Species richness and composition of macroinvertebrate assemblages in the Bavarian Forest National Park: Preliminary results of the stream monitoring

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Abstract
Ongoing monitoring of streams in the Bavarian Forest National Park (BFNP) is focused on the effects of climate changes and natural disturbances on the community composition and diversity of benthic macroinvertebrates in the Bohemian Forest. This study provides the data on macroinvertebrate assemblages of ten streams draining the area of the BFNP (BF streams), which are included in the monitoring survey, and 48 sites distributed evenly in the Große Ohe stream network (GO catchment). The GO catchment serves as a model stream network to study environmental and spatial structuring of macroinvertebrate assemblages on the local scale. We aim to evaluate species richness, abundance and species composition of macroinvertebrates along the main environmental gradients and to consider the possible impact of acidification. Species recorded at all studied sites are compared with available literature data from the BFNP. Altogether 40,682 individuals of 184 species were recorded in our study, 130 and 168 species in the BF streams and GO catchment, respectively. Macroinvertebrate assemblages of the BF streams are significantly influenced by substrate roughness and water quality. Within the GO catchment, stream size and acidity are the main ecological gradients forming the assemblages, with a significant influence of local habitat properties (such as amount of coarse particulate organic matter (CPOM), concentration of ionic aluminium (Al), depth of water, and water chemistry). Species richness of macroinvertebrates is positively related to stream size and negatively to CPOM, whereas their abundance is significantly affected by acidity and Al, being strongly limited in Al>53 µg.l⁻¹. More species of Ephemeroptera, Coleoptera and Diptera, including several acid sensitive species, were found in the GO catchment in comparison with earlier data from the period of strong acidification, which indicates ongoing recovery of streams from acidification. Streams are recently inhabited by numerous moderately acid sensitive species, which is mirrored by their favourable acid status (prevailing acid class 2, predominantly neutral to episodically weakly acidic conditions) assessed based on scoring of acid sensitive species. Acid status based on the overall composition of assemblages shows prevailing acid class 3 (periodically critically acidic conditions) with considerable number of streams of acid classes 4 and 5 indicating strong acid stress. Overall, acid status of streams is not aligned with the altitude, stream size or any habitat property within the model GO catchment suggesting that the stream network is a mosaic of various local conditions determining water chemistry. Thus, macroinvertebrates can find suitable conditions or refugia in some parts of the catchment.

Key words: biodiversity, macroinvertebrates, acidification, acid status assessment, Bohemian Forest, Große Ohe
INTRODUCTION

Springs and streams of the Bavarian Forest National Park (BFNP, German part of the Bohemian Forest) have kept the natural character despite historical local modifications of channels to facilitate timber transportation. Dense stream network is dominated by cold headwater (crenal and epirhittal) streams with relatively heterogeneous catchments, thus offering diverse environment for aquatic biota. In-stream environment is significantly influenced by dead wood in different stadium of decomposition. Dead wood of different size, from branches to large logs forming large cascades and pools or, in extreme cases, completely covering stream channels, is abundant particularly in streams flowing in unmanaged forests. Characteristic phenomenon is the interference of the effects of anthropogenic atmospheric acidification and natural disturbances on the stream water chemistry. Strong atmospheric acidification of headwater streams occurred from the 1960s to 1980s, peaked in the mid-1980s, and was followed by gradual recovery since the 1990s (Alewell et al. 2001, Schäumburg et al. 2010, Beudert & Gietl 2015) caused by significant reduction in sulphur dioxide, nitrogen oxides and ammonia emissions in central Europe (Kopáček et al. 2002, Kopáček & Veselý 2005). Concurrently, rapid dieback of large forest area due to wind storms and/or bark beetle outbreaks peaking in 1997 caused changes in the chemistry of all water fluxes, mainly leaching of nitrate, dissolved organic carbon (DOC) and aluminium to streams draining affected areas and also to lakes (Vrba et al. 2014, Beudert et al. 2015, Beudert & Gietl 2015, Kopáček et al. 2017). Consequent water quality deterioration in streams and increase of episodic acid runoff temporarily slowed down the recovery of streams from acidification (Schäumburg et al. 2010, Hoffmann et al. 2011). Nevertheless, mechanism of episodic acidification of stream water has changed, as it is no longer driven by sulphate, but by DOC, which has to be considered as a natural process (Beudert & Gietl 2015).

