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The effect of channel restoration on ground beetle communities in the floodplain of a channelized mountain stream

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Abstract

Background and purpose: *River regulation works, channelization and floodplain urbanization have reduced the frequency of flooding, incised river channels, and separated them from the surrounding riparian zones. This phenomenon is especially unfavourable for exposed riverine sediment areas (ERS) situated in the transition zone between terrestrial and aquatic environments, and plays a fundamental role in the functioning of riverine ecosystems. We investigated the effects of restoration practise based on eco-friendly structures on riparian ground beetle communities.*

Materials and methods: *Carabids were surveyed in 60 sampling sites of incised and redeposited cross-sections of a mountain stream. At each cross-section geodetic measurements were surveyed and six sampling sites were randomly established at different distances from the water surface.*

Results and conclusions: *Non-metric multidimensional scaling revealed that the dissimilarity in carabid communities between the three benches resulted mainly from differences in hydrological (bankfull discharge, period of flooding, water velocity) and geomorphological parameters (incision and erosion) in the incised and redeposited cross-sections. A GLM indicated that incision-redeposition processes had a significant effect on carabid assemblage parameters and life history traits. The effect of redeposition processes on abundance, species richness, biomass and MIB depended strongly on bench height and flood frequency. The cross-sections where eco-friendly constructions were built and bed material deposition processes were recreated showed increased abundance of ERS specialists: small predators with high dispersal power and a spring breeding strategy. However, the proportion of specialist species in the community was small, which indicates a slow rate of restoration of ERS specialist diversity.*

INTRODUCTION

Human interference in the structure of river channels through various types of regulation works, as well as exploitation of gravel material, has led to vast degradation of riparian environments, currently affecting over 90% of rivers in Europe (*1, 2, 3, 4*). Particularly in the case of mountain rivers, a serious consequence of river channelization has been the loss of natural flow variability and dynamics, resulting in straightening of channels and homogenization of river habitats (*4, 5*). Simplification and straightening of channels may increase water flow velocity and sediment transport. High velocity may also increase channel cutting downstream, leading to incision of the alluvial cover, even exposing the bedrock, and lowering of the water table, not only in the active river channel but in the riparian zone as well (*6, 7, 8*).

The channelization effect may be expected on several levels. First, river channelization leads to a lowering of the water level, so that in time the river becomes a vertically closed system, completely isolated from the riparian zone, which leads to its impoverishment and terrestrialization (*7, 8, 9, 10, 11*). Moreover, exposure of the bedrock as a result of deepening of the river bed reduces the efficiency of sedimentation processes, leading to impoverishment of aquatic diversity (*12, 13, 14*) and the disappearance of areas of exposed riverine sediment constituting a living environment for highly specialized riparian fauna (*11, 15, 16*).

To improve the condition of riparian ecosystems and restore their natural heterogeneity, procedures are carried out to restore the natural hydromorphological processes and multi-threaded character of river channels. By recreating a wide corridor of unimpeded flow, we observe a decrease in flow velocity in the channel and a return to the natural flow regime and redeposition processes (*14, 17*), which are crucial for riparian habitat heterogeneity (*18*). In many cases, however, particularly in highly built-up valleys, different solutions must be sought to reduce the water flow velocity in the channel and thus its incision. To eliminate the negative consequences of incision (mainly associated with flow), environmentally friendly techniques are used, i.e. natural reinforcements constructed of stones or wood, such as rip-rap, gabions, or rapid hydraulic structures. By decreasing hydraulic parameters such as bankfull discharge and water velocity, structures of this kind increase bottom roughness and sedimentation of bed materials (redeposition). As a result of redeposition the morphology of the channel changes and bed material losses are reduced (*19*), leading to restoration of exposed riverine sediment areas (ERS), which are a habitat for numerous riparian specialist species (*20, 21*).

Along natural mountain rivers exposed riverine sediments (ERS) are define as a poory vegetated frequently inundated open areas with fluvially deposited sedminets (*20*). Inundation during flood events provides highly dynamic and patchy ERS habitats with a high diversity of biota and strict adaptations to the dynamic habitats. Among ERS specialists, insects of the family Carabidae are highly abundant (*22, 23, 24, 25*). They have a critical role in linking aquatic and terrestrial food webs (*26, 27*). Key features of their life traits, such as body size (*2, 28, 29*), dispersal ability (*23*) and reproduction strategy (*24, 30, 31*), allow them to live in such specific environments. Several life history traits of ERS carabids specialists are strongly affected by flood disturbance parameters. For example according to Sadler and Bates (*2*), Eyre and Luff (*28*) and Lambeets et al (*29*) small body size and high dispersal power enble them to escape and quickly recolonise ERS areas after flood events. Moreover high tolerance to submersion and reproduce in spring allow them to live in such specific environments (*24,30,31*). Owing to their specific adaptations to this type of environment they are good ecological indicators of the processes taking place in such dynamic ecosystems as ERS (*21, 32, 33*).

The aim of the study was to compare carabid community composition and structure between incised and redeposited sections of the floodplain of a mountain stream. We expected that in redeposited cross- sections where eco-friendly structures were established, the decrease water velocity and improve bed material redeposition contribute to re-creation of exposed riverine sediment specialists communities. We also tested whether life traits of ground beetles characteristic for exposed riverine sediments (ERS) increase with the eco-friendly structures protecting the stream bed.

MATERIALS AND METHODS

The research was conducted in the Western Carpathian Mountains on the Porębianka stream. The Porębianka catchment is situated in the Carpathian Flysch Belt, which is a part of Carpathians known as the Gorce Mountains, with elevation ranging from 370 a.s.l. at the mouth to 1,310 a.s.l. at the highest point. The Porębianka is a fourth-order tributary of the Vistula River. The stream is 15.4 km long and its catchment area comprises 71.8 km^2. Because the stream is quite flashy and experiences frequent bedload movement, many hydraulic structures have been built, such as check dams, artificial rapids, boulder drop structures and concrete drops to protect against flooding and to prevent bank erosion and bedload transport (*17*). The average annual precipitation in the region is 970 mm. Floods typically occur in the summer, with minimum discharge of 0.26 [m^3 s^{-1}] and maximum discharge of 149 [m^3 s^{-1}] for 1960-1980 (Table 1).

