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Anthropogenic transformation of ground beetle assemblages (Coleoptera: Carabidae) in Białowieża Forest, Poland: from primeval forests to managed woodlands of various ages

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The interference of man in the primeval forest of Białowieża (e.g. clear-cutting and reforesting fertile habitats with pine or spruce) brings about changes in carabid assemblages, including a reduction in the proportion of individuals of relict species, reduction in the mean individual biomass (MIB) and in the sum of positive characteristics (SPC; a summary indicator). Human impact in forest ecosystems causes losses of some relict species and a gain of ubiquitous species. I compared the carabid faunas of pristine forests to those of various stages of clear-cut originated succession. Clear-cutting caused a drastic decrease in MIB, a reduction in the proportion of brachypterous species, and an increase in both the number of hygrophilous species and their proportion in the assemblage.

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1. Introduction

The increasing research interest on primeval natural forests is reflected both in the number of publications (e.g., Rackham 1980, Foster *et al.* 1996, Assmann 1999, Bobiec *et al.* 2000, Bircks 2005) and in the attempts to identify and define forests resembling natural ones, at least partially. These forests are referred to as “ancient” or “recent” (Assmann 1999) or “semi-natural woodlands” (Poole *et al.* 2003). Białowieża Primeval Forest is the only lowland forest area in temperate Europe where large tracts of natural forests, with their typical communities, still remain (Wesołowski 1995, Bobiec *et al.* 2000). Perhaps surprisingly, the key to the maintenance of the naturalness was hunting by ruling families. By the fourteenth century, the forest was set aside as a royal forest, and by the sixteenth century 300 royal wardens were employed there. Their main task was to keep the forest free from unwanted intruding, illegal logging and patching (Wesołowski 2005).

Economic use of part of the Białowieża Primeval Forest began as late as the 1920’s. After World War II, only about 600 km^2 of the entire 1,500 km^2 Białowieża Forest were left within Polish territory; the rest now belongs to Belarus. The protected zone in the Polish part of Białowieża Forest includes a national park and nature reserves, while the remaining forests are still exploited for economic purposes and exemplify a variety of types and intensities of anthropic pressure. By anthropic pressure I understand any human activity (irrespective of its temporal or spatial scale) that causes changes to an ecosystem or its constituents. These changes are often deleterious to the system. The presence of both naturally regenerated and managed forest stands in this area provides an opportunity to trace the transformation of natural woodland into managed forests that are the prevalent type of forest at present.

Anthropic pressure in timber forests may take on various forms, from construction of transportation routes and settlement areas to clear-cutting for timber production, or for creation of open areas for various other purposes. Perhaps the most profound impact is that of clear-cutting, after which local macrofaunal assemblages take several dozens of years to regenerate (Szujecki 1971, Szujecki *et al.* 1983, Szyszko 1983, Skłodowski 1995, 1997). As naturally regenerated forest stands are becoming managed (= timber) forests (Wesołowski 2005), the question arises whether a clear-cut originated stand can be restored (through natural re-growth or) by simply planting a new generation of trees and keeping the cutting limited in the area. To study the forest-community resilience, I used ground beetles (Carabidae) as bioindicators of environmental change.

Negative effects of clear-cutting on the macrofauna, and carabid beetles in particular, have been earlier reported by Szyszko (1983), Szujecki *et al.* (1983), Skłodowski (1995), Atlegrim *et al.* (1997), du Bus de Warnaffe and Lebrun (2004), Koivula (2001, 2002), Niemelä *et al.* (1993, 2003) and Pontégnie *et al.* (2005). These papers reveal that small- (e.g., an area of 1,600 m^2) and large-scale clear cutting (up to tens or hundreds of ha) result in an increase in species diversity accompanied by an influx or increased abundance of species associated with open habitats and forest-habitat generalists; however, forest specialists may drastically decrease or even disappear. Atlegrim *et al.* (1997) pointed out that single-tree cutting did not cause such profound changes in carabid assemblages. Because smaller species often prevail in logged areas, the absence of larger species logically means a reduced mean individual biomass (MIB) of the carabid assemblage (Szyszko 1983). All the above-listed results were obtained in managed forests. However, it is less known whether the carabid fauna of primeval forests responds to logging in a similar manner.

Carabid assemblages of mature, primeval forests are characterized by a predominance of large and forest-associated species. These assemblages include relict species that may not tolerate logging (Assmann 1999). In this paper, I study the ecological effects of logging on carabids by comparing faunas of primeval forests to those obtained from clear-cut originated, regenerating (= timber, or managed) forests. The key question is to study the effect of clear-cutting on pristine forests, which is of considerable practical value for nature conservation. More precisely, I study the following hypotheses:

(1) Clear-cutting of a natural forest stand, even if limited in area, results in changes in the number of species, species composition and the structure of carabid assemblages (e.g., a statistically significant decrease in the proportion of relict and hygrophilous species and mean individual biomass);
(2) Tree re-growth of a previously clear-cut stand supports the (presumably slow) restoration of the forest ecosystem, including carabid assemblages. However, regenerated assemblages may be structurally different from the assemblages of primeval forests.
(3) I also examine whether forest type (or soil fertility) of primeval habitats has an impact on the structure and resilience of carabid assemblages.

2. Material and methods

2.1. Study area and carabid sampling

The study was part of a larger research project on the entomo-fauna of the Białowieża Primeval Forest (Szujecki *et al.* 2001). The study was done in the Polish part of the Białowieża Primeval Forest (northern Poland) in two stages. First, in 1999, carabid assemblages were studied in the protected parts of the Primeval Forest (Skłodowski 2003, 2005). In total, 163 plots were selected for that study. At the second stage, in 2003, 90 study plots were set up in stands subjected to different degrees of anthropic pressure. In both stages, five Barber's pitfall traps were installed at each plot

Table 1. Studied forest habitats in Białowieża Forest and their abbreviations used in text. P = primeval forest; C, MC, MD, D and DD refer to forest habitat types (see text); numbers (5, 15, 40, 100) refer to stand age (years since clear-cutting). p = planted pine and s = planted spruce monoculture; C = "Century" forest.

	Mesic coniferous	Mesic mixed coniferous	Mesic mixed deciduous	Mesic deciduous	Damp deciduous
Primeval	P_C	P_MC	P_MD	P_D	P_DD
5-y-old plantation	C5	MC5	MD5	–	DD5
15-y-old plantation	C15	MC15	MD15	–	DD15
40-y-old plantation	C40	MC40	MD40	–	DD40
40-y-old pine monoculture	–	–	MDp	D40p	–
100-y-old pine monoculture	–	–	MD100p	D100p	–
100-y-old spruce monoculture	–	–	MD100s	D100s	–
Old "Century" stand	–	–	MD_C	D_C	–

and serviced four times at six-week intervals, beginning on 1 May. Five traps (0.5 l glass jar with a plastic funnel, 12 cm in diameter, containing 100 ml 70% ethylene glycol) were arranged 15 m apart along each transect. As there were (163 + 90 =) 253 plots, the total number of traps was 1265 in both parts of the study.

Białowieża Primeval Forest consists of a mosaic of fertile habitats that have not been subjected to the destruction and unification typical of managed forests. Two levels of forest soil humidity were selected to study: damp (wet; 70–99% of the soil surface under water during spring) and mesic (fresh; no inundation at any time of the year). Within the mesic habitat, traps were placed in four different forest stand types: coniferous (low fertility habitats with a predominance of *Picea abies*, *Pinus sylvestris* and *Larix decidua*), mixed coniferous, mixed deciduous, and deciduous. The latter two represent high fertility habitats with a predominance of broad-leaved tree species. In the mixed coniferous stands, coniferous tree species constituted 51–90% of all trees, whereas in the mixed deciduous stands 51–90% of the threes were broad-leaved.

The following primeval stand types were selected for investigation in the mesic habitat: coniferous (C), mixed coniferous (MC), mixed deciduous (MD) and deciduous (D); in the damp habitat, deciduous stands (DD) were included (Table 1). Each distinguished primeval forest habitat was represented by equal number of replicates (12 plots for each habitat type).

The effect of anthropic pressure on carabids was studied in analogous forest biotopes (C, MC MD, D and DD). In the C, MC, MD and DD habitats, carabid beetles were studied in 5-, 15- and 40-years-old plantations growing in areas that had been clear-cut earlier. Additional samplings were done in MD and D habitats in 40- and 100-years-old pine monocultures and 100-years-old monocultures of spruce planted in clear-cuts of previous multi-species primeval forest, and in 80-years-old stands growing in areas of large-scale clear-cutting carried out during 1927–1928 by a British company "The Century European Timber Corporation", designated here as "Century". Each variant of anthropic pressure in the study habitats C, MC, MD and DD was replicated three times.

2.2. Ecological-historical types of carabid beetles

For analytical purposes, the carabid species were divided into various groups (Table 2). The "forest relict" species group comprises species that are predominantly found in forests and reproduce there but are seldom or never observed outside closed-forest stands. Species were assigned to this group on the basis of earlier observations in Polish forests and literature (Burakowski *et al.* 1973, 1974, Assman 1999, Turin 2000). A high proportion of relict species in an assemblage presumably indicates the presence of little or no anthropic pressure in a given habitat.

The "brachypterous species" group used in

Table 2. ANOVA for carabid assemblages in four forest habitats. Symbols used in pair-wise *post hoc* tests: 1 = C, 2 = MC, 3 = MD, 4 = DD, and in stands with different ages of dominant trees: 1 = 5-, 2 = 15-, 3 = 40-years-old, and 4 = (un-aged) primeval forest (see Table 1 for abbreviations).