Regular monitoring activities in the BFNP encompass the long-term acidification monitoring and hydrological monitoring of the model catchment with near-natural forest without management intervention. The hydrological monitoring commencing in 1977 has been focused on the water cycle in the Große Ohe catchment and runoff changes caused by the transition from commercial to near-natural forest in this catchment (Beudert & Gietl 2015). The long-term acidification monitoring commenced in 1986 and has been focused on the assessment of recovery from acidification based on water chemistry, macroinvertebrates and diatoms in Seebach, Hinterer Schachtenbach, Vorderer Schachtenbach, Große Ohe, and Rachelsee (LfW 1999, Kifinger et al. 2004, Schäumburg et al. 2008, 2010, Hoffmann et al. 2011, Scheel et al. 2014, LfU 2015). These sites are a part of the network of the ICP Waters, the International Cooperative Programme for assessment and monitoring of the effects of air pollution on rivers and lakes (Skjelkvåle & De Wit 2011). In 2016, a systematic monitoring aiming to evaluate the effects of natural disturbances and climate changes on biodiversity of streams (focusing mainly on macroinvertebrates) started at seven streams distributed throughout the BFNP (Große Deffernik, Kolbersbach, Kleiner Regen, Große Ohe, Kleine Ohe, Sagwasser, and Reschbach). The conceptual framework of the monitoring is analogous to the terrestrial biodiversity survey BIOKLIM (for more details see Bässler et al. 2015). Sampling sites are distributed in seven streams following the altitudinal gradient every 100 altitudinal meters from 600 to 1100 m a.s.l. This monitoring is designed as a long-term study with proposed regular repetition of sampling in the future.

Information on stream macroinvertebrates are, however, incomplete, and generally missing from the pre-acidification period (but see Thiem 1906). Several studies are published in grey literature and, thus, inaccessible for a wider scientific audience (e.g. Eisenreich 1974, Kuhn 1984, Schöll 1987). Some individual records of species are available in faunistic stud-
ies (e.g. HEUBAUER 1975, 1980, SEITZ 1988, 1992, WEINZIERL 1999, SOLDÁN et al. 2012). Probably the first complex faunistic study of stream biodiversity by SCHÖLL (1987, 1989) was focused on the southern (old) part of the current BFNP where catchments of Flanitz, Schwarzach, Große Ohe, Kleine Ohe, and Sagwasser were investigated. Based on the field study conducted in 1984 and 1985, SCHÖLL (1989) reported 182 species (or higher taxa) and pointed out the role of pH in the distribution of species calling for immediate reduction of emissions of acidifying compounds. Another complex faunistic study on four aquatic insect orders (Ephemeroptera, Plecoptera, Coleoptera, and Trichoptera) covered entire Niederbayern and reported 289 species for the Bavarian Forest (SCHULTE & WEINZIERL 1990). The study area, however, included the whole Bavarian Forest, thus, also species found at lower altitudes out of the BFNP were included. The same is true for PITSCH (1994) who studied four aquatic invertebrate groups (Trichoptera, Odonata, Amphipoda, Isopoda) reporting 121 species in the Bavarian Forest, and provided the distribution of individual species in the longitudinal profile of six studied stream systems. Data gathered during the long-term acidification monitoring of streams are unpublished, partially available in the project reports (e.g. KIFINGER et al. 2004, SCHAUMBURG et al. 2010). They document gradual increase of species richness in recovering streams which was slowed down or interrupted by increased effects of episodic acid runoffs after the forest dieback (SCHAUMBURG et al. 2010, HOFFMANN et al. 2011).

In this study, we provide new data on macroinvertebrates inhabiting streams in the BFNP based on the two separate surveys conducted in 2015. Both surveys are the part of the broader transboundary study focusing on the stream biodiversity in the Bohemian Forest. The first survey explores patterns in diversity and assemblage structuring of macroinvertebrates in two neighbouring montane catchments in the non-interventional part of the Bohemian Forest (Šumava in Czech), upper Große Ohe catchment in the BFNP and upper Vydra catchment in the Šumava National Park. The second survey, already mentioned above, investigates stream biota and environmental conditions along the gradient of altitude in order to evaluate the effects of natural disturbances and climate changes on biodiversity of streams in the BFNP.

