

# Aquatic Insects of Man-Made Habitats: Environmental Factors Determining the Distribution of Caddisflies (Trichoptera), Dragonflies (Odonata), and Beetles (Coleoptera) in Acidic Peat Pools

Edyta Buczyńska<sup>1,3,\*</sup> and Paweł Buczyński<sup>2</sup>

<sup>1</sup>University of Life Sciences in Lublin, Department of Zoology, Animal Ecology and Wildlife Management, Akademicka 13, 20–033 Lublin, Poland, <sup>2</sup>Department of Zoology, Maria Curie-Skłodowska University, Akademicka 19, 20–033 Lublin, Poland, and <sup>3</sup>Corresponding author, e-mail: [edyta.buczynska@gmail.com](mailto:edyta.buczynska@gmail.com)

Subject Editor: Philippe Usseglio-Polatera

Received 6 September 2018; Editorial decision 9 January 2019

## Abstract

As degradation of sensitive habitats like *Sphagnum* L. (Sphagnales: Sphagnaceae) peatbogs is endangering their invertebrate fauna, artificial peat pools may offer peatbog insect fauna a chance of survival. The entomofauna of seven peat pools in a peatbog and its surrounding natural marginal zone in SE Poland was investigated at the level of species, assemblages and faunistic metrics, indicating the key environmental drivers of the insect distribution and their implications for the biodiversity and potential conservation of these habitats. The species composition, specialists, and insect assemblages of the peat pools were linked with the fauna typical of both peatbogs and dystrophic pools with an open water surface. The most specialized fauna was found in the pools with the largest *Sphagnum* cover: only tyrphobionts, of all the ecological elements, significantly discriminated the fauna of peat pools and the marginal zone. *Sphagnum* cover was the key structural factor affecting the distribution of all the insects. Additionally, dragonflies were dependent on pH, beetles on temperature, and caddisflies on dissolved oxygen; however, structural factors—apart from *Sphagnum* cover—pool perimeter and emergent vegetation cover were predominant. Our results show that appropriate management of the structural factors of peat pools, especially *Sphagnum* cover, and the provision of different successional stages, can enhance biodiversity and help to maintain a valuable specialist fauna. Even along small environmental gradients and in a homogeneous area, the response of insects is highly differentiated. Dragonflies probably best represent the conservation value of the overall invertebrate fauna of *Sphagnum* bogs.

**Key words:** *Sphagnum* bog, peat pools, Odonata, Coleoptera, Trichoptera

The large-scale excavation of peat for fuel on peatbogs in Europe began in the eighteenth and nineteenth centuries (Ilnicki 2002). Such operations are still continuing on different scales depending on the method of extraction. Peat cutting is environmentally damaging, because destroying substrate, plant cover and biota, and irreversibly changing water regimes. Where heavy machinery is used to extract peat, large areas of bogs are devastated, including surrounding areas, which are important buffer zones. Such activities are particularly destructive on *Sphagnum* bogs. These are among the most seriously endangered ecosystems worldwide (Spitzer and Danks 2006, Kato et al. 2009), because these habitats, which support highly specific flora and fauna, are globally rare. As a result, there are very good reasons for listing them in the International RAMSAR Agreement, Annex 1 of the EU habitats directive and in the Natura 2000 program (EU 2008, Beadle et al. 2015).

Despite the unique character of *Sphagnum* bog habitats, knowledge on their biota is far from satisfactory and very uneven; plants being much more known than animals (Kato et al. 2009). Moreover, researchers often completely ignore *Sphagnum* bogs, claiming that the corresponding fauna is species-poor relative to other habitats and that *Sphagnum* bog conditions are hostile to many taxonomic groups (Desrochers and van Duinen 2006). The vast majority of *Sphagnum* bog species are sensitive specialists. Their populations can collapse very quickly following exposure to stochastic processes. Every bog can be considered as a habitat island (Spitzer et al. 1999, Spitzer and Danks 2006) with a low species capacity and small populations of individual species. No much research has been done on the biodiversity, assemblages, or even microhabitat preferences of particular species in peatbogs (Kato et al. 2009, Drinan et al. 2013, Beadle et al. 2015, Brown et al. 2016). At present, hardly any *Sphagnum* bog is

wholly free from human-induced disturbances (Spitzer and Danks 2006). Yet, too little is known about the interactions between invertebrate assemblages and environmental factors (natural gradients or specific anthropogenic transformations) in peatland pools, lakes, or pits (e.g., Smits et al. 2002, Baars et al. 2015). Thus, in the context of intensifying human pressure, such data are highly attractive, as they are key to the planning of restoration or conservation projects.

All the human interventions in particular environments have not solely negative consequences (Buczyński 2015, Buczyński et al. 2017), although in the case of sensitive *Sphagnum* bogs, caution is always called for. A specific example is the restoration of peatbogs in the British Isles: drainage ditches were dammed, giving rise to pools of water behind the dam which act as a habitat analogous to that of natural peat pools in the same area (Beadle et al. 2015). Similar results can be achieved by the controlled cutting of peat: this leads to the formation of tiny waterbodies – peat pools. Many studies of *Sphagnum* bogs have, thus, focused on newly created systems with the aim of evaluating the potential success of restoration using a variety of biological metrics based on the invertebrate fauna (e.g., Hannigan et al. 2011, Beadle et al. 2015, Elo et al. 2015, Brown et al. 2016). The detailed environmental relationships in old, pre-World War Two peat workings, in which succession has largely restored the original conditions, are poorly understood, especially in comparison with remnants of natural peatbogs since none of them are in the area surveyed. In south-eastern Poland, peat pools do not imitate natural nanotopes. They have rather introduced a new qualitative aspect to the landscape in so far as such pools do not exist in *Sphagnum* habitats in this part of the country. As a result, peat pools may take on considerable importance: they may become refugia for the fauna of peatbogs and their associated small waterbodies. Even in the case of very small or isolated peatbogs, they may become the sole reservoir of species for disturbed habitats. Their significance increases even more during periods of drought: relatively deep peat pools are then the most stable habitats for the peatbog fauna (Buczyński 2015). This is particularly important in the context of global climate warming (Batzer and Boix 2016). Obviously, if peat pools are playing such role, habitat conditions favorable to a particular animal group have to evolve and then require the time necessary for succession to take place.

In this paper, we analyze the occurrence of aquatic insects in diverse, former peatland habitats and in the natural habitat of a single *Sphagnum* peatbog. By choosing these particular study sites, we wished to avoid the effect of geographical differentiation of localities on the results. The selected localities lie close to one another and on one peatbog. They are subject to the same hydrographic, microclimatic, and catchment area regimes, and are colonized from the same local waters. The three orders of insects chosen for this study—Odonata, Coleoptera, Trichoptera—are regarded as good bioindicators of the state of the environment and biodiversity surrogates. Although their biology and ecology are relatively well known, their assemblages, their responses to specific environmental gradients/factors and even the microhabitat preferences of particular species (especially beetles and caddisflies) in peatbogs are poorly understood (e.g., Houghton 2004, Suriano et al. 2011, Ruhi and Batzer 2014).

The aims of this work were to 1) ascertain whether the peat pool fauna (analyzed at the levels of species, assemblages, and ecological metrics) is associated with the peatbog remnant (marginal zone) or whether a completely new faunistic system is appearing; 2) define the key physical and chemical properties of the water and the structural factors of peat pools governing the distribution of dragonflies, beetles, and caddisflies; and 3) specify the microhabitat preferences of particular species from the three orders. In the context of peatland conservation, the results will enable us to state whether artificial peat

pools are a suitable surrogate (secondary) habitat for aquatic insects and how the biodiversity of the study area is linked to the occurrence of a specialized acidophilous fauna.

## Material and Methods

### Study Area and Sampling Procedures

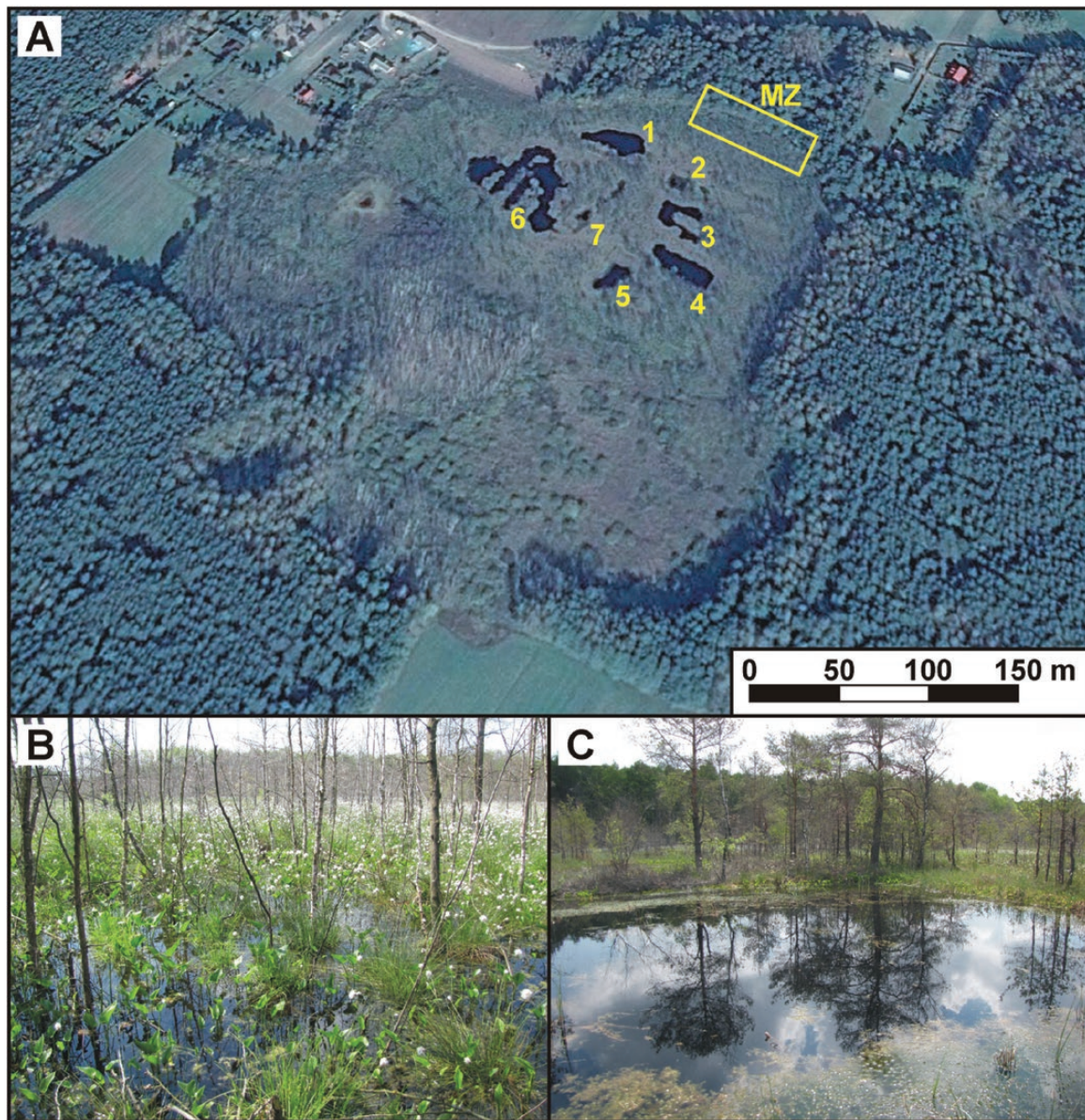
The study was carried out in Western Polesie, a geographical region in the west of the East European Plain. The actual study plot was the Krugle Bagno peatbog (area ca. 6.5 ha) (Fig. 1A) in the village of Zagłębczce (21°01'38"–21°01'59"E, 51°25'00"–51°25'12"N). This is a former continental raised bog, which by the mid-twentieth century had become almost completely exploited. The peat workings subsequently became densely overgrown with transition-bog-like *Sphagnum* mats, which now cover almost the entire area of the Krugle Bagno. Nine peat pools, from 120 to 1,690 m<sup>2</sup> in area, have persisted to the present day. These are shallow waterbodies, no more than ca. 1-m deep, filled with Dy-type sediments. The Krugle Bagno is surrounded by a 50- to 500-m wide belt of largely mixed woodland, with dominant *Pinus sylvestris* L. (Pinales: Pinaceae). Only its north-western part borders on buildings, fallow land, and single fields (Buczyński and Staniec 1998).

