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Abundance, diversity and succession of aquatic Coleoptera and Heteroptera in a cluster of artificial ponds in the North German Lowlands

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ABSTRACT

Our study describes and evaluates environmental influences on assemblages of aquatic Coleoptera and Heteroptera in artificial ponds situated near Lake Steinhude in Lower Saxony (Germany). We determined temporal dynamics and colonization patterns for 14 ponds of different age. In total, we recorded 4941 individuals that represented 87 species of aquatic beetles and bugs. Between 30 and 40 species were found in most of the ponds. Heteropteran species of the families Corixidae and Notonectidae acted as pioneer species in new ponds, while aquatic coleopterans predominated in older ponds. The results of Canonical Correspondence Analyses (CCA) showed that among the key factors affecting community structure were land use, vegetation cover, water chemistry and the age of the ponds. We found that the distribution of adjacent ponds on areas with different land use has a positive influence on the diversity and abundance of the aquatic insect fauna.

Introduction

Many plant and animal species that live in lentic water bodies are endangered by destruction of their natural habitat. Therefore, the construction of artificial ponds and pools is an important measure to compensate for the potential loss of biodiversity. It has been shown that artificial water bodies can achieve high species diversity just after a few years (e.g. Gee et al. 1997). Hence, newly constructed ponds are ideal sites for studies on colonization by aquatic invertebrates. Methodical approaches might entail studying the same water bodies for several years, or comparing similar water bodies of different age.

The composition of aquatic beetle communities can be affected by various environmental factors such as pH (Eyre et al. 1986; Schmidl 2003), electrical conductivity (Eyre et al. 1986), the age of the site (Fairchild et al. 2000; Lundkvist et al. 2001), its size (Nilsson and Svensson 1995), permanence (Lundkvist et al. 2001; Nilsson and Svensson 1995), vegetation (Nilsson and Söderberg 1996) and shading (Lundkvist et al. 2001). For this reason, some authors consider aquatic beetles (especially the Hydradephaga) as suitable indicator species (e.g. Hendrich and Balke 1993; Schmidl 2003). Communities of aquatic Heteroptera, on the other hand, have generally been studied less frequently than aquatic beetles. However, a number of publications indicate that some species of Corixidae seem to have clearly defined habitat demands. For example, the distribution of corixids has been found to correlate with the percentage of organic material in the sediment (Macan 1938, 1954a), electrical conductivity and shape of the water body (Savage 1982), water hardness (Tully et al. 1991) and vegetation (Tully et al. 1991, Macan 1954a). Nonetheless, aquatic Heteroptera are considered less suitable indicator species than aquatic beetles because of their lower species diversity, and the broad ecological amplitude of some species. Moreover, the identification of females of some corixid species is relatively difficult, which may hamper ecological field assessments.

In our study, we monitored 14 ponds of different age that were constructed between 1996 and 2006 in the Nature Reserve (NR) Meerbruchswiesen, a former fen area situated on the western shore of Lake Steinhude in the North German Lowlands. The ponds are inhabited by communities of aquatic coleopterans (Haliplidae, Hygrobiidae, Noteridae, Dytiscidae, Hydrochidae and Hydrophilidae) and water bugs (Heteroptera: Corixidae, Nepidae, Naucoridae and Notonectidae). The main objective of our study was to investigate the temporal dynamics of pond colonization by these two groups of aquatic insects. We assessed regional abundances for 87 species, and evaluated community structures in relation to seral stages and ages of ponds. Canonical Correspondence Analyses (CCA) were conducted to determine the role of environmental factors, including pond surface area, pH, electrical conductivity and total water hardness. As the vegetation of many ponds in the study area is affected by grazing cattle, we also compared grazing intensity and its impact on aquatic communities.

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Material and methods

Study area

The ponds are located in the NR Meerbruchswiesen (Fig. 1), about 35 km northwest of Hannover (Lower Saxony, Germany), at the western shore of Lake Steinhude. The Nature Reserve (NR) covers an area of 1020 ha and is part of the large wilderness reserve Lake Steinhude (RAMSAR, wetland of international importance). Lake Steinhude is situated at the northern border of the Central German Uplands (Hercynian orogenic belt) that is characterized by glacial valleys of the rivers Weser and Aller, and raised bogs in morainal landscapes. The vegetation of the study area is dominated by wet grasslands that are mainly managed as meadows or pastures. The prevailing soil type is peat that originates from the terrestrialization of Lake Steinhude; mineral soils are found only in the western regions of the NR Meerbruchswiesen. A more detailed description of the study area was given by Brandt and Eulner (2004, in German).

Study sites and water parameters

Between 1994 and 2006, 65 temporary and permanent water bodies were constructed in the NR Meerbruchswiesen. For this study, we selected 14 permanent water bodies that differ in age, size and the agricultural land use of the surrounding area (Fig. 1). The ponds were chosen to represent a broad variety of vegetation and seral stages.

All data on age, depth and surface area of the ponds were provided by the Ecological Station Lake Steinhude. For each pond, electrical conductivity and pH were measured potentiometrically using a handheld multi-parameter sonde (WTW Multi 340i SET) in July, August and October 2007. Total water hardness was analyzed in October 2007 using field test kits (Tetratest). The ponds were classified into one of three categories according to the use of the surrounding area. Intensively used pastures, where the vegetation is kept short by grazing cattle, were defined as ‘intensive’, extensively used pastures with remaining areas of high vegetation as ‘extensive’, and fallow land as ‘none’.

Vegetation and ranking of seral stages

The aquatic vegetation, both submerged and emergent species, was recorded in each pond on two occasions, end of July and end of August 2007, during the period of maximum growth. The common plants of each pond were identified and assigned to into five vegetational units:

I. *Glyceria fluitans* community: shore vegetation, consisting mainly of *Glyceria fluitans*, with *Alisma plantago-aquatica* und *Ranunculus flammula*
II. Reeds: banks with different reed plants, including *Carex* spp., *Eleocharis palustris, Equisetum fluviatile, Juncus* spp., *Phalaris arundinacea, Phragmites australis, Sparganium* spp., *Schoenoplectus lacustris, Typha latifolia*
III. Lemnetea: floating community, with one or several small pleustophytic species (*Lemna minor, Riccia fluitans, Spirodela polyrhiza*)
IV. Submerged hydrophytes: *Zannichellia palustris, Utricularia minor*
V. Floating leaf plants: *Nuphar lutea, Nymphaea alba, Potamogeton natans, Hydrocharis morsus-ranae*

On both occasions (July and August 2007), we estimated the percentage of pond area covered by each of the vegetational units and the percentage of open water. Finally, we calculated the arithmetic means for the two estimates for each vegetational unit in each pond.