Variable	df	MS	F	*p*	LSD *post hoc* test
Species richness					
Habitat	3	59.347	6.535	0.001	1, 2 < 3, 4 (*p* = 0.001)
Age	3	18.407	2.027	0.118	
Habitat × Age	9	4.938	0.543	0.837	
Relicts					
Habitat	3	3146.063	14.687	<0.001	4 < 1, 2 < 3 (*p* < 0.001); 2, 3 > 1 (*p* = 0.030)
Age	3	1835.366	8.568	<0.001	4 >1, 2, 3 (*p* = 0.010 to *p* < 0.001)
Habitat × Age	9	803.355	3.710	<0.001	
MIB					
Habitat	3	119846.800	19.914	<0.001	1 < 3 (*p* < 0.001); 4 < 1, 2, 3 (*p* < 0.001); 3 > 2 (*p* < 0.001)
Age	3	105229.200	17.486	<0.001	4 >1, 2, 3 (*p* < 0.001)
Habitat × Age	9	24089.300	4.003	0.003	
SPC					
Habitat	3	15574.560	8.743	< 0.001	4 < 1, 2, 3 (*p* < 0.001)
Age	3	5904.950	3.315	0.024	2 > 3 (*p* = 0.030); 3 < 4 (*p* = 0.003)
Habitat × Age	9	6792.380	3.813	0.001	
Hygrophilous					
Habitat	3	8440.183	34.025	<0.001	4 > 1, 2, 3 (*p* < 0.001)
Age	3	1107.472	4.465	0.006	4 < 1 (*p* = 0.010); 4 < 2 (*p* = 0.003)
Habitat × Age	9	271.367	1.094	0.379	
Brachypterous					
Habitat	3	3592.541	16.439	<0.001	4 < 1, 2, 3 (*p* < 0.001)
Age	3	709.437	3.246	0.027	4 > 3 (*p* = 0.006)
Habitat × Age	9	999.940	4.576	<0.001	

the analysis was distinguished on the basis of observed wing length and wing muscles. Brachypterous carabids have a low power of dispersal, which makes it difficult for them to leave the ploughed clearings quickly or to re-colonize them later on. Hence, a high proportion of brachypterous species in a community indicates an undisturbed habitat (Ribera *et al.* 2001).

”Hygrophilous species” were classified on the basis of earlier observations and data from Burakowski *et al.* (1973, 1974) and Turin (2000). A high proportion of these species in a habitat indicates high moisture levels but may also be due to considerable shading or the presence of coarse woody debris and other factors.

The SPC index used here (see section 2.3.) was based on four different species groups: autumn breeders, large zoophages, forest species and European species (i.e., those with limited geographical ranges, compared to Palaearctic or Holarctic species). The classification was based on observations by the author and Larsson (1939), Burakowski *et al.* (1973, 1974), Szyszko (1983), Szujecki *et al.* (1983) and Turin (2000). The reason for the inclusion of these four groups in the analyses is their predominance in carabid assemblages in mature forests: an abundance of these species indicates the recovery of the forest ecosystem (Szyszko 1983, Szujecki *et al.* 1983, Skłodowski 1995).

2.3. Data analysis

Carabid individuals were determined to species, and their body length was measured with an accuracy of 0.5 mm. This measure was subsequently converted to biomass according to the formula proposed by Szujecki *et al.* (1983). The mean individual biomass (MIB) is the quotient of the sum of biomass of all individuals in an assemblage by their abundance (Szyszko 1983, 2002). The sum of progressive characteristics [SPC; Sklodowski (1997)] was also used. This metric is correlated with the age of the stand in question [$r = +0.93$, $p = 0.0001$, $n = 76$; Sklodowski (1997)] and is calculated as follows:

$$SPC = 74.9 + 102 * LOG\ (stand\ age) \qquad (1)$$

SPC is thus the sum of proportions of those groups of carabids that are dominant in mature forest stands: autumn breeders, large zoophages, forest species and European species (see section 2.2). The two values are coefficients: 74.9 for the model intercept and 102 for the regression slope.

Prior to the statistical analyses, the data were tested for normality of distributions using Shapiro-Wilk's statistic [Statistica; StatSoft, Inc. (1997)]. Species data were log (n) * 100 transformed to improve normality of the distributions. Species richness was standardized to the lowest number of specimens in the samples using Simberloff's rarefaction formula (Krebs 1999).

Two-way ANOVA [Statistica; StatSoft Inc. (1997)] was used to verify the impact of clear-cutting on the abundance and structure of carabid communities. Data were compared in two groups. The first comparison was among areas representing different habitat types (C, MC, MD and DD), with 12 replicates for the primeval forests and 9 replicates for each of the different types of managed (regenerating) forests. The second comparison distinguished different stand ages: 5-, 15- and 40-years-old stands (each with 12 replicates) and "indefinite" (primeval) stands (48 replicates). Equality of variances was verified using Levene's test. A *post hoc* comparison of significant differences in ANOVA was confirmed using the LSD (least significant difference) *post hoc* test. Both ANOVA comparisons were done using data with 1999 and 2003 catches pooled for each stand i.e. analyses were based on stand totals.

Species-composition similarities were compared using Ward cluster analysis based on Euclidean distances [Statistica; StatSoft Inc. (1997)]. To study the distinctiveness of carabid assemblages of the compared habitat types and stand ages, Detrended Correspondence Analysis (DCA) was carried out using CANOCO software (ter Braak & Smilauer 1997–1999).

The hypothesis of slow regeneration of carabid fauna in regenerated forest stands was tested using two-way ANOVA [Statistica; StatSoft Inc. (1997)]. The comparison was carried out in two habitat types: MD and D (both with 24 replicates) in 40- and 100-years-old pine and spruce stands and in 80-years-old regenerated broad-leaved stands. Equality of variances was verified using Levene's test. A *post hoc* comparison of significant differences in ANOVA was confirmed using the LSD (least significant difference) test. The age variants of regenerated stands (40-, 80- and 100-years-old) involved in the slow-regeneration hypothesis were included in Ward analysis of species similarity and DCA gradient analysis. Similarly, I studied whether the structure and abundance of carabid assemblages depends on the fertility of the primeval habitats subject to anthropic pressure.

3. Results

The first stage of the study (year 1999) yielded nearly 60,000 carabid individuals representing 105 species, with a further ca. 30,000 individuals and additional 25 species captured during the second stage (year 2003). Thus, the total number of species was 130, accounting for one-fourth of all carabid species ever recorded within the boundaries of Poland since World War II (Burakowski *et al.* 1973). 50,235 individuals representing 109 species were analysed.

3.1. Effect of clear-cutting on the abundance and structure of carabid assemblages.

Significant differences between characteristics of carabid assemblages from primeval forests vs. those from young, regenerating (5-, 15- and 40-years-old) stands were found (Tables 2–3). However, ANOVA did not indicate differences in species richness between primeval and regenerating stands, although it showed differences in percentages of relict and hygrophilous species and in the values of the SPC and MIB indices (Tables 2–3).

Percentages of relict carabids varied from 15.8%, 36.7%, 44.0% and 53.2% (mean 38.0%)

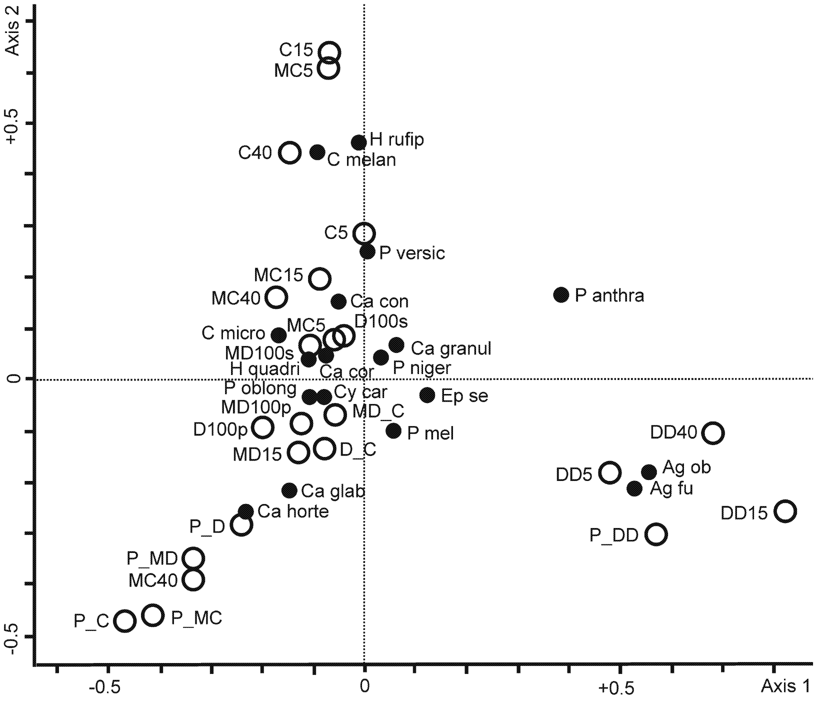


Fig. 1. DCA for the carabid catches presented in Appendix. See Table 1 for abbreviations of habitat codes; species are shown using abbreviations (compare Appendix for full names).

in the assemblages inhabiting the primeval habitats of DD, C, MD and MC types to 6.1%, 9.7% and 17.4% (mean 9.9%) in the assemblages of 5-years-old plantations of C (LSD test, $p = 0.006$), MC (LSD test, $p = 0.001$) and MD (LSD test, $p = 0.01$). Thus, relict species had apparently exhibited a definite group response to human activity. In the assemblages of the restored habitats, two rare relict species, *Carabus intricatus* and *Leistus piceus*, were not found. However, the 5-years-old plantations supported species not found in primeval stands: *C. melanocephalus* (dominance indices 15% in MC habitat, 5% in C and 4% in MD), *P. caerulescens* (12% in MC and 9.6% in MD). At the same time, large forest species were absent from these plantations. On the other hand, these species had high dominance indices in the primeval forests: *C. glabratus* 8% in MC, *C. arcensis* 42.6% in C, where also *C. hortensis* had a value of 35.6% (vs. 1.6% in the 5-years-old plantations; Chi-square statistic = 8.37, $p = 0.004$).

DCA grouped the studied habitats along a gradient of anthropic pressure parallel to the vertical axis (Fig. 1). The four mesic habitats of primeval forest (C, MC, MD and D) scattered close to each other to the bottom-left. Anthropic pressure in the forest areas, resulting from clear-cutting, was followed by forest regeneration, with replacement of formerly dominant deciduous tree species by coniferous trees. Such changes are reflected in Fig. 1 by the displacement of the reference points relative to positions of the points for the primeval forest assemblages. The scores of the damp forest habitats formed a separate cluster to the right from the other habitats, suggesting a vertical course of a moisture gradient. This finding is compatible with the results of an earlier DCA for gradients of fertility and moisture, carried out for carabids collected from the primeval forest habitats only (J. W. Sklodowski, unpubl. data). Cluster analysis also indicated faunal differences between the primeval and regenerating stands. The carabids from the primeval stands (D, MD and MC) were grouped into a distinctive agglomeration (Fig. 2).