Both surveys have started recently and full data are not available yet. This study presents the preliminary results with a special focus on insufficiently known macroinvertebrate diversity of the Bavarian Forest streams. The main aims of the study are to describe species richness and composition of macroinvertebrate assemblages inhabiting main streams draining the BFNP and the model Große Ohe catchment, which together cover all stream types in the studied area. We aim to explore main gradients in species data and factors governing species richness, abundance and composition of macroinvertebrate assemblages. We consider the possible effect of acidification on macroinvertebrates. Last but not least, we aim to provide a species list of the macroinvertebrates found at the studied sites and compare them with available literature data.

**Material and Methods**

**Study sites and data**

Two sets of species and environmental data were evaluated. The first one included species data from 48 sites distributed in the upper Große Ohe catchment (Fig. 1), which were supplemented by detailed environmental data. The second dataset included species data from 10 main rivers draining the area of the BFNP (Fig. 2).
Fig. 1. Map of the GO catchment with the investigated sites (numbers of sites are available in Table 1). Size of symbols indicates discharge of streams.
Große Ohe catchment (GO catchment)

The upper Große Ohe catchment, hereinafter referred as GO, is 19.1 km² large, with the altitudinal gradient from 760 to 1300 m a.s.l. The catchment is 98% forested, with Norway spruce (*Picea abies* (L.)) and European beech (*Fagus sylvatica* L.) being the dominant species ([Beudert & Gietl 2015](#)). Since 1992, bark beetle (*Ips typographus* L.) damaged spruce forests on 58% of the catchment area and converted them into varying succession stages with rapidly growing young spruce ([Beudert et al. 2015](#)). Forty-eight sites (Fig. 1, Table 1) were selected based on four rules: sites to be distributed as much evenly as possible; the proportion of Strahler’s stream orders to reflect their real proportion within the catchment; sites not to be too far from roads or footpath to avoid disturbing protected landscape; and finally, the number of sites not to exceed 50. The same approach was applied in the upper Vydra catchment in the Šumava National Park where 43 sites were selected. In contrast to the Große Ohe, the network of Vydra is less dense and streams are rather low-sloping, flow-

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**Fig. 2.** Map of the BF streams investigated, with seven altitudinal transects and sites studied within them in the monitoring of stream biodiversity. Legend of symbols: blue cross – sites on the BF streams studied in this study (with the name of the sites, see Table 1), red circles – sites on altitudinal transects, green square – sites with additional sampling of insects by Malaise traps.
Table 1. List of sites with coordinates and main environmental characteristics. Nr. – number of site used in Table 3 and Figs. 1, 2, 9; ASW – average stream width, AV – average velocity, TP – total phosphorus, phi – substrate roughness.

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<th>E coord.</th>
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<th>Discharge (m³.s⁻¹)</th>
<th>AV (m.s⁻¹)</th>
<th>Conduct. (µS.cm⁻¹)</th>
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ing on a montane plain covered by spruce forests in different succession stages and large area of raised bogs with dense growth of *Pinus × pseudopumilio* (Willk.) Beck.

Main streams draining the Bavarian Forest NP (BF streams)

Stream network in the BFNP is dominated by rapid headwater streams with coarse to very coarse bed substratum, flowing on heterogeneous and steep terrain. The largest streams draining the area are only between four- and six-meter wide. Ten streams along the NW to SE border of the BFNP were investigated (Fig. 2, Table 1) in order to bring the data on macroinvertebrate variability to help to establish the design of the systematic monitoring of

Fig. 3. Photos of different stream habitats investigated. A – 33_brook with impoundment 2, B – 11_Ra- chelschachtenbach 1, C – 3_Tiefe Seige 1, D – 42_Seebach 5, E – 55_Große Ohe 3, F – 52_Reschbach (see Table 1 for more information on these sites).
streams along the altitudinal gradient. Altitude and type of streams were similar, i.e. epi- to metarhithral streams (average stream width 6 m) with coarse, stones and boulders dominating, bed substrate and altitude about 785 m a.s.l. (Fig. 3, Table 2). Some of the streams were rich on aquatic mosses. Water had near neutral pH; current velocity was relatively high (average velocity 0.67 m.s$^{-1}$), with turbulent flow in all streams.

