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INFLUENCE OF FLOODING AND VEGETATION PATTERNS ON AQUATIC BEETLE DIVERSITY IN A CONSTRUCTED WETLAND COMPLEX

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Abstract: We tested wetland-restoration management techniques to restore and increase the diversity of aquatic beetle assemblages. Three wetland treatments were examined that included: (i) unplanted surface flow (unplanted SF) wetland, (ii) surface flow (planted SF) wetlands planted with aquatic plants, and (iii) subsurface flow (SSF) wetlands. Species richness of aquatic beetles in SF wetlands was highest in spring, while the abundance was lower in the planted SF wetlands than in the unplanted SF wetland. Planted SF wetlands had a slightly higher diversity of beetles than that of the unplanted SF wetland. The planted and unplanted SF wetlands had similar attributes throughout the rest of the year. In SSF wetlands, beetles were significantly more abundant and species rich in spring than either in the planted or in the unplanted SF wetlands. Beetle diversity in SSF wetlands was higher than that in SF wetlands. During the summer, the differences between treatments disappeared. Our results suggested that: (i) vegetation planting was a successful wetland restoration technique, due to the increased habitat diversity, (ii) subsurface flooding provided fishless temporary waters with favorable breeding conditions for aquatic beetles, thus it was also a useful restoration technique, and (iii) significant seasonal differences in abundance and species richness reflected the characteristic breeding habits of aquatic beetles.

Key Words: Coleoptera, multidimensional scaling, temporal dynamics, wetland restoration

INTRODUCTION

Over the last few centuries, Hungary has lost an estimated 97% of its natural wetlands due primarily to agricultural development (Lájer 1998). Drainage of the Hanság wetlands in northwest Hungary occurred from the 18th to 20th century, although much of this area is now a National Park with special bird-refuge areas. The environmental conditions sustaining the wetlands of this area still exist (Timmermann et al. 2006) and a restoration program for wetland communities was initiated in 2001 (Margóczi et al. 2002). The success of the project shows because the restored area became a Ramsar Site (i.e., wetland of international importance designated under the Ramsar Convention) in 2006 (Ramsar Site No. 1644) (Ramsar Convention Secretariat, 2004).

Due to the relatively small number of studies (Margóczi et al. 2002, Timmermann et al. 2006, Kiss 2007, Takács et al. 2007), our knowledge about the wetlands of the Hanság is limited. Similarly, only a few studies deal with the response of aquatic macroinvertebrates to wetland management techniques, such as water level management (Flinn 2005), cattail management (Kostecke et al. 2005), or transplantation of remnant wetland soil (Brown et al. 1997). Information about the responses of macroinvertebrates to surface- vs. subsurface flooding of wetlands is lacking. The positive effects of vegetation on macroinvertebrates in natural wetlands have been described by many authors (e.g., Gregg and Rose 1985, De Szalay and Resh 2000, Strayer and Malcolm 2007). However, the effectiveness of vegetation plantings on faunal recruitment in constructed wetlands is discussed in few publications (e.g., Brady et al. 2002, Keiper and Walton 2002).

The goals of monitoring the Hanság wetland-restoration were to assess the effects of vegetation plantings and hydrology on the diversity of aquatic beetle (Coleoptera) assemblages. Among the macroinvertebrates, water beetles are often suggested as bio-indicators of habitat quality and are used for selecting areas for conservation and management of freshwater habitats (e.g., Painter 1999, Oertli et al. 2005, Sánchez-Fernández et al. 2006). Due to their