Insects were sampled in seven peat pools and the marginal zone (natural remnant) (Fig. 1B and C) during six expeditions in spring (April, May), summer (June, July), and autumn (August, October) of 2013. In April, however, only two pools and the marginal zone could be investigated because the other five pools were still covered with ice. Three 4-m-long transects were marked out around the perimeter of each pool. The standardized sampling method for collecting larval stages involved sweeping along the transects using a 250- $\mu$ m mesh hydrobiological sampler. Insects were sampled to a maximum depth of 0.5 m. The material was sorted in the laboratory and preserved in 70% ethanol. All the specimens were identified to species level, except for some larval stages of Coleoptera, which for lack of identification keys, could only be identified to genus level.

The following physical and chemical water parameters were measured at all sites in situ using a Hanna HI 9828 multiparameter portable meter: water temperature (°C), pH, oxygen reduction potential (mV), dissolved oxygen concentration (ppm), electrical conductivity ( $\mu$ S/cm), total dissolved solids (ppm), and salinity (PSU). The structural parameters distinguishing the pools were surface area – size (m<sup>2</sup>), pool perimeter (km) and *Sphagnum* cover (%). *Sphagnum* cover was calculated from photographs of the pools taken in different months. In addition, three parameters relating to vascular plants were calculated for each pool: i) helophyte cover (*Typha angustifolia* L., *Typha latifolia* L. (Poales: Typhaceae), and *Eleocharis palustris* (L.) Roem. & Schult. (Poales: Cyperaceae)) in the water – helo, ii) emergent vegetation cover (*Carex* spp. (Poales: Cyperaceae), *Juncus* spp. (Juncaceae), and *Eriophorum* spp. (Poales: Cyperaceae)) on the pool shore – helo\_w, and iii) the presence of trees on the shore – trees. Five classes describing these factors were distinguished, coded for further analysis as follows: 0, no plants/trees; 1, plants/trees poorly developed; 2, plants/trees moderately developed; 3, plants/trees well developed; and 4, plants/trees very well developed. The environmental features of each site are detailed in Table 1.

The character of the peatbog's immediate surroundings was analyzed in the field and on the basis of aerial photographs available from Geoportal (<http://geoportal.gov.pl/>); the area and perimeter of each peat pool were calculated using the tools available on the same website.





**Fig. 1.** Study area and study sites: (A) the peatbog and its surroundings (MZ, marginal zone of the peatbog), 1–7: peat pools (Google Earth); (B) marginal zone of the peatbog, (C) peat pool No. 2 (photographs: Paweł Buczyński and Edyta Buczyńska).

## Data Analysis

### Faunistic Metrics

The following faunistic metrics were used: species richness ( $S$ ), abundance ( $N$ ), the Shannon–Wiener diversity index ( $H$ ), Buzas–Gibson’s evenness ( $E$ ), and the Simpson dominance index ( $D$ ). Calculation of the dominance structure for every peat pool and the marginal zone was based on the division into classes proposed by Biesiadka (1980).

The categories of specialists/nonspecialists are commonly used to describe peatbog fauna (Spitzer and Danks 2006). To assess whether the fauna was specialized and typical of the habitat or was composed of nonspecialists (eurytopes), coefficients of naturalness ( $W_n$ s, quantitative formula;  $W_{ni}$ , qualitative formula) were calculated for each study site by substituting the stenotopy index ( $W_{ze}$ ) (taking values from 0 to 16 for each species) into Fischer’s (1996) formula, modified by Czachorowski and Buczyński (1999). Values from 16 to 4 defined specialists: tyrphobionts ( $W_{ze} = 16$ ), species occurring exclusively in peat bogs, and tyrphophiles ( $W_{ze} = 8$  or 4), species typical of peat bogs, but not strictly confined to such habitats. The

lowest values ( $W_{ze} = 2$  or 1) defined non-specialists—eurytopes and random species. The  $W_{ze}$  values were adopted after Czachorowski and Buczyński (1999) and Klausnitzer (1996) or, if data for a particular species were unavailable, defined individually by the authors. The Mann–Whitney and Kruskal–Wallis tests (in combination with Dunn’s post hoc test) were used to detect significant differences in faunistic indices between the sites (habitats) on the sample matrix. The calculations were performed in STATISTICA 11.

### Similarity Analysis: Species and Habitats

Two-way indicator species analysis (TWINSPAN) was used to create the cladogram distinguishing the insect assemblages and to identify the indicator species associated with the acidic waters studied. TWINSPAN was performed in WinTWINSPAN 2.3 (Hill and Šmilauer 2005); species with less than three occurrences (given as frequency) were excluded from the matrix for this analysis.

Hierarchical agglomerative clustering with the Unweighted Pair Group Method with Arithmetic Mean was applied to define

**Table 1.** The environmental variables (mean value  $\pm$  SD and range of values) at eight study sites situated in the peatbog

| Variable                         | MZ                                 | Peat pools                           |                                      |                                      |                                      |                                      |                                      |   |
|----------------------------------|------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|---|
|                                  |                                    | 1                                    | 2                                    | 3                                    | 4                                    | 5                                    | 6                                    | 7 |
| <b>Temp (°C)</b>                 | 15.2 $\pm$ 6.9<br>4.3 to 21.1      | 17.1 $\pm$ 3.8<br>11.0 to 23.3       | 14.8 $\pm$ 4.4<br>9.4 to 19.0        | 16.5 $\pm$ 4.2<br>10.2 to 21.2       | 17.7 $\pm$ 4.8<br>9.9 to 21.7        | 16.7 $\pm$ 5.6<br>9.7 to 23.1        | 16.1 $\pm$ 7.5<br>4.4 to 26.2        |   |
| <b>pH</b>                        | 4.68 $\pm$ 0.77<br>3.96 to 5.91    | 4.45 $\pm$ 0.23<br>4.11 to 4.70      | 4.36 $\pm$ 0.19<br>4.10 to 4.54      | 4.43 $\pm$ 0.21<br>4.17 to 4.70      | 4.87 $\pm$ 0.32<br>4.56 to 5.35      | 4.62 $\pm$ 0.44<br>4.04 to 5.15      | 4.48 $\pm$ 0.18<br>4.28 to 4.81      |   |
| <b>ORP (mV)</b>                  | -98.3 $\pm$ 57.3<br>-139.1 to 15.4 | -126.5 $\pm$ 33.3<br>-170.7 to -92.8 | -148.3 $\pm$ 49.1<br>-205.9 to -88.4 | -109.6 $\pm$ 29.1<br>-142.3 to -80.1 | -133.0 $\pm$ 41.6<br>-195.9 to -92.6 | -117.6 $\pm$ 40.5<br>-179.2 to -76.1 | -106.6 $\pm$ 28.7<br>-137.2 to -74.0 |   |
| <b>DO (mg·d/m<sup>3</sup>)*</b>  | 2.58 $\pm$ 2.14<br>0.00 to 4.87    | 0.58 $\pm$ 0.22<br>0.32 to 0.82      | 0.15 $\pm$ 0.24<br>0.00 to 0.55      | 0.54 $\pm$ 0.85<br>0.00 to 2.01      | 1.53 $\pm$ 2.27<br>0.00 to 5.56      | 1.89 $\pm$ 2.24<br>0.00 to 5.32      | 0.99 $\pm$ 0.48<br>0.47 to 1.81      |   |
| <b>EC (<math>\mu</math>S/cm)</b> | 270 $\pm$ 535<br>20 to 1362        | 32 $\pm$ 27<br>2 to 64               | 31 $\pm$ 8<br>18 to 38               | 31 $\pm$ 14<br>16 to 45              | 29 $\pm$ 20<br>1 to 54               | 37 $\pm$ 23<br>17 to 74              | 40 $\pm$ 21<br>21 to 67              |   |
| <b>TDS (mg·d/m<sup>3</sup>)</b>  | 135 $\pm$ 268<br>10 to 681         | 16 $\pm$ 14<br>1 to 32               | 16 $\pm$ 4<br>9 to 19                | 15 $\pm$ 7<br>8 to 23                | 15 $\pm$ 10<br>0 to 27               | 19 $\pm$ 12<br>8 to 37               | 20 $\pm$ 11<br>10 to 34              |   |
| <b>SAL (PSU)</b>                 | 0.13 $\pm$ 0.27<br>0.01 to 0.68    | 0.01 $\pm$ 0.01<br>0.00 to 0.03      | 0.01 $\pm$ 0.01<br>0.01 to 0.02      | 0.01 $\pm$ 0.01<br>0.00 to 0.02      | 0.01 $\pm$ 0.01<br>0.00 to 0.02      | 0.01 $\pm$ 0.01<br>0.00 to 0.03      | 0.01 $\pm$ 0.01<br>0.00 to 0.02      |   |
| <b>SC (%)</b>                    | -<br>10                            | 66 $\pm$ 17<br>40 to 80              | 3.4 $\pm$ 2.3<br>0 to 5              | 29.6 $\pm$ 3.1<br>5 to 30            | 30 $\pm$ 0<br>30                     | 30 $\pm$ 0<br>30                     | 100 $\pm$ 0<br>100                   |   |
| <b>Size (m<sup>2</sup>)</b>      | -<br>520                           | 120<br>0 to 3                        | 360<br>0 to 3                        | 480<br>0 to 1                        | 220<br>0 to 1                        | 1690<br>0 to 2                       | 120<br>0 to 4                        |   |
| <b>PP (km)</b>                   | -<br>0.122                         | 0.049<br>1.67 $\pm$ 0.82             | 0.189<br>1.67 $\pm$ 0.82             | 0.120<br>1.67 $\pm$ 0.82             | 0.070<br>2.50 $\pm$ 1.22             | 0.430<br>1.50 $\pm$ 0.84             | 0.450<br>0.83 $\pm$ 0.41             |   |
| <b>trees*</b>                    | -<br>2                             | 3<br>0 to 1                          | 2<br>0 to 2                          | 3<br>0 to 2                          | 2<br>0 to 3                          | 2<br>0 to 2                          | 4<br>0 to 1                          |   |
| <b>Helo</b>                      | -<br>0.67 $\pm$ 0.51               | 1.67 $\pm$ 1.03<br>0 to 1            | 0.50 $\pm$ 0.55<br>0 to 3            | 0.67 $\pm$ 0.52<br>0 to 1            | 0.83 $\pm$ 0.41<br>0 to 1            | 1.67 $\pm$ 0.82<br>0 to 2            | 3.00 $\pm$ 1.67<br>0 to 4            |   |
| <b>helo_w</b>                    | -<br>0.83 $\pm$ 0.41               | 1.67 $\pm$ 0.82<br>0 to 1            | 1.67 $\pm$ 0.82<br>0 to 2            | 1.67 $\pm$ 0.82<br>0 to 2            | 2.50 $\pm$ 1.22<br>0 to 3            | 1.50 $\pm$ 0.84<br>0 to 2            | 0.83 $\pm$ 0.41<br>0 to 1            |   |

MZ, marginal zone of the peatbog.

Variables are given as codes (see Study area and sampling procedures) with units. Variables with statistically significant differences are denoted by an asterisk (\*).



the faunistic similarities between the seven peat pools and the marginal zone. A dendrogram based on the Bray–Curtis index was constructed in the PAST 3.18 program (Hammer et al. 2001).

#### Insect Assemblages and Species Versus Environmental Factors

Variation partitioning analysis based on canonical ordination (CCA) was used to display the effects of physical and chemical as well as structural environmental variables in the species composition of each insect order. To construct the matrix only data relating to the species of which there were >1 individual in a sample were used. Stepwise selection with 499 test permutations was employed to filter the significant ( $P < 0.05$ ) parameters primarily responsible for species variation. This showed whether and to what extent species variability within the particular insect assemblages was governed by physical and chemical factors, structural factors, and their potential shared effect (Šmilauer and Lepš 2014). The statistical significance of each fraction (primary factors, secondary factors, and their sum including shared effects) was also evaluated. On this basis, CCA biplots were generated for each group, with significant factors only being taken into account.

Generalized linear models (GLMs) were applied to identify the optimal conditions for the most abundant insect species. Based on the environmental variables that proved to be the most significant for a given insect order, these predictive models indicated the relevant tolerances and optima that might be useful for distinguishing the ecological requirements of a species. In accordance with the recommendations for this analysis (Šmilauer and Lepš 2014), we used a Poisson distribution to construct the models.

Variation partitioning analyses (CCAs) and GLMs were calculated and plotted using CANOCO 5 statistical software (ter Braak and Šmilauer 2012).