Literature data

Comparison of our data collected in 2015 with studies covering the entire Bavarian Forest (Pitsch 1994) and Niederbayern (Schulte & Weinzierl 1990) is complicated as the studies include only the total list of species for the entire area of the Bavarian Forest, i.e. including low altitude streams outside the National Park and in the Danube valley. Therefore, only species recorded by our study and both above-mentioned faunistic studies were included in Table 3. Direct comparison is possible only with Schöll (1987) and Kifinger et al. (2004) that studied the GO catchment (Tables 3, 4). Schöll (1987) studied macroinvertebrates at 14 streams in the GO catchment (included also in our study) in 1984–1985, i.e. in the period of strong acidification. Kifinger et al. (2004) included data from acidification monitoring of four streams in the Große Ohe catchment (Seebach, Vorderer Schachtenbach, Hinterer Schachtenbach, Große Ohe) in 2001–2002, i.e. period after the forest dieback. Both studies concerned with all macroinvertebrates except for Chironomidae, which were not determined. Later reports of the acidification monitoring (SchAumburg et al. 2010, Hoffmann et al. 2011, LFU 2015) did not include the list of recorded species and data on macroinvertebrates were presented only as acid classes for individual rivers or periods based on species data.

Sampling methods and processing of samples

One-shot sampling of macroinvertebrates was conducted in May 2015 at all investigated sites. Sampling was based on a standard multi-habitat scheme designed for sampling major in-stream habitats proportionally according to their share within the sampling section (AQEM CONSORTIUM 2002). Each sample consisted of 20 plots 0.25×0.25 m (1.25 m$^2$) taken from all habitat types with a share of at least 5% coverage at the sampling site. Samples were taken by a standard hydrobiological hand net with 0.5 mm mesh size. Sampling protocol was based on standard AQEM protocol. The cover of different particle sizes on the stream bed was visually estimated and substrate roughness was described by phi (Gordon et al. 1992). Slope was measured using optical level (South NL20) and water velocity was measured by Flo-Mate device (Model 2000; Marsch-McBirney, Frederick, MD, USA). Discharge was calculated from water velocity and depth measured in a cross transect at each site. Samples of macroinvertebrates were fixed with formaldehyde and hand-sorted under the dissecting microscope in the laboratory. Sorted individuals were identified by specialists to as low determination level as possible. Two thirds of the taxa in the final datasets are species (121 species) and the remaining taxa are on higher levels, including 27 groups of species, 33 genera and 3 subfamilies or families. As the majority of taxa was identified to the species level, we use the term “species” for all the taxa throughout the text. Identified individuals were preserved in 70% ethanol or mounted dry and deposited at the Department of Botany and Zoology, Masaryk University in Brno. Only oligochaetes, which were not abundant, were not determined and are not included in the dataset. Semiquantitative sampling was supplemented by collecting of Plecoptera and Trichoptera adults by sweeping of riparian vegetation.

Samples of water for hydrochemical analyses were taken along with the sampling of macroinvertebrates in the Große Ohe catchment (and also in the Vydra catchment), not in the BF streams. Only one-shot sampling of water completed within ten days after the snowmelt-
water outflow is available due to restricted entrance to the area, which is situated in the core zone of both national parks. The area, with abundant fallen trees, windthrows and dead wood, is not safely accessible before the snowmelt in spring and the entrance is strictly restricted due to nesting of capercaillie (*Tetrao urogallus*) until the end of July. Shortly after the sampling, water samples were filtered through 0.4-µm pore size glass-fibre filters (MN-GF5) for the analyses of dissolved compounds. Dissolved organic carbon (DOC) was ana-

Table 2. Environmental characteristics of the 48 sites in the Große Ohe catchment and 10 main rivers draining the Bohemian Forest NP.