Table 1. *The main characteristics of the Porębianka stream.*

Variables	The Porebianka stream
Precipitation [mm]	980
Catchment Area [km^2]	71.8
Channel slope	0.036
Max. Stream width [m]	28
Min. Annual discharge [m^3 s^{-1}]	0.26
Mean annual discharge [m^3 s^{-1}]	1.3
Two years flood $Q_{50\%}$ – the flood of probability of 50% occurrence every 2 years [m^3 s^{-1}]	25
Ten years flood $Q_{10\%}$ – the flood of probability of 10% occurrence every 10 years [m^3 s^{-1}]	89
D_{50} – median diameter of the particle size distribution [mm]	41

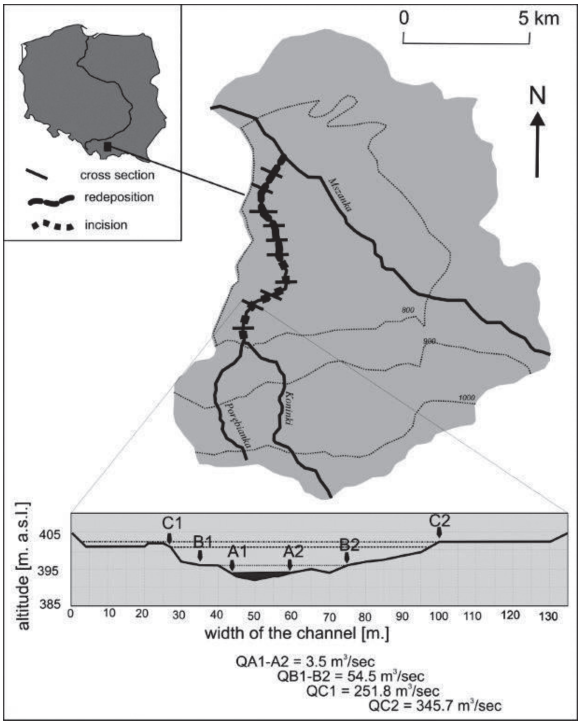

Figure 1. *The location of Porębianka stream and cross sections of incised and redeposited cross-sections. Below: an example of cross-section of the incised channel showing the position of pitfall traps rows at various elevations and benches (A, B, C). Q x-y – calculated bankfull discharge at xy level. Gray shading indicates a low-flow river channel and horizontal lines show calculated bankfull discharges.*

The Porębianka stream was systematically degraded from the 19th century, along its entire length. As a result of concrete reinforcement and channelization the channel became transformed from braided to single-threaded and narrow. Channel narrowing and straightening was associated with incision, lowering the water table by about 2 m between 1911 and 1988 (*17*). To prevent erosion and down-cutting of the channel, many transverse and longitudinal hydrological structures were built. In 2004 a number of eco-friendly structures were built in the lower section of the stream, such as rip-rap and many small boulder drop structures. Currently the entire stream can be divided into two main sections, with processes dominated by redeposition and incision.

Investigations were carried out in both sections, redeposited and incised. In the incised channel four cross-sections were chosen. This section was characterized by single-thread, narrow and straightened channel with bed down-cutting processes and deficit of bed materials/sediments. In the redeposited part, six cross-sections were randomly selected, where channel was more morphologically varied and where eco-friendly structures were built to restore deposition processes and natural state after river training. At each cross-section six sites were selected at the elevated gradually distance to the water surface (benches A, B and C) (Figure 1). Bench A (Figure 1, A_1-A_2 level) was always located the nearest to the adjacent flow channel, not vegetated or covered only by ephemeral grass or herbs (ERS habitats). Bench B (Figure 1, B_1-B_2 level) was the transition zone on intermediate elevation between exposed riverine sediment area and woodlands (typically about 2 meter above the water level). The most clearly develop bench C (Figure 1, C_1, C_2) was the highest and widest, bench characterized by abundant woodland habitats (more than 4 meter above the water level).

At each cross-section land points, elevation and distance were surveyed with a classic optical level Pentax AP-241. Rows of pitfall traps were set up on both sides of the channel. Next, based on the location of the row of pitfall traps and the geometry of the channel, the potential discharge at each level was calculated in terms of volume of running water (*34, 35*). The probability of occurrence of flow at each bench was calculated by Punzet's formula using the Woda 88 computer model (*36*).

Ground beetles were sampled during the growing season from May to September. The pitfall traps (five cylindrical cups with a diameter of 60 mm and depth of 100 mm) filled with ethylene glycol were established in one row at regular 5-metre intervals (*30*) for benches A, B and C along both banks. Sixty sites were established on ten cross-sections (36 in redeposited and 24 in incised cross-sections). Pitfalls traps were emptied monthly and the carabid beetles were stored in 70% ethanol, counted and identified to species.

Similarity/dissimilarity of ground beetle assemblages among all of the sampling sites was analysed by non-metric multidimensional scaling based on the Bray-Curtis similarity matrix. NMDS analysis was performed with WinKyst Software (*37*). The distance between assemblages in relation to channel morphology (incision-redeposition) was analysed by ANOSIM (*38*). Similarity percentage analyses (SIMPER) were performed to determine the relative contribution of the various species to incision and redeposition processes in the channel at each bench. A generalized linear model (GLM) with a Poisson distribution and log-link function (*39*) was used to determine whether there were statistically significant differences in total abundance, richness, biomass and mean individual biomass (MIB) (*40*) in relation to channel modification at three elevations (bench A, B and C). Generalized linear models were also used to examine differences in the abundance of individual life traits across modification at bench A, which is directly connected with changing water discharge. Life traits used in the analysis were habitat specialization (ERS: specialists and generalists; dispersal power: B – brachypterous, D – dimorphic, M – macropterous; food preferences: C – carnivores, H – herbivores; breeding strategy: AB – autumn breeders, SB – spring breeders; and body size classes: large >15 mm, medium 7-15 mm, small <7mm) (*41, 42*).

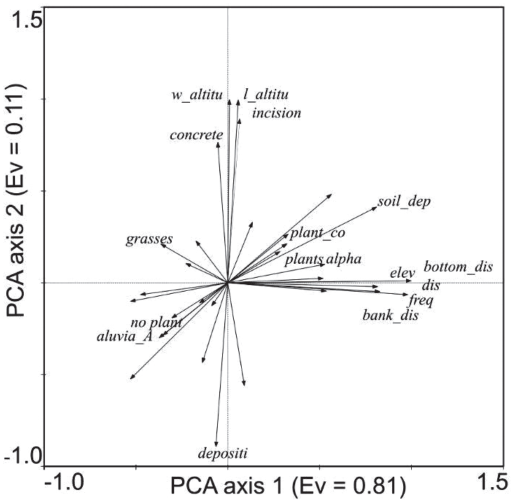

Figure 2. *Results of a principal component analysis performed on the habitat characteristics of 60 localities along 10 cross-sections with various potential flood period and erosion (Abbreviations see Table 2).*

RESULTS

To eliminate the effect of spatial autocorrelation of environmental factors with the location of cross-sections, PCA for environmental parameters was used to test the dimensionality of environmental variables, making it possible to reduce their number to a minimum (Table 2). It was however remarkable that altitude had no influence on environmental and hydrological factors, highly correlating only with the type of river channel (Figure 2). Principal component analysis of environmental factors described 81.2%, 11.1%, 3.1% and 2% of variance for the first four axes, but two of them describe more than 93%. Four groups of environmental factors which depend on one another are associated with the axes (Table 2). The first, which is responsible for most of the variation, is linked with potential bankfull discharge and the period of flooding.