The ponds were arranged in a hypothetical ranking of seral stages that corresponded with particular aquatic vegetation cover. This ranking was based on the assumption that succession in the ponds is mainly characterized by an increase of emergent vegetation (along with a decrease of open water). Therefore, the main ranking criterion for hypothetical seral stages was the percentage of open water.

Sampling of aquatic beetles and bugs

The aquatic beetles and bugs were sampled between May and October 2007. During this period, each pond was sampled seven times, with an interval of about four weeks between two sampling dates. Sampling was carried out between 10 am and 6 pm, using a pond net with a 180 cm long extension rod (volume ca. 8.5 l, mesh size 0.5 mm). For each sample, the pond net was swept about 30 times through the water, so that different vegetational units, substrates and open water areas were proportionally covered.

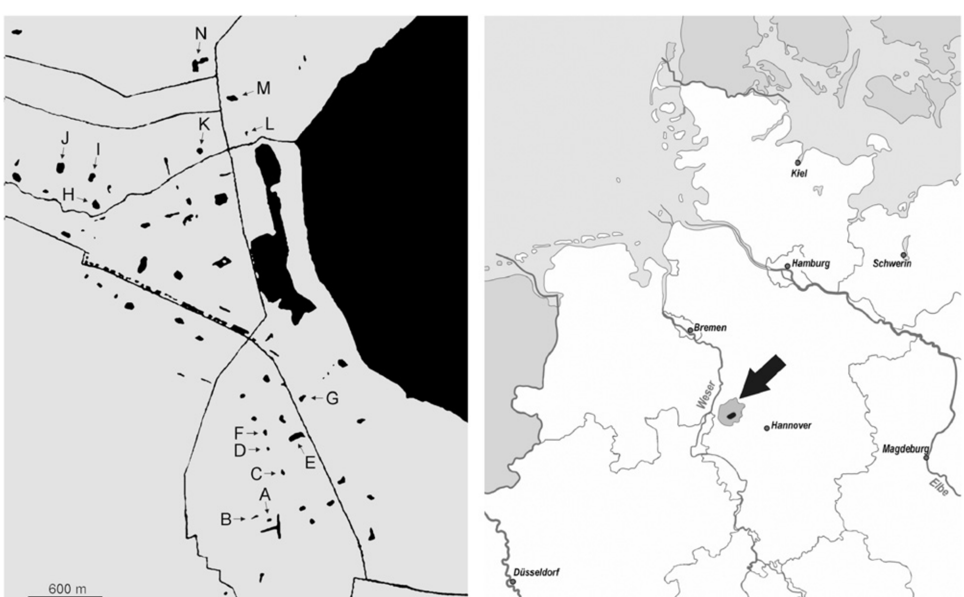

Fig. 1. Locations of the 14 ponds investigated in this study. Left: Map of the western-most region of Lake Steinhude (large black area), and adjacent cluster of artificial ponds (small black areas and dots). The 14 ponds are indicated by capital letters. Right: Overview map of northern Germany (white regions), with black arrow pointing at Lake Steinhude (small black area) in the Nature Reserve Meerbruchswiesen (gray area). Map modified from Lencer, Wikimedia; GNU Free Doc. Lic.

Individuals that could not be identified in the field were preserved in 70% ethanol. The heteropteran *Plea minutissima* occurred in high abundances, i.e., up to 100 individuals, in almost all ponds. However, in this species, discrimination between imagines and larvae is comparatively difficult, and proved to be unfeasible within the time frame of this study. Therefore, *Plea minutissima* was not included in quantitative analysis.

Nomenclature of aquatic Coleoptera follows Freude et al. (1971), Lohse and Lucht (1989) and Löbl and Smetana (2003, 2004), while nomenclature of Corixidae accords with Jansson (1986). Some coleopterans of the genera *Haliplus, Helochares* and *Helophorus* could not be identified to species level; for this reason, they were assigned to groups comprising several species, for example, "*Haliplus* (*Haliplinus*) spp.", "*Helochares* gr. *obscurus/punctatus*" and "*Helophorus* gr. *aquaticus/aequalis*".

Statistical analyses

We calculated dominance indices for all species in each pond using the following formula:

$$D_i = \frac{N_i}{N} \times 100$$

Here D_i represents the dominance of species i, N_i the number of individuals belonging to species i, and N the total number of individuals found at a site. Thus, the dominance of a species at a particular site is expressed as the percentage of individuals belonging to this species. Because female individuals of the genus *Sigara* could not be identified to species level (except for *S. lateralis*), the numbers of male individuals were doubled for these species, assuming that the female/male ratio is 1:1. In these instances, the chance of sex-biased samples was decreased by increasing the sample size (see previous section).

We used Spearman's rank correlation coefficient to evaluate relationships between age or rank of seral stages, and number of individuals or number of species in the ponds. In addition, a one-tailed Mann-Whitney U test was applied to determine whether the numbers of species and individuals in ponds of the use category 'intensive' were significantly lower than those of the category 'extensive'. Here, we assumed that the numbers of individuals obtained from pond net samples are comparable between ponds; possible (slight) differences in water volume were compensated for by the high total number of sweeps with the pond net. All calculations were made using the program XLSTAT-Pro 6.0.

A CCA (ter Braak 1986) was performed to evaluate the influence of different environmental variables on the structure of insect communities in the studied ponds. The environmental factors used in the CCA were the quantitative variables 'age', 'area', 'percentage of open water', 'pH', 'conductivity' and 'total hardness', as well as the nominal variable 'use' (with the categories 'intensive', 'extensive' and 'none'). For standardized quantitative variables the mean was set to zero, and the standard deviation to one. The analysis was performed with the program Multi-Variate Statistical Package (Kovach 1999), and the option 'downweighting of rare species' was chosen to minimize the impact of rare species on the results of the analysis. In an initial analysis, we included all species; subsequently, two separate analyses were conducted for each group of insects, Coleoptera and Heteroptera, to evaluate the influence of the environmental variables between groups.

Although we found single individuals of three-spined sticklebacks (*Gasterosteus aculeatus aculeatus*) in half of the ponds (C, D, F, G, L, M and N), we did not consider the variable 'fish predation' in the CCA. Within the limited time frame of this study, we were neither able to determine exact population sizes for these seven ponds, nor could we confirm or exclude the occurrence of sticklebacks in the remaining ponds. However, we assume that sticklebacks populated the ponds in very small numbers at the time of our study.

Results

Water parameters, vegetation and ranking of seral stages

All water parameters of the ponds are listed in Table 1. The values of total hardness (dH) are comparatively low. Pond B was built on sandy soil, while all other ponds were constructed on peat, with high concentrations of dissolved humic acids. B and L are the only ponds situated on fallow land. The remaining ponds are located on pastures that are usually stocked with cattle from April to November. According to the influence of the cattle, the area around seven ponds was classified as 'extensively used', while the remaining five ponds were assigned to the use category 'intensive'. As the intensive use of the area around pond A only started halfway through the study, this pond does not fit exactly into any category.

