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The response of carabids to landscape simplification differs between trophic groups

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Abstract We studied the response of carabid species richness and density to landscape simplification (measured as percentage cover of non-crop habitat surrounding each study site) in 36 wheat fields using pitfall traps. Carabids were divided to trophic groups following the literature. The number of species from different trophic groups declined with increasing landscape simplification in the order: carnivores > phytophages > omnivores. Density compensation of both carnivores and phytophages suggests that species decline is caused by the loss of specific resources rather than by an overall reduction in food availability. Increasing evenness indicates that a greater share of phytophagous species contributes to density compensation at poorer sites. A comparison with data from complementing studies shows that marked differences in species numbers (carnivores > omnivores > phytophages) are due to a different sensitivity of trophic groups to agricultural management. Since our findings seem to be partly due to increasing sensitivity to landscape changes with trophic rank, and partly to decreasing sensitivity of depauperate communities to local environmental stress, species loss can best be explained by the co-action of factors at local and regional scales. Species richness decline might significantly alter the role of carabids as biocontrol agents.

Keywords Carabidae · Trophic rank · Species richness · Density compensation · Landscape composition

Introduction

Predicting the effect of spatial changes on populations and communities is a major challenge to biodiversity research (Dunning et al. 1992; Bestelmeyer et al. 2003). One essential prerequisite for doing so would be to establish quantitative links between spatial patterns and biodiversity (Gustafson 1998; Tischendorf 2001; Turner et al. 2001). This is, however, very difficult, because each taxon of the enormously rich terrestrial community potentially responds differently to the spatial dynamics and the heterogeneity of its environment (Kareiva 1994; Dauber et al. 2003). One possibility for simplifying this problem is provided by the hypothesis that species-area effects should become stronger as trophic rank increases (Holt et al. 1999). Empirical evidence either challenges (Borrvall et al. 2000; Woodward and Hildrew 2002) or supports (Kruess 2003; Thies et al. 2003) this hypothesis. However, aggregation into functional groups not only makes it possible to detect spatial influences across broad ecological groups, rather than being reliant on the presence of a few key indicator species, but may also help in predicting associated influences on ecosystem functioning (Cole et al. 2002).

Species at higher trophic ranks depend on spatial composition at larger scales than local patches, since they are more likely to have large home ranges (e.g. Ritchie and Olf 1999). This suggests that landscape effects are different for different trophic groups. We have tested this hypothesis by investigating the impact of landscape simplification on carabid communities inhabiting wheat fields. Landscape simplification should lead to a significant decline in the effective area, since carabids critically depend upon a variety of habitats within their movement range for the provision of alternate food sources, as well as refuge and overwintering sites (Bommarco 1999; Fournier and Loreau 2002). Though most carabids are unspecialised carnivores, several species are either phytophagous or omnivorous (Thiele 1977). Species belonging to the omnivorous

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group are normally carnivorous but supplement their diets with seeds or vegetative parts of plants (Jorgensen and Toft 1997). In accordance with Holt et al. (1999), we asked the following questions: (1) does the decline in effective area associated with landscape simplification affect the species richness of carabids?; (2) if so, is this effect stronger for carnivorous (high trophic rank) than for phytophagous (lower trophic rank) species?; and (3) are omnivorous species, as opportunistic generalists, less sensitive to landscape effects than other trophic groups?

Materials and methods

Study area and study sites

The study was conducted in 36 agricultural landscapes situated in two regions of central Germany: the Lahn-Dill-Bergland northwest of the city of Giessen (LDB, $n=19$) and southern Lower Saxony around the city of Göttingen (SLS, $n=17$). LDB is dominated by a small-scale mosaic of forests (48% total cover of the region), low-input agricultural systems (17% total cover) and grassland (18% total cover), while SLS mainly consists of cropland-grassland mosaics, dominated by intensive agricultural land use (about 75% total cover), and by patchily distributed fragments of semi-natural habitats such as fallows, grasslands, hedges and a few forest remnants. We focused on an area comprising about 600 km² in each of the two regions. During the study period, from May to July, average temperature and average rainfall in LDB were 14.3°C and 181.5 mm. Corresponding values in SLS were 16.9°C and 155.5 mm (data from the meteorological station in Göttingen and Hessisches Landesamt für Umwelt und Geologie, Wiesbaden).