In the assemblages inhabiting the 5- and 15-years-old plantations, the proportion of hygrophilous species was significantly higher than in the assemblages from primeval stands (Table 2); for example, 47.7% vs.13.4% in C, 26.1% vs. 19.7% in MC and 22.8% vs. 16.4% in MD (LSD test; p for pair-wise differences varied between

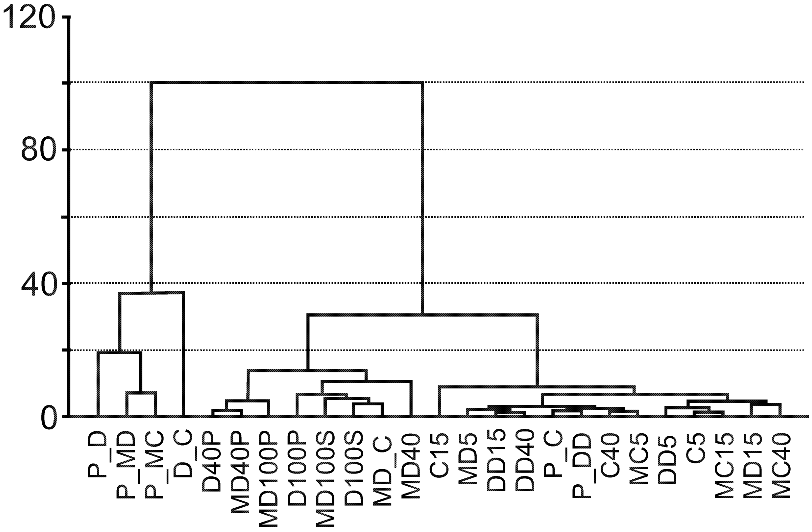


Fig. 2. Cluster analysis for the carabid catches from primeval and managed forests at the Białowieża area. Compare Table 1 for habitat codes.

0.040 and 0.001). Also the mean percentages of hygrophilous species in assemblages of the 40-years-old plantations and the primeval stands differed markedly (Table 2).

The proportion of brachypterous species was higher in the primeval stands compared to their baseline (= mean value for each habitat separately) proportion: in C habitat, from a baseline of 87.2% to 76.3% in the 5-years-old plantations and to 53.4% in the 15-years-old plantations (LSD test, $p = 0.002$), in MC habitat from a baseline of 81.1% to 44.1% in the 5-years-old plantations (LSD test, $p = 0.002$), in MD habitat from a baseline of 69.9% to 57.8% ($F = 6.670$, $p < 0.001$). The primeval stands hosted higher proportions of brachypterous species than did 5-years-old plantations. In the marshy DD habitats, on the other hand, clear-cutting increased the proportion of brachypterous individuals from 29% to 52% (LSD test, $p = 0.014$). In the 40-years-old plantations, the proportion of this group decreased to 22.3%, corresponding to its reference in the primeval stands.

ANOVA for the mean individual biomass (MIB) and the SPC index (Table 2) revealed a significant discrepancy of the community indices between the primeval habitats [with the highest MIB values (293 mg/individual) and SPC (246.8)] and the 5- years-old plantations (with the lowest MIB values 160.6; LSD test, $p = 0.0001$) and the 40-years-old plantations [with the lowest SPC values (232); LSD test; $p = 0.034$].

3.2. Resilience of carabid fauna in the regenerated stands

The numbers of carabid species (rarefaction standardized) in the 80-years-old Century stands exceeded the species numbers of 100-years-old pine and spruce plantations (Table 3). In the MD habitat, the mean species richness of 80-years-old Century stands was significantly higher than in the assemblages from primeval stands: 9.57 vs. 6.2 (LSD test, $p = 0.008$). No significant differences in species richness were found between the primeval and others stands.

In the assemblages inhabiting the 40-, 80- and 100-years-old stands, the proportion of relict species was significantly lower than in the assemblages from primeval stands (from 8.3% to 16% vs. 35.7%; LSD test, $p < 0.0001$). Percentages of brachypterous carabids varied widely across the regenerated and primeval habitats, e.g., 78.3% and 78.4% in the assemblages inhabiting 40- and 100-years-old pine stands on MD habitats to 55.3% in the assemblages of primeval forest. The primeval stands hosted lower proportions of brachypterous species than did monocultures of pine and spruce growing in the fertile habitats of MD and D.

In assemblages inhabiting younger (40-years-old) stands, the proportion of hygrophilous species was significantly higher than in the assemblages from older (80-years-old) stands (51.0% vs. 24.3%; LSD test, $p < 0.001$) and in the prime-

Table 3. ANOVA for carabid assemblages in two fertile forest habitats. Symbols used in pair-wise *post hoc* tests: 1 = MD, 2 = MC, and in stands with different ages of dominant trees: 1 = 40-, 2 = 80-, 3 = 100-years-old, and 4 = (un-aged) primeval forest (see Table 1 for abbreviations).

Variable	df	MS	F	*p*	LSD *post hoc* test
Species richness					
Habitat	1	1.176	0.103	0.750	
Age	3	31.980	2.798	0.050	1 < 2 (*p* = 0.007); 3 < 2 (*p* = 0,037)
Habitat × Age	3	21.532	1.884	0.147	
Relicts					
Habitat	1	9.849	0.094	0.760	
Age	3	2352.114	21.546	<0.001	4 > 1, 2, 3 (*p* < 0.001)
Habitat × Age	3	495.497	4.749	0.006	
MIB					
Habitat	1	10017.000	0.895	0.350	
Age	3	118475.200	10.584	<0.001	4 > 1, 2, 3 (*p* < 0.001)
Habitat × Age	3	25398.900	2.269	0.094	
SPC					
Habitat	1	334.098	0.277	0.601	
Age	3	6280.280	5.213	0.004	1 > 2 (*p* = 0.008); 1 > 3 (*p* = 0.015); 1 > 4 (*p* = 0.003)
Habitat × Age	3	1086.107	0.902	0.448	
Hygrophilous					
Habitat	1	933.267	1.639	0.207	
Age	3	3019.507	5.303	0.003	1 > 2, 4 (*p* = 0.001); 1 > 3 (*p* = 0.010); 2, 3 > 4 (*p* = 0.001)
Habitat × Age	3	948.384	1.666	0.189	
Brachypterous					
Habitat	1	347.705	0.694	0.409	
Age	3	1826.846	3.649	0.020	1 > 2 (*p* < 0.001); 1 > 4 (*p* = 0.030); 2 < 4 (*p* = 0.007)
Habitat × Age	3	91.362	0.183	0.908	

val stands (51.0% vs. 15.6%; LSD test, *p* = <0.001). Also, in the assemblages inhabiting the 100-years-old stands, the proportion of hygrophilous species was significantly higher than in the assemblages from primeval forests (LSD test, *p* <0.001). The proportion of brachypterous species was also lower in the primeval than in the 40-years-old stands (63.2% vs. 77.8%; LSD test, *p* = 0.03). ANOVA for the MIB revealed a significant discrepancy of the community indices between the primeval habitats (297.8 mg/individual) and the 40-, 80- or 100-years-old stands (227.9 [LSD test; *p* = 0.027], 169.2 [*p* <0.001], 231.8 [*p* = 0.007], respectively).

3.3. Effect of soil fertility on forest carabid assemblages.

The numbers of carabid species (rarefaction standardized) in fertile primeval D and DD (9.2 and 9.7) stands exceeded the species richness of poorer primeval C and MC stands (6.0 and 7.4; LSD test, *p* <0.001; Table 2). The proportions of relict species in the carabid assemblages of the primeval DD habitats was significantly lower than in the primeval C, MC and MD habitats (15.8% vs. 36.7%, 53.2% and 44.0%, respectively; LSD test, *p* <0.0001). Also the proportion of relict species was higher in the primeval assemblages of fertile MC and MD habitats compared to their proportion in poorer primeval habitat C (53.2% and 44.0% vs. 36.7%; LSD test, *p*= 0.001 and 0.03, respectively).

The proportion of brachypterous species was also lower in the primeval stands DD compared to their proportion in the primeval stands of C, MC and MD (37.4% vs. 70.6%, 63.3% and 69.3%; LSD test, *p* <0.0001)

ANOVA for MIB (Table 2) revealed significant differences in the community indices be-

Table 4. Dominant and co-dominant species, with dominance indices >5%, in selected MMC and MMD habitats. For column names, see Table 1.

Species	P_MD	MD5	MD40	MD100p	MD100s	MD_C	P_MC	MC5	MC40
C. hortensis	46.8	–	28.2	10.0	5.0	–	43.3	7.2	
P. oblongopunctatus	18.6	–	17.4	13.8	34.2	18.5	10.2	–	21.8
C. glabratus	11.1	7.9	15.8	–	–	–	13.3	–	
P. niger	10.5	17.7	11.4	46.0	27.5	33.0	6.7	21.1	20.6
C. arcensis	6.5	5.5	9.0	5.4	–	–	13.2	–	10.1
E. secalis	–	12.1	–	–	–	–	–	–	
P. versicolor	–	9.6	–	–	–	–	–	11.9	
H. quadripunctatus	–	5.1	–	–	–	–	–	–	
C. caraboides	–	–	–	5.4	–	–	–	–	
C. granulatus	–	–	–	–	7.0	–	–	–	
P. melanarius	–	–	–	–	6.1	23.0	–	–	
C. nemoralis	–	–	–	–	–	6.4	–	–	
C. melanocephalus	–	–	–	–	–	–	–	15.5	15.6
H. rufipes	–	–	–	–	–	–	–	7.7	

tween fertile primeval MD habitats (with the highest MIB 303.1 mg/individual) and other primeval habitats: MC (218.3), C (178.0) and DD (86.6) (LSD test, $p < 0.001$). On the other hand, in the assemblages inhabiting damp primeval habitats of the type DD, the SPC index was significantly lower than in the assemblages from others primeval stands of types C, MC and MD (184.3 vs. 236.1, 242.0 and 260.0, respectively; LSD test, $p < 0.001$).