<table>
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<th>Variables</th>
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<th>BF streams</th>
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<td></td>
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lysed in the filtrate with a LiquiTOC analyser (Foss/Heraeus). Dissolved phosphate ($P_d$) was determined by the molybdate method after perchloric acid digestion and acid neutralising capacity (ANC) by Gran titration. Fractionation of Al was analysed in filtered samples. Ionic Al (Al$_i$) was obtained as the difference between dissolved and organically-bound Al. Concentrations of major ions were analysed by ion chromatography. All concentrations used in this study were above the detection limits and accuracy of the analyses was checked using ion balance control including ionic Al forms and organic acid anions for each sample according to KOPÁČEK et al. (2000). More details on the analytical methods, their accuracy, and precision are given in KOPÁČEK et al. (2004).

Data evaluation

Differences in the species richness and abundance at sites of GO catchment and BF streams were tested by non-parametric Mann-Whitney U test. Rarefaction curves were performed to evaluate the possible impact of different number of individuals on species richness in the datasets. For each sampling site, acid class scored by species was calculated. Species with unknown affiliation to acid classes based on BRAUKMANN & BISS (2004) were excluded from the analysis. Two approaches of acid class assessment were used: (i) Based on maximum sensitivity of bioindicators – species are cumulatively added from acid sensitive to acid very resistant till the threshold is reached. Calculation is based on abundance classes of species (according to ALF et al. 1992), when threshold is 4, or based on dominance of species, when threshold is 10% (BRAUKMANN 2001, BRAUKMANN & BISS 2004). (ii) Based on the composition of all classified species when the acid class expresses mean value of acid classes scored by all species included in the analysis. The value is weighted average of acid class based on species abundances.

Multidimensional statistic methods were used to describe the variability in species data from the GO catchment and BF streams. Non-Metric Multidimensional Scaling (NMDS) was used to project sites in 2-dimensional ordination space. NMDS was calculated on Bray-Curtis dissimilarity matrix obtained from ln(x+1) transformed species data. We applied NMDS via a wrapper function metaMDS of the vegan package (OKSANEN et al. 2017), which performs several random starts and rotates the final projection so that the variance is maximized on the first dimension. Once the NMDS ordination was finalized, we searched for environmental variables that would enable the interpretation of general gradients represented by NMDS dimensions using visualisation techniques and by fitting smooth surfaces onto the ordination via Generalized Additive Models (GAM). We also searched for species that best followed these gradients with the same methods, but with expected Poisson distributed errors. Environmental variables for constrained ordinations were selected based on Spearman correlations. Variables with R>0.65 were excluded from the analyses. Forward selection was performed to select variables explaining the highest percent of variability for db-RDA (via ordiR2step function of the vegan package, OKSANEN et al. 2017).

All statistical analyses were carried out in R (R CORE TEAM 2017) using the following packages: “vegan” (OKSANEN et al. 2017), “ggplot2” (WICKHAM 2009), “Hmisc” (HARRELL 2017), “RColorBrewer” (NEUWIRTH 2014) and “goeveg” (GORAL & SCHELLENBERG 2017).

RESULTS

GO catchment and BF streams: species richness and abundance

In total, 40,682 individuals and 184 species were recorded in the BF streams and GO catchment (Table 3, 5); 114 species were common, 16 and 54 species were found only in the BF streams and GO catchment, respectively. Eight endangered (2 – stark gefährdet) or vulner-
able (3 – gefährdet) species based on the Bavarian/German Red list (BiNOT et al. 1998, ANONYMUS 2005) were found: Ameletus inopinatus (3/2), Rhithrogena hercynia (–/2), Perla marginata (3/3), and Leuctra alpina (3/3), Brachycentrus montanus (3/–), Hydropsyche silvenii (3/2), Drusus chrysotus (3/3), and Chaetopteryx major (3/3). The total number of species was higher in the GO catchment (168 species) than in the BF streams (130 species). However, higher species richness per site (i.e. alpha diversity) was found in the BF streams (Mann-Whitney U test, p<0.001, Fig. 4) which indicates higher habitat heterogeneity there. The total abundance per a site was also higher in the BF streams (Mann-Whitney U test, p = 0.006, Fig. 4). Higher number of species found in the GO catchment was influenced more by higher beta diversity within the catchment than higher number of individuals found, as the rarefaction curves reach their asymptotes (Fig. 5). The most species-rich groups were Chironomidae and Trichoptera (Table 5). Less species of Chironomidae, Coleoptera, and Plecoptera were found in the BF streams than in the GO catchment.