The second axis mostly describes geomorphological incision and erosion. The third axis describes plant cover as the main factor, while the fourth is significantly correlated with the angle of the bank. Loadings were qualitatively designated as high for absolute values (> 0.60). Four main groups of factors were ordinated (Table 2): two of these (Factor 1s and 3) are hydrological processes of inundation, and two are geomorphological processes (incision and redeposition) (Factors 2 and 4).

Then two-way analysis of variance was performed between the environmental gradients revealed in PCA and incision-redeposition and bench classes. Axis 1 is significantly dependent on the bench ($F=69.9$, $p<0.0001$). Axis 2 depends on the river section (incision-redeposition), $F=216$, $p<0.0001$. The third and fourth axes are also bench-dependent ($F= 9.12$, $p<0.0001$ and $F=14.92$, $p<0.0001$, respectively). This comparison indicated that only altitude variation depended on incision-redeposition

Table 2. *The loadings of environmental parameters to the first four axes of PCA.*

Description	abbreviation	axis 1	axis 2	axis 3	axis 4
bankfull discharge [m3/s]	dis	1.00	0.01	0.00	-0.01
maximum depth of the river [m]	bottom_dis	1.00	0.01	0.00	-0.01
frequency of flood [years]	freq	0.98	-0.07	0.09	0.08
height from the water level [m]	elev	0.83	-0.05	-0.03	-0.05
distance to the bank [m]	bank_dis	0.82	-0.02	-0.13	-0.34
soil depth to the host rock [m]	soil_dep	0.81	0.41	-0.09	0.00
distance from the water level [m]	w_altitu	0.01	1.00	0.08	0.01
altitude above sea level [m a.s.l.]	l_altitu	0.06	0.99	0.08	0.00
incision of the river [0-1]	incision	0.06	0.89	-0.02	0.14
occurence of concrete regulation [0-1]	concrete	-0.05	0.76	-0.04	-0.01
deposition of aluvial material [0-1]	depositi	-0.06	-0.89	0.02	-0.14
absence of plants on the river bank [0-1]	no plant	-0.30	-0.19	0.67	-0.21
occurence of alluvia on the bench A [0-1]	aluvia_A	-0.35	-0.29	0.62	-0.02
presence of plants on the river bank [0-1]	plants	0.28	0.17	-0.73	0.02
percentage of plant cover [%]	plant_co	0.32	0.21	-0.86	0.33
presence of grasses on the bench A [0-1]	grasses	-0.36	0.21	-0.01	0.66
angle between the bank slope and water surface [o]	alpha	0.53	0.10	-0.43	-0.70

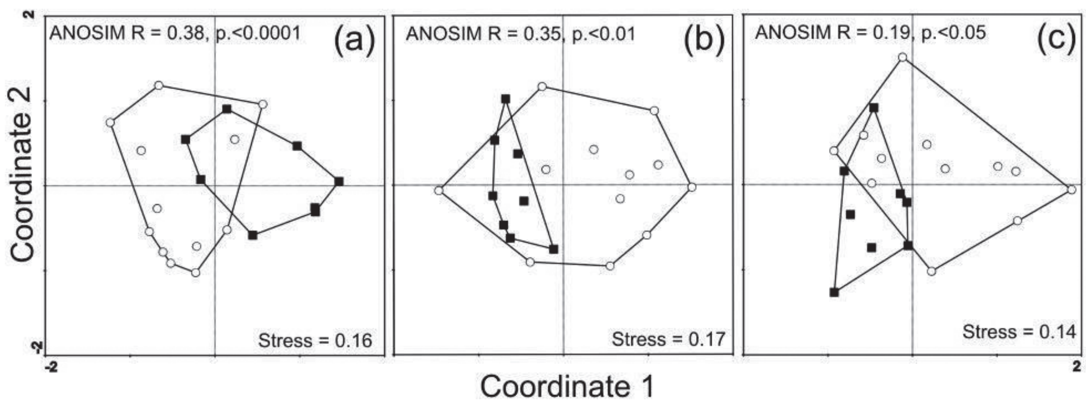

Figure 3. *Non-metric multidimensional scaling of ground beetles on three benches (a-c). The division into incised (square) and redeposited (open circle) is significant.*

processes, but the range of altitude (78 m) is very narrow and has no biological significance.

A total of 6,000 specimens belonging to 102 species (Coleoptera, Carabidae) were collected. The most abundant species, comprising almost 50% of the total sample, were *Poecilus versicolor* (20%), *Pterostichus melanarius* (11%), *Abax parallelepipedus* (7%) and *Pterostichus niger* (7%). All of these are characterized by broad ecological range, preferring mostly woodland habitats. The most numerous riverine specialist, *Chleanius nitidulus*, was 20th in total abundance, accounting for no more than 2% of the overall sample size. Thirty species were collected as singletons and doubletons, most of which were exposed riverine sediment specialists (ERS specialists) (*Bembidion ascendens* and *Bembidion punctulatum*).

Non-metric NMDS showed differences in ground beetle assemblages on all benches depending on the type of cross-section (Figure 3). In all cases assemblages from incised sites differ significantly from recently redeposited areas. The significance level, however, decreases as elevation increases. The assemblages from bench A (ERS) are the most distinct, whereas the assemblages from bench three (C) overlap, while still mostly having different composition.