4. Discussion

4.1. Carabid assemblage variation among the compared forest habitats

Cluster analysis indicated faunal differences between primeval and regenerating stands (Fig. 2). The carabid samples from the primeval stands were grouped into separate agglomerations. One included the assemblages inhabiting the fertile MC, MD and D habitats of the primeval stands. However, the D primeval habitat assemblage appear located among the regenerated stands sampled within the "Century" area that otherwise formed a distinct cluster of samples. The other group, consisting of the assemblages of the poor C habitat and the marshy DD habitat, shared a branch together with the young 5- to 40-years-old plantations. The carabid assemblages in the 40- and 100-years-old pine and spruce monocultures also formed a separate agglomeration, which can be attributed both to the considerable shading of the litter and the reduction of its composition to one component, viz. pine or spruce needles. Such litter decomposes more slowly than mixed litter. The resulting thickness was about 10 cm, probably supporting e.g. *Pterostichus niger* and *P. melanarius* (Table 4).

Also DCA separated the assemblages from the primeval stands of two areas on the diagram at various levels of moisture (Fig. 1). The horizontal axis could be related to an altitude gradient. However, the arrangement of all assemblages suggested a gradient of anthropic pressure increasing upward along the vertical axis, as the scores of the assemblages of the youngest plantations were located at the top. Considering also the number of carabid species disappearing from the primeval stands while harvesting, and the number of alien species that colonize new plantations on clear-cuts, the result is one of profound changes in the ecosystem.

4.2. Effect of clear-cutting and litter quality on carabid assemblages

Niemelä *et al.* (1993) distinguished three general carabid responses to logging: (1) an increase in abundance of species characteristic of dry and open conditions; (2) an initial decrease of forest generalist species that reestablish with forest regeneration; and (3) canopy closure and disappearance of some forest specialists which seem unable to re-establish populations in cut-over stands (but see Spence *et al.* 1996).

In carabid assemblages of clear-cuts, forest specialists are apparently replaced by non-forest (e.g., *Amara* and *Harpalus*) species, resulting in a local increase in species diversity (Beaudry *et al.* 1997). Open habitat carabids, for example, are efficient in colonizing clear-cuts: the first individuals may colonize small (<0.5 ha) clear-cut openings within months (Koivula & Niemelä 2003). Contrary to these findings, the present study showed no change in the mean number of species following clear-cutting. However, I found few non-forest species [*P. versicolor*, *E. secalis* (MD), *C. melanocephalus* and *H. rufipes* (MC)] in the group of co-dominants in the carabid assemblages of the 5-years-old plantations. In the 15- and 40-years-old plantations, these species had apparently been replaced by the forest specialists *C. hortensis*, *C. glabratus* and *P. oblongopunctatus* (Table 4).

The forest generalist *Pterostichus niger* was a dominant species in the 5-years-old plantations. However, it has also been reported as being a dominant species in 40-years-old and older managed stands (Szyszko 1983, Sklodowski 1995). Its locomotor ability resembles those of the flightless *C. hortensis* and *C. glabratus* that were present in low numbers in the regenerating clear-cuts. Studies of movement patterns of *C. hortensis* and *C. glabratus* have indicated that these species do not enter open areas (Sklodowski 1999, 2002, Assmann & Günther 2000). Furthermore, *C. hortensis* is associated with humic soils and *C. glabratus* with abundant mosses (Niemelä *et al.* 1996). Also forest litter is important for carabid beetles: litter thickness and composition stimulate the occurrence of forest-associated carabids (Guillemain *et al.* 1997, Koivula *et al.* 1999, Koivula 2001, Magura *et al.* 2001, Koivula & Niemelä 2003). Baguette (1993) associated the occurrence of *P. oblongopunctatus* with the “moder” type of litter, a forest floor type in which there is a distinct litter and decomposing layer and humus layer that gradually changes into, and is partly mixed with, the underlying mineral soil (Kimmins 1997). However, according to Baguette (1993), *P. niger* and *P. melanarius* are associated with thick litter covering humic soils. Similar micro-habitat associations with litter have been observed for *C. hortensis* (Turin 2000).

The above explains why the destruction of litter and mosses during top-soil preparation in clear-cuts has negative effects on the abundance of e.g. *C. hortensis* and *C. glabratus*, while it may not affect the colonization of clear-cuts by *P. niger*, as shown in a recent capture-recapture experiment (Skłodowski 2002). This difference probably accounts for the dominance of the latter species in carabid assemblages in the 5-years-old plantations in Białowieża.

In spite of the lack of litter, *P. niger* was dominant in the carabid assemblages of 5-years-old plantations, whereas the eurytopic *P. melanarius*, relatively similar in terms of body size and diet, was not numerous there. Perhaps the more flattened body of *P. niger* allows it to easily penetrate micro-crevices in furrows created by ploughing. The slightly stockier *Pterostichus melanarius* was a co-dominant in the carabid assemblages of mature stands planted in the “Century” area and in the pine and spruce monocultures. Because this species was recorded only in very low abundance in the primeval stands, the higher abundance in regenerating areas apparently serves as an indicator of stand disturbance. However, Poole *et al.* (2003) found *P. melanarius* more abundantly in semi-natural but “mature” oak woodland than in oak plantations.

4.3. Relict and brachypterous carabids, and clear-cutting

However, perhaps a more important indicator of destruction of primeval stands is the depletion of relict species (Assmann 1999). In this study, the proportion of the ten relict forest species decreased in Białowieża Forest from 85% to 25% along with increasing anthropic pressure. Clear-cutting, even if not particularly intense in terms of area covered, leads to the disappearance of species characteristic of older stands, such as *L. piceus*, *C. intricatus* and *C. glabratus*. In order to complete their life cycle, these species need a well-developed humic litter layer that is often destroyed by clear-cutting. The extensive areas subjected to the large-scale clear-cutting by the "Century" 80 years ago are still deficient in these species. Clearly, clear-cutting leads to the destruction of forest micro-habitats, the importance of which has previously been pointed out e.g. by Niemelä *et al.* (1996).

Clear-cutting of primeval stands in mesic habitats also decreases the proportion of brachypterous species giving way to macropterous and wing-dimorphic species in carabid assemblages. In the damp habitats, the proportion of brachypterous species increased following a clear-cut, which can be attributed to inundation of the habitat. Brachypterous species may find it difficult to escape from a flooded habitat devoid of trees that used to act as natural transpiration "pumps" during the spring floods.

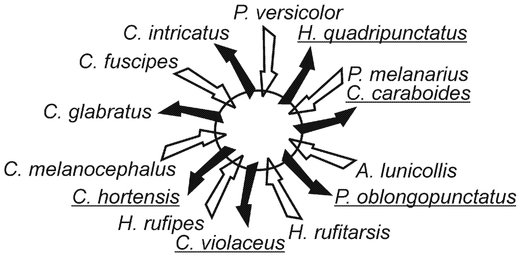
Kotze & O'Hara (2003) suggested that wing-dimorphic species may survive better in highly altered environments than do brachypterous species. In my study, however, individuals of wing-dimorphic species did not achieve higher dominance values than did brachypterous individuals, which may suggest that clear-cutting had no significant effects on the latter as a group. Still, the documented over 50% reduction in MIB (390 mg/individual vs. 160 mg/individual) and 20% decrease in SPC (293 vs. 232) indicate profound changes. Another sign of change in the studied carabid assemblages and in the habitats was the increased proportion of hygrophilous species in the carabid assemblages of the 5-years-old plantations. This change should be ascribed to the felling of trees that had earlier removed water from the otherwise rather moist soil in Białowieża. Removal of the trees may increase habitat moisture, and consequently hygrophilous species seize this opportunity. However, eventually the subsequent growth of trees leads to restoration of the water-level adjusting system of trees and a gradual reduction of this group of species.

4.4. Effect of fertility of forest habitat on carabid assemblages

The structure of carabid assemblages appeared to be related to habitat fertility. The carabid species richness was higher in the fertile habitats MC and MD (7.4 and 9.2, respectively) than in the poor habitat C (6.0). The MIB and SPC, which reflect the successional phase of the assemblages, were also higher in the fertile habitats MC and MD (MIB: 218 mg/individual and 303 mg/individual; SPC: 242 and 260, respectively), compared to the poor habitat C (MIB: 178; SPC: 236). The fertile but water-logged DD stands had high mean species richness (9.7), coupled with low MIB (87) and SPC (184), and these also supported brachypterous species that are apparently not resistant to disturbances (Szyszko 1990, Ribera *et al.* 2001). The differences between these indices suggest an improvement in the quality of carabid assemblages with increasing fertility. Here, the term "quality" should be understood as referring to carabid assemblages of very old forests, with high MIB and SPC values and high proportions of brachypterous and relict species. For this reason, the degree of deterioration of an assemblage following clear-cutting is related to the degree of organization of the assemblage prior to this disturbance (Szyszko 1990).

4.5. Conclusions: restoration of carabid fauna in regenerating stands

Restoration of carabid fauna in managed stands may take up to 80 or 100 years (Szyszko 1983, Skłodowski 1995). There are two plans of regeneration of the ecosystem: regeneration of the litter-soil habitat and vertical growth of the forest stand. The regeneration process of the carabid fauna was documented by comparing the faunas of 40-, 80- and 100-years-old stands. This process clearly included (1) a slight gradual increase in MIB from 227 to 231 mg/individual (vs. 298 in primeval habitats), (2) an increase in the proportion of hygrophilous species to 24% in the 80-years-old stands (compared to 15% in primeval habitats), (3) a persistent, reduced proportion of relict species, and (4) a long-persisting elevated species richness (e.g., 9.6 in 80-years-old stands vs. 6.2 in primeval forests). As is evident from the above comparison between 80-years-old and primeval stands, the regeneration of carabid assemblages after clear-cutting is a very slow process. The absence of the forest relict species *C.*



No. lost species	Habitat type	No. added species
23	5-y-old (C, MC)	15
17	5-y-old (MD, D)	18
5	100-y-old pine (MD, D)	27
5	100-y-old spruce (MD, D)	30
7	old "Century" stand (MD)	24
7	old "Century" stand (D)	30

Fig. 3. The "snowball" effect. While harvesting, relict species (black arrows) are being replaced by ubiquitous species (white arrows). The underlined species may return to the logged areas after a reforestation and/or some decades of forest re-growth.

glabratus from the 100-years-old stands, for example, appears to indicate incomplete regeneration of the carabid assemblages there.