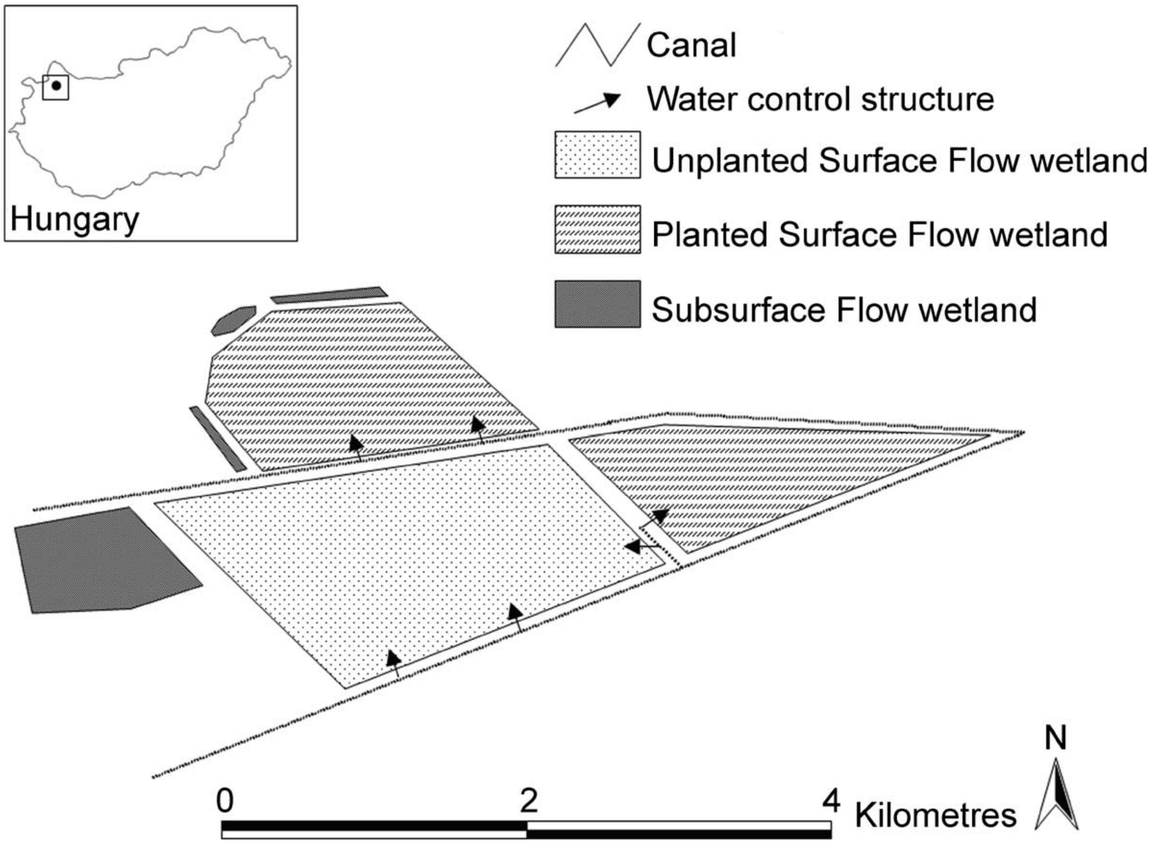

Figure 1. Geographical location of the Hanság Wetland Restoration Area and the arrangement of the constructed wetland basins.

ecological demands and physiological features (feeding, microhabitat preferences, body size, flying capacity, etc.), many species are sensitive to changes in environmental conditions (Hebauer 1986, Fairchild et al. 2000, 2003), resulting in rapid changes in their assemblages (Foster 1987, Ribera and Foster 1992). They occur in most aquatic habitats in considerable abundance compared to other macroinvertebrate taxa (Ribera and Foster 1992), and the group is taxonomically well-known in Hungary (Csabai 2003). The importance of seasonal dynamics of water beetles has been highlighted by several authors (e.g., Bosi 2001, Fairchild et al. 2003); thus we evaluated seasonal dynamics of beetle assemblages in response to restoration techniques.

In this study we tested the hypothesis that the planting of aquatic plants in surface flow (SF) wetlands had a positive effect on the abundance and diversity of aquatic beetle assemblages due to enhanced plant colonization and the association of most aquatic beetles with the presence of aquatic vegetation. We also tested the hypothesis that beetle assemblages in subsurface flow (SSF) wetlands were different from the SF wetlands. In addition, we investigated the hypothesis that seasonal differences between the wetland treatment types were also important due to the phenology of aquatic beetles.

METHODS

Study Area and Management

The wetland-restoration area was established in 2001 by flooding 460 ha in the South-Hanság, 15 km North of Csorna, Hungary (Figure 1). There were three types of treatments, following the nomenclature of The Interstate Technology and Regulatory Council Wetlands Team (ITRC 2003): (i) one unplanted surface flow (SF) wetland, (ii) two SF wetlands planted with aquatic plants, and (iii) four subsurface flow (SSF) wetlands formed from an increased water table.

In the case of SF wetlands (with and without planting) the flooding-water was transported by gravity, from two neighboring canals. The SF wetlands, covering altogether 430 ha, were made in three basins separated from each other with artificial retaining banks. The basins were then connected to the canals, and concrete water control structures were installed to control water-levels (Takács et al. 2007). The operating water depth was between 10 and 80 cm. The quality of the flood-water was not ideal for fen restoration, due to high concentration of nutrients (Margóczi et al. 2002).