A difference in composition of ground beetles was also shown by the SIMPER analysis (Table 3). There was a

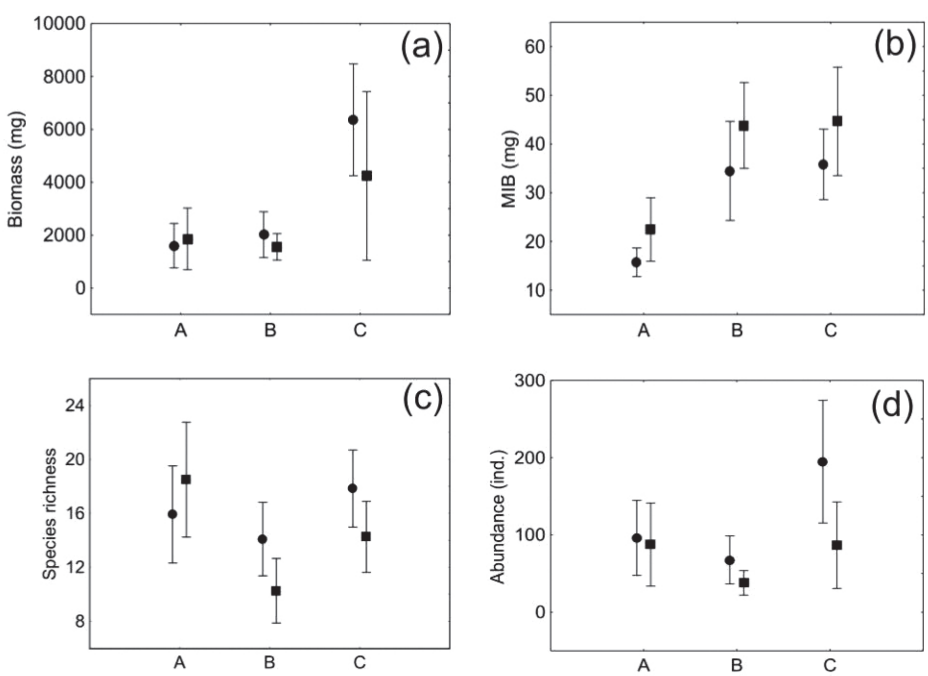

Figure 4. *The mean ground beetle assemblage structure parameters in relation to stream benches (A, B, C) and stream morphology (circle – redeposition of bed material, square – incision).*

Table 3. *SIMPER analysis of dissimilarity of ground beetles that contribute more than 1% of the variance between redeposited and incised cross-sections on three benches.*

	Taxon	Mean abundance (Redeposition)	Mean abundance (Incision)	Average dissimilarity	Contribution %
Bench A	*Poecilus versicolor* (Sturm, 1824)	**28.80**	5.75	13.84	15.89
	Chlaenius nitidulus (Schrank, 1781)	**11.20**	0.50	4.97	5.71
	Agonum sexpunctatum (Linné, 1758)	**8.25**	0.75	3.79	4.35
	Poecilus cupreus cupreus (Linné, 1758)	**5.25**	1.50	3.04	3.50
	Poecilus lepidus lepidus (Leske, 1785)	**4.75**	0.13	2.24	2.57
	Amara ovata (Fabricius, 1792)	**4.08**	0.38	2.15	2.47
	Anisodactylus binotatus (Fabricius, 1787)	**3.33**	0.88	1.92	2.21
	Carabus granulatus granulatus Linné, 1758	**3.00**	2.75	1.71	1.96
	Bembidion varicolor (Fabricius, 1803)	**1.42**	0.75	1.74	2.00
	Bembidion fasciolatum (Duftschmid, 1812)	**1.00**	0.00	1.04	1.19
	Bembidion ruficorne (Sturm, 1825)	**0.83**	0.25	0.85	0.98
	Pterostichus melanarius (Illiger, 1798)	2.50	**14.60**	7.73	8.88
	Platynus assimilis (Paykull, 1790)	0.08	**12.40**	5.57	6.40
	Elaphrus riparius (Linné, 1821)	0.00	**6.13**	2.97	3.41
	Pterostichus oblongopunctatus (Fabricius, 1787)	0.33	**5.63**	3.12	3.59
	Amara spreta Dejean, 1831	0.33	**5.13**	2.66	3.05
	Asaphidion flavipes (Linné, 1761)	0.00	**3.63**	1.91	2.19
	Pterostichus niger (Schaller, 1783)	1.58	**3.50**	2.07	2.38
	Carabus convexus Fabricius, 1775	0.83	**3.25**	1.74	2.00
	Abax parallelepipedus (Piller et Mitterpacher, 1783)	0.17	**3.00**	1.81	2.07
	Bembidion testaceum (Duftschmid, 1812)	1.42	**1.63**	2.15	2.47
	Loricera pilicornis (Fabricius, 1775)	0.25	**1.13**	0.86	0.98
Bench B	*Poecilus versicolor* (Sturm, 1824)	**20.10**	0.88	15.03	19.60
	Amara ovata (Fabricius, 1792)	**7.83**	0.25	6.63	8.65
	Carabus granulatus granulatus Linné, 1758	**6.00**	2.88	4.70	6.13
	Calathus erratus (C. R. Sahlberg, 1827)	**3.42**	0.00	2.89	3.76
	Carabus violaceus Linné, 1787	**2.92**	0.25	2.87	3.75
	Pterostichus niger (Schaller, 1783)	**2.17**	1.63	2.63	3.43
	Poecilus lepidus lepidus (Leske, 1785)	**1.67**	0.00	1.32	1.72
	Abax parallelus (Duftschmid, 1812)	1.75	**6.75**	6.50	8.48
	Abax parallelepipedus (Piller et Mitterpacher, 1783)	4.50	**6.50**	5.66	7.38
	Pterostichus oblongopunctatus (Fabricius, 1787)	2.17	**4.38**	4.59	5.99
	Carabus convexus Fabricius, 1775	3.00	**4.00**	4.33	5.65
	Pterostichus melanarius (Illiger, 1798)	2.58	**3.63**	3.75	4.89
	Platynus assimilis (Paykull, 1790)	0.33	**2.88**	2.80	3.65
	Carabus coriaceus Linné, 1758	0.33	**0.88**	1.01	1.32
Bench C	*Poecilus versicolor* (Sturm, 1824)	**48.20**	2.63	13.26	17.86
	Pterostichus melanarius (Illiger, 1798)	**33.50**	11.10	10.47	14.10
	Pterostichus niger (Schaller, 1783)	**22.70**	8.50	7.88	10.62
	Amara aenea (De Geer, 1774)	**9.00**	0.50	2.42	3.26
	Pterostichus oblongopunctatus (Fabricius, 1787)	**7.42**	1.88	3.61	4.86
	Carabus convexus Fabricius, 1775	**6.50**	1.75	2.52	3.39
	Carabus violaceus Linné, 1787	**5.58**	4.00	2.58	3.48
	Calathus erratus (C. R. Sahlberg, 1827)	**5.58**	0.00	1.13	1.52
	Amara ovata (Fabricius, 1792)	**4.50**	0.00	1.52	2.05
	Platynus assimilis (Paykull, 1790)	**4.42**	1.00	2.25	3.03
	Amara communis (Panzer, 1797)	**2.83**	0.38	1.02	1.37
	Abax parallelepipedus (Piller et Mitterpacher, 1783)	15.60	**21.60**	7.19	9.68
	Abax parallelus (Duftschmid, 1812)	7.75	**14.40**	4.87	6.56
	Abax ovalis (Duftschmid, 1812)	0.42	**5.63**	2.30	3.10
	Carabus ulrichii Germar, 1824	1.75	**2.75**	1.39	1.88