These changes are accompanied by a replacement process where relict forms, particularly rare ones, seem to be permanently lost to the habitat. They may return to the biocoenosis being restored but not until the first hundred post-disturbance years have passed. The effects of anthropic pressure have been compared to a snowball that loses some of the snow (here, relict species) as it rolls, while at the same time new snow (here, ubiquitous species) sticks to it (Witkowski 2000; see also Fig. 3). All these findings point to profound changes in carabid assemblages following a drastic human-caused alteration of pristine forest environment. That is why primeval forests should be subject to strict protection with any human interference reduced to a minimum.

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References

Assmann, T. 1999: The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). — Biodiversity and Conservation 8: 1499–1517.

Assmann, T. & Günther, J. M. 2000: Relict populations in ancient woodlands: genetic differentiation, variability and power of dispersal of *Carabus glabratus* (Coleoptera, Carabidae) in north-western Germany. — In: Brandmayr *et al.* (eds.), Natural history and applied ecology of carabid beetles: 197–206. Pensoft. 304 pp.

Atlegrim, O. Sjöberg, K. & Ball, J. P. 1997: Forestry effects on a boreal ground beetle community in spring: selective logging and clear-cutting compared. — Entomologica Fennica 8:19–26.

Baguette, M. 1993: Habitat selection of carabid beetles in deciduous woodlands of southern Belgium. — Pedobiologia 37: 365–378.

Beaudry, S., Duchesne, L. & Côté, B. 1997: Short-term effects of three forestry practices on carabids assemblages in a jack pine forest. — Canadian Journal of Forest Research 27: 2065–2071.

Bircks, H. J. B. 2005: Mind the gap: how open were European primeval forests? — Trends in Ecology and Evolution. 20: 154–156.

Bobiec, A., Burt, H., Meijr, K., Zuyderduyn, C., Haga, J. & Vlaanderen, B. 2000: Rich deciduous forest in Białowieża as a dynamic mosaic of developmental phases: premises for nature conservation and restoration management. — Forest Ecology and Management 130: 159–175.

Burakowski, B., Mroczkowski, M., & Stefanska, J. 1973–1974: Katalog Fauny Polski, Chrzaszcze Coleoptera, Biegaczowate Carabidae, Vol. XXIII, t. 3–4. — PWN. [In Polish.]

du Bus de Warnaffe, G. & Lebrun, P. 2004: Effects of forest management on carabid beetles in Belgium: implications for biodiversity conservation. — Biological Conservation 118: 219–234.

Foster, D. R., Orwig, D. A. & McLachlan, J. S. 1996: Ecological and conservation insights from reconstructive studies of temperate old-growth forests. — Trends in Ecology and Evolution 11: 419–424.

Guillemain, M., Loreau, M. & Daufrense, T. 1997: Relationship between the regional distribution of carabid beetles (Coleoptera, Carabidae) and the abundance of their potential prey. — Acta Oecologia 18: 465–483.

Kimmins, J. P. 1997: Forest Ecology. A Foundation for Sustainable Management. Second Edition. — Prentice Hall. 598 pp.

Koivula, M. 2001: Carabid beetles (Coleoptera, Carabidae) in boreal managed forests – meso-scale ecological patterns in relation to modern forestry. — PhD thesis, University of Helsinki. 120 pp.

Koivula, M. 2002: Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). — Forest Ecology and Management 167: 103–121.

Koivula, M., Punttila, P., Haila, Y. & Niemelä, J. 1999: Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. — Ecography 22: 424–435.

Koivula, M. & Niemelä, J. 2003: Gap felling as a forest harvesting method in boreal forests: responses of carabid beetles (Coleoptera, Carabidae). — Ecography 26: 179–187.

Kotze, D. J. & O'Hara, R. B. 2003: Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. — Oecologia 135: 138–148.

Krebs, C. J. 1999: Ecological methodology. Second edition. — Addison Wesley Longman. 620 pp.

Larsson S. G. 1939: Entwicklungstypen und Entwicklungszeiten der Dänischen Carabiden. — Entomologiske Meddelelser 20: 273–562.

Magura, T., Ködöböcz, V., Tóthmérész, B. 2001: Effects of habitat fragmentation on carabids in forest patches. – Journal of Biogeography 28: 129–138.

Niemelä, J., Langor, D. & Spence, J. R. 1993: Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in Western Canada. — Conservation Biology 7: 551–561.

Niemelä, J., Haila, Y. & Punttila, P. 1996: The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. — Ecography 19: 352–368.

Pontégnie, M., du Bus de Warnaffe, G. & Lebrun, P. 2005: Impacts of silvicultural practices on the structure of hemi-edaphic macrofauna community. — Pedobiologia 49: 199–210.

Poole, A., Gromally, M. & Skeffington, M. 2003: The flora and carabid fauna of a mature and regenerating semi-natural oak woodland in south-east Ireland. — Forest Ecology and Management 177: 207–220.

Rackham, O. 1980: Ancient Woodland. — Arnold, London.

Ribera, I., Dolédec, S., Downie, I. S. & Foster, G. N. 2001: Effect of land disturbance and stress on species traits of ground beetles assemblages. — Ecology 82: 1112–1129.

Sklodowski, J. 1995: Antropogenne przeobrażenia zespołów biegaczowatych (Col. Carabidae) w ekosystemach borów sosnowych Polski. [Anthropogenic changes in carabid assemblages (Col. Carabidae) in pine forest ecosystems In Poland.] — In: A. Szujecki *et al.* (eds.), Antropogeniczne przeobrażenia epigeicznej i glebowej entomofauny borów sosnowych: 17–174. Katedra Ochrony Lasu i Ekologii. Fundacja "Rozwój SGGW", Warszawa. [In Polish.]

Skłodowski, J. 1997: Interpretacja stanu środowiska leśnego za pomocą modelu SCP/SBO zgrupowan biegaczowatych (Col. Carabidae). Interpretation of state of environment by using SPC/MIB model of carabids assemblages. — In: Mazur, S. *et al.* (eds.), Waloryzacja ekosystemów lesnych metodami zooindykacyjnymi. VI Sympozjum Ochrony Ekosystemów Lesnych. Jedlnia 2–3 grudnia 1996: 69–87. Fundacja Rozwój SGGW. [In Polish.]

Skłodowski, J. 1999: Movement of selected carabid species (Col. Carabidae) through a pine forest-fallow ecotone. — Folia Forestalia Polska Ser. A. 41: 5–23.

Skłodowski, J. 2002: System kolonizacji zrębu zupełnegoi przez biegaczowate oraz możliwości jego doskonalenia. System of colonization clear-cut area by carabid beetles and possibility of its improving — Wydawnictwo SGGW, Warsaw Agricultural University Press. 134 pp. [In Polish with English summary.]

Skłodowski, J. 2003: Epigeic Carabid assemblages of the Białowieża Primeval Forest. — In: Bauer T. *et al.* (eds.), How to protect or What we know about Carabid Beetles. From knowledge to application – from Wijster (1969) to Tuczno (2001): 259–272. Warsaw Agricultural University Press.

Skłodowski, J. 2005: Intraspecific body size differentiation in *Carabus* assemblages in the Białowieża Primeval Forest, Poland. — In: Lövei G. L. & Toft, S. (eds.), European Carabidology 2003. Proceedings of the 11th European Carabidologist Meeting: 291–303. DIAS Report No. 114.

Spence, J. R., Langor, D. W., Niemelä, J., Carcamo, H. A. & Currie, C. R. 1996: Northern forestry and carabids: The case for concern about old-growth species. — Annales Zoologici Fennici 33: 302–302.

StatSoft Inc. 1997: Statistica for Windows (Computer program manual). — Tulsa, OK, USA.

Szyszko, J. 1983: State of Carabidae (Col.) fauna in fresh pine forest and tentative valorisation of this environment. — Warsaw Agricultural University Press.

Szyszko J. 1990: Planning of prophylaxis in threatened pine forest biocenoses based on an analysis of the fauna of epigeic Carabidae. — Warsaw Agricultural University Press.

Szyszko, J. 2002: Carabids as an efficient indicator of the quality and functioning of forest ecosystems useful in forest management. — In: Szyszko, J. *et al.* (eds.), How to protect or What we know about Carabid Beetles. From knowledge to application – from Wijster (1969) to Tuczno (2001): 301–318. Warsaw Agricultural University Press. 378 pp.

Szujecki, A. 1971: The effect of clear-cutting upon the community of litter inhabiting Staphylinids (Col. Staphylinidae) in fresh pine forests. — Folia Forestalia Polska Ser. A. 18: 5–45.

Szujecki, A., Mazur, S., Perliński, S. & Szyszko, J. 1983: The process of forest soil macrofauna formation after afforestation of farmland. — Warsaw Agricultural University Press.

Szujecki, A., Sławska, M., Skłodowski, J., Smoleński, M., Perliński, S., Mazur S., Łęgowski, D., Tracz, H., Sawoniewicz, J., Mokrzycki, T., Borowski, J., Rutkiewicz, A. & Byk, A. 2001: Próba szacunkowej waloryzacji lasów Puszczy Białowieskiej metodą zooindykacyjną. — Wydawnictwo SGGW, Warsaw Agricultural University Press. 411pp. [In Polish.]

ter Braak, C.J.F. & Smilauer, P. 1997: CANOCO for Windows v. 4.02. — Centre for Biometry Wageningen, The Netherlands.

Turin, H. 2000: De Nedrelandse loopkevers. Verspreiding en oecologie (Coleoptera: Carabidae). Nationaal Natuurhistorisch Museum Naturalis. — KNNV Uitgeverij. 662 pp. [In Dutch.]

Wesołowski, T. 1995: Value of Białowieża forest for the conservation of white-backed woodpecker *Dendrocopos leucotos* in Poland. — Biological Conservation 71: 69–75.

Wesołowski, T. 2005: Virtual conservation: how the European Union is turning a blind eye to its vanishing primeval forests. — Conservation Biology 19: 1349–1358.