## Results

### The Insect Fauna of Peat Pools: Species Richness and Diversity Indices

In total, 1,837 insects from 76 species were caught. Beetles were the species-richest assemblage (51), followed by dragonflies (16), and caddisflies (9) (Table 2). The marginal zone supported 56% of all the species recorded, the individual pools 25–44% and the pools combined 92.5%. About 9% of the species were exclusive to the marginal zone, from 1 to 6% were found in the individual pools, but as many as 44% in the peat pools combined. The dominance structures were the most evenly balanced among the beetles, but distinctly less so among the dragonflies and caddisflies, though at roughly the same level. The largest numbers of taxa—predominantly dragonflies and beetles—were recorded in the marginal zone. The diversity index was also the highest there. Taxa richness was the highest in pools 1 and 4, and the lowest in pool 7. Peat pools 1 and 7 exhibited the greatest faunal diversity; the diversity indices for the other pools were much the same. The dominance in peat pools 1–6 was very similar; this value was very low only in pool 7 and in the marginal zone. The evenness index was the highest in the most densely vegetated peat pool 7, identical in the marginal zone and pool 5, and slightly lower in the other pools (Table 2).

### Cluster Analysis: Habitats, Insect Assemblages, and Indicators Within Divisions

The faunistic similarities between several peat pools and the marginal zone were relatively high (Bray–Curtis index > 0.5). The highest similarity (>60%) was between pools 4 and 6, then between pools 3 and 1, and also between pool 2 and the marginal zone (Fig. 2). The

first four of these pools formed a separate cluster, connected with the densely vegetated pool 2 and the marginal zone. The very densely vegetated pool 7 and pool 5 were faunistically the most distinct. The analysis of qualitative faunistic similarities (Jaccard index) between the fauna of all the peat pools and the peatbog remnant showed that 45% of the taxa were common to the whole area, whereby this percentage consisted only of dragonflies and beetles, as caddisflies were absent from the marginal zone. The Jaccard index was higher for dragonflies (up to 62.5%) and lower for beetles (41.6%).

TWINSpan yielded three assemblages of species (Fig. 3): assemblage A1 was dominated by beetles, A2 contained similar numbers of odonates and coleopterans, whereas assemblage B comprised all three insect orders. At higher levels (divisions), these assemblages consisted of species with both steno- and eurytopic habitat requirements or life strategies. In lower divisions, species pairs or groups with more strictly defined requirements were formed. The indicator species of the first division included members of the three orders, whereas divisions 2–6 consisted exclusively of dragonflies and beetles, the former being prevalent (Fig. 3). For example, *Hygrotus decoratus* defined the habitat type opposite to that of *Graphoderus cinereus* (division 2), whereas there were two indicator dragonflies for division 4: the tyrphophilous *Leucorrhinia pectoralis* versus the eurytopic *Libellula quadrimaculata*. In division 5, the opposing species were *Leucorrhinia pectoralis* and *Lestes virens*. The most important indicator species in the lowest divisions of the study area was *Leucorrhinia pectoralis*, which was replaced by *Leucorrhinia rubicunda* and key representatives of the other two orders in the higher divisions.

### Specialization of the Insect Fauna: Naturalness Indices and Distribution of Specialists

The fauna most typical of *Sphagnum* peatbogs, as demonstrated by the overall value of the naturalness indices, inhabited peat pools 2 and 7 with the largest *Sphagnum* mats (Table 3). The deciding factors in this respect were the dragonflies in pool 2 and the beetles in pool 7; pool 5 also had a highly specific odonate fauna ( $W_{ns}$  and  $W_{ni} > 6$ ). The least habitat-specific fauna colonised pools 1, 4, and 6. The most highly specialized caddisfly species were present in pool 6, and with regard to the species composition, in pools 3 and 4. In general, our results show that the best development conditions for each insect order prevailed in different pools. Sometimes, these conditions were at opposite extremes: for example, pool 5 was a key area for odonates but was unattractive to trichopterans, whereas pool 7 was important to beetles but unfavourable or nonoptimal for the other orders. The values of both indices for the marginal zone were only moderately high, and lower than for some of the pools, although in the case of the peatbog remnant, one could have expected higher values (Table 3). The differences between  $W_{ns}$  and  $W_{ni}$  at the sample level between the sites studied were statistically significant (Kruskal–Wallis test for  $W_{ns}$ :  $P = 0.024$ , for  $W_{ni}$ :  $P = 0.018$ ). In turn, the differences between the marginal zone and all the peat pools combined were not statistically significant (Mann–Whitney test for  $W_{ns}$ :  $P = 0.929$ , for  $W_{ni}$ :  $P = 0.578$ ).

Comparison of the proportions of ecological groups—in terms of species richness—in individual peatbogs showed a very similar distribution pattern over the study area (Fig. 4A). The proportions of ecological groups in the three orders of insects (Fig. 4B) showed a total absence of tyrphobionts and a large percentage of tyrphophiles among trichopterans, a high proportion of tyrphophilous odonates (82% of the total dragonfly fauna) and similar proportions of tyrphophiles and nonspecialists in terms of

**Table 2.** List of the insect species collected. Wze, stenotopy index; 1–7, peat pools; MZ, marginal zone of the peatbog. %N, percentage of a species in the total number of individuals. Eudominants (>10%) are given in bold.

| Taxon                                       | Code    | Wze | Dominance at study sites [%] |      |      |      |      |      |      | %N   |      |
|---|---------|-----|------------------------------|------|------|------|------|------|------|------|------|
|   |         |     | Peat pools                   |      |      |      |      |      | MZ   |      |      |
|   |         |     | 1                            | 2    | 3    | 4    | 5    | 6    |      |      | 7    |
| ODONATA                                     |         |     |                              |      |      |      |      |      |      |      |      |
| Lestidae                                    |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Lestes dryas</i> Kirby                   | Les_dry | 2   | –                            | –    | –    | –    | –    | –    | –    | 0.6  | 0.1  |
| <i>Lestes sponsa</i> (Hansem.)              | Les_spo | 2   | 1.5                          | –    | 0.7  | 0.9  | –    | 0.7  | –    | 10.3 | 2.2  |
| <i>Lestes virens</i> (Charp.)               | Les_vri | 4   | 57.6                         | 17.4 | 41.6 | 20.2 | 11.8 | 27.7 | –    | 17.4 | 28.0 |
| Coenagrionidae                              |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Coenagrion bastulatum</i> (Charp.)       | Coe_has | 4   | 20.5                         | –    | 8.8  | 5.2  | 8.8  | 2.0  | –    | 0.6  | 5.8  |
| <i>Coenagrion puella</i> (L.)               | Coe_pue | 1   | 11.4                         | 0.7  | 13.9 | 15.9 | –    | 17.6 | –    | 0.6  | 10.0 |
| <i>Coenagrion pulchellum</i> (Vander L.)    | Coe_pul | 2   | 0.8                          | –    | –    | –    | –    | –    | –    | –    | 0.1  |
| <i>Nehalennia speciosa</i> (Charp.)         | Neh_spe | 8   | –                            | 4.7  | 0.7  | –    | 44.1 | 1.4  | –    | 7.1  | 3.6  |
| Aeshnidae                                   |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Aeshna cyanea</i> (O.F. Müll.)           | Aes_cya | 1   | –                            | –    | –    | 0.4  | –    | –    | –    | –    | 0.1  |
| <i>Aeshna subarctica</i> Walk.              | Aes_sub | 16  | –                            | 0.7  | –    | –    | –    | –    | –    | –    | 0.1  |
| Corduliidae                                 |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Cordulia aenea</i> (L.)                  | Cor_aen | 2   | –                            | –    | –    | 3.0  | –    | –    | –    | –    | 0.7  |
| Libellulidae                                |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Leucorrhinia dubia</i> (Vander L.)       | Leu_dub | 16  | 1.5                          | 5.4  | 2.2  | 1.7  | –    | 2.7  | –    | 2.6  | 2.5  |
| <i>Leucorrhinia pectoralis</i> (Charp.)     | Leu_pec | 4   | 5.3                          | 34.9 | 28.5 | 44.2 | 26.5 | 42.6 | –    | 38.1 | 33.5 |
| <i>Leucorrhinia rubicunda</i> (L.)          | Leu_rub | 8   | 1.5                          | 33.6 | 2.2  | 7.7  | 5.9  | 3.4  | 25.0 | 13.5 | 10.3 |
| <i>Libellula quadrimaculata</i> L.          | Lib_qua | 2   | –                            | 0.7  | 1.5  | 0.4  | –    | 2.0  | 75.0 | 7.1  | 2.1  |
| Libellulidae: Sympetrinae juv.              | –       | –   | –                            | 1.3  | –    | –    | –    | –    | –    | –    | 0.2  |
| <i>Sympetrum danae</i> (Sulz.)              | Sym_dan | 8   | –                            | 0.7  | –    | 0.4  | 2.9  | –    | –    | 0.6  | 0.4  |
| <i>Sympetrum vulgatum</i> (L.)              | Sym_vul | 1   | –                            | –    | –    | –    | –    | –    | –    | 1.3  | 0.2  |
| N=  | –       | –   | 132                          | 149  | 137  | 233  | 34   | 148  | 4    | 155  | 992  |
| COLEOPTERA                                  |         |     |                              |      |      |      |      |      |      |      |      |
| Gyrinidae                                   |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Gyrinus</i> sp.                          | –       | –   | –                            | –    | 1.4  | –    | –    | –    | –    | –    | 0.1  |
| Halipidae                                   |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Haliplus ruficollis</i> (De Geer)        | Hal_ruf | 2   | –                            | –    | –    | –    | 1.1  | –    | –    | –    | 0.1  |
| <i>Haliplus wehncke</i> Gerh.               | Hal_weh | 4   | –                            | –    | –    | 1.1  | –    | –    | –    | –    | 0.1  |
| Noteridae                                   |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Noterus clavicornis</i> (De Geer)        | Not_cla | 2   | 1.0                          | –    | –    | –    | –    | –    | –    | >0.1 | 0.1  |
| <i>Noterus crassicornis</i> (O.F. Müll.)    | Not_cra | 4   | 19.2                         | 19.0 | 32.4 | 22.1 | 18.3 | 31.1 | 15.8 | 12.4 | 19.6 |
| Dytiscidae                                  |         |     |                              |      |      |      |      |      |      |      |      |
| <i>Acilius canaliculatus</i> (Nic.)         | Aci_can | 2   | 6.1                          | –    | –    | 1.1  | –    | –    | –    | –    | 1.0  |
| <i>Acilius sulcatus</i> (L.)                | Aci_sul | 4   | 2.0                          | –    | 5.4  | 4.2  | –    | –    | –    | –    | 1.4  |
| <i>Agabus</i> sp.                           | –       | –   | 4.0                          | –    | 4.1  | –    | –    | –    | –    | 2.8  | 1.7  |
| <i>Bidessus unistriatus</i> (Goeze)         | Bid_uni | 8   | –                            | 2.4  | 1.4  | –    | 2.2  | –    | 1.8  | –    | 0.8  |
| <i>Cybister lateralmarginalis</i> (De Geer) | Cyb_lat | 2   | 6.1                          | –    | –    | 2.1  | –    | 2.2  | –    | –    | 1.2  |
| <i>Dytiscus circumflexus</i> Fabr.          | Dyt_cir | 2   | 1.0                          | –    | –    | –    | –    | –    | –    | –    | 0.1  |
| <i>Dytiscus dimidiatus</i> Bergstr.         | Dyt_dim | 4   | 2.0                          | –    | –    | –    | –    | 6.7  | –    | –    | 0.7  |
| <i>Dytiscus marginalis</i> L.               | Dyt_mar | 2   | 6.1                          | 1.2  | 5.4  | 9.5  | –    | –    | –    | 1.7  | 3.2  |
| <i>Graphoderus austriacus</i> (Sturm)       | Gra_aus | 2   | 2.0                          | –    | 1.4  | 2.1  | 4.3  | 2.2  | –    | 12.4 | 4.4  |
| <i>Graphoderus cinereus</i> (L.)            | Gra_cin | 2   | 18.2                         | –    | 5.4  | 11.6 | 4.3  | 26.7 | –    | 7.3  | 8.6  |
| <i>Hydaticus seminiger</i> (De Geer)        | Hyd_sem | 2   | –                            | 2.4  | –    | –    | –    | –    | –    | –    | 0.3  |
| <i>Hydaticus stagnalis</i> (Fabr.)          | Hyd_sta | 2   | –                            | –    | –    | –    | –    | –    | –    | 0.6  | 0.1  |
| <i>Hydaticus transversalis</i> (Pontopp.)   | Hyd_tra | 2   | –                            | –    | –    | –    | –    | –    | –    | 1.7  | 0.4  |
| <i>Hydroglyphus geminus</i> (Fabr.)         | Hyd_gem | 1   | 1.0                          | –    | –    | 1.1  | –    | –    | 3.5  | –    | 0.6  |
| <i>Hydroporus angustatus</i> Sturm          | Hyd_ang | 8   | –                            | –    | 1.4  | –    | 1.1  | –    | 3.5  | 2.8  | 1.2  |
| <i>Hydroporus erythrocephalus</i> (L.)      | Hyd_ery | 8   | 2.0                          | 1.2  | 1.4  | –    | –    | –    | –    | 2.3  | 1.1  |
| <i>Hydroporus incognitus</i> Sharp          | Hyd_inc | 8   | –                            | –    | –    | –    | –    | –    | 3.5  | 2.3  | 0.8  |
| <i>Hydroporus obscurus</i> Sturm            | Hyd_obs | 16  | –                            | 1.2  | 1.4  | –    | –    | –    | 7.0  | 1.1  | 1.1  |
| <i>Hydroporus scalesianus</i> Steph.        | Hyd_sca | 16  | –                            | –    | –    | –    | –    | –    | 1.8  | –    | 0.1  |
| <i>Hydroporus striola</i> (Gyll.)           | Hyd_str | 8   | –                            | –    | –    | –    | –    | –    | –    | 10.7 | 2.6  |
| <i>Hydroporus tristis</i> (Payk.)           | Hyd_tri | 8   | –                            | –    | –    | –    | 1.1  | –    | –    | –    | 0.1  |
| <i>Hydroporus</i> sp.                       | –       | –   | –                            | –    | –    | –    | –    | –    | –    | 4.0  | 1.0  |
| <i>Hygrotus decoratus</i> (Gyll.)           | Hyg_dec | 8   | 3.0                          | 7.1  | 5.4  | 1.1  | –    | –    | 15.8 | 1.7  | 3.6  |
| <i>Hygrotus impressopunctatus</i> (Schall.) | Hyg_imp | 2   | –                            | 4.8  | –    | 1.1  | 2.2  | –    | –    | 0.6  | 1.1  |
| <i>Hygrotus inaequalis</i> (Fabr.)          | Hyg_in  | 2   | 4.0                          | 10.7 | –    | 9.5  | 6.5  | 6.7  | 3.5  | 1.7  | 5.0  |
| <i>Hygrotus versicolor</i> (Schall.)        | Hyg_ver | 2   | 1.0                          | –    | 1.4  | –    | –    | –    | –    | 0.6  | 0.4  |