The first vegetational unit that appeared in most of the newly constructed ponds was the *Glyceria fluitans* community (unit I). This community was replaced in the course of succession by different species that formed reed banks (unit II). The vegetational units III, IV and V played only a minor role in succession and did not appear in every pond. The percentage of open water in the ponds ranged from 5% to 99.5% (Table 2). A *Glyceria fluitans* community was found in 13 ponds, and represented the major part of the vegetated area in seven ponds. Reeds were the main vegetational unit in the remaining seven ponds. More than half of the area of ponds B, C and L was covered with reeds. The vegetational unit Lemnetea occurred in six ponds, covering up to 14.5% of the total pond surface. Submerged hydrophytes and floating leaf plants were found only in some of the ponds (Table 2).

The youngest ponds (H, F and K) with a high percentage of open water were placed on the first ranks of the hypothetical ranking of seral stages (Table 2). Ranking positions 4–7 are occupied by another young pond (M) and three ponds with vegetation strongly affected by cattle (A, E, N). Ponds with an intermediate percentage of open water were placed on the ranks 8–11. Succession was most advanced in the oldest ponds B and L and the small pond C. Although pond C has the lowest percentage of open water, it received a lower rank than B and L because a larger *Glyceria fluitans* community was still present in pond C.

Abundance, distribution and succession of aquatic beetles (Coleoptera) and bugs (Heteroptera)

We recorded a total number of 4941 individuals, 2414 aquatic bugs and 2527 beetles, that represented 87 species (Appendix 1). The heteropteran families with the highest number of individuals were Pleidae (not counted), Corixidae (1823), followed by Naucoridae (214) and Notonectidae (367). Among coleopteran families, we found the highest abundances for Hydrophilidae (999), Noteridae (770), and Dytiscidae (633). The species-richest families were the coleopteran Dytiscidae (36) and Hydrophilidae (20), followed by the heteropteran Corixidae (17). In the course of our investigation, we recorded all known German species of the families Nepidae, Naucoridae, Hygrobiidae and Noteridae.

The most abundant species found in the study area were the heteropterans *Plea minutissima* (Pleidae) and *Corixa punctata* (Corixidae), and the coleopterans *Noterus crassicornis* (Noteridae) and *Helophorus minutus* (Hydrophilidae). These four species usually inhabit water bodies with rich vegetation (Klausnitzer 1996; Wachmann et al. 2006). *Hesperocorixa castanea* (Corixidae) had a higher dominance than *Corixa punctata* (Appendix 1), but all individuals of *H. castanea* except one were found only in pond B.

Table 1
Structural, physical and chemical parameters of the ponds (September 2007).

Pond	Age (years)	Area (m^2)	Max. depth (m)	Land use	pH	EC ($\mu S^* cm^{-1}$)	Total hardness (°dH)
A	5.8	600	> 1.0	Intensive[a]	6.9 ± 1.01	205 ± 68.6	4
B	10.8	500	0.9	None	5.7 ± 0.81	42 ± 3.1	0–1
C	5.8	750	> 1.0	Extensive	5.9 ± 0.26	98 ± 7.9	3
D	5.8	550	0.8	Extensive	6.6 ± 0.35	144 ± 16.5	4
E	6.8	2300	0.6	Intensive	6.3 ± 0.15	171 ± 16.4	4
F	1.0	640	0.8	Extensive	5.6 ± 0.20	170 ± 12.9	4
G	6.8	1600	0.8	Extensive	6.3 ± 0.12	195 ± 44.8	5
H	1.0	3160	1.0	Intensive	6.4 ± 0.29	332 ± 48.3	8
I	6.8	2000	0.7	Extensive	6.1 ± 0.21	97 ± 15.0	2
J	6.8	2700	0.7	Extensive	6.3 ± 0.50	106 ± 7.6	3
K	1.9	1820	1.8	Intensive	7.4 ± 0.75	483 ± 27.9	12
L	10.0	2500	0.7	None	6.7 ± 0.21	228 ± 38.7	7
M	2.8	1500	0.7	Extensive	6.4 ± 0.15	134 ± 3.1	4
N	9.6	1200	1.5	Intensive	8.1 ± 0.99	301 ± 23.9	7

Data for pH and electrical conductivity (EC) are mean values and standard deviations based on three measurements.

[a] Intensive use of the area surrounding pond A began in August 2007.

Table 2
Ranking of seral stage and percentage of pond area covered by different vegetational units.

Rank of seral stage	Pond	Open water (%)	*Glyceria fluitans* community (%)	Reeds (%)	Lemnetea (%)	Submersed hydrophytes (%)	Floating leaf plants (%)
1	H	99.5	0.5	0	0	0	0
2	F	95.0	5.0	0	0	0	0
3	K	94.0	3.0	2.0	0	0	1.0
4	A	90.0	10.0	0	< 0.5	0	0
5	M	85.0	11.0	3.0	1.0	0	0
6	E	87.5	4.5	6.0	2.0	0	0
7	N	87.5	2.5	10.0	0	0	< 0.5
8	J	80.0	11.0	9.0	0	0	0
9	G	60.0	5.0	20.0	14.5	0	0.5
10	I	55.0	25.0	20.0	0	< 0.5	0
11	D	55.0	10.0	35.0	< 0.5	0	0
12	C	5.0	7.5	77.5	< 0.5	0	10.0
13	L	32.5	< 0.5	59.0	0	2.0	6.5
14	B	16.0	0	64.0	0	20.0	0

The four most abundant species accounted together for more than 40% of the total number of recorded individuals.

Thirteen species (six Heteroptera and seven Coleoptera) of the 87 species found in the study area are listed in the Red Data Book of Germany (Geiser 1997; Günther et al. 1997), and twelve species (one Heteroptera and eleven Coleoptera) in the Red Data Book of Lower Saxony (Haase 1996; Melber 1998) (Table 3). Many of the endangered species were rare in the study area; however, *Sigara semistriata, Notonecta obliqua* und *Graphoderus zonatus* were caught regularly in different ponds. *Agabus congener* occurred in some ponds, but only at the beginning of the study.

The highest number of species was found in pond L (46), followed by pond I (44). The ponds with the lowest numbers of species were N (14) and H (17). Between 30 and 40 species were present in most of the ponds. More than half of the species in the youngest ponds F and H were Heteroptera, while coleopteran species predominated in the remaining ponds. Coleopteran species accounted for more than three quarters of the species in ponds A, G and L (Fig. 2).