Abundance of macroinvertebrates in the GO catchment was significantly correlated with three mutually related variables, positively with pH and ANC, and negatively with AI concentration (Table 6). Abundance increased with increasing pH being variable above 5.5 at sites with different ANC, while it was variable in AI, from 0 to 53 µg.l⁻¹ and steeply decreased in its higher concentrations (Fig. 6). Species richness was, however, not correlated with acidity and was slightly positively related to discharge and negatively to coarse particulate organic matter (CPOM) in the substrate (Table 6). Relations of species richness and abundance were not evaluated in the BF streams because of low number of sites.

**Composition of macroinvertebrate assemblages and its relation to environmental variables**

**GO catchment**

Stream network of the GO catchment included relatively wide range of stream sizes, from small streamlets 0.3 m wide with discharge $4.10^{-5} \text{ m}^3\text{s}^{-1}$ to a 6-m-wide stream with dis-
Table 3. List of species found in the GO catchment and BF streams. Frequency/mean abundance and list of sites (see site numbers in Table 1) where each species was found, are shown. Species/taxa are sorted according to their frequency in the GO catchment. The following literature data are shown: records from the GO catchment (Sch = Schöll 1987, Kif = Kifinger et. al. 2004) and from the area of Bavarian Forest National park and surrounding area (BFNP: S&W = Schulte & Weinzierl 1990, Pit = Pitsch 1994). “+” = species was found, “−” = species was not found, “n.i.” = group is not included/determined in the study. Acid class values according to Brauckmann & Biss (2004) are shown in the last column. Explanatory notes for acid classes: species occurring in 1 – continuously neutral (not acidic) waters, 2 – predominantly neutral to episodically weakly acidic, 3 – periodically critically acidic, 4 – periodically very acidic, and 5 – permanently very acidic.