Table 2. Continued

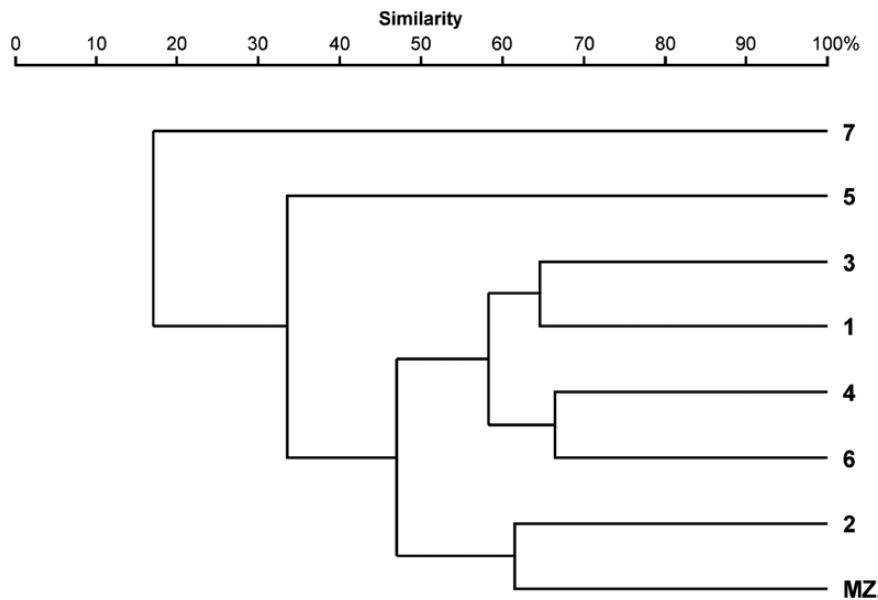
| Taxon                                    | Code    | Wze | Dominance at study sites [%] |             |             |             |              |             |             | %N   |      |
|--|---------|-----|------------------------------|-------------|-------------|-------------|--------------|-------------|-------------|------|------|
|  |         |     | Peat pools                   |             |             |             |              | MZ          |             |      |      |
|  |         |     | 1                            | 2           | 3           | 4           | 5            | 6           | 7           |      |      |
| <i>Hyphydrus ovatus</i> (L.)             | Hyh_ova | 2   | –                            | –           | –           | –           | –            | –           | –           | 0.6  | 0.1  |
| <i>Ilybius</i> sp.                       | –       | –   | –                            | –           | –           | 1.1         | –            | –           | –           | >0.1 | 0.1  |
| <i>Laccophilus hyalinus</i> (De Geer)    | Lac_hya | 1   | –                            | –           | –           | 1.1         | >0.1         | –           | –           | >0.1 | 0.1  |
| <i>Laccophilus poecilus</i> Klug         | Lac_poe | 8   | <b>12.1</b>                  | <b>23.8</b> | <b>16.2</b> | <b>24.2</b> | <b>37.6</b>  | 8.9         | –           | 12.4 | 17.7 |
| <i>Porhydrus lineatus</i> (Fabr.)        | Por_lin | 4   | 1.0                          | –           | 2.7         | 1.1         | –            | 2.2         | –           | –    | 0.7  |
| <i>Rhantus suturalis</i> (MacL.)         | Rha_sut | 2   | 1.0                          | –           | –           | –           | 1.1          | –           | –           | –    | 0.3  |
| Helophoridae                             |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Helophorus granularis</i> (L.)        | Hel_gra | 4   | –                            | 1.2         | –           | –           | –            | –           | 1.8         | –    | 0.3  |
| Hydrochidae                              |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Hydrochus crenatus</i> (Fabr.)        | Hyd_cre | 2   | –                            | 2.4         | –           | 1.1         | –            | 2.2         | –           | 1.1  | 0.8  |
| Hydrophilidae                            |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Anacaena limbata</i> (Fabr.)          | Ana_lim | 2   | –                            | 1.2         | –           | –           | 1.1          | –           | –           | –    | 0.3  |
| <i>Anacaena lutescens</i> (Steph.)       | Ana_lut | 8   | –                            | –           | –           | –           | –            | –           | 3.5         | 2.3  | 0.8  |
| <i>Anacaena</i> sp.                      | –       | –   | –                            | –           | –           | 2.1         | –            | –           | –           | 0.6  | 0.4  |
| <i>Cercyon analis</i> (Payk.)            | Cre_ana | 2   | 1.0                          | –           | –           | –           | –            | –           | –           | –    | 0.1  |
| <i>Coelostoma orbiculare</i> (Fabr.)     | Coe_orb | 2   | –                            | 1.2         | –           | –           | –            | –           | –           | 1.1  | 0.4  |
| <i>Enochrus affinis</i> (Thunb.)         | Eno_aff | 8   | 1.0                          | 3.6         | 4.1         | –           | –            | 2.2         | 8.8         | 2.8  | 2.5  |
| <i>Enochrus coarctatus</i> (Gredl.)      | Eno_coa | 8   | –                            | –           | –           | –           | –            | –           | –           | 0.6  | 0.1  |
| <i>Enochrus melanocephalus</i> (Ol.)     | Eno_mel | 8   | –                            | 1.2         | –           | 1.1         | 1.1          | 2.2         | 7.0         | 1.1  | 1.4  |
| <i>Enochrus ochropterus</i> (Marsh.)     | Eno_och | 8   | –                            | –           | –           | –           | 3.2          | –           | –           | –    | 0.4  |
| <i>Enochrus quadripunctatus</i> (Herbst) | Eno_qua | 2   | 1.0                          | –           | –           | 1.1         | –            | –           | 3.5         | 0.6  | 0.7  |
| <i>Enochrus testaceus</i> (Fabr.)        | Eno_tes | 2   | –                            | 1.2         | –           | –           | –            | >0.1        | –           | –    | 0.1  |
| <i>Enochrus</i> sp.                      | –       | –   | 1.0                          | –           | –           | –           | –            | 2.2         | –           | 0.6  | 0.4  |
| <i>Helochares obscurus</i> (O.F. Müll.)  | Hel_obs | 2   | 3.0                          | <b>13.1</b> | 8.1         | –           | 5.4          | 2.2         | <b>12.3</b> | 3.4  | 5.4  |
| <i>Hydrobius fuscipes</i> (L.)           | Hyb_fus | 2   | –                            | –           | –           | –           | –            | –           | 1.8         | >0.1 | 0.1  |
| <i>Hydrochara caraboides</i> (L.)        | Hyd_car | 2   | –                            | –           | 1.4         | –           | –            | –           | 1.8         | 1.1  | 0.6  |
| <i>Laccobius minutus</i> (L.)            | Lac_min | 2   | –                            | –           | –           | –           | 1.1          | –           | –           | >0.1 | 0.1  |
| <i>Laccobius</i> sp.                     | –       | –   | –                            | 1.2         | –           | –           | >0.1         | –           | –           | 5.1  | 1.4  |
| Scirtidae                                |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Elodes</i> sp.                        | –       | –   | –                            | –           | –           | 1.1         | –            | –           | –           | >0.1 | 0.1  |
| <i>Microcara testacea</i> (L.)           | Mic_tes | 8   | –                            | –           | –           | –           | 1.1          | –           | –           | >0.1 | 0.1  |
| <i>Scirtes</i> sp.                       | –       | –   | –                            | –           | –           | –           | 5.4          | –           | 3.5         | –    | 1.0  |
| Curculionidae                            |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Tanysphyrus lemnae</i> (Payk.)        | Tan_lem | 1   | –                            | –           | –           | –           | 2.2          | 2.2         | –           | –    | 0.4  |
| N=                                       | –       | –   | 99                           | 84          | 74          | 95          | 93           | 45          | 57          | 177  | 724  |
| TRICHOPTERA                              |         |     |                              |             |             |             |              |             |             |      |      |
| Polycentropodidae                        |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Cyrnus insolutus</i> McL.             | Cyr_ins | 8   | 2.7                          | –           | –           | –           | –            | –           | –           | –    | 0.8  |
| <i>Holocentropus dubius</i> (Ramb.)      | Hol_dub | 8   | <b>35.1</b>                  | –           | <b>90.2</b> | <b>56.3</b> | –            | <b>50.0</b> | –           | –    | 60.3 |
| Leptoceridae                             |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Oecetis furva</i> (Ramb.)             | Oec_och | 2   | <b>13.5</b>                  | –           | –           | –           | –            | –           | –           | –    | 4.1  |
| Limnephilidae                            |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Limnephilus stigma</i> Curt.          | Lim_sti | 8   | –                            | –           | –           | –           | –            | 10.0        | –           | –    | 0.8  |
| Phryganeidae                             |         |     |                              |             |             |             |              |             |             |      |      |
| <i>Agrypnia obsoleta</i> (Hag.)          | Agr_obs | 8   | –                            | –           | –           | –           | –            | 10.0        | –           | –    | 0.8  |
| <i>Agrypnia varia</i> (Fabr.)            | Agr_var | 4   | <b>45.9</b>                  | –           | 7.3         | <b>37.5</b> | <b>100.0</b> | –           | –           | –    | 27.3 |
| <i>Oligotricha striata</i> (L.)          | Oli_str | 4   | –                            | –           | –           | 3.1         | –            | –           | –           | –    | 0.8  |
| <i>Phryganea bipunctata</i> Retz.        | Phr_bip | 1   | –                            | –           | –           | –           | –            | 20.0        | –           | –    | 1.7  |
| <i>Phryganea grandis</i> L.              | Phr_gra | 4   | 2.7                          | –           | 2.4         | 3.1         | –            | 10.0        | –           | –    | 3.3  |
| N=                                       | –       | –   | 37                           | 0           | 41          | 32          | 1            | 10          | 0           | 0    | 121  |
| Taxa richness (S)                        |         |     | 37                           | 29          | 30          | 36          | 26           | 28          | 20          | 43   |      |
| Number of individuals (N)                |         |     | 268                          | 233         | 252         | 360         | 128          | 203         | 61          | 332  |      |
| Shannon-Wiener index (H)                 |         |     | 2.75                         | 2.48        | 2.54        | 2.58        | 2.59         | 2.31        | 2.71        | 3.1  |      |
| Buzas-Gibson's evenness (E)              |         |     | 0.42                         | 0.41        | 0.42        | 0.36        | 0.51         | 0.36        | 0.75        | 0.51 |      |
| Dominance index (D)                      |         |     | 0.11                         | 0.12        | 0.11        | 0.12        | 0.12         | 0.16        | 0.08        | 0.06 |      |

Wze, stenotopy index; 1–7, peat pools; MZ, marginal zone of the peatbog. %N, percentage of a species in the total number of individuals.