Landscape analysis

We used the percentage cover of non-crop area ['non-crop (%)'] as a parameter for landscape simplification. This parameter is closely correlated to other landscape metrics such as habitat type diversity (cf. Thies et al. 2003). A total of 36 independent, non-overlapping circular landscape sectors were selected to form a gradient from complex and structurally rich landscapes (>85% non-crop area) to extremely simple and structurally poor landscapes (<15% non-crop area). The sectors had a radius of 0.75 km, since ecologically effective impacts of the surrounding landscape on carabid assemblages occur within this range (Östman et al. 2001; Jeanneret et al. 2003; Weibull et al. 2003). Simple and complex landscapes were geographically interspersed, ranging from 12 to 72% and 40 to 90% of non-crop area in SLS and LDB, respectively. One conventionally managed winter-wheat field was chosen as a study site at the center of each landscape sector. Calculation of the parameter 'non-crop (%)' was based on land-use maps derived either from intensive field inspections (SLS) or GIS-sup-

ported stereoscopic analysis of black and white aerial photographs (scale: approx. 1:10,000; LDB). Decreasing 'non-crop (%)' is termed 'landscape simplification' in the following text.

Sampling

Carabids were sampled using pitfall traps. Each trap consisted of a 500-ml polyethylene beaker (diameter 85 mm) and was filled with approx. 170 ml ethylene glycol-water solution (1:1). A detergent was added to reduce surface tension. Acrylic glass covers (250 × 250 mm) were positioned approximately 10 cm above the traps to prevent flooding by rain. Four pitfall traps were placed at the center of each site, forming a line with about 10 m between neighbouring traps. Sampling took place in 2001 at two-weekly intervals between 3 and 30 May, and 18 June and 2 July. All carabid individuals were determined to the species level and sorted to trophic groups according to their feeding type (Skuhrový 1959; Lindroth 1992; Ribera et al. 2001). Criteria for dividing species into trophic groups were reports of adult beetles feeding solely on animal material (carnivorous), feeding solely on plant material (phytophagous), or feeding on both (omnivorous).

Statistical analysis

Site-specific estimates of species richness and activity density of all carabid communities were calculated from pooled pitfall catches of each site. The overall effect of landscape simplification on total species richness of carabids was analysed by linear regression. Twelve species for which only sparse information on their feeding behaviour was available were not considered within the analyses (see Appendix). Effects of the two categorical factors 'trophic group' (carnivorous, phytophagous, omnivorous) and 'region' (LDB, SLS) as well as of the continuous factor 'non-crop (%)' on species richness and activity density were analysed using general linear models (GLM). A potential non-linear effect of the continuous factor was considered by additionally including [non-crop (%)]² in the model. Since this factor did not affect any of the dependent variables, presentation of the results is confined to the linear factor. Means were compared using the Tukey HSD-test ($P < 0.05$). We additionally calculated the local evenness (E_H) for each of the three trophic groups based on the Shannon-Weaver index (Southwood and Henderson 2000) to get an estimate of changes in the dominance structure along the landscape gradient. The correlation between E_H and 'non-crop (%)' was analysed by linear regression. Differences in the slope of the regression lines were compared by using analysis of covariance. Homogeneity of variances was tested using Levene's test. Data were checked for normal distribution using the Kolmogorov-Smirnov test. All statistical treatments were performed using the STATISTICA for Win-

dows package 6.0 and SPSS for Windows package 11.0 (StatSoft, Tulsa, USA; SPSS, Ill., USA). Arithmetic means \pm standard errors are given in text.

Neither the results of the GLM nor the analysis of covariance are affected by different numbers of species within the three trophic groups, because these techniques test statistical effects against the error mean square of the complete sample. However, since graphic presentation of the interactions between 'feeding types' and 'non-crop (%)' was made difficult by differences in species numbers, the richness of the three feeding types was standardized by subtracting species richness of the individual feeding groups at each value of 'non-crop (%)' from that of the corresponding richness at the highest 'non-crop (%)' (89.9%). This procedure does not affect the regression coefficients, the slope of the regression lines, or the level of significance.