<table>
<thead>
<tr>
<th>Group / species</th>
<th>Frequency / mean abund.</th>
<th>Sites</th>
<th>GO catchm.</th>
<th>BFNP Acid class</th>
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<tbody>
<tr>
<td></td>
<td>GO catchm.</td>
<td>BF streams</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Sch</td>
<td>Kif</td>
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<tr>
<td><strong>Ephemeroptera</strong></td>
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<td><em>Baetis alpinus</em> (Pictet, 1843)</td>
<td>28 / 35</td>
<td>10 / 91,5</td>
<td>4, 9, 10, 11, 12, 14, 15, 16, 17, 18, 19, 20, 22, 23, 27, 28, 29, 30, 32, 33, 34, 35, 38, 39, 40, 42, 44, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58</td>
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<tr>
<td><em>Ameletus inopinatus</em> Eaton, 1887</td>
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<td>3 / 3,3</td>
<td>3, 6, 9, 10, 11, 12, 13, 14, 15, 16, 17, 19, 20, 25, 26, 27, 28, 30, 32, 33, 34, 37, 39, 40, 42, 44, 49, 50, 52</td>
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<tr>
<td><em>Baetis rhodani</em> (Pictet, 1843)</td>
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<td>8 / 17,9</td>
<td>4, 18, 22, 27, 30, 32, 33, 34, 35, 38, 39, 40, 42, 44, 45, 46, 48, 50, 52, 53, 54, 55, 56, 57, 58</td>
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<td>9 / 15</td>
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<td><em>Habrophlebia lauta</em> Eaton, 1884</td>
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<td>4, 18, 20, 27, 30, 33, 34, 38, 40, 42, 45, 46, 48, 54, 56</td>
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<td><em>Rhithrogena iridina</em> (Kolenati, 1839) / <em>R. picteti</em> Sowa, 1971</td>
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<td>3 / 3,7</td>
<td>14, 22, 23, 30, 32, 33, 34, 35, 38, 40, 53, 55, 56</td>
<td>-</td>
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<td><em>Ecdyonurus picteti</em> (Meyer-Dür, 1864)</td>
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<td>12, 22, 30, 34, 35, 38, 39, 40, 49, 51, 54</td>
<td>-</td>
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<tr>
<td><em>Nigrobaetis niger</em> (Linnaeus, 1761)</td>
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<td>2 / 5,5</td>
<td>27, 34, 35, 39, 45, 47, 48, 55, 56</td>
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<td><em>Ecdyonurus venosus</em> (Fabricius, 1775)</td>
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<td>6 / 3,5</td>
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<tr>
<td>Group / species</td>
<td>Frequency / mean abund.</td>
<td>Sites</td>
<td>GO catchm.</td>
<td>BFNP</td>
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<td><strong>Epeorus assimilis</strong> Eaton, 1885</td>
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<td><strong>Habroleptoides confusa</strong> Sartori &amp; Jacob, 1986</td>
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<td><strong>Habrophlebia fusca</strong> (Curtis, 1834)</td>
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<td>9 / 18,2</td>
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<td><strong>Leuctra braueri</strong> Kempny, 1898</td>
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<td>10 / 63,9</td>
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<td>Frequency / mean abund.</td>
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<td>GO catchm.</td>
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<td>Sch</td>
<td>Kif</td>
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<td>Amphinemura sulcicollis (Stephens, 1836)</td>
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<td>Isoperla goertzi Illies, 1952 / I. rivulorum (Pictet, 1841) / I. silesica Illies, 1952</td>
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<td>+</td>
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<td>Nemoura cinerea (Retzius, 1783)</td>
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<td>11 / 55 10 / 71,5</td>
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<td>Nemurella pictetii Klapálek, 1900</td>
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<td>1, 7, 8, 10, 25, 35, 43, 46, 47</td>
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<tr>
<td>Leuctra hippopus Kempny, 1899</td>
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<tr>
<td>Group / species</td>
<td>Frequency / mean abund.</td>
<td>Sites</td>
<td>GO catchm.</td>
<td>BF streams</td>
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<td>GO catchm.</td>
<td>BF streams</td>
</tr>
<tr>
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<td></td>
<td></td>
<td>Sch</td>
<td>Kif</td>
</tr>
<tr>
<td><em>Perlodes cf. microcephalus</em> (Pictet, 1833)</td>
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<td>3 / 2,7</td>
<td>28, 40, 42, 44, 52, 53, 55</td>
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<td><em>Nemoura marginata</em> group</td>
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<td>0 / 0</td>
<td>21, 26</td>
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<tr>
<td><em>Chloroperla tripunctata</em> (Scopoli, 1763)</td>
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<td>1 / 4</td>
<td>44, 51</td>
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<tr>
<td><em>Protonemura meyeri</em> (Pictet, 1841)</td>
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<td>1 / 3</td>
<td>48, 56</td>
<td>+</td>
</tr>
<tr>
<td><em>Perla marginata</em> (Panz, 1799)</td>
<td>0 / 0</td>
<td>2 / 5</td>
<td>57, 58</td>
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</tr>
<tr>
<td><em>Protonemura praecox</em> (Morton, 1894)</td>
<td>0 / 0</td>
<td>1 / 10</td>
<td>50</td>
<td>–</td>
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<tr>
<td><strong>Trichoptera</strong></td>
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<td><em>Limnephilidae g. sp. juv.</em></td>
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<tr>
<td><em>Plectrocnemia conspersa</em> (Curtis, 1834)</td>
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<td>3 / 1,3</td>
<td>1, 2, 3, 4, 6, 7, 8, 9, 10, 11, 13, 14, 15, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 39, 40, 43, 46, 49, 50, 51</td>
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<td>10 / 4,6</td>
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<tr>
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<td>3 / 4,7</td>
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<tr>
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<td>0 / 0</td>
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<tr>
<td><em>Odontocerum albicorne</em> (Scopoli, 1763)</td>
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<td>8 / 10,5</td>
<td>14, 16, 18, 20, 22, 26, 27, 28, 30, 31, 33, 34, 39, 40, 41, 42, 44, 45, 48, 49, 52, 53, 54, 55, 56, 57, 58</td>
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<tr>
<td>Group / species</td>
<td>Frequency / mean abund.</td>
<td>Sites</td>
<td>GO catchm.</td>
<td>BFNP</td>
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<td>GO catchm.</td>
<td>BF streams</td>
<td></td>
<td>Sch</td>
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<td>9 / 23,2</td>
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<td>+</td>
</tr>
<tr>
<td>Rhyacophila tristis Pictet, 1834</td>
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<td>6 / 3,8</td>
<td>10, 12, 14, 16, 18, 20, 30, 32, 34, 37, 38, 39, 41, 44, 49, 51, 52, 54, 56, 58</td>
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<td>Potamophylax latipennis (Curtis, 1834) / P. luctuosus (Piller &amp; Mitterpacher, 1783)</td>
<td>13 / 3,1</td>
<td>4 / 2,8</td>
<td>1, 8, 10, 11, 20, 21, 29, 34, 38, 40, 41, 44, 48, 49, 54, 55, 56</td>
<td>+</td>
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<tr>
<td>Rhyacophila fasciata Hagen, 1859 / R. vulgaris Pictet, 1834 / R. obliterata McLachlan, 1863</td>
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<td>8 / 4,9</td>
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<td>Hydropsyche tenuis Navás, 1932</td>
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<td>9 / 20,9</td>
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<td>Chaetopteryx villosa (Fabricius, 1798)</td>
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<td>Lithax niger (Hagen, 1859)</td>
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<td>1 / 2</td>
<td>12, 18, 21, 22, 30, 31, 33, 34, 35, 39, 41, 53</td>
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<td>6 / 5,7</td>
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<td>1 / 2</td>
<td>4, 6, 7, 9, 12, 13, 15, 18, 28, 34, 53</td>
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<td>2 / 1,5</td>
<td>8, 10, 22, 24, 25, 35, 37, 38, 46, 51, 53</td>
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<td>2 / 14</td>
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<tr>
<td>Drusus annulatus (Stephens, 1837)</td>
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<td>1 / 4</td>
<td>8, 12, 17, 22, 25, 32, 33, 35</td>
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<td>Drusus discolor (Rambur, 1842)</td>
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<td>2 / 3,5</td>
<td>9, 10, 12, 13, 18, 28, 44, 49, 51</td>
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<td>3 / 1,7</td>
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Table 3. Continued