Eudominants (>10%) are given in bold.

species richness of Odonata and Coleoptera assemblages. At the sample level, the most significant differences (Kruskal–Wallis test,  $P \leq 0.03$ ) were in mean abundance ( $P = 0.03$ ), species richness

( $P = 0.01$ ), and proportions of ecological groups in terms of species richness or abundance ( $P = 0.01$ ), applied almost exclusively to the tyrphobionts.



**Fig. 2.** Dendrogram from Unweighted Pair Group Method with Arithmetic Mean cluster analysis for the study sites based on the numbers of individual insect taxa (Bray–Curtis index). MZ, marginal zone of the peatbog; 1–7, peat pools.

### The Effects of Environmental Factors on the Distribution of the Entomofauna

Three environmental factors—one physical and chemical as well as two structural—were significant for each of the insect groups (Table 4). Both sets of variables were equally important for dragonflies and beetles, whereas structural factors were more important for caddisflies. The shared effects were different: extremely low for beetles, higher for odonates, and the highest for trichopterans.

For dragonflies, the key factors were pH, *Sphagnum* cover, and pool perimeter (Fig. 5A, Table 4). The occurrence of the three *Leucorrhinia* species was most closely related with pH and *Sphagnum* cover. They were all closely associated with intermediate pH. In addition, *Leucorrhinia rubicunda* was the most strongly associated with moderately overgrown peat pools. *Coenagrion hastulatum* inhabited the pools with the longest perimeter; and *Cordulia aenea* with intermediate perimeter.

Beetles were significantly dependent on temperature, *Sphagnum* cover and emergent vegetation cover (Fig. 5B, Table 4). Among species strongly associated with the first factor, *Laccophilus poecilus* and *Tanytarsus lemnae* belong to more thermophilous species in contrast to *Hygrotus inaequalis* and *Acilius sulcatus*. *Anacaena lutescens*, *Helophorus granularis*, *Hydaticus seminiger*, and *Helochaeres obscurus* were strictly associated with larger *Sphagnum* cover, whereas *Graphoderus cinereus* and *Noterus crassicornis* were related to poorly overgrown sites. *Tanytarsus lemnae*, *Noterus crassicornis*, *Hygrotus versicolor*, and *Acilius sulcatus* were associated the most with the emergent vegetation cover: the first species with the densest cover, the second and third with moderate, and the last species with the thinnest cover.

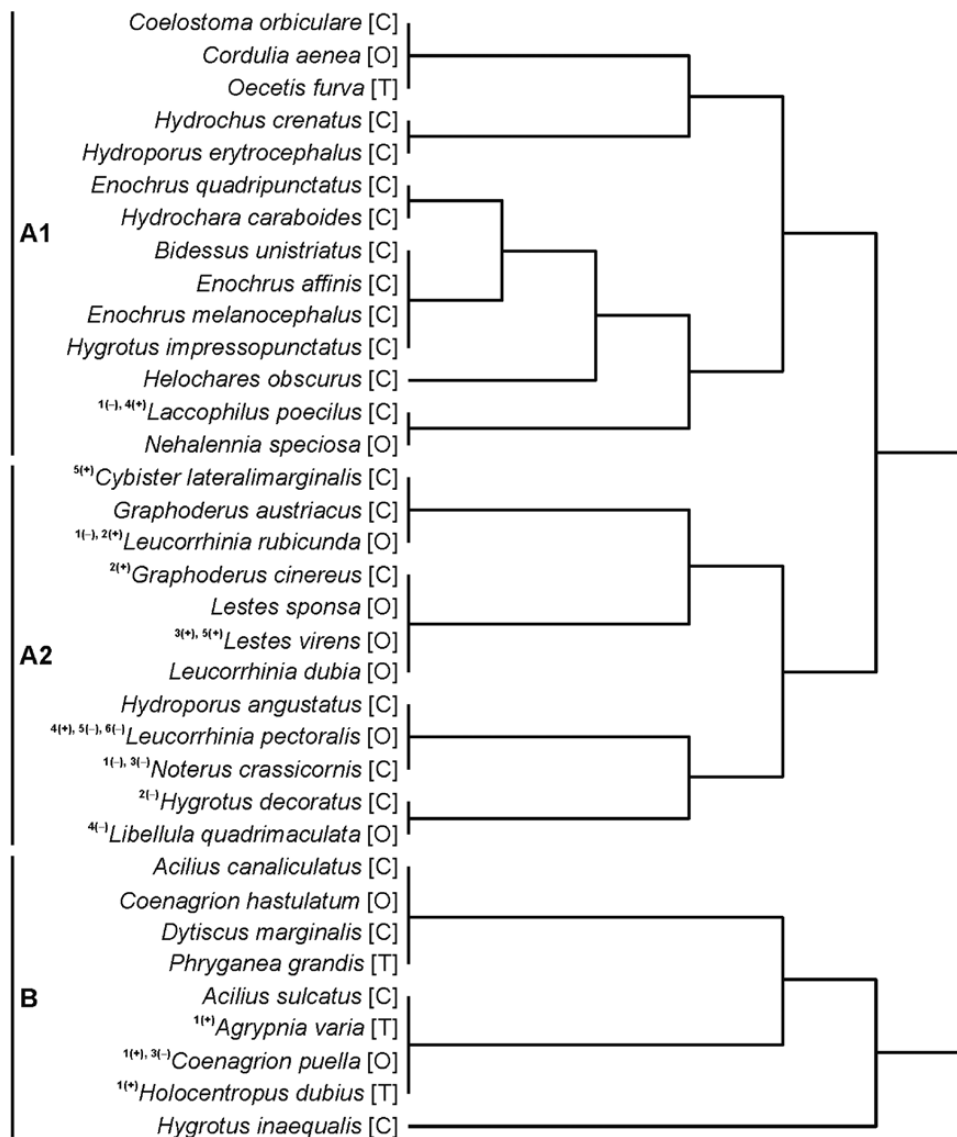
Dissolved oxygen, *Sphagnum* cover, and pool perimeter were the most significant factors for caddisflies (Fig. 5C, Table 4). Since acidic habitats favor a rather species-poor caddisfly fauna, few close relationships between these variables and species were found: *Holocentropus dubius* was strongly related with intermediate oxygen levels and waterbodies with intermediate perimeter, whereas *Agrypnia varia* and *Phryganea grandis* were more typical of lower oxygen levels and pools with the shortest perimeter.

### Occurrence Patterns of Particular Insect Species Versus Their Key Habitat Factors

Among the dragonflies, *Leucorrhinia pectoralis* displayed the broadest and *Lestes virens* the narrowest pH tolerance (Fig. 6). *Leucorrhinia rubicunda* and *Lestes virens* clearly preferred low pH, their numbers falling with decreasing acidity. The abundance of *Nehalennia speciosa* increased with pH (optimum pH, 5.78), whereas the abundance of *Leucorrhinia pectoralis* was almost the same over the observed pH range. The two *Leucorrhinia* species preferred pools with large *Sphagnum* cover: the optimum value for *Leucorrhinia rubicunda* was 61% (tolerance 17%) and 46% for *Leucorrhinia pectoralis* (tolerance 23%). *Nehalennia speciosa* exhibited the same optimum as *Leucorrhinia pectoralis*, but with a lower tolerance (14%). The two *Coenagrion* species associated with thinly vegetated habitats had optima of 16% (*Coenagrion hastulatum*) and 23% (*Coenagrion puella*). Apart from *Leucorrhinia rubicunda* and *Nehalennia speciosa*, the optimum peat pool perimeter for dragonflies was similar and ranged between 0.22 and 0.3 km. Tolerance ranges were also similar, the widest being for *Leucorrhinia pectoralis* (0.4) and the narrowest for *Coenagrion hastulatum* (0.09).

The respective thermal optima of the beetles *Hygrotus inaequalis* and *Helochaeres obscurus* were 13.2 and 16.2°C, both displaying similar tolerances (3.8 and 4.5°C) (Fig. 6). *Laccophilus poecilus* and *Graphoderus cinereus* were the most thermophilous species, their abundance increasing with water temperature. *Noterus crassicornis* had a thermal optimum of 16°C but also the broadest thermal tolerance (7.7°C). *Hygrotus inaequalis* and *Laccophilus poecilus* preferred the pools with large *Sphagnum* cover (61 and 49%) and exhibited similar tolerances (≈25%). In turn, *Graphoderus cinereus* had the narrowest tolerance and optimum at 19%. The abundance of *Noterus crassicornis* dropped with increasing *Sphagnum* cover. The reverse applied to *Helochaeres obscurus*, which was more abundant in more densely vegetated habitats. The emergent vegetation cover affected *Hygrotus inaequalis* and *Helochaeres obscurus*, which exhibited similar occurrence patterns with respective optima of 2.2 and 3. *Laccophilus poecilus* displayed a distinct preference for the most developed emergent vegetation, *Noterus crassicornis* was most abundant where the cover of this vegetation was moderate and *Graphoderus cinereus* where it was thin.





**Fig. 3.** TWINSpan cladogram showing insect assemblages (A1, A2, B) typical of acidic habitats. [C], Coleoptera; [O], Odonata; [T], Trichoptera. Indicator species (positive and negative) for divisions 1–6 are provided.

Among caddisflies, *Holocentropus dubius* exhibited a far greater demand for oxygen than *Agrypnia varia*: the optimum and tolerance of the former were 2.53 and 2.31 ppm, respectively, those of the latter were 0.85 and 1.12 ppm (Fig. 6). *Holocentropus dubius* distinctly preferred peat pools without *Sphagnum* mats; its abundance falling with increasing moss cover. *Agrypnia varia* clearly avoided both open pools and pools with dense plant cover, exhibiting an optimum at 18% with a tolerance of 7.4%. By colonizing pools of varying sizes, and hence with different perimeters, *Holocentropus dubius* achieved its optimum at a value of 0.27 km. In contrast, *Agrypnia varia* preferred smaller peat pools (optimum of 0.12 km).

## Discussion

### General Features of the Insect Fauna of Peatland Habitats

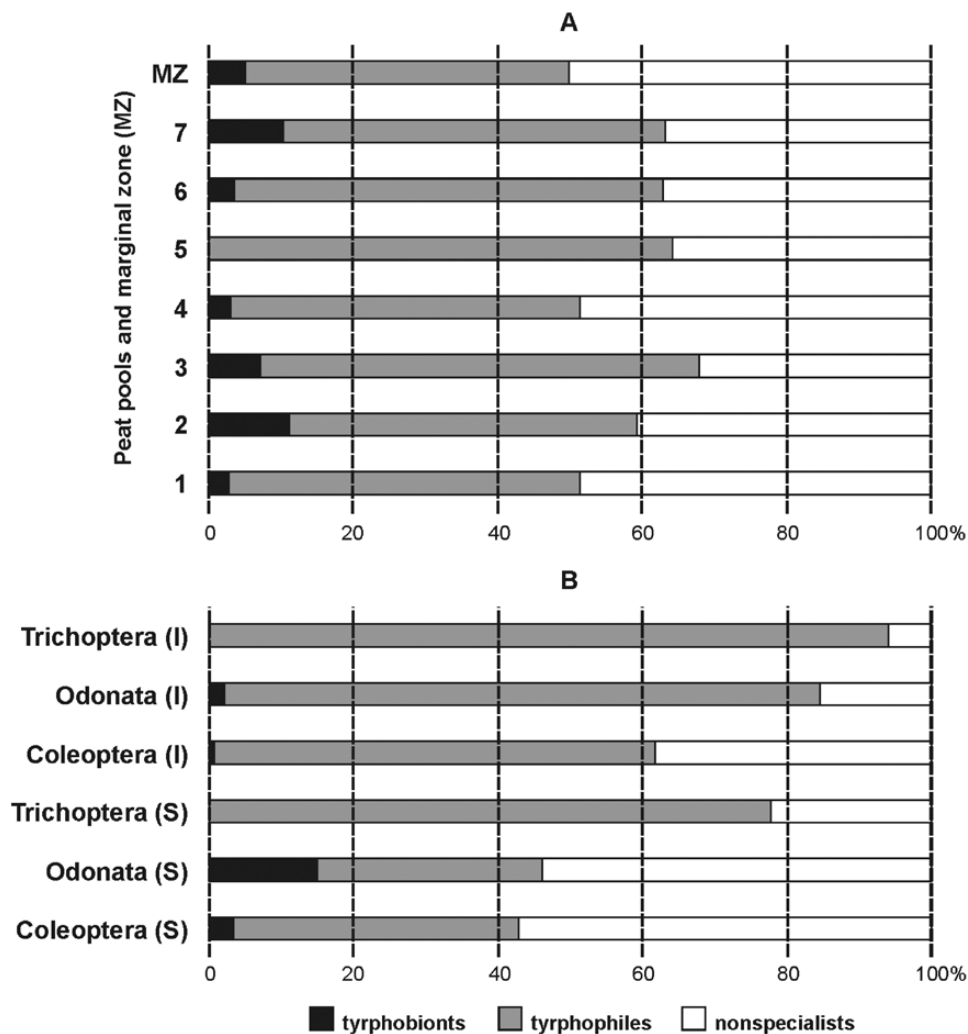
The species richness of beetles and dragonflies in the study area can be regarded as typical of peatlands (Smits et al. 2002, Drinan et al. 2013, Elo et al. 2015, Brown et al. 2016), but the caddisfly fauna was species-poorer in comparison to similar studies (Smits et al. 2002, Hannigan and Kelly-Quinn 2012), despite having the highest