general consistent increase in exposed riverine sediment specialists on redeposited sites on bench A (e.g. *Chlaenius nitidulus*, *Bembidion varicolor*, *Bembidion fasciolatum* and *Bembidion ruficorne*), where the eco-friendly constructions had been built. Otherwise, *Elaphrus riparius* and *Asaphidion flavipes*, which are characteristic for riparian zones, were more abundant on incised cross-sections. There were also differences on other benches, but trends in species distribution are not clear. On bench B, which is mostly a transition zone between exposed riverine sediments and riparian forest, the most abundant species are characteristic of open areas (*Poecilus versicolor* and *Amara ovata*). However, the incised bench B is much more occupied by woodland species (e.g. *Abax parallelus*, *Abax parallelepipedus* and *Pterostichus oblongopunctatus*). Species characteristic of redeposited riparian forest are more diverse, representing open area and woodland specialists (*Poecilus versicolor*, *Amara aenea* or *Amara communis*), while in the incised habitats we find only woodland species (*Abax* species).

The distribution of ground beetle community structure parameters, total biomass, MIB, species richness and abundance is presented in Figure 4.

The generalized linear model indicated that incision-redeposition processes have a significant effect on most of the parameters (Table 4). The total biomass increases with elevation from the water table and distance from the water surface (from bench A, which has been most disturbed by flooding, to bench C), but the influence of channel modification on this parameter can be seen. On bench A the total biomass is lower on redeposited cross-sections, while on benches B and C the opposite effect is observed. Mean individual biomass increases along the gradient of habitat disturbances (from bench A to bench C), but more significantly, incision increases MIB on each bench. Species richness is not modification-dependent, but in combination with terrace type we have opposite results for bench A and the two other benches. On the most disturbed bench A the mean number of species is higher on incised cross-sections, while on the more stable bench B and C the number of species decreased at incised sites. The mean total abundance is always higher on redeposited than incised cross-sections on all investigated benches.

Table 4. *GLM for the bench (A, B, C) and channel type (incised, redeposited).*

Structure parameters	df	Wald parameters	p
Biomass			
Intercept	1	7780881.04	0.0000
Bench	2	46077.63	0.0000
Channel type	1	946.25	0.0000
Bench*Channel type	2	1903.11	0.0000
MIB			
Intercept	1	19892.56	0.0000
Bench	2	163.55	0.0000
Channel type	1	31.31	0.0000
Bench*Channel type	2	1.22	0.5442
Richness			
Intercept	1	6022.71	0.0000
Bench	2	17.78	0.0001
Channel type	1	3.52	0.0606
Bench*Channel type	2	8.99	0.0111
Abundance			
Intercept	1	81612.74	0.0000
Bench	2	560.93	0.0000
Channel type	1	252.09	0.0000
Bench*Channel type	2	124.37	0.0000

The life traits distribution on incised and redeposited exposed riverine sediments is presented in Figure 5. Only habitat generalists and predators were not significantly affected by redeposition of bed material (Table 5). In the parts of the Porębianka stream which had previously been regulated and incised, generalist species are dominant on ERS (Figure 5). There is, however, a significant positive effect of redeposition on ERS specialists, suggesting a continual increase in the proportion of ERS specialists in the ERS community after the construction of eco-friendly structures. Dispersal abilities also differ between types of channel modification, with higher abundance of brachypterous and dimorphic species at incised sites and greater abundance of macropterous species at redeposited sites. Feeding preferences differ between categories.

Stream restoration had no effect on predator species, but herbivorous ground beetles were more abundant at redeposited sites.

Breeding strategies are similar in both life strategy groups. Spring and autumn breeders are more abundant on modified redeposited cross-sections. The distribution of abundance in the three body-size groups differs between cross-section categories. On redeposited sites small and medium-sized species are more abundant. Large ground beetles, which are not natural elements of exposed riverine sediments, are more abundant on the incised ERS.

DISCUSSION

This study addressed the effects of redeposition processes in a stream channel on carabid beetle communities inhabiting a channelized riparian zone, showing significant effect of „eco-friendly" structures on community composition and life history pattern on formerly incised channel. Numerous authors have emphasized the severe negative impact of river channelization on the functioning of riparian ecosystems (*11, 43*), particularly for areas