Individuals of the phytophagous coleopteran family Hydrophilidae mainly occurred during late seral stages with much vegetation, while Dytiscidae and Noteridae were most abundant in intermediate seral stages (Fig. 3).

The pioneer species recorded in young ponds were mainly different heteropteran species of the families Corixidae and Notonectidae (*Notonecta glauca*). Coleopteran species with the highest abundance in the early seral stages were *Hygrotus inaequalis*, *Hydroporus planus, Laccophilus minutus* and *Rhantus suturalis* (Dytiscidae), *Helophorus minutus, Anacaena lutescens* and *Helochares obscurus/H. punctatus* (Hydrophilidae).

The role of environmental factors in colonization dynamics

Low numbers of species and individuals were recorded in the youngest ponds near the beginning of succession (Fig. 3). Older ponds in advanced seral stages were generally inhabited by more individuals (except pond N). However, the numbers of species reveal no obvious trend in relation to pond age and/or seral stage (Fig. 2).

Spearman's rank correlation coefficients detected a slightly significant positive correlation ($p = 0.046$) between the number of individuals and the rank (seral stage) of a pond (Table 4). However, the number of species is not correlated with ranks of seral stages, and no significant correlation could be found between the age of a pond and the number of individuals or species (Table 4).

Ponds with an 'intensive' use of the surrounding area (E, H, K, N) had a mean number of 102 individuals and a mean number of 24 species, while the mean number of individuals in ponds of the category 'extensive' is 390 and the mean number of species is 34. The Mann-Whitney U test showed that the numbers of individuals and species are significantly lower ($p = 0.009/p = 0.044$) in ponds

Table 3
Red List categories of the species found in the study area (according to Geiser, 1997; Günther et al., 1997; Haase, 1996; and Melber, 1998).

Species	Red List category Germany	Red List category Lower Saxony (Lower Saxonian Lowland)	Total number of individuals found
Cymatia bonsdorffii	2/3		2
Cymatia rogenhoferi	R	R	1
Hesperocorixa castanea	2/3		500
Sigara semistriata	2/3		42[a]
Sigara scotti	2/3		1[a]
Notonecta obliqua	V		100
Haliplus fulvus	3	3	1
Hygrobia hermanni	3		8
Hydroporus obscurus	3		4
Agabus congener		3	21
Ilybius subaeneus		3	5
Graphoderus zonatus	3	3	27
Dytiscus circumflexus		3	1
Cybister lateralimarginalis	3	1	7
Enochrus melanocephalus		3	1
Enochrus ochropterus		3	6
Hydrochara caraboides	V	3	3
Hydrophilus piceus	2	2	3

The categories are: 1 = Critically endangered, 2 = Endangered, 3 = Vulnerable, V = Near threatened, R = Extremely rare species (or species with geographical restriction).
[a] Only males were recorded.

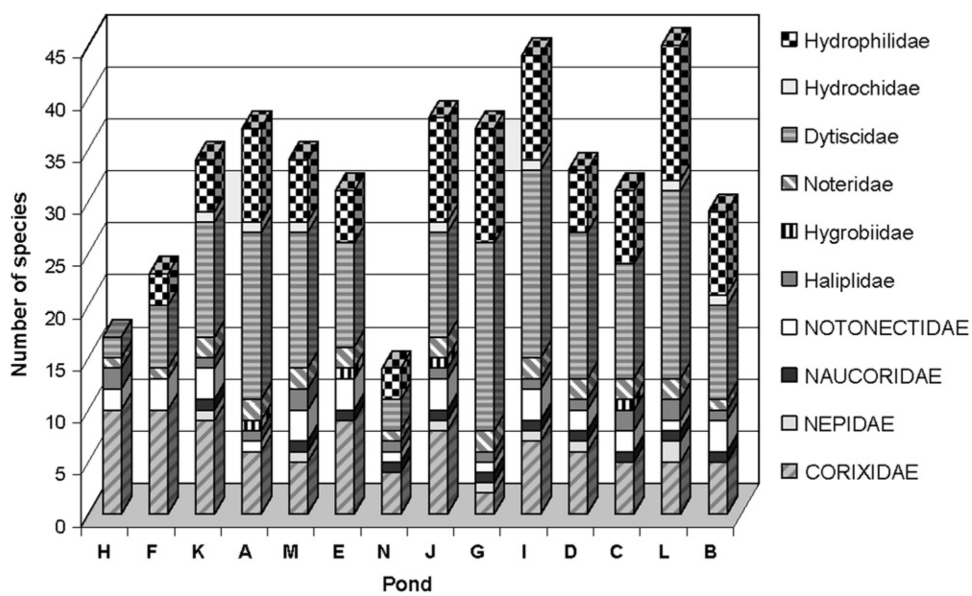

Fig. 2. Number of coleopteran and heteropteran (in capital letters) species per family recorded in each of the 14 ponds. Ponds are ranked according to seral stage (H = lowest-ranking, B = highest-ranking pond).

of the use category 'intensive' than in the category 'extensive'. Pond A was omitted from this calculation because the intensity of cattle grazing around this pond changed halfway through the study.

Canonical Correspondence Analyses

All species

The first axis of the CCA, run with the dominance values of all species, has an eigenvalue of 0.348 (Table 5; Fig. 4). This eigenvalue is relatively low, but the first four axes together explain more than 50% of the total variance in the data set. Fig. 4 shows that the environmental variables 'age', 'pond area' and 'percentage of open water' explain the distribution of species best. The vectors for 'age' and 'open water' point in opposite directions; this negative correlation reflects the decrease of open water over time. The fourth axis of the CCA (not shown in Fig. 4) is highly correlated with pH.

Aquatic beetles

The first four axes of this CCA had low eigenvalues (Fig. 6), but explain, nonetheless, more than 54% of the total variance. These values show that the variance in the data set is generally low and that differences between assemblage compositions of aquatic beetles in the fourteen ponds were comparatively small. The first axis is strongly correlated with the variable 'age', while the second axis seems to represent a chemical gradient, since it correlates with pH, conductivity and total water hardness. The third axis shows a high correlation with pond area.