proportion of specialists (tyrphophiles). Dragonflies and beetles were represented by both tyrphobionts and tyrphophiles, but more than half of their species were nonspecialists. Habitat-dependent insect species are key to this habitat type, constitute also a species pool for the colonisation of new sites (van Duinen et al. 2007, Drinan et al. 2013), and are the best bioindicators of successional changes (Spitzer and Danks 2006). The presence of habitat specialists is important, but the proportion between them and eurytopic species (opportunists) is crucial. Their proportions in the peat pools studied here were evenly balanced, possibly indicating that these relatively old waterbodies have achieved a state of faunistic equilibrium. The predominance of opportunists on the *Sphagnum* bogs, with high richness and diversity, might even be a consequence of negative processes (pollution, deforestation of drainage basin, inflow of nutrients, increase in trophic, lowering groundwater table, and drying out), taking place in these habitats (Bernard et al. 2002). Diversity metrics alone are not a sufficient tool for reliably assessing *Sphagnum* bog fauna, especially in the context of peatland conservation. Such metrics must be complemented by i) a greater knowledge of the basic life history of insect assemblages as well as of rare and specialist peatbog species or (ii) the use of additional metrics (van Duinen et al. 2007, Drinan et al. 2013, Brown et al. 2016). Our

**Table 3.** Values of qualitative naturalness (Wns) and quantitative naturalness (Wni) indices for each peat pool (1–7) and the marginal zone of the peatbog (MZ)

| Index                    | Site       |             |      |      |             |      |             | MZ   |
|--------------------------|------------|-------------|------|------|-------------|------|-------------|------|
|                          | Peat pools |             |      |      |             |      |             |      |
|                          | 1          | 2           | 3    | 4    | 5           | 6    | 7           |      |
| <b>All insect orders</b> |            |             |      |      |             |      |             |      |
| Wns                      | 4.06       | 5.81        | 5.46 | 4.00 | 4.92        | 4.85 | 5.95        | 4.84 |
| Wni                      | 3.98       | 5.80        | 4.82 | 4.23 | 5.64        | 3.99 | <b>6.00</b> | 4.90 |
| <b>Odonata</b>           |            |             |      |      |             |      |             |      |
| Wns                      | 5.13       | 7.44        | 5.44 | 4.73 | 6.00        | 5.44 | 5.00        | 5.00 |
| Wni                      | 3.86       | <b>6.28</b> | 3.92 | 3.96 | <b>6.12</b> | 3.93 | 3.50        | 4.74 |
| <b>Coleoptera</b>        |            |             |      |      |             |      |             |      |
| Wns                      | 3.41       | 5.00        | 5.50 | 3.33 | 4.59        | 4.00 | <b>6.06</b> | 4.77 |
| Wni                      | 3.65       | 4.96        | 4.94 | 4.22 | 5.47        | 3.67 | <b>6.18</b> | 5.05 |
| <b>Trichoptera</b>       |            |             |      |      |             |      |             |      |
| Wns                      | 5.20       | –           | 5.33 | 5.00 | 4.00        | 5.80 | –           | –    |
| Wni                      | 5.24       | –           | 7.61 | 6.23 | 4.00        | 6.20 | –           | –    |

The highest scores are given in bold.



**Fig. 4.** Proportions of ecological groups (tyrphobionts, tyrrophiles, and nonspecialists) at particular study sites (A) and within the three insect orders (B). S, species richness; I, abundance.

**Table 4.** Results of variance partitioning analysis (CCAs) for Odonata, Coleoptera, and Trichoptera

| Taxon/variance       |      | Environmental variable          | %C   | P     | pseudo-F |
|----------------------|------|---------------------------------|------|-------|----------|
| Odonata              |      |                                 |      |       |          |
| TVE (%)              | 66   |                                 |      |       |          |
| VE <sub>FC</sub> (%) | 35.3 | pH                              | 40   | 0.002 | 4.5      |
| VE <sub>ST</sub> (%) | 36.3 | <i>Sphagnum</i> cover           | 21.8 | 0.026 | 2.3      |
|                      |      | Pool perimeter                  | 20.7 | 0.024 | 2.4      |
| SE (%)               | 5.6  |                                 |      |       |          |
| Coleoptera           |      |                                 |      |       |          |
| TVE (%)              | 52.3 |                                 |      |       |          |
| VE <sub>FC</sub> (%) | 25.7 | Temperature                     | 22   | 0.04  | 1.6      |
| VE <sub>ST</sub> (%) | 26.7 | <i>Sphagnum</i> cover           | 29.1 | 0.004 | 2.3      |
|                      |      | Coverage of emergent vegetation | 24.6 | 0.004 | 2        |
| SE (%)               | 0.1  |                                 |      |       |          |
| Trichoptera          |      |                                 |      |       |          |
| TVE (%)              | 88.6 |                                 |      |       |          |
| VE <sub>FC</sub> (%) | 41.5 | Dissolved oxygen                | 32.2 | 0.049 | 2.5      |
| VE <sub>ST</sub> (%) | 54.4 | <i>Sphagnum</i> cover           | 35.5 | 0.008 | 3.6      |
|                      |      | Pool perimeter                  | 24.3 | 0.046 | 3.1      |
| SE (%)               | 10.9 |                                 |      |       |          |

TVE, total variance explained; VE<sub>FC</sub>, variance explained by physical and chemical factors; VE<sub>ST</sub>, variance explained by structural factors; SE, shared effect; %C, percent contribution of a particular variable; P, significance level of the effect tested by Monte Carlo permutation test; pseudo-F, value of the pseudo-F ratio statistic

study indicates that naturalness indices may be useful tools for analyzing the specialization potential of peat pools. In comparison with the values observed in other *Sphagnum* bogs in Poland (Czachorowski and Buczyński 1999), those obtained in this study were high for caddisflies and intermediate for dragonflies, underscoring the crucial part played by such pools in the survival of the specialist peatbog fauna.

Even among small and rather homogeneous sites, like those explored here, distinct differences in the fauna have emerged from species richness and composition, with major implications for biodiversity. Even if each kind of site and microhabitat had its own contribution to biodiversity, the peat pools combined—with 44% of exclusive species and 15 specialists—made the most valuable contribution to the biodiversity of aquatic insects on the peatbog studied. On the basis of these data, one can risk stating that if the marginal zone becomes degraded or dries out—even as a result of climate warming—the permanent pools should provide refugia for almost the entire peatbog fauna, an aspect also emphasized by Batzer and Boix (2016).

This study has demonstrated that peat pools may be as valuable as primary peatbog habitats for the occurrence of specialist insects (with regard to species composition) or even more so (naturalness indices), since particular assemblages or species are dependent on different stages of succession (Buczyński 2015). This also applies to the early successional stages: peat pools with open water and floating-leaved and/or submerged vegetation provide an opportunity for the restoration of assemblages typical of small lakes surrounded by peatbogs, with both limnophilous and tyrophilous species. In turn, the pools with the most extensive *Sphagnum* cover were faunistically the most specialized (maximum values of Wns and Wni) and similar to the marginal zone (especially with regard to odonates), and hence to a natural habitat. As a result, the peat pool insect fauna to a large extent relates to the last remnants of this habitat, whereas habitat diversity promotes acidophilous and acid-tolerant species characteristic of dystrophic pools.

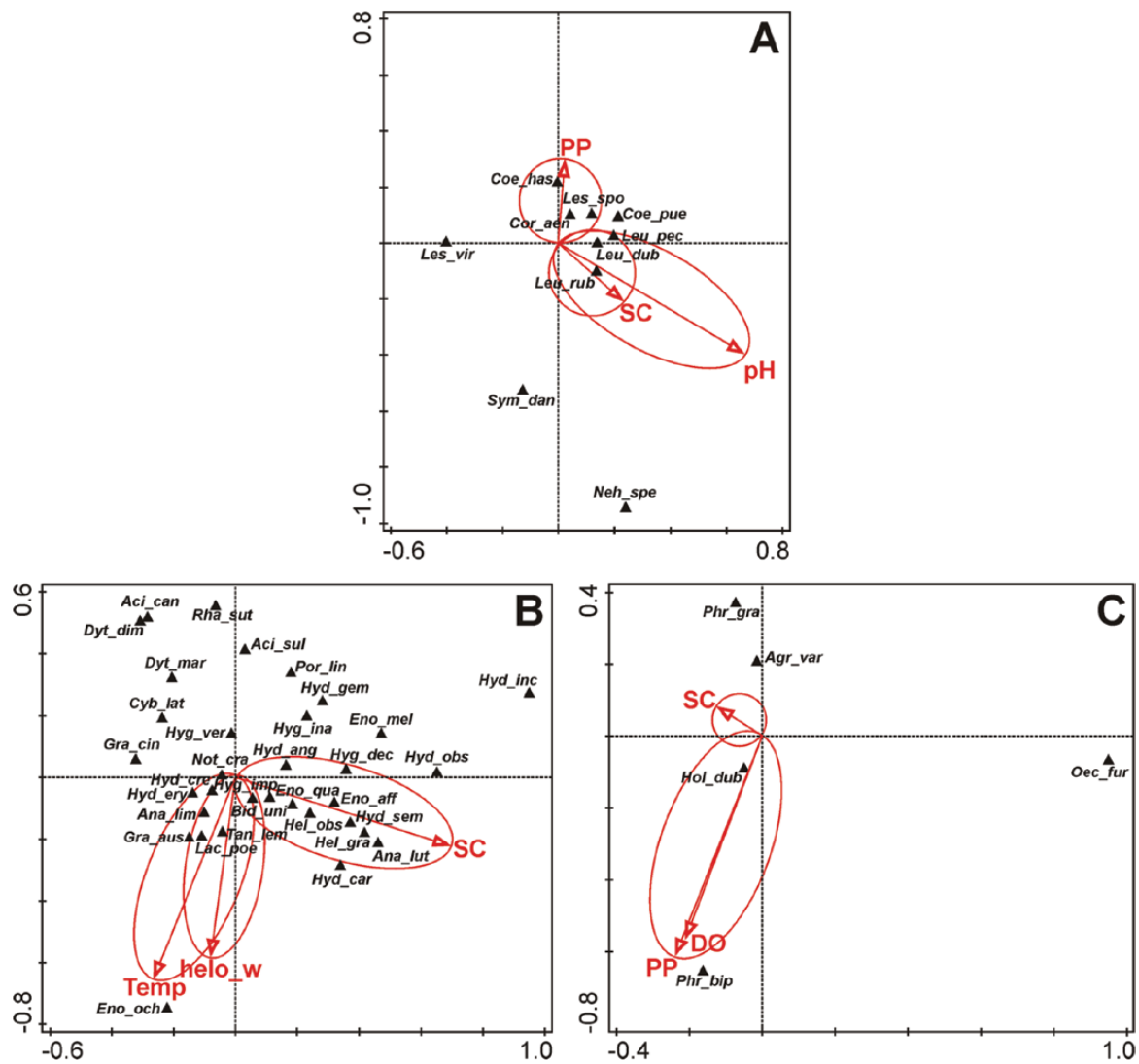
### Environmental Factors Affecting the Distribution of Insects in Peat Pools

The *Sphagnum* cover of the pools was the most significant factor in this man-made habitat governing the distribution of all the studied

insect groups. The same key factor was found for aquatic macroinvertebrates in Scragh bog (Hannigan and Kelly-Quinn 2012), with a rather similar percentage of explained variation in fauna (23 vs. 24.5%). In accordance with Heino (2010), moss cover increases the number of predatory species. Heino's explanation of this phenomenon can also be extrapolated to our peat pools: the lentic macroinvertebrates of such habitats may be more dependent on the quantity of terrestrial-based rather than aquatic-based detritus. The trees on the pool shores (although significantly different at the various sites) were not crucial for insects as providers of either shade or allochthonous detritus.