Results

A total of 14,108 carabids belonging to 84 species were trapped at the 36 sites (see Appendix). The GLM revealed significant effects of the factor 'trophic group' on carabid species richness (Table 1). This reflects that species richness of carnivores (13.61 ± 3.27) was significantly higher than that of both phytophages (2.94 ± 1.98) and omnivores (4.72 ± 1.09), and that species richness of omnivores was significantly higher than that of phytophages (Tukey HSD test).

Linear regression analysis revealed that total species richness of carabids significantly declined with landscape simplification ($r^2 = 0.31$, $P < 0.001$, $n = 36$ fields). However, significant 'trophic group' \times 'non-crop (%)' interactions revealed by the GLM indicate trophic group-specific differences (Table 1). Species richness of carnivorous and phytophagous carabids significantly decreased with decreasing 'non-crop (%)', while no effect of this parameter on omnivorous carabids could

Table 1 General linear model results on effects of 'trophic group' (carnivorous, phytophagous, omnivorous), region (LDB, SLS), and the percentage of non-crop habitat in the surrounding landscape, both linear [non-crop (%)] and non-linear [non-crop (%)²] on species richness ($r^2 = 0.88$) and activity density ($r^2 = 0.57$) of carabids in winter-wheat fields

	DF	Species richness		Activity density	
		F	P	F	P
Trophic group	2	13.15	<0.001	5.80	<0.01
Region	1	1.49	0.22	1.89	0.17
Non-crop (%)	1	1.19	0.27	0.03	0.87
Non-crop (%) ²	1	0.61	0.43	0.15	0.70
Region \times trophic group	2	0.64	0.53	3.43	<0.05
Region \times non-crop (%)	1	0.93	0.08	0.68	0.41
Trophic group \times non-crop (%)	2	4.76	0.01	0.66	0.52

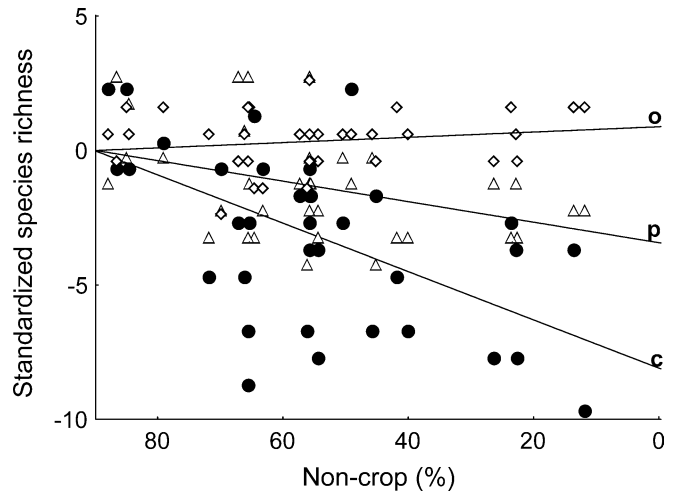


Fig. 1 Impact on landscape simplification, i.e., decreasing cover of [non-crop (%)], on the 'standardized species richness' of carabid trophic groups inhabiting wheat fields located in Central Germany ($n = 36$ fields). Trophic groups of carabids include carnivores [c, filled circles, $n = 45$ species; $F = 16.23$, $r^2 = 0.32$, $P < 0.001$, $y = -8.09 + 0.09 \times \text{non-crop} (\%)$], phytophages [p, triangles, $n = 21$ species; $F = 6.41$, $r^2 = 0.16$, $P = 0.02$, $y = -3.43 + 0.04 \times \text{non-crop} (\%)$], and omnivores [o, diamonds, $n = 6$ species; $F = 1.24$, $r^2 = 0.03$, $P = 0.2$, $y = 0.88 - 0.001 \times \text{non-crop} (\%)$]

be established (Fig. 1). Analysis of covariance showed that, due to strong internal variability, the apparently steeper slope for carnivorous than for phytophagous carabids could only be statistically confirmed at the $P < 0.06$ level ($F = 3.68$). The richness decline of these two groups with landscape simplification was significantly stronger than that of omnivores (carnivores: $F = 17.67$, $P < 0.001$, phytophages: $F = 17.3$, $P < 0.002$). Evenness of carnivores and phytophages in complex landscapes was higher than that of omnivores (Fig. 2). It