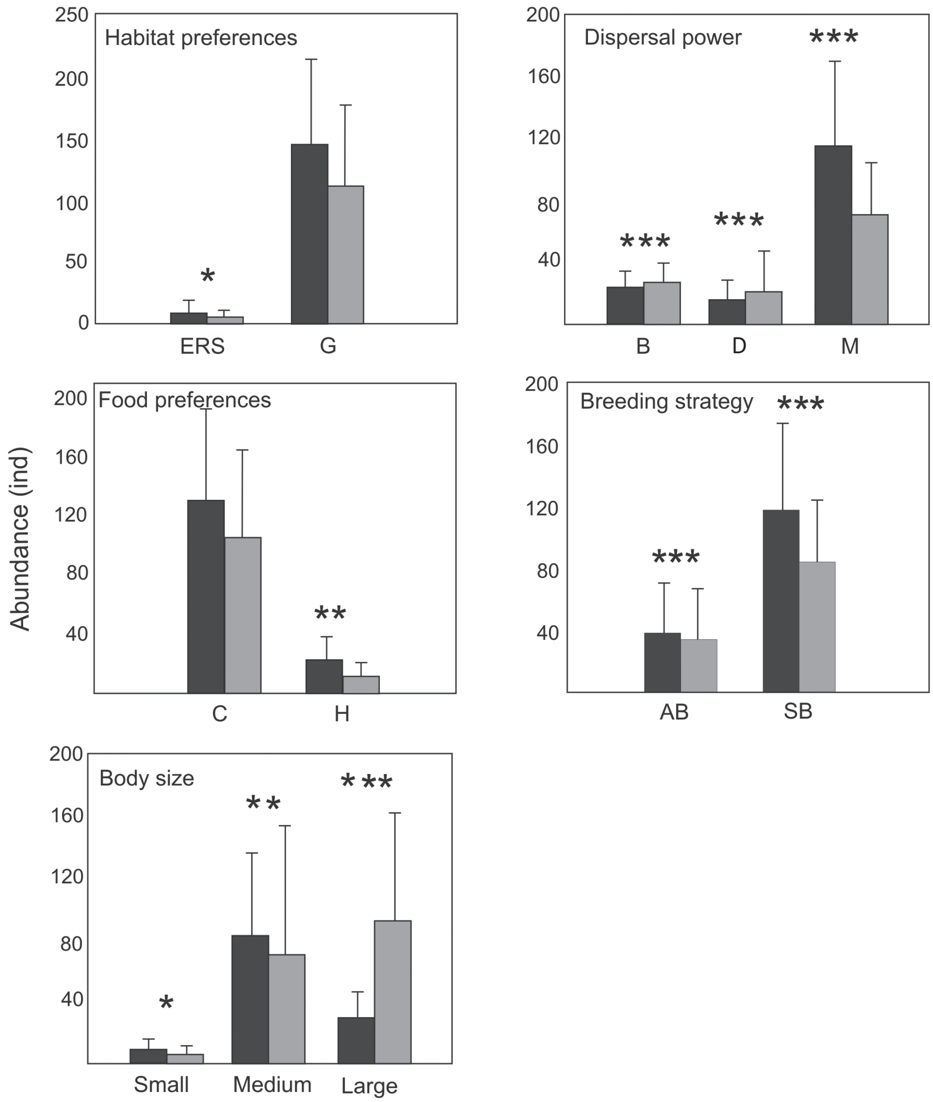

Figure 5. *Mean abundance (mean ±SE) of life history traits of ground beetles of redeposited (darker) and incised (lighter) channels on the exposed riverine sediments. The differences between channel types were tested using generalized linear models (Wald statistics *<0.05, ** <0.01, *** < 0.001).*

in the direct vicinity of the shoreline (known as exposed riverine sediments) (*44*). The disappearance of ERS areas as a result of channel incision disturbs natural riparian heterogeneity, leading to homogenization and terrestrialization of the floodplain. These changes have a detrimental effect on groups of riparian specialist species, for which unstable exposed riverine sediment areas (ERS) are a natural habitat (*21*), reducing their diversity or even eliminating them (*28*).

To limit the impact of these negative processes and restore the diversity of riparian zones, engineering techniques that are 'close to nature' are increasingly chosen, creating the possibility of unimpeded development of morphological processes (redeposition of gravel bed material and restoring the natural mosaic character of the shore zones (*14*). The results of our study indicate variation on all three benches in the carabid species composition between severely incised cross-sections and those with redeposition of bottom material, although as elevation increases and the frequency of flooding decreases (from bench A to B to C), these differences gradually become less perceptible (Figure 3). This was mainly due to differences in hydrological parameters such as bankfull discharge and period of flooding, as well as geomorphological parameters such as incision and erosion in the two types of channel (PCA) (Figure 2). In the sections where eco-friendly structures were established for restoration purposes, the decrease in bankfull discharge and water velocity led to an increase in bottom roughness and sedimentation of bottom material. The ERS areas restored in this manner gave specialist species the opportunity to recolonize. In cases of restoration of a natural, wide and multi-threaded river channel with many naturally flood-

Table 5. *GLM for life traits abundance of ground beetles.*

Life trait		Intercept	p	Channel modification	p
		Wald Statistics		Wald Statistics	
Exposed Riverine Sediment specialists	ERS	2470.67	0.00	5.86	0.0155
Generalists	G	26602.55	0.00	1.00	0.3175
Carnivores	C	29325.25	0.00	0.96	0.3284
Herbivores	H	1256.80	0.00	8.13	0.0044
Autumn breeders	AB	2205.23	0.00	33.49	0.0000
Spring breeders	SB	25997.75	0.00	22.32	0.0000
Brachypteres	B	847.08	0.00	22.01	0.0000
Dimorphic	D	1439.68	0.00	17.70	0.0000
Macropteres	M	22707.30	0.00	31.42	0.0000
Small (<7mm)	Small	251.89	0.00	6.60	0.0102
Medium (7-15mm)	Medium	17965.08	0.00	7.26	0.0071
Large (>15mm)	Large	9744.96	0.00	239.34	0.0000

ed ERS areas, this process has been reported to take place rapidly (*3, 43, 45*). In our case, however, the results do not confirm precisely this type of changes. When we consider the proportion of particular carabid species in the two types of cross-section (incised and redeposited), we see a small proportion of riparian specialist species in individual assemblages (Table 3, Figure 5). In the case of the incised cross-sections this is the result of stabilization of environmental conditions on the banks (*11*), the total disappearance of ERS, and the influx to all benches of generalist species with a wide ecological amplitude, characteristic of woodland habitats (e.g. *Poecilus versicolor*, *Pterostichus melanarius* or *Abax parallelepipedus*). In the case of the redeposited cross-sections, we presume that the slow increase in the proportion of riparian specialist species results first of all from the intensive exploitation of the entire valley, leaving the stream with a single-threaded stream. In this case the restoration measures taken (redeposition of bed material) favour the re-creation of unstable ERS environments, although their range and size is spatially limited to a narrow, single-threaded active channel. Secondly, the absence of natural ERS areas in the vicinity of the restored cross-section, which might have functioned as refuges for rare and often specialized species of carabids migrating into restored zones, may have been due to the severe modification of the floodplain in the entire Porębianka stream.

The differences in riparian carabid community organization between incised and redeposited cross-sections also reflect parameters of the structure of individual communities. According to Datry et al. (*46*), changes in communities inhabiting particular floodplains probably reflect changes in species resilience to inundation and changes in species habitat preferences from flood-adapted to flood-avoiding species (*18, 47*). Because on the higher situated benches B and C the frequency of flooding is considerably lower than on bench A, more stable environmental conditions lead to an increase in the abundance, species richness, total biomass and MIB of the carabid assemblages (*46*). Significantly, a similar effect can be observed in analysing the structure of Carabidae assemblages inhabiting bench A in the incised cross-sections. Severe incision of the channel stabilizes environmental conditions on benches, thereby substantially reducing the habitat diversity of the banks (*11, 43*). A reduced frequency of bank inundation creates possibilities for the colonization of ERS by species from higher elevations and elimination of specialized ERS species (well-adapted to the dynamic flow conditions typifying unmodified sections). In the sections where eco-friendly techniques reduced the water flow velocity, restoring deposition of bottom material, we can observe a slow stage of restoration of riparian specialist communities. This process can best be seen in the communities inhabiting bench A. The habitats situated closest to the shoreline and thus most dependent on the frequency of flooding mainly contain species of small body size and high dispersal capacity (*23, 24*). These traits allow them to escape quickly during periods of flooding and to recolonize the banks after the water level recedes. Our results confirm a visible decrease in total biomass and MIB on bench A in comparison with the benches situated farther from the shoreline (Figure 4).