Two SF basins were stocked with the following aquatic plant species (SF planted wetlands) to facilitate the restoration process: A*corus calamus* L., *Alisma plantago-aquatica* L., *Butomus umbellatus* L., *Ceratophyllum demersum* L., *C. submersum* L., *Eleocharis palustris* (L.) R. et Sch., *Hippuris vulgaris* L., *Hottonia palustris* L., *Iris pseudacorus* L., *Hydrocharis morsus-ranae* L., *Lemna gibba* L., *Menyanthes trifoliata* L., *Myriophyllum verticillatum* L., *Nuphar lutea* (L.) Sm., *Nymphaea alba* (L.), *Nymphoides peltata* (Gmel.) Kuntze, *Potamogeton crispus* L., *P. natans* L., *P. pectinatus* L., *Ranunculus lingua* L., *Sparganium emersum* Rehm., *Stratiotes aloides* L., *Typha latifolia* L., and *Utricularia vulgaris* L. The plantings were conducted in 2001 in late spring and early summer. Basins were stocked with plants by seed sowing (e.g., *A. plantago-aquatica*), transplanting rhizomes (e.g., *N. alba*, *N. lutea*, *M. trifoliata*, *I. pseudachorus*, *B. umbellatus*), and setting out seedlings (e.g., *I. sibirica*, *E. palustris*, *S. emersum*, *N. peltata*) or shoots (e.g., *C. submersum*, *C. demersum*, *P. natans*, *P. crispus*, *P. pectinatus*, *M. verticillatum*). Plantings of some species were not successful: *A. calamus*, *C. submersum*, *H. vulgaris*, *H. palustris*, *L. gibba*, *P. crispus*, *M. verticillatum*, *R. lingua*, *S. emersum*, and *U. vulgaris* disappeared from the SF planted wetland basins.

In the third basin, there was no deliberate planting, and only natural colonization of hydrophytes occurred (unplanted SF wetland). Lack of artificial planting led to considerable colonization by *Carex riparia* Curt., *Typha latifolia* L., *Phragmites australis* Cav., *Persicaria amphibia* (L.) Gray, *M. spicatum* L., *C. demersum* L., and *U. vulgaris* L (Margóczi et al. 2002).

Surface flooding increased the water table around the neighboring lowlands, spontaneously generating four subsurface flow (SSF) wetlands. These were small (altogether 30 ha), shallow temporary water bodies (water level <40 cm). Subsoil water and nutrients were filtered by the peat soil, so these water-bodies were more similar to fens than to the SF wetlands. These SSF wetlands were rich in vegetation, but lacked most vertebrate predators (birds, fishes). Some of the SSF wetlands dried out occasionally during the study, depending on the water table levels; one sampling site was dry by late summer, and another by early autumn.

Sampling

Samples were taken during the vegetation period of 2004 in early and late spring (April, May), early and late summer (July, August), and autumn (October). Preliminary samples were taken in November of 2003 and March of 2004 to determine the 19 sampling sites, which were chosen to represent all characteristic habitat-types of the area. Nine sampling sites were in planted SF wetlands, five sampling sites were in unplanted SF wetlands, and five sampling sites were in the four SSF wetlands. Each sampling site was 10–15 m in length depending on the accessibility of the water and the water depth. At every sampling site, four random sampling stations (0.5 × 0.5 m) were selected for collecting aquatic beetles.

The beetles were captured by sweeping with a D-frame sweep net (mesh size 200 µm, mouth area 830 cm^2, depth 20 cm, length of the handle 170 cm) just above the substrate and through the submerged or emergent vegetation. Four net sweeps (length 50 cm/sweep) were made at each sampling station. The captured specimens were preserved in glass-vials filled with 70% ethanol. Only adult beetles were identified in the laboratory, using keys and descriptions by Csabai (2000) and Csabai et al. (2002) and nomenclature following Csabai (2003). Abundance was estimated as the total number of adult beetles collected at each sampling site.

Data Analysis

A nested ANOVA design was used to compare abundance and species richness among sampling dates and treatments. Different treatments (unplanted SF wetlands, planted SF wetlands, and SSF wetlands) were nested in different sampling dates. Comparisons of dates and treatments were made using Tukey's honest significant differences (HSD) test (Statistica 5.0; Statistica 1995).

Diversity profiles were calculated using the Rényi one-parametric diversity index family (Tóthmérész 1998), which includes a scalable comparison of the diversity of the assemblages. Some of the frequently used diversity statistics are sensitive to rare (e.g., Shannon index of diversity) or very common species (e.g., Berger-Parker dominance index). In the case of one-parametric diversity index families, changing the scale parameter modifies the sensitivity of the diversity index (varying sensitivities to the rare or abundant species). The change in sensitivity can then be displayed graphically by plotting the calculated diversity value against the scale parameter. This curve is characteristic of the diversity profile of the assemblage. If two diversity profiles intersect each other, then these assemblages cannot be unequivocally ordered, as the one assemblage is more diverse for the rare species, while another is more diverse for the frequent species. Rényi diversity, $HR(\alpha)$ is defined as:

$$HR(\alpha)=\frac{1}{1-\alpha}\left(\log\sum_{i=1}^{S}p_i^{\alpha}\right),$$

where p_i is the relative frequency of the i-th species, S the total number of species, and α is the scale parameter ($\alpha \geq 0$, $\alpha \neq 1$). The scale parameter automatically takes its values along the x-axis. It is important to note some special capabilities of the Rényi index family. First, when the value of the scale parameter is zero ($\alpha = 0$), the value of the Rényi diversity is the logarithm of the number of species of the assemblage. In this case the method is extremely sensitive to the contribution of rare species to the diversity of the assemblage. Second, when the value of the scale parameter approaches 1, then the Rényi diversity is identical to the Shannon diversity index. In this case the *HR* value is sensitive to rare species. Third, when α=2, the Rényi diversity is related to the quadratic diversity. In this case the index starts to be more sensitive to the frequent species than to the rare ones. Finally, when the value of the scale parameter is large the Rényi diversity is related to the Berger-Parker dominance index that is determined only by the relative abundance of the most common species.