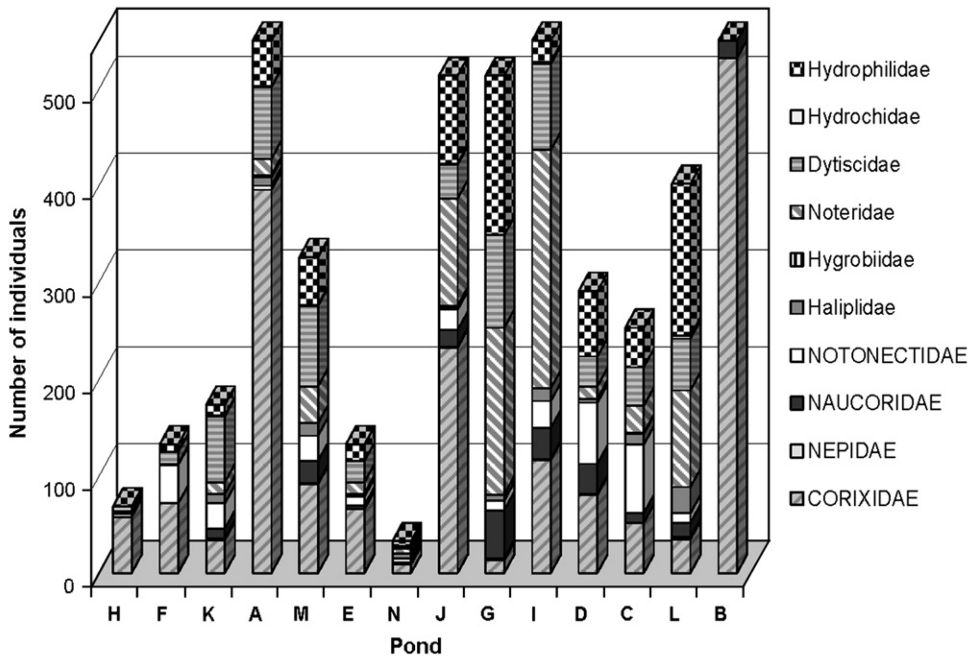

Fig. 3. Number of coleopteran and heteropteran (in capital letters) individuals per family recorded in each pond. Ponds are ranked according to seral stage (H = lowest-ranking, B = highest-ranking pond).

Table 4
Spearman's rank correlation coefficients and p values between ranks of seral stages and age of ponds, based on total numbers of recorded species and individuals (both Coleoptera and Heteroptera).

	Species ($n = 86$)		**Individuals ($n = 4941$)**	
	Correlation	p value	Correlation	p value
Rank of seral stage	0.318	0.269	0.542	0.046
Age	0.256	0.378	0.443	0.112

Water bugs

The eigenvalues of axes resulting from the CCA performed with the dominance values of the water bug species (Fig. 6) are higher than those from the CCA for all species (Fig. 4). The first four axes together account for more than 58% of the variance in the data set. These results indicate that the composition of water bug communities in ponds in the study area is more variable than that of the aquatic beetle communities. The first axis is distinctly correlated with the percentage of open water and the three categories of the nominal variable 'use'. The second and third axes do not reveal an obvious correlation with one or several of the variables, while the fourth axis is strongly correlated with pH, conductivity and total water hardness. The aquatic heteropteran species show a good separation along the axes in the ordination diagram. According to the diagram, the species *Sigara iactans* (15), *S. distincta* (13) and *S. lateralis* (17) mainly live in ponds with a high percentage of open water, while *Notonecta obliqua* (22) and *Hesperocorixa sahlbergi* (8) prefer older ponds with rich vegetation.

Discussion

Succession of aquatic beetles and bugs

The first insects that colonized the newly created pond in the study area belong to the family Corixidae. Individuals of this family could be observed in the new ponds just a few weeks after construction. The water boatmen *Sigara lateralis*, *S. iactans* and *S. falleni* can be regarded as true pioneer species as they disappear in the course of the succession of pond vegetation, probably because they are displaced by species that are better competitors. Hebauer (1988) also lists *Sigara lateralis* as a pioneer species, but he regards *Sigara falleni* as an ubiquist. Many of the other heteropteran species found in the youngest ponds are also ubiquists, for example, *Notonecta glauca* and *Corixa punctata*. These species were found in the older ponds as well, they were not restricted to a certain seral stage. The three heteropteran species of the genus *Hesperocorixa* (*H. castanea*, *H. linnaei* and *H. sahlbergi*) occurred mainly in ponds with abundant vegetation. These observations coincide with the findings of Macan (1954a, b).

Most of the species in the youngest ponds were Heteroptera, while the abundance and diversity of Coleoptera increased in course of succession. Unlike corixid and notonectid heteropterans, the carnivorous hydradephagan water beetles seem to depend on established prey populations. In addition, many aquatic coleopteran species need water plants for egg laying or as a hideout. Only some ubiquistic beetle species with low habitat requirements were found in early seral stages. The aquatic Hydrophilidae are mainly phytophagous, and therefore mainly inhabit ponds with rich vegetation. However, a small vegetation belt around the shore seems to be sufficient for the coleopterans *Helophorus minutus*, *Anacaena lutescens* and *Helochares obscurus*/*H. punctatus*, as they occurred also during early seral stages. Most of the individuals of the highly abundant coleopteran species *Noterus crassicornis* and *Helophorus minutus* were caught in ponds of intermediate seral stages, with extensive *Glyceria fluitans* communities.

One might expect that the number of aquatic coleopteran and heteropteran species generally increases with the age of a pond. For example, Nilsson and Danell (1981) observed that the number of dytiscid species (based on larval records) increased over time. However, in this study we did not find a significant correlation between the number of bug and beetle species and the age of a pond. One reason for this finding might be a rapid colonization of the newly created ponds, leading to a high number of species just

Table 5
Eigenvalues, percentages of variance explained by each axis, and Intraset correlations (correlation between constrained site scores and environmental variables) of the three Canonical Correspondence Analyses.

Variable	Axis 1			Axis 2			Axis 3			Axis 4		
	All	Beetles	Bugs	All	Beetles	Bugs	All	Beetles	Bugs	All	Beetles	Bugs
Eigenvalue	0.348	0.276	0.381	0.249	0.164	0.312	0.213	0.127	0.26	0.158	0.119	0.185
Percentage of total variance	18.524	22.073	19.641	13.222	13.142	16.109	11.323	10.149	13.424	8.416	9.506	9.561
Age	−0.670	−0.832	0.363	−0.112	−0.145	0.348	0.469	−0.157	0.469	0.277	0.160	0.224
Area	−0.073	−0.352	−0.372	0.865	−0.279	−0.668	0.090	0.754	0.417	−0.234	−0.451	−0.108
Percentage of open water	0.526	0.334	−0.604	0.591	−0.272	−0.598	−0.297	0.318	−0.250	0.080	0.252	0.117
pH	−0.075	0.048	−0.121	0.420	−0.860	−0.487	−0.366	−0.227	−0.190	0.810	0.252	0.729
Conductivity	0.313	0.452	−0.375	0.410	−0.663	−0.454	−0.385	0.033	−0.297	0.581	−0.095	0.590
Total hardness	0.193	0.399	−0.246	0.411	−0.663	−0.556	−0.483	0.000	−0.324	0.504	−0.263	0.501
Intensive	0.604	0.461	−0.729	0.458	−0.574	−0.251	−0.086	0.212	−0.198	0.517	0.508	0.429
Extensive	−0.343	−0.149	0.575	−0.235	0.645	−0.258	−0.389	−0.064	−0.191	−0.658	−0.051	−0.538
None	−0.339	−0.393	0.207	−0.292	−0.159	0.729	0.674	−0.187	0.558	0.233	−0.592	0.166

'All' indicates all species of aquatic beetles and bugs.