Pool perimeter was a significant factor for odonates and trichopterans, although, interestingly, the actual size of a peat pool had not a significant effect for any of the three orders—this corresponds with the results of Hannigan and Kelly-Quinn (2012). The perimeter, however, may be significant for territorial insects like dragonflies (Corbet 1999): a longer perimeter will provide a potentially greater number of territories for males and will enhance their reproductive success. For caddisflies, it will provide a larger food base, with more detritus for case-bearing species and more favorable microhabitats for net attachment of predatory species. The significant association of beetles with vegetation of waterbodies, including peat pools, has frequently been evoked: for example, the herb and shrub cover as well as the number of plant species were crucial for coleopterans in a raised bog in Belarus (Sushko 2007). The present results also confirmed such relationships: beetles were dependent on the emergent vegetation cover. Many species preferred moderately or poorly developed helophytes which may be related to easier dispersion and foraging of coleopterans within this vegetation zone (Klausnitzer 1996).

The pH value was crucial for dragonflies. This parameter has very often been shown to be one of the main drivers of aquatic invertebrate distribution in peatlands (Smits et al. 2002, Więcek et al. 2013, Baars et al. 2015), including Odonata (Elo et al. 2015). Many odonate species are perfectly adapted to low pH. *Leucorrhinia dubia* and *Leucorrhinia rubicunda* are regarded as species largely restricted to acidic habitats (Rychła et al. 2011), which corresponds with our CCA results. One of the reasons why certain dragonfly species are



**Fig. 5.** Ordination CCA biplots showing the distribution of Odonata (A), Coleoptera (B), and Trichoptera (C) species in peat pools versus significant environmental factors (pH; SC, *Sphagnum* cover; PP, pool perimeter; helo\_w, emergent vegetation cover on peat pool shores; Temp, water temperature; DO, dissolved oxygen concentration). The taxon codes are given in Table 2.

relatively abundant at low pH is the zero or limited predation pressure from fish under these conditions (Corbet 1993). Fish were present in these peat pools, but their influence was attenuated by the presence of thick *Sphagnum* mats, providing to larvae effective shelter from predators (Henrikson 1993).

Temperature was a key factor of distribution for beetles, as was water dissolved oxygen content for caddisflies. This result is fairly typical, given that trichopterans are regarded as the most sensitive of the three orders analyzed here to oxygen deficits (Lock and Goethals 2012). The links between beetles and specific thermal conditions may be due to their diverse requirements during larval development (Nilsson and Svensson 1994). The most temperature-dependent species in our pools preferred low to moderate values (4.3–11°C). Natural waterbodies on *Sphagnum* bogs are typically subject to marked temperature fluctuations, from low to very high (Sternberg 1993). Deeper and larger peat pools may be refuges for species preferring low temperatures.

Structural factors, which are easy to control simply by managing the succession, offer interesting prospects for the active conservation of peat pools. The results of CCAs indicated that certain species

preferred different degrees of vegetation cover. For instance, when creating a peat pool, it can be modified according to the needs of a particular species. *Leucorrhinia rubicunda*, for example, distinctly preferred the most densely vegetated peat pools, in contrast to other *Leucorrhinia* spp. Moreover, some physical and chemical properties of peat pools can be manipulated. For example, water temperature, crucial for beetles, depends to a large extent on shading, i.e., on the presence or absence of trees lining the pool shore. Smits et al. (2002) drew attention to a similar, practical aspect of using their results (underlining, like us, the importance of pH, vegetation structure and open water) for restoration management in Estonia, whereby their research focused on an intact raised bog system. The present findings and recommendations can be regarded as complementary to those describing systems of the following type: restored (rewetted) pools versus natural undisturbed peatland pools or artificial remnant sites (van Duinen et al. 2003, Hannigan et al. 2011, Elo et al. 2015, Brown et al. 2016). Our case extends these systems to include the remnants of a natural habitat (transition bog) versus ca. 80-yr-old peat pools, as a new type of anthropogenic lentic habitat in the study area.



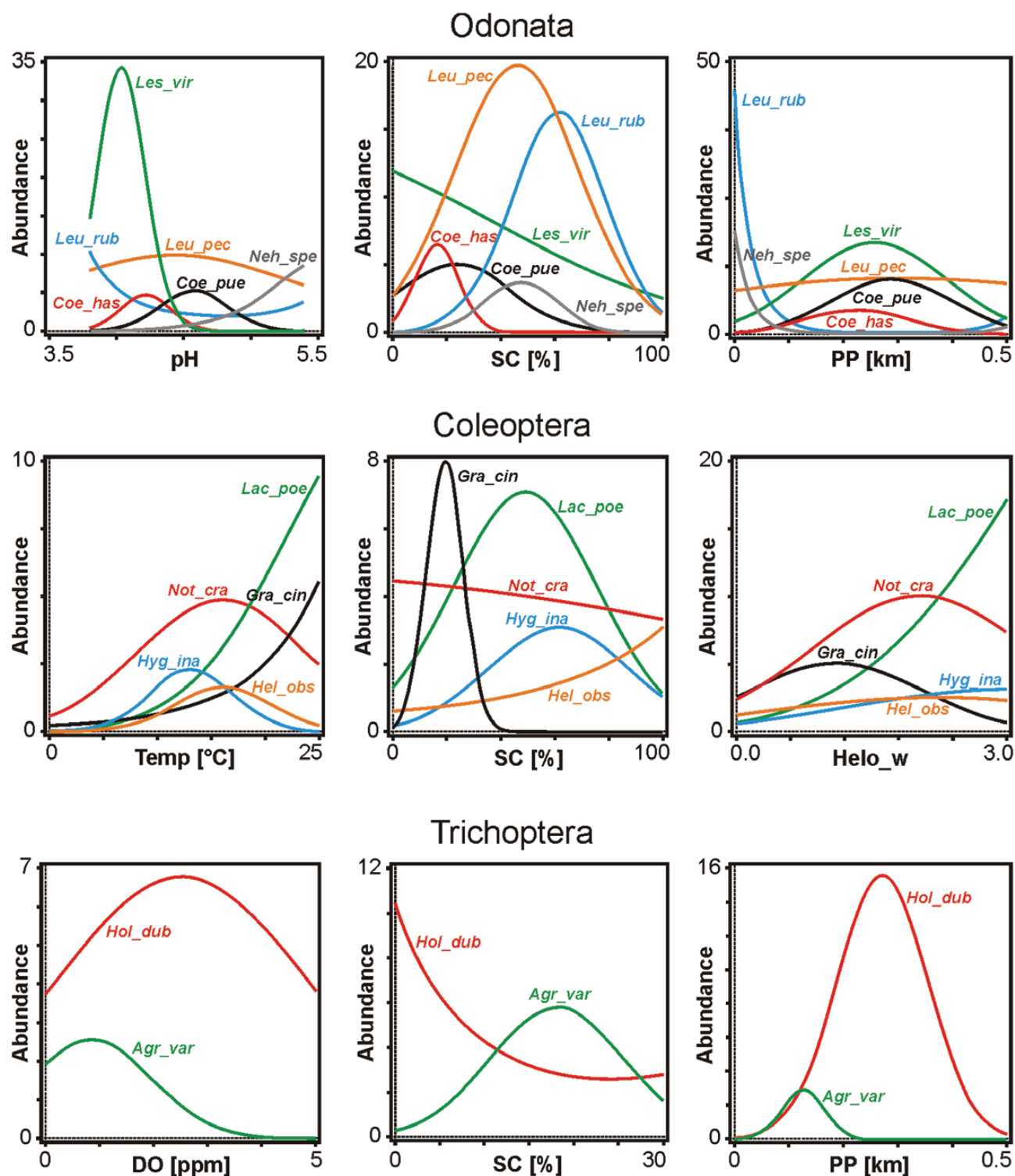


Fig. 6. Response curves of the most frequent Odonata, Coleoptera, and space is lacking Trichoptera species to significant environmental variables using GLM (pH; SC, *Sphagnum* cover; PP, pool perimeter; helo\_w, emergent vegetation cover on peat pool shores; Temp, water temperature; DO, dissolved oxygen concentration). The taxon codes are given in Table 2.

### The Species Level: From Habitat Preferences to Conservation Aspects

The distribution, species richness, rarity, and description of habitat preferences of particular species or assemblages may be useful in the conservation context of *Sphagnum* bogs. The presence of legally protected and endangered species raises the natural value of an area

and facilitates formal and practical conservation actions. In our study area, we found just three of the 15 dragonfly species legally protected in Poland (Regulation of the Minister of the Environment 2016): *Aeshna subarctica*, *Leucorrhinia pectoralis*, and *Nehalennia speciosa*. The last-mentioned species is also on the IUCN Red List of Threatened Species (category EN; Bernard et al. 2009). *Aeshna*

*subarctica* was recorded only in the peat pools, and *Nehalennia speciosa* and *Leucorrhinia pectoralis* in both the marginal zone and the peat pools.

Even though the invertebrate species of *Sphagnum* bogs in Europe are quite well known (Batzer and Boix 2016), the search for the best indicators of this kind of habitat continues, as the requirements and responses of particular species to specific factors remain still unknown. Promising results for *Sphagnum* bogs have been achieved for carabid beetles and ants as indicators for conservation planning (Brigić et al. 2017), and also spiders, whose assemblages have been found to depend on peatbog successional stages (Buchholz 2016). The first indicator level (TWINSPAN) in the present results pointed out two opposite groups: one dominated by eurytopes preferring the open water surface and the other by tyrphophiles from the well-vegetated peat pools. Thus, as in the case of the spiders, the stage of succession was a key factor to distinguish different indicators representative of all the insect orders in the peat pools. Odonates and beetles were lower division indicators, mostly replicating the tyrphophile—eurytope opposition. As in Brigić et al. (2017), the discriminant species were tyrphophiles; these authors failing to record any tyrphobiont species. In contrast, we found this element to be the rarest, but no species from this category turned out to be suitable as an indicator. Also, worth emphasizing is the fact that TWINSPAN designated species from all the orders as first-level indicators, which has confirmed that assessment of *Sphagnum* bogs should be based on the widest possible taxonomic range of insects. In the present case, each of the three insect orders had an important contribution. Nevertheless, dragonflies were the best indicators, as they are generally regarded as good indicators of changes in *Sphagnum* peatbogs and are well used in restoration monitoring studies (Elo et al. 2015). Specifically, the tyrphophilous *Leucorrhinia pectoralis* and *Leucorrhinia rubicunda* were key species at all levels. GLM analysis revealed that these two species had different pH and perimeter requirements, as well as different optima with regard to *Sphagnum* cover. Among the beetle species, only *Hygrotus decoratus* (tyrphophile) and *G. cinereus* (eurytope) were of any use for discriminating waterbodies, whereby the absence of endangered/protected species in this group makes them, in our opinion, less suitable indicators for the conservation of this type of habitat.

Umbrella species—another faunistic tool used in conservation practice—indicate important habitats potentially worth protecting and define the various processes/changes taking place in these areas, especially the negative ones. Our GLM results have corroborated the good umbrella species status of *Leucorrhinia pectoralis* for *Sphagnum* bogs and waterbodies bounded by *Sphagnum*, including anthropogenic peat pools (Bernard et al. 2002). In our study area, it was the most numerous species and exhibited the broadest tolerance among the odonates toward significant habitat factors governing its populations. Our detailed data on the habitat requirements of this species in peat pools closely resemble those given by Wildermuth (2001) regarding the optimal habitat conditions created for *Leucorrhinia pectoralis* in fens. They indicate that active conservation of this species on *Sphagnum* bogs can be just as effective. *Nehalennia speciosa* is one of the prime target species protected along with *Leucorrhinia pectoralis*, since the optima and tolerances of both species are convergent, especially with respect to *Sphagnum* cover. Worth underlining is the fact that *Nehalennia speciosa*, a rare IUCN red-listed species, was present in five of the eight peat pools (including the marginal zone), which shows that it can function well in both primary and secondary habitats (Bernard and Wildermuth 2005). The factor that might limit its occurrence in our peat pools is pH. Our results show that its response curve is quite different

from that of the other odonates, its optimal pH being 5.8 (tolerance = 0.5). The optimum pH range for its Polish populations is 4.0–5.5 (Bernard and Wildermuth 2005).