Composition of the beetle assemblages was evaluated using non-metric multidimensional scaling (NMDS). Dissimilarity in abundance data was compared using the Bray-Curtis index (Legendre and Legendre 1998). On the scatterplots provided by the NMDS ordination, the *a priori* classes (i.e. SF planted wetland, SF unplanted wetland, SSF wetland) were denoted by convex hulls. Segregation among the convex hulls indicates dissimilarities among classes. The more segregated the convex hulls are, the more different the classes are. Diversity profiles and multivariate analyses were calculated using the R statistical environment (R-Development Core Team 2005).

RESULTS

A total of 3,895 individuals of aquatic beetles belonging to 66 taxa were collected in 2004 (Table 1). *Noterus crassicornis* was the most frequent species at 39.7% dominance. Proportions of subdominant species were as follows: *N. clavicornis* (11.4%), *Helochares obscurus* (7.3%), *Anacaena limbata* (5.3%), *Hydrobius fuscipes* (4.0%), *Enochrus testaceus* (3.2%) and *Cymbiodyta marginella* (2.9%). The proportions of the remaining 59 taxa were below 2%.

Analysis of variance indicated significant differences both in abundance (among dates: $F_{4,89} = 3.5$, $P = 0.01$; among treatments: $F_{10,89} = 2.4$, $P = 0.01$), and in species richness (among dates: $F_{4,89} = 3.4$, $P = 0.012$; among treatments: $F_{10,89} = 3.3$, $P = 0.001$). Significant differences were detected in abundance for early spring vs. late summer ($P = 0.008$) and early spring vs. autumn ($P = 0.021$), and a marginal difference for early spring vs. early summer ($P = 0.069$), suggesting notable changes through time. Differences were more pronounced in late summer and autumn (Figure 2). A significant difference in species richness existed between early spring and early summer ($P = 0.003$), and marginal differences existed for late spring vs. early summer ($P = 0.081$) and early summer vs. late summer ($P = 0.094$; Figure 3). No significant difference in either abundance or species richness was found between the planted and unplanted SF wetlands. Abundance in the SSF wetlands differed marginally from that in the planted SF wetlands ($P = 0.064$; Figure 2). Species richness in SSF wetlands was higher than that found in planted ($P = 0.025$), and non-planted SF wetlands ($P = 0.016$; Figure 2).

The Rényi diversity profiles of the three habitat types (planted and unplanted SF wetlands, SSF wetlands) were different; the curves of the assemblages did not intersect (Figure 3), allowing us to rank the assemblages by their diversity. Beetle diversity of the SSF wetlands was higher than the SF wetlands, while the diversity of planted SF wetlands was only slightly higher than the unplanted SF wetland, considering both rare (low scale parameter values) and dominant species (high scale parameter values).

Using NMDS ordination, we demonstrated the differences in abundance data of the three different habitat types (Figure 4). The separation of the SSF wetlands from the SF wetlands was large in the cases of early and late spring samples (Figure 4A, B), and homogenization was recognizable in early summer and autumn samples (Figure 4C, E). The dissimilarity of late summer samples was rather conspicuous due to the drying of some SSF wetlands (Figure 4D). In general, planted and unplanted SF wetlands were not separated, as there was a high degree of overlap between the convex hulls of these habitat types over the whole sampling period (Figure 4). The ordination of pooled abundance data of all sampling dates showed only the separation of SSF wetlands from SF wetlands, whereas a direct separation of data points between planted and unplanted SF wetlands was not detectable.

DISCUSSION

Despite the relatively low surface area, the wetlands in the Hanság wetland restoration area

Table 1. Mean number of aquatic beetles (± S.E) captured in planted and unplanted surface flow wetlands, and in subsurface flow wetlands, from South-Hanság, Hungary, from early spring to autumn, 2004.