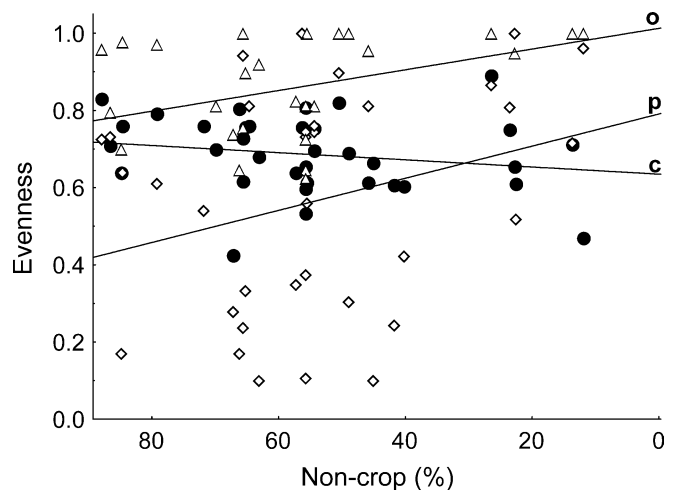


Fig. 2 Impact on landscape simplification, i.e., decreasing cover of 'non-crop (%)', on the evenness (E_H) of carabid trophic groups inhabiting wheat fields located in central Germany ($n = 36$ fields). Trophic groups of carabids include carnivores [c, filled circles, n.s.], phytophages [p, triangles, $F = 5.08$, $r^2 = 0.16$, $P < 0.05$, $E_{Hp} = 1.1 - 0.002 \times \text{non-crop} (\%)$], and omnivores [o, diamonds, $F = 3.32$, $r^2 = 0.09$, $P = 0.07$, $E_{Ho} = 0.7 - 0.004 \times \text{non-crop} (\%)$]

significantly increased with landscape simplification for phytophages and omnivores, but remained unchanged for carnivores.

Significant effects of the factor 'trophic group' on activity density (Table 1) indicate the significantly higher numbers of carnivores (265.97 ± 139.33) than of phytophages (6.75 ± 7.09) and omnivores (121.25 ± 141.77). Moreover, omnivore density was significantly higher than that of phytophages. In contrast to species richness and evenness, however, activity density of none of the three trophic groups was affected by the surrounding landscape (Table 1). Significant 'region' × 'trophic group' interactions are due to the much higher activity density of omnivores in LDB (181.79 ± 172.82) than in SLS (53.59 ± 33.94 ; Tukey HSD test). However, this was solely caused by the species *Poecilus cupreus* (Lineé 1758) which reached very high densities in LDB (approx. factor 10). Activity density of both carnivores and phytophages did not differ between regions.

Discussion

The results of this study clearly prove the differential response of carabid trophic groups to landscape composition. Since effects of the factor 'region' were confined to the density of just one omnivorous species, data do not seem to be biased by systematic differences between the two study regions. We have shown that the species richness of carnivores is very sensitive, that of phytophages less sensitive and that of omnivores insensitive to landscape simplification. All questions posed in the introduction section have thus been answered positively.

Assuming that the erosion of perennial habitats in the vicinity of wheat fields reduces the 'effective area' for carabids (Bommarco 1999), the finding that species of high trophic rank (carnivores) respond much more strongly than those of lower trophic rank (phytophages) is consistent with the rank dependency theory (Holt et al. 1999). According to this theory, two processes might explain the effect of landscape simplification on the species richness of these two groups: (1) processes operating directly upon the dynamics of the different populations; and (2) spatial constraints impinging on the food sources of these populations. Direct changes in the effective area are most probably due to the decline of supplemental habitats for hibernation and reproduction (Desender 1982; Wallin and Ekblom 1988). Evidence for indirect landscape effects via food constraints comes from investigations on carabid prey (Dombos 2001; Lagerlöf et al. 2002) and from the decline of arable weed diversity with landscape simplification found in a complementary study (Gabriel et al. 2002). The latter may have adversely affected both phytophagous species (critically dependent on the availability of seeds, preferably of grasses, umbellifers and crucifers; Thiele 1977) and carnivorous species (profiting from the large number of insect

species hosted by weeds; Marshall et al. 2003). The weak relationship between omnivore species richness and landscape simplification confirms the ability of opportunistic generalists to flexibly persist on different resources (Jorgensen and Toft 1997; Holt et al. 1999).