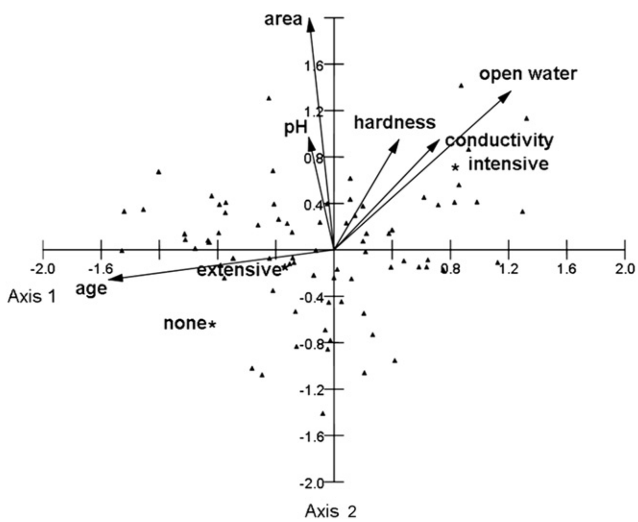

Fig. 4. Ordination diagram of the Canonical Correspondence Analysis for all species. The first two axes are shown. The categories of the nominal variable 'use' are indicated by asterisks (*). Species are represented by small triangles.

after one or two years. After the formation of a stable species community, only few new species may be able to colonize a pond, while some pioneer species disappear. As a result, the number of species increases only slightly. A study by Gee et al. (1997) supports this assumption; they also found no correlation between the number of macroinvertebrate species and the age of a water body after one year of observation.

Some studies have shown that size or density of vegetated areas are correlated with the number of macroinvertebrate species in a water body (Friday 1987; Nilsson and Söderberg 1996). Therefore, we expected to find a positive correlation between the rank of seral stage and the number of species in the ponds we investigated. However, we detected a significant positive correlation only between the seral stage and the number of individuals, but not between seral stage and the number of species. We assume that dense vegetation around the shores existed already in early seral stages, and that this vegetation belt allowed for an early colonization by many species. Another important factor, however, is probably the increased food supply during later seral stages. The amount of plants, algae, detritus and prey increased in the course of succession, and phytophagous, algophagous, detritophagous and carnivorous species benefited alike from this development. However, more data are needed to find out if this is a general trend in lentic water bodies. Since sampling with a pond net usually yields better results (higher number of individuals) in open water than in dense vegetation, the real differences in the numbers of individuals between ponds of different seral stages are probably even higher than observed.

Influence of grazing cattle

The lower abundances of both aquatic coleopterans and heteropterans in ponds located on intensively used pastures are probably correlated with the low amounts of vegetation in these ponds. Typical pond vegetation can develop only slowly in ponds on these pastures. The growth of plants is slowed down by grazing and damage by cattle hooves. In some ponds, most plants were eaten by cattle.

In pond A, the negative impact of cattle on the bug and beetle communities was most pronounced. Here, the vegetation was largely destroyed by cattle in August. The number of aquatic bug and beetle individuals sank from 141 in July to 46 in August, and in the same period, the number of species decreased from 17 to nine. In most of the other ponds, we recorded higher numbers of individuals in August than in July.

Many species depend on aquatic plants for egg laying or nutrition, while some carnivorous species need vegetation for successful hunting strategies. Apart from that, the vegetation is important because it serves as a hideout, especially in ponds with vertebrate predators (fish). For example, the low numbers of species and individuals in pond N (exposed to intensive grazing) were probably caused by high fish predation combined with a lack of hiding places.

In ponds situated on fallow land, the growth of the vegetation was not disturbed and the portion of open water decreased quickly. We studied only two ponds on fallow land, L and B, and these are also the oldest ponds. Pond L has rich vegetation with many different plant species, and it is the study site with the highest number of aquatic bug and beetle species. In contrast, the number of species in pond B is relatively low, with one predominating species (*Hesperocorixa castanea*). Pond B is the smallest of the fourteen ponds, and dries out except for a small area in months with low precipitation. This seems to explain the low number of species. Since only two ponds on fallow land were studied, it is not possible to make a general statement about this use category.

According to our results, we assume that the distribution of adjacent ponds on areas with different use intensities has a positive influence on the diversity of the aquatic coleopteran and heteropteran fauna.

The impact of environmental factors

The low eigenvalue of the first CCA axis performed with all species implies that the distribution of species cannot be explained by a distinct main gradient. This is not surprising, since only similar water bodies in a small study area were analyzed. The distribution of species is mainly correlated with the environmental variables 'age', 'pond area' and 'pH'. It is difficult to determine which variables cause the differences in species distributions because these environmental variables are correlated with each other (e.g., percentage of open water with area and age), or with other variables that were not considered. For example, pH is mainly influenced by CO_2 concentrations, and electrical conductivity is a sum of all ions.

In the ordination diagram for coleopterans, many species appear close to the centre (Fig. 5). In contrast to heteropteran species, the distribution of coleopterans exhibits only vague or ambiguous correlations with environmental variables. This distribution pattern could indicate a preference for intermediate values of the environmental variables; alternatively, it may as well be interpreted as a low correlation with these variables. It should be noted that many aquatic coleopteran species are ubiquists that have no special habitat requirements. However, those species that do have special habitat requirements are mostly rare, and should not affect the CCA results too much because we used the option *downweighting of rare species*. The factors 'age', 'pH', 'conductivity' and 'total hardness' appear to have the highest impact on the composition of aquatic beetle communities in the study area. These results coincide with the findings of other authors: Eyre et al. (1986) identified pH and conductivity as important factors for the distribution of Dytiscidae, while Fairchild et al. (2000) and Lundkvist et al. (2001) found that site age is an important factor for aquatic beetles (i.e., Dytiscidae). The expanse of water vegetation is apparently of minor importance for many species of aquatic Coleoptera.

The crucial factor for the distribution of aquatic heteropteran species seems to be the percentage of open water, and thus, a combination of age, area and use intensity of a pond. Some species preferred water bodies with a high percentage of open water and emigrated in the course of succession or were displaced by other species, while other species mainly inhabited water bodies with rich vegetation. Many species of Corixidae, in particular, showed a preference for a certain amount of vegetation, which accords with results of other studies (Macan and Macfadyen 1941; Macan 1954a; Tully et al. 1991).