Species	Planted Surface Flow wetland	Unplanted Surface Flow wetland	Subsurface Flow wetland
Haliplidae			
Haliplus heydeni Wehncke, 1875	1.7 ± 0.6	0.0 ± 0.0	0.6 ± 0.4
Haliplus ruficollis (De Geer, 1774)	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
Peltodytes caesus (Duftschmid, 1805)	0.8 ± 0.4	0.4 ± 0.4	1.0 ± 0.8
Dytiscidae			
Acilius canaliculatus (Nicolai, 1822)	0.3 ± 0.2	0.2 ± 0.2	4.4 ± 2.2
Acilius sulcatus (Linnaeus, 1758)	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
Agabus uliginosus (Linnaeus, 1761)	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Agabus undulatus (Schrank, 1776)	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.2
Bidessus nasutus Sharp, 1887	0.2 ± 0.1	0.0 ± 0.0	0.4 ± 0.4
Bidessus unistriatus (Goeze, 1777)	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
Colymbetes fuscus (Linnaeus, 1758)	0.9 ± 0.3	0.8 ± 0.5	4.8 ± 3.0
Cybister lateralimarginalis (De Geer, 1774)	1.6 ± 0.4	1.4 ± 0.7	0.0 ± 0.0
Dytiscus dimidiatus Bergsträsser, 1778	0.0 ± 0.0	0.4 ± 0.4	0.0 ± 0.0
Dytiscus marginalis Linnaeus, 1758	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
Hydaticus seminiger (De Geer, 1774)	0.2 ± 0.1	0.0 ± 0.0	1.4 ± 1.0
Hydaticus transversalis (Pontoppidan, 1763)	0.2 ± 0.2	0.4 ± 0.4	1.6 ± 1.4
Hydroglyphus geminus (Fabricius, 1792)	4.1 ± 2.3	0.2 ± 0.2	5.0 ± 4.5
Hydroporus angustatus Sturm, 1835	0.3 ± 0.3	0.0 ± 0.0	3.2 ± 1.5
Hydroporus erythrocephalus (Linnaeus, 1758)	0.1 ± 0.1	0.0 ± 0.0	0.6 ± 0.4
Hydrovatus cuspidatus (Kunze, 1818)	0.2 ± 0.1	0.6 ± 0.4	0.0 ± 0.0
Hygrotus impressopunctatus (Schaller, 1783)	2.4 ± 2.0	0.4 ± 0.2	5.6 ± 2.1
Hygrotus inaequalis (Fabricius, 1776)	2.1 ± 1.2	4.0 ± 3.3	4.4 ± 3.1
Hygrotus parallellogrammus (Ahrens, 1812)	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Hyphydrus ovatus (Linnaeus, 1761)	0.1 ± 0.1	0.0 ± 0.0	8.8 ± 8.3
Ilybius ater (De Geer, 1774)	0.0 ± 0.0	0.4 ± 0.2	0.0 ± 0.0
Ilybius fenestratus (Fabricius, 1781)	1.7 ± 0.7	2.0 ± 1.3	0.2 ± 0.2
Ilybius quadriguttatus (Lacordaire, 1835)	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
Ilybius subaeneus (Erichson, 1837)	0.3 ± 0.2	2.2 ± 1.5	0.0 ± 0.0
Laccophilus minutus (Linnaeus, 1758)	0.8 ± 0.4	3.0 ± 1.8	1.2 ± 0.6
Laccophilus poecilus Klug, 1834	3.8 ± 0.9	5.2 ± 1.7	1.8 ± 0.9
Liopterus haemorrhoidalis (Fabricius, 1787)	0.1 ± 0.1	1.2 ± 1.0	1.0 ± 0.8
Platambus maculatus (Linnaeus, 1758)	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Rhantus bistriatus (Bergsträsser, 1778)	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
Rhantus frontalis (Marsham, 1802)	1.2 ± 1.1	1.0 ± 0.5	2.2 ± 1.2
Rhantus suturalis (MacLeay, 1825)	1.3 ± 0.5	2.0 ± 0.9	2.2 ± 1.2
Noteridae			
Noterus clavicornis (De Geer, 1774)	30.1 ± 6.2	23.0 ± 10.1	11.6 ± 10.1
Noterus crassicornis (O.F.Müller, 1776)	81.6 ± 26.2	98.0 ± 38.9	64.6 ± 26.9
Spercheidae			
Spercheus emarginatus (Schaller, 1783)	0.0 ± 0.0	0.4 ± 0.2	0.6 ± 0.2
Hydrochidae			
Hydrochus elongatus (Schaller, 1783)	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2
Hydrochus flavipennis (Küster, 1852)	0.0 ± 0.0	0.2 ± 0.2	6.8 ± 6.8
Hydrophilidae			
Anacaena limbata (Fabricius, 1792)	7.3 ± 2.0	2.2 ± 0.5	25.8 ± 8.1
Anacaena lutescens (Stephens, 1829)	0.1 ± 0.1	0.0 ± 0.0	0.6 ± 0.6
Berosus frontifoveatus Kuwert, 1888	0.1 ± 0.1	0.4 ± 0.4	1.0 ± 0.4
Berosus signaticollis (Charpentier, 1825)	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 0.5
Cercyon granarius Erichson, 1837	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Cercyon sternalis (Sharp, 1918)	0.0 ± 0.0	0.2 ± 0.2	0.6 ± 0.6
Coelostoma orbiculare (Fabricius, 1775)	1.6 ± 0.6	0.0 ± 0.0	0.6 ± 0.2
Cymbiodyta marginella (Fabricius, 1792)	1.7 ± 0.6	4.0 ± 1.9	15.8 ± 8.1
Enochrus bicolor (Fabricius, 1792)	0.0 ± 0.0	0.6 ± 0.6	5.2 ± 3.3

Table 1. Continued.

