	Harpalus (s. str.) atratus Latreille , 1804.	H_atra	11.8	20.68	5
74	Harpalus (s. str.) autumnalis (Duftschmid , 1812).	H_autum	8.9	9.82	162
75	Harpalus (s. str.) flavicornis flavicornis Dejean , 1829.	H_flavi	8.6	8.97	1
76	Harpalus (Pseudoophonus) griseus (Panzer , 1796).	H_grise	10.5	15.20	4
77	Harpalus (s. str.) hirtipes (Panzer , 1796).	H_hirt	13.5	29.50	26
78	Harpalus (s. str.) latus (Linné , 1758).	H_latus	9.3	11.03	116
79	Harpalus (s. str.) luteicornis (Duftschmid , 1812).	H_lutei	7.5	6.25	37
80	Harpalus (Cryptophonus) melancholicus Dejean , 1829.	H_melan	10.3	14.45	13
81	Harpalus (s. str.) picipennis (Duftschmid , 1812).	H_pici	6.3	3.95	56
82	Harpalus (s. str.) pumilus Sturm , 1818.	H_pumil	5.5	2.76	68
83	Harpalus (s. str.) rubripes (Duftschmid , 1812).	H_rubri	10.3	14.45	491
84	Harpalus (Pseudoophonus) rufipes (De Geer , 1774).	H_rufip	13.8	31.26	1048
85	Harpalus (s. str.) rufipalpis rufipalpis Sturm , 1812.	H_rufipa	9.9	13.01	1
86	Harpalus (s. str.) serripes serripes (Quensel , 1806).	H_serri	10.1	13.72	6
87	Harpalus (Semiophonus) signaticornis (Duftschmid , 1812).	H_signa	6.9	5.02	1
88	Harpalus (s. str.) smaragdinus (Duftschmid , 1812).	H_smara	9.8	12.67	59
89	Harpalus (s. str.) tardus (Panzer , 1796).	H_tard	9.7	12.33	479
90	Licinus (s. str.) depressus (Paykull , 1790).	L_depre	10.2	14.08	30
91	Leistus ferrugineus (Linné , 1758).	L_ferru	7.2	5.62	101
92	Leistus fulvibarbis Dejean, 1826	L_ful	7.5	6.25	3
93	Leistus piceus piceus Frölich , 1799.	L_pice	8.3	8.17	19
94	Loricera (s. str.) pilicornis pilicornis (Fabricius , 1775).	L_pilic	7.4	6.04	14
95	Leistus rufomarginatus (Duftshidt, 1812)	L_ruf	8.9	9.82	4
96	Leistus spinibarbis (Fabricius, 1775)	L_spin	8.3	8.17	26

	Species	Abreviation	Body size (mm)	biomass (mg)	Total abundance
97	Lebia (Lamprias) chlorocephala (J. J. Hoffmann , 1803).	Le_chlo	6.8	4.83	2
98	Microlestes minutulus (Goeze , 1777).	M_minut	3.1	0.61	12
99	Microlestes plagiatus (Duftschmid , 1812).	M_plag	2.9	0.51	143
100	Notiophilus aquaticus (Linné , 1758).	N_aqua	5	2.15	60
101	Notiophilus biguttatus (Fabricius , 1779).	N_bigu	5	2.15	48
102	Nebria brevicollis (Fabricius, 1792)	N_brev	11.5	19.32	559
103	Notiophilus germinyi Fauvel in Grenier , 1863.	N_germ	4.9	2.03	2
104	Notiophilus palustris (Duftschmid , 1812).	N_palu	5.2	2.38	28
105	Notophilus rufipes Curtis, 1829	N_ruf	5.3	2.50	9
106	Ophonus (Metophonus) cordatus (Duftschmid , 1812).	O_cord	8.5	8.70	84
107	Oxypselaphus obscurus (Herbst , 1784).	Ox_obsc	5.5	2.76	3
108	Paranchus albipes (Fabricius , 1796).	P_albi	7.8	6.94	1
109	Panagaeus (s. str.) cruxmajor (Linné , 1758).	P_crux	8.1	7.66	7
110	Poecilus (s. str.) cupreus cupreus (Linné , 1758).	P_cupr	12.1	22.10	2226
111	Poecilus (s. str.) lepidus lepidus (Leske , 1785).	P_lepid	12.9	26.16	117
112	Poecilus (s. str.) versicolor (Sturm , 1824).	P_versi	10.7	15.97	3022
113	Platynus assymilis	Pl_ass	11	17.18	53
114	Pterostichus (Eosteropus) aethiops Panzer , 1796.	Pt_aet	12.8	25.63	3
115	Pterostichus (Cheporus) burmeisteri burmeisteri Heer , 1838.	Pt_bur	13.5	29.50	1
116	Pterostichus madidus (Fabricius, 1775)	Pt_mad	15.5	42.47	431
117	Pterostichus (Morphnosoma) melanarius melanarius (Illiger , 1798).	Pt_melan	15.7	43.93	601
118	Pterostichus (Platysma) niger niger (Schaller , 1783).	Pt_niger	18.5	67.74	904
119	Pterostichus (Pseudomasesus) nigrita (Paykull , 1790).	Pt_nigr	11	17.18	3
120	Pterostichus (Bothriopterus) oblongopunctatus (Fabricius , 1787).	Pt_obl	11.4	18.88	7326
121	Pterostichus (Pseudomasesus) rhaeticus Heer , 1837.	Pt_rhaet	9.6	12.00	1
122	Pterostichus (Phonias) strenuus (Panzer , 1796).	Pt_stren	6.1	3.63	56
123	Pterostichus vernalis (Panzer, 1795)	Pt_ver	6.7	4.64	15
124	Syntomus truncatellus (Linné , 1761).	S_trun	2.8	0.46	6
125	Stomis (s. str.) pumicatus pumicatus (Panzer , 1796).	Sto_pum	6.90	5.02	1
126	Trichotichnus (s. str.) laevicollis laevicollis (Duftschmid , 1812).	T_laevi	7.6	6.48	4
127	Zabrus (s. str.) tenebrioides tenebrioides Goeze , 1777.	Za_ten	14.6	36.27	13