As hypothesized, differences are observed in life history parameters of carabids between the redeposited and incised cross-sections. These parameters have been used in many ecological studies and studies on environmental disturbances *(18, 24, 45, 48, 49, 50).* Our results show that redeposition leads to an increase in abundance of species whose life traits describe riparian specialists. In restored cross-sections there is an increase in abundance of macropteric predators with small body size and a spring developmental cycle (Figure 5). These are parameters characterizing ERS specialist species, enabling them not only to survive repeated periods of flooding, but also to permanently colonize these unstable environments (*18, 21, 23, 24*).

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APPENDIX

List of Carabid species and their habitat preferences, mean body size, life traits (C-carnivores, H – herbivores, A – autumn breeders, S – spring breeders, B – brachypters, D-dimorphics, M – macropters) and Total abundance

No.	Species name	Habitat preferences	Mean body size [mm]	Food preferences	Breeding strategy	Dispersal power	Total abundance
1	*Abax (s. str.) ovalis* (Duftschmid, 1812).	G	14.3	C	S	B	68
2	*Abax (s. str.) parallelepipedus* (Piller et Mitterpacher, 1783).	G	18.6	C	S	B	470
3	*Abax (s. str.) parallelus* (Duftschmid, 1812).	G	15.1	C	S	B	309
4	*Acupalpus (s. str.) elegans* (Dejean, 1829).	G	4.4	H	S	M	1
5	*Agonum (s. str.) muelleri* (Herbst, 1784).	G	8.1	C	S	M	15
6	*Agonum (s. str.) sexpunctatum* (Linné, 1758).	G	8.7	C	S	M	122
7	*Amara (Celia) bifrons* (Gyllenhal, 1810).	G	6.3	H	S	M	1
8	*Amara (Celia) cursitans* C. Zimmermann, 1832.	G	7.7	H	S	M	1
9	*Amara (Celia) ingenua* (Duftschmid, 1812).	G	9.6	H	S	M	2
10	*Amara (Celia) praetermissa* (C. R. Sahlberg, 1827).	G	6.8	H	A	M	5
11	*Amara (Curtonotus) aulica* (Panzer, 1796).	G	12.5	H	A	M	13
12	*Amara (Percosia) equestris* (Duftschmid, 1812).	G	8.9	H	A	M	2
13	*Amara (Zezea) plebeja* (Gyllenhal, 1810).	G	6.8	H	S	M	2
14	*Amara (s. str.) aenea* (De Geer, 1774).	G	7.5	H	S	M	128
15	*Amara (s. str.) communis* (Panzer, 1797).	G	6.6	H	S	M	53
16	*Amara (s. str.) curta* Dejean, 1828.	G	6.6	H	S	M	2
17	*Amara (s. str.) famelica* C. Zimmermann, 1832.	G	7.8	H	S	M	1
18	*Amara (s. str.) familiaris* (Duftschmid, 1812).	G	6.4	H	S	M	8
19	*Amara (s. str.) littorea* C. G. Thomson, 1857.	G	7.7	H	S	M	1
20	*Amara (s. str.) montivaga* Sturm, 1825.	G	8.2	H	S	M	30
21	*Amara (s. str.) nitida* Sturm, 1825.	G	7.4	H	S	M	1
22	*Amara (s. str.) ovata* (Fabricius, 1792).	G	9	H	S	M	204
23	*Amara (s. str.) schimperi* Wencker, 1866.	G	7.7	H	S	M	34
24	*Amara (s. str.) similata* (Gyllenhal, 1810).	G	8.7	H	S	M	30
25	*Amara (s. str.) spreta* Dejean, 1831.	G	7.8	H	S	M	49
26	*Anchomenus (s. str.) dorsalis* (Pontoppidan, 1763).	G	6.8	C	S	M	1
27	*Anisodactylus (Hexatrichus) poeciloides* (Stephens, 1828).	G	10.7	H	S	M	9
28	*Anisodactylus (Pseudanisodactulus) signatus* (Panzer, 1796).	G	12.5	H	S	M	2
29	*Anisodactylus (s. str.) binotatus* (Fabricius, 1787).	G	11.1	H	S	M	49
30	*Asaphidion caraboides* (Schrank, 1781).	ERS	6.1	C	S	M	1
31	*Asaphidion flavipes* (Linné, 1761).	ERS	4.4	C	S	M	30
32	*Badister (Baudia) dilatatus* Chaudoir, 1837.	G	5.4	C	S	M	1
33	*Badister (s. str.) bullatus* (Schrank, 1798).	G	5.4	C	S	M	3
34	*Bembidion (Bembidionetolitzkya) ascendens* (K. Daniel, 1902).	ERS	7.1	C	S	M	1
35	*Bembidion (Bembidionetolitzkya) fasciolatum* (Duftschmid, 1812).	ERS	5.9	C	S	M	12
36	*Bembidion (Bembidionetolitzkya) geniculatum* (Heer, 1837).	ERS	5.1	C	S	M	4
37	*Bembidion (Bembidionetolitzkya) tibiale* (Duftschmid, 1812).	ERS	6	C	S	M	5
38	*Bembidion (Bembidionetolitzkya) varicolor* (Fabricius, 1803).	ERS	5.3	C	S	M	23
39	*Bembidion (Euperyphus) testaceum* (Duftschmid, 1812).	ERS	5	C	S	M	31
40	*Bembidion (Metallina) lampros* (Herbst, 1784).	G	3.6	C	S	D	14
41	*Bembidion (Metallina) properans* (Stephens, 1828).	G	4	C	S	D	6
42	*Bembidion (Neja) nigricorne* (Gyllenhal, 1827).	G	3.8	C	S	D	1
43	*Bembidion (Peryphus) cruciatum bualei* Jacquelin du Val, 1852.	ERS	5	C	S	M	6
44	*Bembidion (Peryphus) tetracolum Say*, 1823.	ERS	5.4	C	S	D	13