Species	Planted Surface Flow wetland	Unplanted Surface Flow wetland	Subsurface Flow wetland
Enochrus coarctatus (Gredler, 1863)	0.8 ± 0.5	1.0 ± 1.0	12.6 ± 6.0
Enochrus fuscipennis (Thomson, 1884)	0.0 ± 0.0	0.2 ± 0.2	0.6 ± 0.4
Enochrus melanocephalus (Olivier, 1792)	0.0 ± 0.0	0.6 ± 0.4	0.2 ± 0.2
Enochrus ochropterus (Marsham, 1802)	0.6 ± 0.3	0.2 ± 0.2	4.0 ± 2.3
Enochrus quadripunctatus (Herbst, 1797)	0.1 ± 0.1	0.0 ± 0.0	3.8 ± 1.7
Enochrus testaceus (Fabricius, 1801)	6.7 ± 1.3	6.4 ± 2.9	6.6 ± 1.7
Helochares lividus (Forster, 1855)	0.4 ± 0.2	0.2 ± 0.2	0.0 ± 0.0
Helochares obscurus (O.F.Müller, 1776)	16.6 ± 3.2	16.0 ± 4.3	11.0 ± 2.8
Hydrobius fuscipes (Linnaeus, 1758)	2.3 ± 1.3	3.2 ± 1.5	23.8 ± 13.8
Hydrochara caraboides (Linnaeus, 1758)	1.9 ± 0.6	1.6 ± 1.1	2.8 ± 0.9
Hydrochara flavipes (Steven, 1808)	0.4 ± 0.2	0.0 ± 0.0	1.0 ± 1.0
Hydrophilus piceus (Linnaeus, 1758)	0.6 ± 0.3	0.2 ± 0.2	0.2 ± 0.2
Laccobius bipunctatus (Fabricius, 1775)	0.0 ± 0.0	0.6 ± 0.4	1.6 ± 0.8
Laccobius minutus (Linnaeus, 1758)	0.1 ± 0.1	0.8 ± 0.5	0.4 ± 0.2
Limnoxenus niger Zschach, 1788	2.8 ± 1.0	4.8 ± 2.4	2.2 ± 1.3
Limnichidae	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Hydraenidae	0.3 ± 0.2	0.0 ± 0.0	0.2 ± 0.2
Dryopidae	0.2 ± 0.2	0.2 ± 0.2	0.6 ± 0.4

were species rich; approximately 60% of the known beetle species of the Fertő-Hanság National Park (Merkl 2002) occurred in our investigation, while the area of the wetlands represented only 2% of the park. Common species collected in this study (e.g., *Noterus crassicornis*, *N. clavicornis*, *Helochares obscurus*, *Anacaena limbata*) and acidophilous, marsh- and fen-related species (e.g., *Cymbiodyta marginella*, *Enochrus coarctatus*, *Laccophilus poecilus*, *Acilius canaliculatus*) were represented in high numbers in the water bodies of the area as well. The species characteristic of astatic, shallow waterbodies (e.g., *Hydrobius fuscipes*, *Hygrotus inaequalis*) were also found in the study area. The presence of these groups indicated that the wetland-complex provided diverse habitat-types for aquatic beetles.

Our results confirmed the findings of several authors who found that the aquatic beetle and macroinvertebrate assemblages are clearly different between larger, permanent water bodies (like SF wetlands in our case) and smaller temporary waters (like the SSF wetlands of the restored area). Mechanisms such as inundation and flooding regulation (Quinn et al. 2000) as well as physical and chemical conditions (Cuppen 1986, Ribera and Foster 1992, Collinson et al. 1995 Heino 2000) often explain differences in macroinvertebrate composition between permanent and temporary waters. Others suggest that biological interactions like shading (Lundkvist et al. 2001), predator pressure, and productivity (Collinson et al. 1995, Batzer and Wissinger 1996) are also important factors.

Macroinvertebrate assemblages of temporary waters are often characterized by rapidly developing and very active species (Wellborn et al. 1996). In these assemblages, predaceous insects can become very abundant and they are often the top predators. These top predators are large-bodied (due to the absence of size-selective fish predation) and generalists (Batzer and Wissinger 1996). Also the proportion of macroinvertebrate taxa may differ in temporary and permanent waters, e.g., temporary pools have especially diverse beetle and midge communities (Batzer and Wissinger 1996). Along the hydrological gradient from temporary to permanent waters, the relative abundance and dominance structure can vary (see Tarr et al. 2005).