Witkowski, Z. J. 2000: Restytucja owadów w Polsce w świetle teorii ekologicznej, zaleceń Unii Europejskiej i krajowych doświadczeń. [Recovery of insects in Poland in light of ecological theory, recommendation of European Union and local experience.] — Wiad. Entomol. 18 Suppl. 2: 251–273. [In Polish with English summary.]

Appendix. Carabid beetles collected in primeval and anthropogenic habitats (see Table 1 for habitat abbreviations). Species characteristics: r = relict, b = brachypterous, and h = hygrophilous. The subsequent columns (except “Other” and “Sum”) show values for different habitats (for coding, see Table 1). The numbers refer to dominance indices exceeding 5%; “1” is used when a dominance index was <5%; and “+” indicates that only a few specimens were found. Other = catches of carabids in other anthropogenic variants (not included in the analysis).

Species	Charact.	P_C	P_MC	P_MD	P_D	P_DD	C5	C15	C40	MC5	MC15	MC40	MD5	MD15
Agonum assimile (Paykull, 1790)	r, h	0	0	+	+	5.4	0	0	0	0	0	+	0	0
A. dorsale (Pontoppidan, 1763)		0	0	0	0	0	0	0	0	0	0	0	0	0
A. fuliginosum (Duftschmid, 1812)	h	+	+	+	+	10.1	0	+	0	0	+	0	+	0
A. gracilis (Sturm, 1824)	h	0	0	0	0	+	0	0	0	0	0	0	0	0
A. livens (Gyllenhal, 1810)	h	0	0	+	+	1	0	0	0	0	0	0	0	0
A. micans (Nicolai, 1822)	h	0	0	0	0	+	0	0	0	0	0	0	0	0
A. obscurum (Herbst, 1784)	h	+	+	+	+	9.2	0	+	1	0	0	+	0	1
A. piceus (Linnaeus, 1758)	h	0	0	0	0	+	0	0	0	0	0	0	0	0
A. sexpunctatum (Linnaeus, 1758)	h	0	0	0	0	+	0	0	0	0	0	0	0	0
A. viduum (Panzer, 1797)	h	+	0	0	+	+	0	0	0	0	0	0	0	+
Amara aenea (De Geer, 1774)		0	0	+	0	0	1	0	0	0	0	0	0	0
A. apricaria (Paykull, 1790)		0	0	0	0	0	0	0	0	0	0	0	+	0
A. aulica (Panzer, 1797)		0	0	0	0	0	0	0	0	0	0	0	0	0
A. bifrons (Gyllenhal, 1810)		+	0	0	0	0	0	0	0	+	+	0	0	0
A. brunnea (Gyllenhal, 1810)	r	+	+	+	+	+	0	+	0	0	0	+	+	+
A. consularis (Duftschmid, 1812)		0	0	0	0	0	0	0	0	0	0	0	0	0
A. communis (Panzer, 1797)		0	0	+	+	0	+	+	0	0	0	0	+	+
A. eurynota (Panzer, 1797)		0	0	0	0	0	0	0	0	0	0	0	0	0
A. familaris (Duftschmid, 1812)		0	0	0	0	0	0	0	0	0	0	0	+	+
A. fulva (Müller, 1776)		0	0	0	0	0	0	0	0	0	0	0	0	0
A. lunicollis Schiødte, 1837		0	0	0	+	0	+	+	0	+	0	0	1	+
A. majuscula Chaudoir, 1850		0	0	0	0	+	0	0	0	0	0	0	0	0
A. ovata (Fabricius, 1792)		0	0	0	0	0	0	0	0	0	0	0	0	0
A. plebeja (Gyllenhal, 1810)	h	0	+	+	0	0	0	0	0	+	0	0	+	+
A. tibialis (Paykull, 1798)		0	0	0	0	0	0	0	0	+	0	0	0	0
Anisodactylus binotatus (Fabricius, 1792)	h	0	+	0	0	0	0	0	0	0	0	0	0	0
Broscus cephalotes (Linnaeus, 1758)		0	0	0	0	0	0	0	0	0	0	0	+	0
Bembidion gilvipes Sturm, 1825	h	0	0	0	+	0	0	0	0	0	0	0	0	0
B. lampros (Herbst, 1784)		0	0	+	+	+	0	0	0	0	0	0	+	0
B. mannerheimi C. R. Sahlberg, 1827	h, b	0	+	0	0	0	0	0	0	0	0	0	0	0
B. nigricorne Gyllenhal, 1827		0	0	0	0	0	+	0	0	0	0	0	+	+
B. properans (Stephens, 1828)		0	0	0	+	0	0	0	0	0	0	0	0	0
B. pygmaeum (Fabricius, 1792)		0	0	0	0	0	0	0	0	0	0	0	0	0
B. quadrimaculatum (Linnaeus, 1761)		0	0	0	0	0	0	0	0	0	0	0	0	0
B. semipunctatum (Donovan, 1806)	h	0	0	0	0	0	0	0	0	0	0	0	0	+
Badister bullatus (Schrank, 1798)		0	0	+	+	0	0	0	0	0	0	0	+	0
B. dilitatus Chaudoir, 1837	h	0	0	0	+	+	0	0	0	0	0	0	0	0
B. drosiger (Duftschmid, 1812)	h	0	0	0	0	0	0	0	0	0	0	0	0	0
B. lacertosus Sturm, 1815		0	0	+	+	+	0	0	0	0	0	+	1	+
B. sodalis (Duftschmid, 1812)	h, b	0	0	0	0	+	0	0	0	0	0	0	0	0
B. unipustulatus Bonelli, 1813	h	0	0	0	0	0	0	0	0	1	0	0	0	0
Carabus arcensis Herbst, 1784	b	42.6	13.2	6.5	9.8	1	0	+	+	1	6.6	10.1	5.5	1
C. cancellatus Illiger, 1798	b	+	+	+	+	+	1	+	1	1	1	+	1	1
C. coriaceus Linnaeus, 1758	b	1	1	+	+	+	1	+	1	1	0	1	1	1
C. convexus Fabricius, 1775	b	+	+	+	+	+	+	0	0	0	1	+	1	+
C. glabratus Paykull, 1790	r, b	1	13.3	11.1	1	1	+	0	0	0	1	+	7.9	10.4
C. granulatus Linnaeus, 1758	h, b	0	+	+	+	1	+	1	1	0	1	1	1	0
C. hortensis Linnaeus, 1758	r, b	+	43.3	46.8	19.9	6.2	+	+	+	7.2	1	1	1	9.5
C. intricatus Linnaeus, 1761	r, b	0	+	+	+	0	0	0	0	0	0	0	0	0
C. nemoralis O. F. Müller, 1764		+	1	1	1	1	1	+	8.4	0	1	+	+	1
C. violaceus Linnaeus, 1758	r, b	8.1	1	+	+	+	1	+	+	1	+	1	0	1

Calathus erratus (C. R. Sahlberg, 1827)		+	0	+	+	0	0	+	0	0	+	0	+	0
C. fuscipes (Goeze, 1777)		0	0	0	0	0	0	+	0	1	0	0	0	0
C. melanocephalus (Linnaeus, 1758)		0	0	0	0	0	5	38.7	21.3	15.5	1	15.6	1	0
C. micropterus (Duftschmid, 1812)	r, b	1	+	1	+	+	0	1	17.1	0	5.8	1	1	6.5
Clivina fossor (Herbst, 1784)	h	0	0	+	+	+	0	0	0	0	+	0	0	0
Calosoma inquisitor (Linnaeus, 1758)		0	+	0	+	0	0	0	0	0	+	+	0	0
Cychrus caraboides (Linnaeus, 1758)	h, b	1	1	1	1	1	1	1	+	1	1	1	1	5.9
Chlaeniellus nigricornis (Fabricius, 1787)	h	+	0	0	0	+	0	0	0	0	0	0	+	0
Cicindela sylvatica Linnaeus, 1758		+	0	0	0	0	0	0	0	0	0	0	0	0
Cymindis macularis Mannerheim in Fischer von Waldheim, 1824		0	0	0	0	0	0	0	0	0	0	0	0	0
Dolichus halensis (Schaller, 1783)		0	0	0	0	0	0	0	0	0	0	0	0	0
Dromius agilis (Fabricius, 1787)		0	0	+	0	+	0	0	0	0	0	0	0	0
D. fenestratus (Fabricius, 1794)		0	0	0	0	0	0	0	0	0	0	0	0	0
D. schneideri Crotch, 1871		0	0	0	0	0	0	0	0	0	0	0	0	0
D. sigma (Rossi, 1790)	h	0	0	0	0	0	0	0	0	0	0	0	+	0
Dyschirius globosus (Herbst, 1783)		0	0	+	+	1	0	+	0	0	+	0	+	0
Elaphrus cupreus Duftschmid, 1812	h	+	0	+	0	+	0	0	0	0	0	0	0	0
Epaphius rivularis (Gyllenhal, 1810)	h, b	0	0	0	0	0	+	+	0	0	0	0	0	0
E. secalis (Paykull, 1790)	b	+	+	1	1	1	12.5	8.4	9.4	1	12.4	1	12.1	1
Harpalus affinis (Schrank, 1781)		0	0	0	0	0	0	0	0	0	0	0	0	0
H. anxius (Duftschmid, 1812)		0	0	0	0	0	0	0	0	0	0	0	0	0
H. fuliginosus (Panzer, 1809)		0	0	+	+	0	0	0	0	0	+	0	0	0
H. griseus (Panzer, 1797)		0	0	+	0	0	0	0	0	0	+	0	0	0
H. latus (Linnaeus, 1758)		+	+	+	+	+	+	+	0	1	+	+	1	+
H. luteicornis (Duftschmid, 1812)		0	0	0	0	0	0	0	0	0	0	0	0	0
H. neglectus Serville, 1821		0	0	0	0	0	0	0	0	0	0	0	0	0
H. picipennis (Duftschmid, 1812)		0	0	0	0	0	0	0	0	0	0	0	0	0
H. progrediens Schauberger, 1922		0	0	0	0	0	0	0	0	0	0	0	0	0
H. quadripunctatus Dejean, 1829	r	+	+	+	+	+	1	+	1	1	+	1	5.1	1
H. rubripes (Duftschmid, 1812)		0	0	0	0	0	0	0	0	+	0	0	0	0
H. rufipes (De Geer, 1774)		0	+	+	+	0	1	+	+	7.7	+	+	+	+
H. rufitarsis (Illiger, 1778)		0	0	+	0	0	0	0	0	1	+	0	0	+
Harpalus signaticornis (Duftschmid, 1812)	0	0	0	0	0	+	0	0	0	0	0	0	+	
H. smaragdinus (Duftschmid, 1812)		0	0	0	0	0	0	0	0	0	0	0	0	0
H. tardus (Panzer, 1796)		0	0	0	0	0	0	0	+	1	0	0	0	0
H. tenebrosus (Schauberger, 1929)		0	0	0	0	0	0	0	0	0	0	+	0	0
Lebia chlorocephala (Hoffmannsegg, 1803)	0	0	0	0	0	0	0	0	0	0	0	0	0	
Leistus ferrugineus (Linnaeus, 1758)	h	0	0	0	0	+	+	+	0	0	0	+	0	0
L. piceus Froelich, 1979	r, b	0	0	+	+	+	0	0	0	0	+	0	0	+
L. rufescens (Fabricius, 1775)	h	+	0	+	0	+	0	0	0	0	0	0	+	+
Loricera pilicornis (Fabricius, 1775)		+	0	+	+	1	0	0	0	0	0	0	0	0
Licinus depressus (Paykull, 1790)	b	0	0	0	0	0	0	0	0	0	0	0	0	0
Masoreus wetterhalli (Linnaeus, 1767)		0	0	0	0	+	0	0	0	1	0	0	0	0
Miscodera arctica (Paykull, 1798)		0	0	0	0	0	0	0	0	1	0	0	0	0
Microlestes minutulus (Goeze, 1777)		0	0	0	0	0	0	0	0	0	0	0	+	+
Nebria brevicollis (Fabricius, 1792)		0	0	+	1	6.1	0	0	0	0	0	0	0	0
Notiophilus aesthuans (Motschulsky, 1864)	0	0	0	+	+	0	0	0	0	0	0	0	0	
N. aquaticus (Linnaeus, 1758)		0	0	+	0	0	0	0	0	0	0	0	0	0
N. biguttatus (Fabricius, 1799)		+	+	+	+	0	0	0	+	0	0	+	0	0
N. germinyi Fauvel in Grenier, 1863		+	+	+	0	0	0	0	+	1	+	0	+	0
N. palustris (Duftschmid, 1812)		+	+	+	+	0	0	0	0	0	0	0	1	0
Oodes helopioides (Fabricius, 1792)	h	0	0	0	0	+	0	0	0	0	0	0	0	0
Ophonus puncticollis (Paykull, 1798)		0	0	0	0	0	0	0	0	0	0	0	0	0
Panagaeus bipustulatus (Fabricius, 1775)	0	0	0	0	0	0	0	0	0	0	0	0	0	
P. cruxmajor (Linnaeus, 1758)	h	0	+	0	0	+	+	0	0	0	0	0	0	0
Patrobus atrorufus (Strøm, 1768)	r, h, b	+	+	+	+	1	0	0	0	0	0	0	0	0
Pterostichus aethiops (Panzer, 1797)	b	+	+	0	1	1	2.5	1	+	0	+	+	+	+
P. anthracinus (Illiger, 1798)	h	+	0	0	+	1	0	0	0	0	0	0	0	+
P. cupreus (Linnaeus, 1758)		0	0	0	+	0	0	0	0	+	0	0	0	+