Carnivores and phytophages declined in richness but not in abundance. Though we cannot exclude that our data are biased by varying trapping efficiencies between trophic groups, no indication for such an effect could be found in the literature. We are thus confident that the mechanisms involved are mainly due to both behavioural and numerical responses to landscape simplification (Östman 2002). Density compensation might indicate release from interspecific competition (cf. Lawton and Brown 1993). More importantly, however, it shows that species at poorer sites have enough resources to support the same number of individuals as richer sites (cf. Findley and Findley 2001). We thus conclude that landscape effects on the richness of carnivorous and phytophagous carabids mediated by nutritional constraints are due to the loss of specific resources rather than to an overall reduction in food availability. This is consistent with the specialized consumers assumption underlying the 'trophic rank hypothesis' of Holt et al. (1999). Considering the taxon-specific responses of invertebrate prey [e.g., Collembola: Dombos (2001); earthworms: Lagerlöf et al. (2002); ants: Dauber et al. (2003)] and food plants [e.g., herbs vs. grasses: Bruun (2000)] to spatial features of agricultural landscapes, the composition of food sources may have dramatically changed along the landscape gradient without necessarily altering total energy gain.

Results from complementary studies suggest that agricultural management increases the richness of carnivorous and omnivorous carabids, but decreases that of phytophagous carabids (Purtauf et al. 2004). The marked differences in species numbers found on arable land in the present study seem thus to be the result of differences in the sensitivity of trophic groups to the selective forces exerted by agricultural management. In particular, the impoverished community of phytophages on arable land provides an alternate scenario to the 'trophic-rank hypothesis', because resident species of depauperate communities may enjoy lower extinction risk due to a high potential for density compensation (McGrady-Steed and Morin 2000). Accordingly, the moderate loss of phytophagous carabids with landscape simplification as compared to carnivorous species could also be explained by the high resistance of the few remaining species to additional stress associated with the spatial composition of the surrounding area. In a similar vein, a significant increase in evenness (i.e., homogenization of the dominance structure) shows that the share of phytophagous species contributing to density compensation increases with landscape simplification. However, community impoverishment does not explain the somewhat intermediate response of omnivores, i.e., no change in richness or abundance but marked increase in even-

ness. Moreover, both carnivores and phytophages exhibited density compensation despite marked differences in species numbers, community abundance, and evenness change. We thus hypothesize that the patterns found in the present study can best be explained by the co-action of local processes underlying the 'depauperate community hypothesis' (McGrady-Steed and Morin 2000) and regional processes underlying the 'trophic-rank hypothesis' (Holt et al. 1999). This confirms that landscape effects on species richness can only be evaluated by considering local as well as regional processes in a group-specific way (Gaston and Lawton 1990; Dauber et al. 2003). Since the correlative approach of our study does not provide causal explanations, further studies have to identify the proximate drivers for the different response patterns of phytophagous and carnivorous carabids.

The loss of carnivorous and phytophagous carabids with landscape simplification may significantly affect biocontrol of agricultural pests. Some carnivores are able to suppress aphids (Kromp 1999; Schmidt et al. 2003) and slugs (Bohan et al. 2000; Symondson et al. 2002). Phytophages control arable weeds via seed predation (Honek et al. 2003). The striking evidence for density compensation along the species richness gradient might nevertheless suggest that most of the landscape effects can be compensated by the abundance increase of

the remaining species (Ruesink and Srivastava 2001). However, knowledge on the modulation of biodiversity/function relationships by processes taking place at the landscape level is very poor (Bengtsson et al. 2002). The same holds for patterns such as density compensation by species differing in resource requirements or changes in the dominance structure (Wolters 2001). Considering the rapid change of Europe's agricultural landscape (Stanners and Bordeau 1995; Jongman 2002), the functional implications of processes such as those reported in this study have to be quantified with high priority, because there are good reasons for assuming that a loss of biodiversity makes systems more vulnerable to disturbances (Scheffer et al. 2001).