Conclusions

Our study shows that constructed ponds in the Nature Reserve (NR) Meerbruchswiesen are characterized by high abundances and species diversity of aquatic beetles and bugs. A considerable number of these species are classified as endangered in the Red Data Books of Lower Saxony and Germany. The occurrence of the dytiscid beetle *Cybister lateralimarginalis* is inasmuch remarkable as this species is critically endangered in Lower Saxony (Table 3).

We found that the artificial ponds are a suitable refuge for endangered species. The ponds are colonized rapidly; the two-year-old pond K was already a home to 36 species of Coleoptera and Heteroptera. It is likely that the ponds also host many other macroinvertebrate species (e.g., Odonata or Mollusca). Based on our study, we consider the construction of small water bodies for conservation purposes in the NR Meerbruchswiesen very successful. Therefore, the construction of artificial ponds has the potential to compensate for destruction or loss of natural lentic water bodies.

We are aware of the fact that there are numerous open questions and unresolved issues that need to be addressed in future investigations of similar study objects. For example, we do not know the long-term variability of successional patterns in newly constructed ponds, or how different environmental characteristics affect ecological stability. To answer these questions it may be necessary to include additional variables such as predation and substrate composition, and disentangle the impact of correlated variables in a framework of sensitivity analysis.

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Appendix 1

Dominance values of all species in all ponds investigated (ranked from H to B). CCA numbers correspond with numbers in diagrams of Canonical Correspondence Analysis (Figs. 4, 5 and 6).

See Table A1.

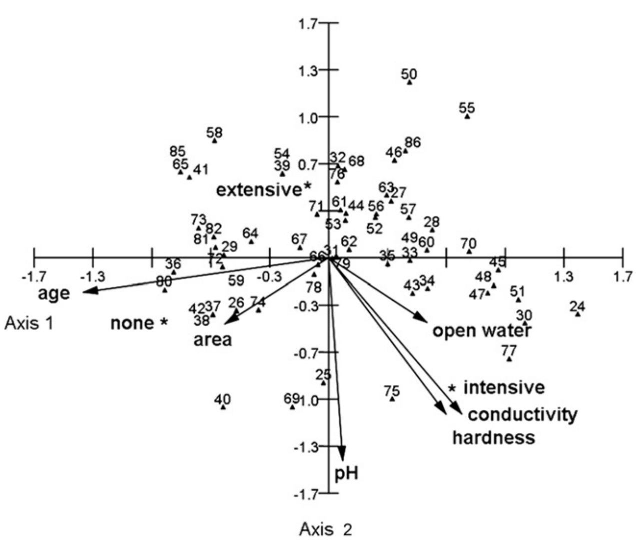

Fig. 5. Ordination diagram (first two axes) of the Canonical Correspondence Analysis of all coleopteran species. The categories of the nominal variable 'use' are indicated by asterisks (*). Species are represented by small triangles; ID numbers of species are also listed in Appendix 1 as CCA numbers.

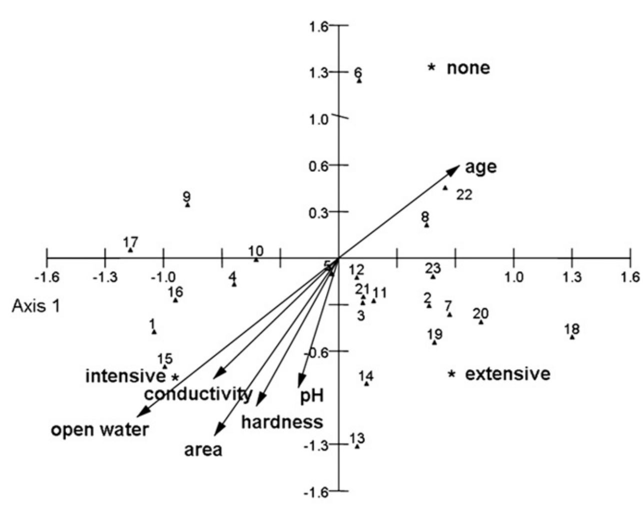

Fig. 6. Ordination diagram of the Canonical Correspondence Analysis (first two axes) of all heteropteran species. See Fig. 4 for more details.

Table A1

Species	CCA no.	H	F	K	A	M	E	N	J	G	I	D	C	L	B
Heteroptera															
Corixidae															
Callicorixa praeusta (FIEB.)	4		0.8		0.6		7.5		0.2						
Corixa punctata (ILL.)	5		15.0	4.6	17.3	26.1	26.3		6.6	2.1	6.4	9.3	11.9	2.2	3.1
Cymatia bonsdorffii (C.R.SBG.)	1	1.4		0.6											
Cymatia coleoptrata (F.)	2	1.4	1.5	6.9			0.8	3.0			1.3	10.0		0.7	0.6
Cymatia rogenhoferi (FIEB.)	3			0.6											
Hesperocorixa castanea (THOMS.)	6		0.8												70.4
Hesperocorixa linnaei (FIEB.)	7	2.9		1.7		0.3	1.5		3.5	0.4	3.0	3.8	2.0	4.2	1.1
Hesperocorixa sahlbergi (FIEB.)	8	1.4	4.5			0.3					0.1	2.7	3.6		0.3
Paracorixa concinna (FIEB.)	9				0.5										
Sigara distincta (FIEB.)	13	5.8				1.2			22.2		0.9				
Sigara falleni (FIEB.)	14		1.5	1.1			1.5	12.1	2.7						
Sigara iactans JANSS.	15	26.1					3.0	6.1	6.6						
Sigara lateralis (LEACH)	17	33.3	13.5	1.7	40.4	0.3	6.0	6.1			0.1				
Sigara limitata (FIEB.)	10	5.8	7.5		0.6				0.4			0.7	0.8		
Sigara scotti (DGL. & SC.)	16	2.9													
Sigara semistriata (FIEB.)	11	2.9	7.5	1.1	0.3		1.5		3.1		4.9	1.4	2.4	1.0	
Sigara striata (L.)	12		1.5	1.1			1.5							0.5	
Nepidae															
Nepa cinerea L.	18					0.3				0.4		0.3		0.2	
Ranatra linearis (L.)	19			1.1					0.2		0.1			0.2	
Naucoridae															
Ilyocoris cimicoides (L.)	20			5.7		7.1	3.0	6.1	3.3	9.7	4.6	10.7	4.0	3.7	2.8
Notonectidae															
Notonecta glauca L.	23	2.9	18.0	7.5	0.6	4.9	4.5	12.1	2.7	1.9	3.3	16.8	16.6	2.5	2.1
Notonecta obliqua GALL.	22	1.4	6.8	0.6		0.9	1.5		0.4		0.4	4.8	11.5		5.0
Notonecta viridis DELC.	21		5.3	6.9		2.1	0.8		1.0		0.3				0.3
Pleidae															
Plea minutissima LEACH	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]
Coleoptera															
Haliplidae															
Haliplus (*Haliplinus*) spp.	25	1.4		5.7	1.4	3.7		15.2	0.4	1.2	1.9	1.4	3.6	6.5	0.1
Haliplus fulvus (F.)	26													0.2	
Peltodytes caesus DUFTSCH.	24	1.4				0.3							0.8		
Hygrobiidae															
Hygrobia hermanni (F.)	27				0.3		2.3		0.4				0.4		
Noteridae															
Noterus clavicornis (DEG.)	28			6.3	1.7	4.9	0.8		0.6	4.9	0.9	1.4	8.7	0.7	2.0
Noterus crassicornis (MÜLL.)	29	1.4	0.8	0.6	0.9	6.7	8.3	15.2	21.0	28.6	34.4	3.1	2.4	24.1	
Dytiscidae															
Acilius canaliculatus (NICOL.)	63		0.8		0.2	1.8	0.8				0.1	1.4		1.0	
Acilius sulcatus (L.)	62					0.6			0.2						
Agabus bipustulatus (L.)	48			1.1	0.3		1.5				0.1				0.1
Agabus congener (THUNB.)	50		1.5		0.2				0.2	2.1		0.7	2.6		
Agabus nebulosus (FORST.)	49				0.8										
Coelambus confluens (F.)	33				0.2										
Coelambus impressopunctatus (SCH.)	32		0.8		0.6	0.6	0.8			1.9	0.7		0.4	1.0	
Colymbetes fuscus (L.)	58									0.4	0.3				0.1
Cybister lateralimarginalis (DEG.)	65								0.2	0.2					
Dytiscus circumflexus F.	64										0.1				
Graphoderus cinereus (L.)	61					0.6	0.8		0.4	0.2					
Graphoderus zonatus (HOPPE)	60			1.1	0.2	1.8	1.5			0.6	0.4	0.3	0.4	0.2	
Graptodytes pictus (F.)	45			0.6							0.1		1.2	0.2	
Guignotus pusillus (F.)	31			0.6	0.3	1.2				0.4	0.3	0.3		1.2	0.6
Hydaticus seminiger (DEG.)	59													0.5	