The spring heterogeneity and summer homogenization of SF and SSF wetlands verified the results of several authors (Galewski 1971, Fernando and Galbraith 1973, Schaeflein 1989, Van Duinen et al. 2004) who found that in spring most of the aquatic beetles seek out astatic, quickly warming, shallow, temporary water bodies for mating and breeding. After the breeding period, which is generally early summer, the imagos return to their original habitats, to the larger, permanent water bodies (i.e., the SF wetlands). This process was also demonstrated for several beetle species using a mark and recapture study (Davy-Bowker 2002). Returning to larger water bodies might be the consequence, among others, of diminished food resources, or the drying up of the temporary pools (Davy-Bowker 2002).

To facilitate the establishment of plant species to achieve a more natural habitat, it is a common

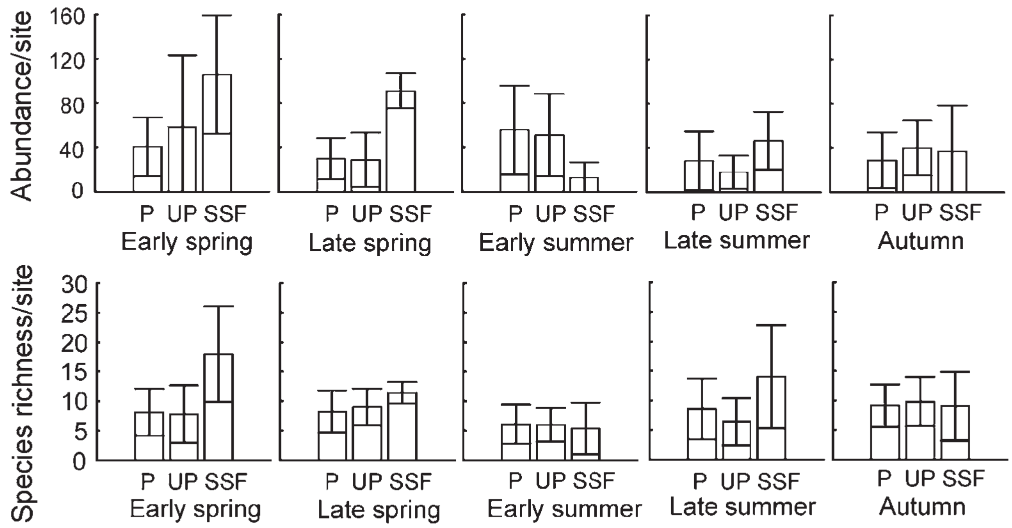

Figure 2. Mean abundance (± S.D.) and mean number of aquatic beetle species (± S.D.) collected from planted surface flow wetlands (P), unplanted surface flow wetland (UP) or subsurface flow wetland (SSF), from early spring to autumn, 2004.

procedure to inoculate desired plant species (Brady et al. 2002). Breeding habits of aquatic beetles seem to explain the differences between the planted and unplanted SF wetlands. In larger water bodies, breeding aquatic beetles prefer waters overgrown by emerged and submerged vegetation following winter hibernation. Many aquatic beetles prefer breeding in waters with dense aquatic vegetation, as it provides food and cover for larvae and imagos (Hebauer 1986, De Szalay and Resh 2000), as well as for other macroinvertebrate taxa (Nicolet et al. 2004). The experiments of Brady et al. (2002) confirm this hypothesis; they found similarities in invertebrate community structures between inoculated and natural water bodies and significant differences between inoculated and control areas without vegetation. However, the abundances of some groups, including Coleoptera, were much lower in the vegetated mesocosms of that investigation. This is in contradiction with our results. Brady et al. (2002) investigated their wetland mesocosms 82 days after inoculation, whereas we took samples three years after plantings. The timing of the experiment of Brady et al. (2002) might have precluded colonization by aerial invertebrate taxa that have fall or spring emergence. In contrast, we studied the restoration area through multiple vegetation periods. Thus, we suggest that across a larger spatial and time scale, aquatic plantings have a positive effect on aquatic beetle assemblages. Other authors also emphasize the positive correlations between aquatic vegetation and macroinvertebrate diversity (Stewart and Downing 2008) and abundance (e.g., Streever et al. 1995, Kurashov et al. 1996, Hornung and Foote 2006, Strayer and Malcolm 2007), indicating that vegetation planting is a useful wetland restoration management technique. Besides providing food and cover, aquatic vegetation increases physical heterogeneity and creates additional living spaces for macroinvertebrates (Gregg and Rose 1985). Considering their potential effect, we propose plantings of aquatic plants by similar wetland restoration projects to increase the rate of colonization and diversity of aquatic beetles.