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Appendix

Table 2 lists all of the species recorded during this study

Table 2 Species recorded

Species name	Feeding group	Abundance (mean \pm SD)	Distribution
<i>Abax ovalis</i> (Duftschmid 1812)	c	0.02 \pm 0.16	1
<i>A. parallelepipedus</i> (Piller et Mitterpacher 1783)	c	0.91 \pm 1.96	11
<i>Acupalpus meridianus</i> (Linné 1767)	c	0.02 \pm 0.16	1
<i>Agonum muelleri</i> (Herbst 1785)	c	1.88 \pm 3.29	17
<i>A. sexpunctatum</i> (Linné 1758)	c	0.13 \pm 0.54	3
<i>Asaphidion flavipes</i> (Linné 1761)	c	6.30 \pm 9.98	29
<i>Bembidion femoratum</i> Sturm 1825	c	0.02 \pm 0.16	1
<i>B. guttula</i> (Fabricius 1792)	c	0.02 \pm 0.16	1
<i>B. lampros</i> (Herbst 1784)	c	10.8 \pm 15.2	29
<i>B. lunulatum</i> (Fourcroy 1785)	c	0.13 \pm 0.54	3
<i>B. obtusum</i> Serville 1821	c	2.55 \pm 3.47	22
<i>B. tetracolum</i> (Say 1823)	c	2.55 \pm 8.64	5
<i>Brachinus crepitans</i> (Linné 1758)	c	0.11 \pm 0.66	1
<i>B. explodens</i> (Duftschmid 1812)	c	0.41 \pm 1.55	5
<i>Calathus fuscipes</i> (Goeze 1777)	c	2.25 \pm 5.94	19
<i>Calathus melanocephalus</i> (Linné 1761)	c	0.08 \pm 0.28	3
<i>Carabus auratus</i> Linné 1759	c	6.58 \pm 14.8	16
<i>C. auronitens</i> Fabricius 1792	c	0.08 \pm 0.36	2
<i>C. cancellatus</i> Illiger 1798	c	5.86 \pm 16.2	10
<i>C. convexus</i> Fabricius 1775	c	1.13 \pm 6.49	3
<i>C. granulatus</i> Linné 1758	c	20.5 \pm 27.1	29
<i>C. monilis</i> Fabricius 1792	c	0.02 \pm 0.16	1
<i>C. purpurascens</i> Fabricius 1787	c	0.22 \pm 0.59	6
<i>Clivina fossor</i> (Linné 1758)	c	0.63 \pm 1.70	10
<i>Cychrus caraboides</i> (Linné 1758)	c	0.08 \pm 0.28	3
<i>Dyschirius globulosus</i> (Herbst 1783)	c	0.02 \pm 0.16	1
<i>Leistus ferrugineus</i> (Linné 1758)	c	0.02 \pm 0.16	1
<i>Loricera pilicornis</i> (Fabricius 1775)	c	14.8 \pm 10.0	36
<i>Molops piceus</i> (Panzer 1793)	c	0.02 \pm 0.16	1
<i>Nebria brevicollis</i> (Fabricius 1792)	c	4.19 \pm 5.77	24
<i>N. salina</i> Fairmaire 1854	c	23.4 \pm 31.8	31
<i>Notiophilus biguttatus</i> (Fabricius 1779)	c	2.16 \pm 3.35	18

during this study, giving their feeding group (c carnivorous, o omnivorous, p phytophagous, ? no classification possible), abundance (number of individuals per site), and distribution (number of sites where each species was found)

Table 2 (Contd)