No analysis of the fauna of *Sphagnum* bogs at the species level can ignore questions of genetic diversity and conservation. Climate change is adversely affecting the network of surface waters and waterlogged habitats in many parts of Europe (Dokulil 2013), which may increase the isolation of habitat islands like peatbogs and cause many of them to disappear. With a too small number of localities and when a certain critical isolation threshold is exceeded, metapopulations, together with genetic material (e.g., Sternberg 1995, Korkeamäki and Suhonen 2002), may be seriously altered. Detrimental demographic processes may then ensue, causing numbers to fall below the Minimum Viable Population level (Traill et al. 2007).

## Acknowledgments

We are grateful to the anonymous reviewers and Professor Philippe Usseglio-Polatera for their constructive suggestions for improving the manuscript. We also thank Professor Bernard Staniec for his help with the fieldwork and Dr hab. Rafał Gosik for identifying the Curculionidae. This study was financially supported by the Fundamental Research Funds for the University of Life Sciences (no. DS-06 ‘Faunistic and ecological research of invertebrates in aquatic water bodies and ecosystems’) and Maria Curie-Skłodowska University (no. BS-P-11\_010\_13\_1-13 ‘Research on biodiversity and threats of selected groups of invertebrates, amphibians and reptiles, with elements of ecology’).

## References Cited

- Baars, J., D. A. Murray, E. Hannigan, and M. Kelly-Quinn. 2015. Macroinvertebrate assemblages of small upland peatland lakes in Ireland. *Proc. R. Ir. Acad.* 114B: 233–248.
- Batzer, D., and D. Boix. (eds.). 2016. Invertebrates in freshwater wetlands: an international perspective on their ecology. Springer, Cham, Switzerland.
- Beadle, J. M., L. E. Brown, and J. Holden. 2015. Biodiversity and ecosystem functioning in natural bog pools and those created by rewetting schemes. *Wiley Interdiscipl. Rev. Water.* 2: 65–84.
- Bernard, R., and H. Wildermuth. 2005. *Nehalennia speciosa* (Charpentier, 1840) in Europe: a case of a vanishing relict (Zygoptera: Coenagrionidae). *Odonatologica.* 34: 335–378.
- Bernard, R., P. Buczyński, and G. Tończyk. 2002. Present state, threats and conservation of dragonflies (Odonata) in Poland. *Nat. Conserv.* 59: 53–71.
- Bernard, R., P. Buczyński, G. Tończyk, and J. Wendzonka. 2009. A distribution atlas of dragonflies (Odonata) in Poland. Bogucki Wydawnictwo Naukowe, Poznań, Poland.
- Biesiadka, E. 1980. Water beetles (Coleoptera) of the eutrophic lake Zbęczy (Leszno voiv.). *Pol. Ecol. St.* 6: 263–275.
- ter Braak, C. J. F., and P. Šmilauer. 2012. Canoco reference manual and user’s guide: software for ordination (version 5.0). Microcomputer Power, Ithaca, NY.
- Brigić, A., J. Bujan, A. Alegro, V. Šegota, and I. Ternjej. 2017. Spatial distribution of insect indicator taxa as a basis for peatbog conservation planning. *Ecol. Ind.* 80: 344–353.
- Brown, L. E., S. J. Ramchunder, J. M. Beadle, and J. Holden. 2016. Macroinvertebrate community assembly in pools created during peatland restoration. *Sci. Total Environ.* 569–570: 361–372.
- Buchholz, S. 2016. Natural peatbog remnants promote distinct spider assemblages and habitat specific traits. *Ecol. Ind.* 60: 774–780.
- Buczyński, P. 2015. Dragonflies (Odonata) of anthropogenic waters in middle-eastern Poland. Mantis, Olsztyn, Poland.
- Buczyński, P., and B. Staniec. 1998. Waloryzacja godnego ochrony torfowiska Krugle Bagno (Pojezierze Łęczyńsko-Włodawskie) w oparciu o wybrane elementy jego fauny. *Rocz. Nauk. Pol. Tow. Ochr. Przynr. “Salamandra”.* 2: 95–107.

- Buczyński, P., A. Szlauer-Łukaszewska, G. Tończyk, and E. Buczyńska. 2017. Groyes: a factor modifying the occurrence of dragonfly larvae (Odonata) on a large lowland river. *Mar. Freshw. Res.* 68: 1653–1663.
- Corbet, P. S. 1993. Are Odonata useful as bioindicators? *Libellula*. 12: 91–102.
- Corbet, P. S. 1999. Dragonflies. Behaviour and ecology of Odonata. Harley, Colchester, United Kingdom.
- Czachorowski, S., and P. Buczyński. 1999. Wskaźnik naturalności biocenozy – potencjalne narzędzie w monitorowaniu stanu ekologicznego torfowisk Polski, na przykładzie Odonata i Trichoptera, pp. 153–158. *In* S. Radwan, R. Kornijów (eds.), *Problemy aktywnej ochrony ekosystemów wodnych i torfowiskowych w polskich parkach narodowych*. Wydawnictwo Uniwersytetu Marii Curie-Skłodowskiej Lublin, Poland.
- Desrochers, A., and G. J. van Duinen. 2006. Peatland fauna, pp. 67–100. *In* R. K. Wieder, D. H. Vitt (eds), *Boreal peatland ecosystems. Ecological studies (analysis and synthesis)*, vol 188. Springer, Berlin, Germany.
- Dokulil, M. T. 2013. Impact of climate change on European inland waters. *Inland Waters*. 4: 27–40.
- Drinan, T. J., G. N. Foster, B. H. Nelson, J. O'Halloran, and S. S. C. Harrison. 2013. Macroinvertebrate assemblages of peatland lakes: assessment of conservation value with respect to anthropogenic land-cover change. *Biol. Conserv.* 158: 175–187.
- van Duinen, G. J. A., A. M. Brock, J. T. Kuper, R. S. Leuven, T. M. Peeters, J. G. Roelofs, G. Van Der Welde, W. C. E. P. Verberk, and H. Esselink. 2003. Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. *Wetl. Ecol. Manag.* 11: 447–459.
- van Duinen, G. J. A., W. C. E. P. Verberk, and H. Esselink. 2007. Persistence and recolonisation determine success of bog restoration for aquatic invertebrates: a comment on Mazerolle *et al.* (2006). *Freshw. Biol.* 52: 381–382.
- Elo, M., J. Penttinen, and J. S. Kotiaho. 2015. The effect of peatland drainage and restoration on Odonata species richness and abundance. *BMC Ecol.* 15: 11.
- EU [European Commission]. 2008. Natura 2000. <http://ec.europa.eu/environment/nature/natura2000/>. Accessed 13 March 2018.
- Fischer, J. 1996. Bewertungsverfahren zur Quellenfauna. *Crunoecia*. 5: 227–240.
- Hammer, Ř., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electronica*. 4: 1–9.
- Hannigan, E., and M. Kelly-Quinn. 2012. Composition and structure of macroinvertebrate communities in contrasting open-water habitats in Irish peatlands: implications for biodiversity conservation. *Hydrobiologia*. 692: 19–28.
- Hannigan, E., R. Mangan, and M. Kelly-Quinn. 2011. Evaluation of the success of mountain blanket bog pool restoration in terms of aquatic macroinvertebrates. *Proc. R. Ir. Acad.* 111B: 95–105.
- Heino, J. 2010. Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. *Hydrobiologia*. 418: 229–242.
- Henrikson, B. I. 1993. *Sphagnum* mosses as a microhabitat for invertebrates in acidified lakes and the colour adaptation and substrate preference in *Leucorrhinia dubia* (Odonata, Anisoptera). *Ecography*. 16: 143–153.
- Hill, M. O., and P. Šmilauer. 2005. TWINSpan for Windows version 2.3. Centre for Ecology & Hydrology and University of South Bohemia, Česká Budějovice, Czech Republic.
- Houghton, D. C. 2004. Utility of caddisflies (Insecta: Trichoptera) as indicators of habitat disturbance in Minnesota. *J. Freshw. Ecol.* 19: 97–108.
- Ilnicki, P. 2002. Torfowiska i torf. Wydawnictwo Akademii Rolniczej im. Augusta Cieszkowskiego w Poznaniu, Poznań, Poland.
- Kato, Y., Y. Takemon, and M. Hori. 2009. Invertebrate assemblages in relation to habitat types on a floating mat in Mizorogaike Pond, Kyoto, Japan. *Limnology*. 10: 167–176.
- Klausnitzer, B. 1996. Käfer im und am Wasser. Westarp Wissenschaften, Spektrum Akademischer Verlag, Oxford, United Kingdom.
- Korkeamäki, E., and J. Suhonen. 2002. Distribution and habitat specialization of species affect local extinction in dragonfly Odonata populations. *Ecography*. 25: 459–465.
- Lock, K., and P. L. Goethals. 2012. Distribution and ecology of the caddisflies (Trichoptera) of Flanders (Belgium). *Ann. Limnol. Int. J. Lim.* 48: 31–37.
- Nilsson, A. N., and B. W. Svensson. 1994. Dytiscid predators and culicid prey in two boreal snowmelt pools differing in temperature and duration. *Ann. Zool. Fennici*. 31: 365–376.
- Regulation of the Minister of the Environment of 12 December 2016 on the species protection of animals (Journal of Laws, item 2183). <http://prawo.sejm.gov.pl/isap.nsf/download.xsp/WDU20160002183/O/D20162183.pdf>. Accessed 13 March 2018.
- Ruhi, A., and D. P. Batzer. 2014. Assessing congruence and surrogacy among wetland macroinvertebrate taxa towards efficiently measuring biodiversity. *Wetlands*. 34: 1061–1071.
- Rychła, A., J. Benndorf, and P. Buczyński. 2011. Impact of pH and conductivity on species richness and community structure of dragonflies (Odonata) in small mining lakes. *Fundam. Appl. Limnol.* 179: 41–50.
- Šmilauer, P., and J. Lepš. 2014. *Multivariate analysis of ecological data using Canoco 5*, 2 ed. Cambridge University Press, Cambridge, United Kingdom.
- Smits, M. J. A., G. A. Van Duinen, G. J. C. G. M. Bosman, A. M. T. Brock, J. Javois, J. T. Kuper, T. M. J. Peeters, M. A. J. Peeters, H. Esselink. 2002. Species richness in a species poor system: aquatic macroinvertebrates of Nigula raba, an intact raised bog system in Estonia, pp. 283–291. *In* G. Schmilewski and L. Rochefort (eds), *Proceeding of the International Peat Symposium on Peat in Horticulture – Quality and Environmental Challenges*. Pärnu, Estonia, September 3–6. International Peat Society, Jyväskylä, Finland.
- Spitzer, K., and H. V. Danks. 2006. Insect biodiversity of boreal peat bogs. *Annu. Rev. Entomol.* 51: 137–161.
- Spitzer, K., A. Bezděk, and J. Jaroš. 1999. Ecological succession of a relict central European peatbog and variability of its insect biodiversity. *J. Insect Conserv.* 3: 97–106.
- Sternberg, K. 1993. Hochmoorschlenken als warme Habitatsinseln im kalten Lebensraum. *Telma*. 23: 125–146.
- Sternberg, K. 1995. Populationsökologische Untersuchungen an einer Metapopulation der Hochmoor Mosaikjungfer (*Aeshna subarctica elisabethae* Djakonov, 1922) (Odonata, Aeshnidae) im Schwarzwald. *Z. Ökol. Natenschutz*. 4: 53–60.
- Suriano, M. T., A. A. Fonseca-Gessner, F. O. Roque, and C. G. Froehlich. 2011. Choice of macroinvertebrate metrics to evaluate stream conditions in Atlantic Forest, Brazil. *Environ. Monit. Assess.* 175: 87–101.
- Sushko, G. 2007. Beetles (Coleoptera) of raised bogs in North-Western Belarus (Belarusian Land O'Lakes). *Baltic. J. Coleopterol.* 7: 207–214.
- Traill, L. W., C. J. A. Bradshaw, and B. W. Brook. 2007. Minimum viable population size: A meta-analysis of 30 years of published estimates. *Biol. Conserv.* 139: 159–166.
- Więcek, M., P. Martin, and M. Gąbka. 2013. Distribution patterns and environmental correlates of water mites (Hydrachnidia, Acari) in peatland microhabitats. *Exp. Appl. Acarol.* 61: 147–160.
- Wildermuth, H., 2001. Das Rotationsmodell zur Pflege kleiner Moorgewässer – Simulation naturgemäßer Dynamik. *Naturschutz Landschaftsplan*. 33: 269–273.