The primary objective of the restoration of Hanság wetland area was to produce suitable habitats for vertebrates (mainly birds). It also

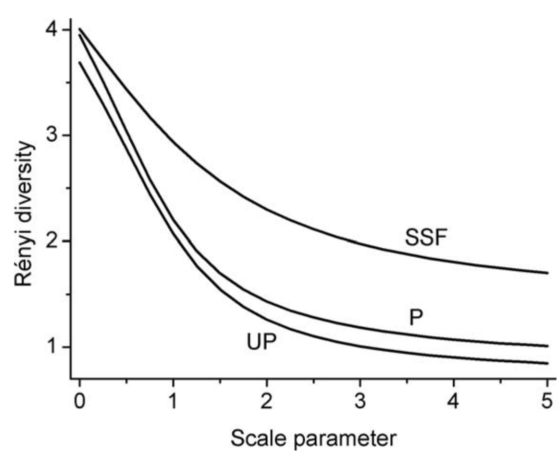

Figure 3. Diversity profiles of wetland beetle assemblages sampled from the Hanság wetland restoration area. Subsurface flow (SSF) wetlands have the most diverse assemblages followed by planted surface flow (P) and unplanted surface flow (UP) wetlands.

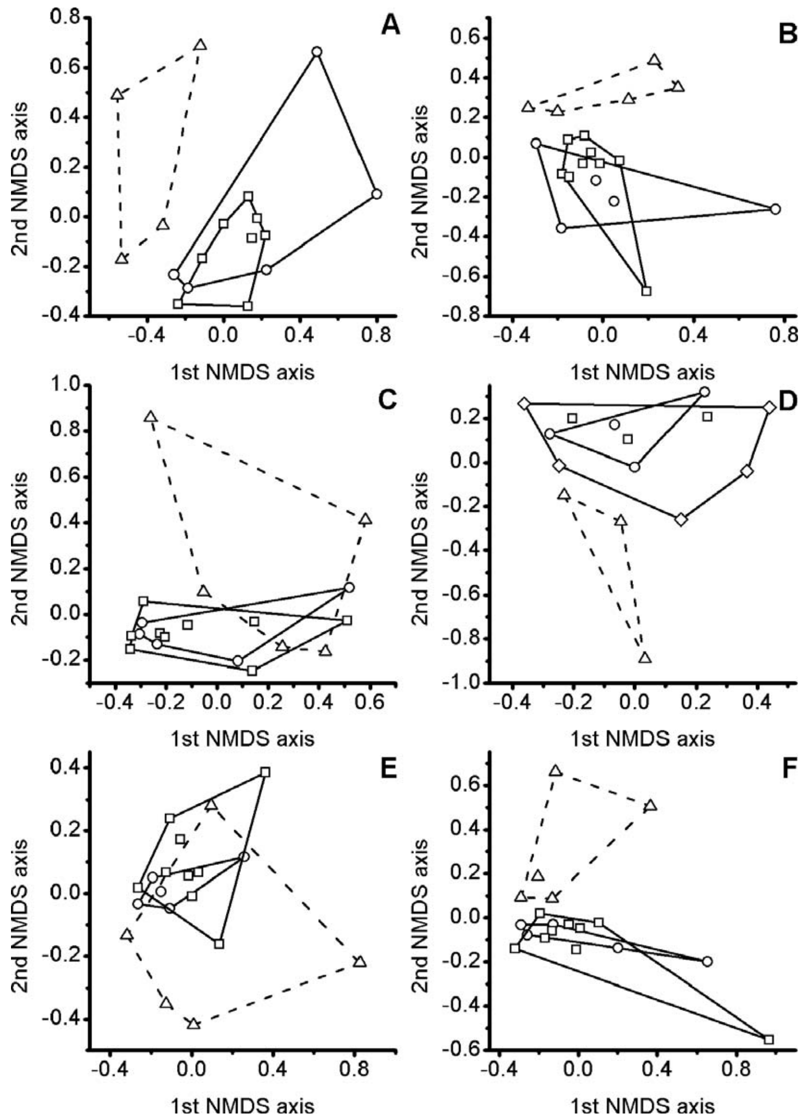

Figure 4. NMDS ordinations of aquatic beetle assemblages sampled from the Hanság wetland restoration area from early spring to autumn, 2004. A: early spring, B: late spring, C: early summer, D: late summer, E: early autumn, F: whole year. Notations: square – planted surface flow wetlands; circle – unplanted surface flow wetland; triangle – subsurface flow wetland.

increased habitat for aquatic invertebrates — a primary prey source for many waterfowl and shore birds. The SSF wetlands, formed by inundating the wetland basins, play a vital role in this process. An important consequence for conservation is that the smaller, shallow SSF wetlands play a crucial role in the preservation of biodiversity. Therefore, they have to be considered as important factors during the construction and management of these wetland complexes as several authors suggest (e.g., Wood et al. 2003, Nicolet et al. 2004). During the spring, SSF wetlands play an especially important role in maintaining aquatic beetle diversity by providing breeding sites. Therefore, management should facilitate the presence of SSF wetlands during this time period. To achieve this task, in the Hanság restoration area, a relatively high water table level is necessary in the SF wetlands, which is supported by the neighboring canals and water control structures. The presence of the different types of wetlands increases the landscape heterogeneity which is an important factor in conserving aquatic macroinvertebrate diversity (Verberk et al. 2006).

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