P. diligens (Sturm, 1824)	h	0	+	+	+	1	0	0	0	0	0	+	+	+
P. melanarius (Illiger, 1798)		+	+	+	6.9	4	1	1	+	0	1	1	1	1
P. minor (Gyllenhal, 1827)	h	0	0	0	0	+	0	0	0	0	0	0	+	0
P. niger (Schaller, 1783)	h	10	6.7	10.5	10.3	12.3	49.7	22.5	12.9	21.1	40.4	20.6	17.7	24.9
P. nigrita (Paykull, 1790)	h	+	+	+	+	1	0	+	+	0	0	+	0	0
P. oblongopunctatus (Fabricius, 1787)		7	10.2	18.6	30.5	10.5	5	5.6	11.9	1	10.7	21.8	1	13.1
P. quadrifoveolatus Letzner, 1852		0	0	0	0	0	0	0	0	0	0	0	0	0
P. strenuus (Panzer, 1797)		0	+	+	+	+	0	0	0	0	+	0	+	+
P. vernalis (Panzer, 1796)		0	0	0	0	+	0	0	0	0	0	0	0	0
Poecilus versicolor (Linnaeus, 1758)		+	+	+	0	+	1	+	1	11.9	+	1	9.6	1
P. punctulatus (Schaller, 1783)		0	0	0	0	0	0	0	+	0	0	0	0	0
P. lepidus (Leske, 1787)	b	0	0	0	+	+	+	0	0	+	0	0	0	0
Synuchus nivialis (Illiger, 1798)		0	0	+	+	0	+	+	0	+	+	0	+	0
Stomis pumicatus (Panzer, 1796)		+	+	0	+	+	+	+	0	0	0	+	0	+
Syntomus foveatus (Fourcroy, 1785)	b	0	+	0	0	0	0	0	0	0	0	0	0	0
S. truncatellus (Linnaeus, 1761)		0	0	0	0	0	0	0	0	0	0	0	+	0
T. quadristriatus (Schrank, 1781)		0	+	0	+	0	0	0	0	0	0	0	0	0
Trichocellus placidius (Gyllenhal, 1827)		0	0	0	0	0	0	0	0	0	0	0	+	0
Microlestes maurus (Sturm, 1827)	h	+	0	0	0	0	0	0	0	0	0	0	0	0
Total		2,011	7897	10,107	9,766	2,779	360	729	310	194	346	601	543	758

Appendix. Continued.

Species	MD40	DD5	DD15	DD40	MDp	MD100p	D40p	D100p	MD100s	D100s	MD_C	D_C	Other	Sum
Agonum assimile (Paykull, 1790)	0	+	1	1	0	0	0	+	0	0	0	+	52	274
A. dorsale (Pontoppidan, 1763)	0	0	+	0	0	0	0	0	0	0	0	0	111	112
A. fuliginosum (Duftschmid, 1812)	+	12.7	1	15.8	+	+	0	+	0	0	0	+	10	520
A. gracilis (Sturm, 1824)	0	0	0	0	0	0	0	0	0	0	0	0	1	8
A. livens (Gyllenhal, 1810)	0	1	1	14.9	0	0	0	+	0	0	0	0	0	206
A. micans (Nicolai, 1822)	0	0	0	0	0	0	0	0	0	0	0	0	0	3
A. obscurum (Herbst, 1784)	+	1	12.1	11.2	0	0	0	0	0	+	+	0	11	455
A. piceus (Linnaeus, 1758)	+	4.1	+	5.6	0	0	0	+	0	0	0	0	1	60
A. sexpunctatum (Linnaeus, 1758)	0	+	0	0	0	0	0	0	0	0	0	0	0	3
A. viduum (Panzer, 1797)	0	1	+	0	0	0	0	0	0	0	0	0	0	42
Amara aenea (De Geer, 1774)	0	0	0	1	0	0	0	0	0	0	0	0	112	132
A. apricaria (Paykull, 1790)	0	0	0	0	0	0	0	0	0	0	0	0	10	11
A. aulica (Panzer, 1797)	0	0	0	0	0	0	0	0	0	0	0	0	13	13
A. bifrons (Gyllenhal, 1810)	0	0	0	1	0	0	0	0	0	0	0	0	75	83
A. brunnea (Gyllenhal, 1810)	+	0	0	0	0	+	0	0	+	0	+	1	60	181
A. consularis (Duftschmid, 1812)	0	0	0	0	0	0	0	0	0	0	0	0	121	121
A. communis (Panzer, 1797)	0	+	+	0	0	0	0	0	0	0	+	0	97	111
A. eurynota (Panzer, 1797)	0	0	0	0	0	0	0	0	0	0	0	0	9	9
A. familaris (Duftschmid, 1812)	0	0	0	0	0	0	0	0	0	0	0	0	0	2
A. fulva (Müller, 1776)	0	0	0	+	0	0	0	0	0	0	0	0	12	13
A. lunicollis Schiødte, 1837	0	0	0	1	0	0	0	0	0	0	0	+	80	107
A. majuscula Chaudoir, 1850	0	0	0	0	0	0	0	0	0	0	0	0	1	2
A. ovata (Fabricius, 1792)	0	0	0	0	0	0	0	0	0	0	0	0	8	8
A. plebeja (Gyllenhal, 1810)	0	0	0	1	0	0	0	0	0	0	0	0	32	59
A. tibialis (Paykull, 1798)	0	0	0	0	0	0	0	0	0	0	0	0	68	69
Anisodactylus binotatus (Fabricius, 1792)	0	0	0	0	0	0	0	0	0	0	0	0	46	47
Broscus cephalotes (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	81	85
Bembidion gilvipes Sturm, 1825	0	0	0	0	0	0	0	0	0	0	0	0	0	1
B. lampros (Herbst, 1784)	0	0	0	+	0	0	+	0	0	0	0	0	24	32
B. mannerheimi C. R. Sahlberg, 1827	+	0	0	0	0	0	0	0	0	0	0	0	0	3
B. nigricorne Gyllenhal, 1827	+	0	0	0	0	0	0	0	0	0	0	0	8	12