Species name	Feeding group	Abundance (mean \pm SD)	Distribution
<i>N. aquaticus</i> (Linné 1758)	c	1.02 \pm 1.64	15
<i>N. palustris</i> (Duftschmid 1812)	c	0.97 \pm 1.40	17
<i>Platynus assimilis</i> (Paykull 1790)	c	1.13 \pm 5.49	7
<i>P. dorsalis</i> (Pontoppidan 1763)	c	60.3 \pm 64.7	36
<i>Poecilus versicolor</i> (Sturm 1824)	c	23.6 \pm 58.2	18
<i>Pterostichus madidus</i> (Fabricius 1775)	c	0.02 \pm 0.16	1
<i>P. melanarius</i> (Illiger 1798)	c	76.7 \pm 73.1	35
<i>P. niger</i> (Schaller 1783)	c	1.22 \pm 4.49	7
<i>P. nigrita</i> (Paykull 1790)	c	0.02 \pm 0.16	1
<i>P. oblongopunctatus</i> (Fabricius 1787)	c	0.02 \pm 0.16	1
<i>P. vernalis</i> (Panzer 1766)	c	0.38 \pm 0.76	9
<i>Syntomus truncatellus</i> (Linné 1761)	c	0.02 \pm 0.16	1
<i>Trechus quadristriatus</i> (Schrank 1781)	c	14.5 \pm 24.7	28
<i>Amara similata</i> (Gyllenhal 1811)	o	0.61 \pm 1.72	8
<i>Bembidion quadrimaculatum</i> (Linné 1761)	o	0.11 \pm 0.31	4
<i>Carabus nemoralis</i> Müller 1794	o	3.94 \pm 7.68	22
<i>Harpalus affinis</i> (Schrank 1781)	o	4.63 \pm 4.01	33
<i>Poecilus cupreus</i> (Linné 1758)	o	76.6 \pm 133.1	32
<i>Pseudophonus rufipes</i> (Degeer 1774)	o	6.5 \pm 16.2	25
<i>Amara aenea</i> (Degeer 1774)	p	0.38 \pm 0.64	11
<i>A. aulica</i> (Panzer 1797)	p	0.02 \pm 0.16	1
<i>A. communis</i> (Panzer 1797)	p	0.11 \pm 0.31	4
<i>A. consularis</i> (Duftschmid 1812)	p	0.36 \pm 1.47	3
<i>A. convexior</i> Stephens 1828	p	0.02 \pm 0.16	1
<i>A. eurynota</i> (Panzer 1797)	p	0.33 \pm 0.98	6
<i>A. familiaris</i> (Duftschmid 1812)	p	1.00 \pm 2.51	12
<i>A. lunicollis</i> Schiödte 183	p	0.30 \pm 0.62	8
<i>A. montivaga</i> Sturm 1825	p	0.13 \pm 0.35	5
<i>A. ovata</i> (Fabricius 1792)	p	0.25 \pm 0.64	6
<i>A. plebeja</i> (Gyllenhal 1810)	p	3.97 \pm 6.40	23
<i>Harpalus honestus</i> (Duftschmid 1812)	p	0.08 \pm 0.36	2
<i>H. latus</i> (Linné 1758)	p	0.27 \pm 0.51	9
<i>H. rubripes</i> (Duftschmid 1812)	p	0.36 \pm 0.59	11
<i>H. rufibarbis</i> (Fabricius 1792)	p	0.05 \pm 0.23	2
<i>H. rufitarsis</i> Duftschmid 1812	p	0.05 \pm 0.23	2
<i>H. schaubergianus</i> Puel 1937	p	0.02 \pm 0.16	1
<i>H. signaticornis</i> (Duftschmid 1812)	p	0.11 \pm 0.39	3
<i>H. tardus</i> (Panzer 1797)	p	0.41 \pm 1.53	6
<i>Synuchus vivalis</i> (Illiger 1798)	p	0.25 \pm 0.5	8
<i>Zabrus tenebroides</i> (Goeze 1777)	p	0.02 \pm 0.16	1
<i>Anisodactylus binotatus</i> (Fabricius 1787)	?	0.22 \pm 0.63	5
<i>Badister sodalis</i> (Duftschmid 1812)	?	0.25 \pm 1.18	3
<i>Demetrias atricapillus</i> (Linné 1758)	?	0.86 \pm 1.41	15
<i>H. anxius</i> (Duftschmid 1812)	?	0.05 \pm 0.33	1
<i>H. azureus</i> (Fabricius 1775)	?	0.08 \pm 0.36	2
<i>Molops elatus</i> (Fabricius 1801)	?	0.13 \pm 0.59	2
<i>P. burmeisteri</i> Heer 1841	?	0.25 \pm 0.60	6
<i>P. strenuus</i> (Panzer 1797)	?	0.22 \pm 0.54	6
<i>Stomis pumicatus</i> (Panzer 1796)	?	0.11 \pm 0.39	3
<i>Trechoblemus micros</i> (Herbst 1783)	?	0.05 \pm 0.23	2
<i>Trechus secalis</i> (Paykull 1790)	?	0.11 \pm 0.39	3
<i>Trichotichnus laevicollis</i> (Duftschmid 1812)	?	0.02 \pm 0.16	1

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