Table A1 (*continued*)

Species	**CCA no.**	**H**	**F**	**K**	**A**	**M**	**E**	**N**	**J**	**G**	**I**	**D**	**C**	**L**	**B**
Hydroporus angustatus STRM.	36								0.2	0.4	0.6			1.2	
Hydroporus erythrocephalus (L.)	41								0.2	0.4	0.7			0.2	0.4
Hydroporus gyllenhali SCHIÖDTE	38													0.5	
Hydroporus obscurus STRM.	42										0.1			0.7	
Hydroporus palustris (L.)	39				0.5			3.0		0.2	0.3		0.4	1.5	
Hydroporus planus (F.)	43	4.3		3.4	1.4	0.9	2.3	3.0	1.0	2.9	3.0	1.7	3.2		0.1
Hydroporus pubescens (GYLL.)	44					0.3	0.8			0.2	0.1			0.2	
Hydroporus striola GYLL.	40									0.2					
Hydroporus umbrosus (GYLL.)	37										0.1			0.7	
Hygrotus decoratus (GYLL.)	35			0.6		0.3								0.2	0.4
Hygrotus inaequalis (F.)	34		0.8	4.6	0.9	4.6	1.5	3.0	1.2	3.3	3.2	1.0	4.3	0.5	0.1
Hyphydrus ovatus (L.)	30			0.6	0.2	0.3						0.3			
Ilybius ater (DEG.)	52											0.3	0.4	0.2	
Ilybius fenestratus (F.)	51			1.1			1.5								
Ilybius obscurus (MARSH.)	54									0.2					
Ilybius subaeneus ER.	53											0.3			
Laccophilus minutus (L.)	47	2.9	2.3	24.1	5.3	12.0	5.3		2.9	4.5	2.0	2.1	3.2	2.0	1.0
Porhydrus lineatus (F.)	46									0.2		0.3	0.4		
Rhantus exsoletus (FORST.)	57				0.2							0.3			
Rhantus notatus (F.)	56				0.2							0.7			
Rhantus suturalis (MAC LEAY)	55		3.0	1.1	0.2	0.3			0.4	0.4	0.3	0.7	0.4	0.7	0.1
Hydrochidae															
Hydrochus carinatus GERM.	66			0.6	0.2	0.3			0.2		0.3			0.7	0.7
Hydrophilidae															
Anacaena limbata (F.)	73									0.2				0.2	
Anacaena lutescens STEPH.	74		1.5	0.6		6.7		6.1	1.8	1.6	1.7	0.7	1.6	14.2	0.4
Berosus stignaticollis (CHARP.)	86												0.8		0.3
Cymbiodyta marginella (F.)	83													1.7	
Enochrus affinis (THUNB.)	81					0.3	1.5		0.8	0.4	3.0			3.0	0.6
Enochrus coarctatus (GREDL.)	82					0.6			0.6	0.2	1.1			0.7	0.3
Enochrus melanocephalus (OLIV.)	77			0.6											
Enochrus ochropterus (MRSH.)	78				0.5				0.2		0.1			0.2	
Enochrus quadripunctatus (HERBST)	79				1.4		1.5							1.5	0.3
Enochrus testaceus (F.)	80								0.4	0.4	0.1			1.5	
Helochares obscurus (MÜLL.) / *H. punctatus* SHARP	76		2.3		2.3	4.3	0.8		1.4	7.2	2.6	2.1	5.9	4.7	1.0
Helophorus aquaticus (L.) / *H. aequalis* THOMS.	68				0.3					0.4					
Helophorus grandis ILL.	67				0.3	0.3			0.2		0.4	0.3		0.2	
Helophorus granularis (L.)	70			0.6	0.5		0.8				0.1	0.3	0.4		0.1
Helophorus minutus (F.)	71		2.3	4.0	16.9	2.8	8.3	6.1	11.9	20.0	12.9	18.9	6.3	5.0	5.4
Helophorus obscurus MULS.	69				1.4			3.0		0.2			0.4		
Hydrobius fuscipes (L.)	72				0.8				0.4	1.4	2.1	0.7	0.4	4.7	
Hydrochara caraboides (L.)	84													0.5	
Hydrophilus piceus (L.)	85								0.2	0.2					
Laccobius minutus L.	75			0.6										0.7	
Total number of individuals		69	133	174	663	326	133	33	514	514	698	291	253	402	705
Total number of species		17	23	34	37	34	31	14	38	37	44	33	31	46	29

[a] Because individuals of the heteropteran *Plea minutissima* were highly abundant in most ponds, this species was not included in quantitative analysis.

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