B. properans (Stephens, 1828)	0	0	0	0	0	0	0	0	0	0	0	0	17	18
B. pygmaeum (Fabricius, 1792)	0	0	0	0	0	0	0	0	0	0	0	0	2	2
B. quadrimaculatum (Linnaeus, 1761)	0	0	0	0	0	0	0	0	0	0	0	0	5	5
B. semipunctatum (Donovan, 1806)	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Badister bullatus (Schrank, 1798)	0	+	+	0	0	0	0	0	0	+	0	0	15	32
B. dilitatus Chaudoir, 1837	0	+	+	0	0	0	0	0	0	0	0	0	1	16
B. drosiger (Duftschmid, 1812)	0	+	1	0	0	0	0	0	+	+	0	+	63	82
B. lacertosus Sturm, 1815	+	+	+	0	+	0	0	+	0	+	+	0	17	72
B. sodalis (Duftschmid, 1812)	0	0	0	0	0	0	0	0	+	0	0	+	4	11
B. unipustulatus Bonelli, 1813	0	0	0	+	0	0	0	0	0	0	0	0	1	5
Carabus arcensis Herbst, 1784	9	1	0	+	16.3	5.4	10.9	9.1	+	+	13.4	+	84	3,980
C. cancellatus Illiger, 1798	+	0	+	0	0	+	0	13.9	1	1	+	+	167	637
C. coriaceus Linnaeus, 1758	1	+	0	0	1	+	+	+	+	+	+	1	30	447
C. convexus Fabricius, 1775	+	+	+	0	0	+	0	+	+	13.2	0	1	75	431
C. glabratus Paykull, 1790	15.8	+	1	+	1	1	1	+	+	1	+	1	61	2,199
C. granulatus Linnaeus, 1758	+	8.6	+	1	0	1	0	5.1	7	14.1	+	1	531	1,363
C. hortensis Linnaeus, 1758	28.2	1	1	0	6.4	10.0	9	11.2	5	1	1	8.9	1,004	11,907
C. intricatus Linnaeus, 1761	0	0	0	0	0	0	0	0	0	0	0	0	0	24
C. nemoralis O. F. Müller, 1764	1	+	+	0	+	+	+	6.7	+	1	6.4	+	224	1,401
C. violaceus Linnaeus, 1758	+	+	0	0	+	1	1	+	0	0	+	0	279	827
Calathus erratus (C. R. Sahlberg, 1827)	0	0	0	5.3	0	0	0	+	0	0	0	0	207	234
C. fuscipes (Goeze, 1777)	0	0	0	1	0	0	0	0	0	0	0	0	174	189
C. melanocephalus (Linnaeus, 1758)	+	0	+	1	0	+	0	+	1	+	+	+	299	885
C. micropterus (Duftschmid, 1812)	1	+	0	0	+	+	+	+	0	0	+	0	6	772
Clivina fossor (Herbst, 1784)	0	0	0	0	+	0	0	0	0	0	0	0	28	35
Calosoma inquisitor (Linnaeus, 1758)	0	0	0	0	0	+	0	+	+	+	+	+	53	88
Cychrus caraboides (Linnaeus, 1758)	1	1	+	0	5.8	5.4	1	1	+	1	1	1	337	1,380
Chlaeniellus nigricornis (Fabricius, 1787)	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Cicindela sylvatica Linnaeus, 1758	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Cymindis macularis Mannerheim in Fischer von Waldheim, 1824	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Dolichus halensis (Schaller, 1783)	0	0	0	0	0	0	0	0	0	0	0	0	19	19
Dromius agilis (Fabricius, 1787)	0	0	0	0	0	0	0	0	0	0	0	0	1	3
D. fenestratus (Fabricius, 1794)	0	0	0	+	0	0	0	0	0	0	0	0	0	1
D. schneideri Crotch, 1871	0	0	0	+	0	0	0	0	0	0	0	0	0	2
D. sigma (Rossi, 1790)	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Dyschirius globosus (Herbst, 1783)	0	0	0	+	0	0	0	0	0	0	0	0	1	42
Elaphrus cupreus Duftschmid, 1812	0	+	0	+	0	0	0	0	0	0	0	0	0	12
Epaphius rivularis (Gyllenhal, 1810)	0	1	+	1	0	0	0	0	0	0	0	0	7	39
E. secalis (Paykull, 1790)	1	1	8	0	0	+	+	1	1	+	+	1	547	1,471
Harpalus affinis (Schrank, 1781)	0	0	0	0	0	0	0	0	0	0	0	0	141	141
H. anxius (Duftschmid, 1812)	0	0	0	0	0	0	0	0	0	0	0	0	1	1
H. fuliginosus (Panzer, 1809)	0	0	0	0	0	0	0	0	+	0	0	0	6	18
H. griseus (Panzer, 1797)	0	0	0	1	0	0	0	0	0	0	0	+	196	204
H. latus (Linnaeus, 1758)	+	+	+	0	+	+	+	+	+	+	1	+	96	351
H. luteicornis (Duftschmid, 1812)	0	0	0	0	0	0	0	0	0	0	0	0	1	1
H. neglectus Serville, 1821	0	0	0	0	0	0	0	0	0	0	0	0	1	1
H. picipennis (Duftschmid, 1812)	0	0	0	0	0	0	0	0	0	0	0	0	12	12
H. progrediens Schauberger, 1922	0	0	0	0	0	0	0	0	0	0	0	0	1	1
H. quadripunctatus Dejean, 1829	+	+	0	0	+	+	1	1	1	1	1	1	113	709
H. rubripes (Duftschmid, 1812)	0	0	0	1	0	0	0	0	0	0	0	0	78	83
H. rufipes (De Geer, 1774)	0	+	+	+	+	0	+	+	+	+	+	+	2,332	2,401
H. rufitarsis (Illiger, 1778)	0	0	0	0	0	0	0	0	0	0	0	0	28	41
Harpalus signaticornis (Duftschmid, 1812)	0	0	0	+	0	0	0	0	0	0	0	0	68	72
H. smaragdinus (Duftschmid, 1812)	0	0	0	0	0	0	0	0	0	0	0	0	3	3
H. tardus (Panzer, 1796)	0	0	0	1	0	0	0	0	0	0	0	0	59	72
H. tenebrosus (Schauberger, 1929)	0	0	0	0	0	0	0	0	0	0	0	0	2	3
Lebia chlorocephala (Hoffmannsegg, 1803)	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Leistus ferrugineus (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	8
L. piceus Froelich, 1979	+	0	0	0	0	0	0	0	0	0	0	+	0	21

L. rufescens (Fabricius, 1775)	0	0	+	0	0	0	0	0	0	0	0	0	0	12
Loricera pilicornis (Fabricius, 1775)	0	+	+	+	0	0	0	0	0	0	0	0	5	76
Licinus depressus (Paykull, 1790)	0	0	0	0	0	0	0	0	0	0	0	0	4	4
Masoreus wetterhalli (Linnaeus, 1767)	0	0	+	+	0	0	0	0	0	0	0	0	5	14
Miscodera arctica (Paykull, 1798)	0	0	0	0	0	0	0	0	0	0	0	0	2	4
Microlestes minutulus (Goeze, 1777)	+	0	0	0	0	0	0	0	0	0	0	0	1	5
Nebria brevicollis (Fabricius, 1792)	0	0	0	0	0	0	0	+	0	+	+	+	6	507
Notiophilus aesthuans (Motschulsky, 1864)	0	0	0	0	0	+	0	0	0	0	0	0	7	20
N. aquaticus (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	+	1	3
N. biguttatus (Fabricius, 1799)	0	0	0	0	0	+	0	+	0	0	0	0	43	90
N. germinyi Fauvel in Grenier, 1863	+	+	+	0	0	0	0	+	0	+	+	0	29	45
N. palustris (Duftschmid, 1812)	+	0	0	0	0	0	0	0	0	0	0	0	2	49
Oodes helopioides (Fabricius, 1792)	0	1	0	+	0	0	0	0	0	0	0	0	0	15
Ophonus puncticollis (Paykull, 1798)	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Panagaeus bipustulatus (Fabricius, 1775)	0	0	0	0	0	0	0	0	0	0	0	0	4	4
P. cruxmajor (Linnaeus, 1758)	0	0	+	0	0	0	0	0	0	0	0	0	10	14
Patrobus atrorufus (Strøm, 1768)	0	1	5.3	1	0	+	0	+	0	0	0	1	2	278
Pterostichus aethiops (Panzer, 1797)	0	0	+	0	0	+	0	+	0	1	1	1	17	328
P. anthracinus (Illiger, 1798)	0	0	5.3	0	0	+	0	0	0	0	+	+	136	282
P. cupreus (Linnaeus, 1758)	+	0	0	0	0	0	0	0	0	0	0	+	56	68
P. diligens (Sturm, 1824)	+	1	+	+	+	+	0	+	+	+	+	+	25	139
P. melanarius (Illiger, 1798)	+	11.4	8.2	0	5.2	1	0	9.3	6.1	6.7	23.0	25.4	966	3,567
P. minor (Gyllenhal, 1827)	0	1	1	1	0	0	0	0	0	+	0	0	1	37
P. niger (Schaller, 1783)	11.4	30.9	22.4	6.2	43.7	46	43.8	12.2	27.5	24.9	33.0	17.1	1,665	9,625
P. nigrita (Paykull, 1790)	0	0	1	+	0	+	0	0	0	0	0	0	8	106
P. oblongopunctatus (Fabricius, 1787)	17.4	1	1	+	14.1	13.8	17.9	13.6	34.2	15.1	18.5	19.7	2,153	12,228
P. quadrifoveolatus Letzner, 1852	0	0	0	0	0	0	0	0	0	0	0	0	10	10
P. strenuus (Panzer, 1797)	+	1	+	+	0	+	0	0	0	0	0	0	15	134
P. vernalis (Panzer, 1796)	0	+	0	0	0	0	0	0	0	0	0	0	9	13
Poecilus versicolor (Linnaeus, 1758)	+	+	1	0	1	1	1	1	1	1	1	1	905	1364
P. punctulatus (Schaller, 1783)	0	0	0	0	0	0	0	0	0	0	0	0	16	18
P. lepidus (Leske, 1787)	0	0	0	+	0	0	0	0	0	0	0	0	253	327
Synuchus nivialis (Illiger, 1798)	0	0	+	+	0	0	+	0	0	0	0	0	38	55
Stomis pumicatus (Panzer, 1796)	0	+	1	+	0	0	0	+	0	+	+	+	13	65
Syntomus foveatus (Fourcroy, 1785)	0	0	0	0	0	0	0	0	0	0	0	0	2	3
S. truncatellus (Linnaeus, 1761)	0	0	0	0	0	0	0	0	0	0	0	0	6	9
T. quadristriatus (Schrank, 1781)	+	0	0	0	0	0	0	0	0	0	0	0	3	8
Trichocellus placidius (Gyllenhal, 1827)	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Microlestes maurus (Sturm, 1827)	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Total	1,229	676	588	322	935	1,263	952	1,334	1,016	952	2,134	2,433	14,861	65,096