No.	Species name	Habitat prefer-ences	Mean body size [mm]	Food prefer-ences	Breeding strategy	Dispersal power	Total abun-dance
45	*Bembidion (Phyla) obtusum* Audinet-Serville, 1821.	ERS	3.1	C	S	D	1
46	*Bembidion (Princidium) punctulatum* Drapiez, 1821.	G	5	C	S	M	2
47	*Bembidion (Sinechostictus) ruficorne* (Sturm, 1825).	ERS	6.7	C	S	M	12
48	*Bembidion (Trepanedoris) doris* (Panzer, 1797).	ERS	3.4	C	S	M	2
49	*Bradycellus (s. str.) caucasicus* (Chaudoir, 1846).	G	3.8	H	S	B	1
50	*Calathus (Neocalatchus) erratus* (C. R. Sahlberg, 1827).	G	9.7	C	A	B	113
51	*Carabus (Eucarabus) ulrichii* Germar, 1824.	G	27.5	C	A	B	49
52	*Carabus (Megodontus) violaceus* Linné, 1787.	G	28.5	C	A	B	148
53	*Carabus (Oreocarabus) glabratus* Paykull, 1790.	G	28	C	A	B	1
54	*Carabus (Oreocarabus) linnei* Panzer, 1810.	G	18.5	C	S	B	22
55	*Carabus (Procrustes) coriaceus* Linné, 1758.	G	36.5	C	A	B	52
56	*Carabus (Tachypus) cancellatus excisus* Dejean, 1826.	G	23.5	C	S	B	20
57	*Carabus (Tomocarabus) convexus* Fabricius, 1775.	G	17	C	S	B	196
58	*Carabus (s. str.) arcensis* Herbst, 1784.	G	18	C	S	B	2
59	*Carabus (s. str.) granulatus* Linné, 1758.	G	19.5	C	S	D	187
60	*Chlaenius (Chlaeniellus) nitidulus* (Schrank, 1781).	ERS	11.5	C	S	M	141
61	*Chlaenius (Chlaeniellus) tibialis* Dejean, 1826.	ERS	11.1	C	S	M	20
62	*Clivina collaris* (Herbst, 1784).	G	5.4	C	S	M	8
63	*Elaphrus (Elaphroterus) aureus* P. W. J. Müller, 1821.	ERS	6.7	C	S	M	1
64	*Elaphrus (s. str.) riparius* (Linné, 1821).	ERS	7	C	S	M	49
65	*Harpalus (Pseudoophonus) griseus* (Panzer, 1796).	G	10.5	H	S	M	2
66	*Harpalus (Pseudoophonus) rufipes* (De Geer, 1774).	G	13.8	H	S	M	18
67	*Harpalus (s. str.) affinis* (Schrank, 1781).	G	10.2	H	S	M	11
68	*Harpalus (s. str.) atratus* Latreille, 1804.	G	11.8	H	S	D	18
69	*Harpalus (s. str.) froelichii* Sturm, 1818.	G	9.4	H	S	M	1
70	*Harpalus (s. str.) hirtipes* (Panzer, 1796).	G	13.5	H	S	M	2
71	*Harpalus (s. str.) latus* (Linné, 1758).	G	9.3	H	S	M	8
72	*Harpalus (s. str.) luteicornis* (Duftschmid, 1812).	G	7.5	H	S	M	16
73	*Harpalus (s. str.) marginellus* Gyllenhal, 1827.	G	10.8	H	S	M	2
74	*Laemostenus (Pristonychus) terricola* (Herbst, 1784).	G	15.1	C	A	D	4
75	*Loricera (s. str.) pilicornis* (Fabricius, 1775).	G	7.4	C	S	M	12
76	*Molops (Molops) piceus* (Panzer, 1793).	G	12	C	S	B	20
77	*Nebria (Boreonebria) rufescens* (Strom, 1768).	ERS	10.2	C	S	M	3
78	*Nebria (s. str.) brevicollis* (Fabricius, 1792).	G	11.5	C	A	M	25
79	*Notiophilus germinyi* Fauvel in Grenier, 1863.	G	4.9	C	A	D	1
80	*Notiophilus palustris* (Duftschmid, 1812).	G	5.2	C	S	D	5
81	*Oodes helopioides* (Fabricius, 1792).	G	8.7	C	S	M	13
82	*Ophonus (Metophonus) cordatus* (Duftschmid, 1812).	G	8.5	H	A	M	8
83	*Ophonus (Metophonus) laticollis* Mannerheim, 1812.	G	9.5	H	S	M	7
84	*Oxypselaphus obscurus* (Herbst, 1784).	G	5.5	C	S	D	4
85	*Panagaeus (s. str.) cruxmajor* (Linné, 1758).	G	8.1	C	S	M	3
86	*Patrobus assimilis* Chaudoir, 1844.	G	7.8	C	S	B	3
87	*Patrobus atrorufus* (Strom, 1768).	G	8.5	C	A	B	5
88	*Platynus (s. str.) assimilis* (Paykull, 1790).	G	11	C	S	M	197
89	*Poecilus (s. str.) cupreus* (Linné, 1758).	G	12.1	C	S	M	87
90	*Poecilus (s. str.) lepidus* (Leske, 1785).	G	12.9	C	A	D	80

No.	Species name	Habitat preferences	Mean body size [mm]	Food preferences	Breeding strategy	Dispersal power	Total abundance
91	*Poecilus (s. str.) sericeus* (Fischer von Waldheim, 1824).	G	12.6	C	A	D	19
92	*Poecilus (s. str.) versicolor* (Sturm, 1824).	G	10.7	C	S	M	1238
93	*Pterostichus (Bothriopterus) oblongopunctatus* (Fabricius, 1787).	G	11.4	C	S	M	214
94	*Pterostichus (Cheporus) burmeisteri* Heer, 1838.	G	13.5	C	A	B	7
95	*Pterostichus (Cryobius) unctulatus* (Duftschmid, 1812).	G	6.9	C	S	B	1
96	*Pterostichus (Morphnosoma) melanarius* (Illiger, 1798).	G	15.7	C	A	D	698
97	*Pterostichus (Petrophilus) foveolatus* (Duftschmid, 1812).	G	13.3	C	S	B	2
98	*Pterostichus (Phonias) strenuus* (Panzer, 1796).	G	6.1	C	S	D	11
99	*Pterostichus (Platysma) niger* (Schaller, 1783).	G	18.5	C	A	M	426
100	*Pterostichus (Pseudomasesus) nigrita* (Paykull, 1790).	G	11	C	S	M	13
101	*Stenolophus (s. str.) teutonus* (Schrank, 1781).	ERS	6.6	C	S	M	3
102	*Trichotichnus (s. str.) laevicollis* (Duftschmid, 1812).	G	7.6	H	S	D	23