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<th>Frequency / mean abund.</th>
<th>Sites</th>
<th>GO catchm.</th>
<th>BF streams</th>
<th>Acid class</th>
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<td>BF streams</td>
<td>GO catchm.</td>
<td>BF streams</td>
<td>Sch</td>
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<td>1 / 4</td>
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<td>+</td>
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<td>7 / 10,4</td>
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<td>4 / 4,8</td>
<td>9, 14, 28, 38, 42, 49, 51, 57, 58</td>
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<td>+</td>
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<tr>
<td>Rhyacophila glareosa McLachlan, 1867</td>
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<td>3 / 2</td>
<td>9, 10, 12, 15, 18, 49, 50, 51</td>
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<td>Crunoecia cf. irrorata (Curtis, 1834)</td>
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<td>Wormaldia occipitalis (Pictet, 1834)</td>
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<td>Agapetus fuscipes Curtis, 1834</td>
<td>3 / 74,7</td>
<td>2 / 21</td>
<td>21, 24, 29, 57, 58</td>
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<td>Driasus chrysotus (Rambur, 1842)</td>
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<td>Anomalopterygella chauviniana (Stein, 1874)</td>
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<td>3 / 2,7</td>
<td>44, 48, 52, 55, 58</td>
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<td>Allogamus auricollis (Pictet, 1834)</td>
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<td>2 / 1</td>
<td>40, 52, 56</td>
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<td>Halesus radiatus (Curtis, 1834)</td>
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<td>1 / 2</td>
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<td>Micrasema longulum McLachlan, 1876</td>
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<td>1 / 1</td>
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<td>Micropterna lateralis (Stephens, 1837)</td>
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<td>0 / 0</td>
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<td>Agapetus ochripes Curtis, 1834</td>
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<td>3 / 2</td>
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<td>Brachycentrus montanus Klapálek, 1892</td>
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<td>1 / 12</td>
<td>58</td>
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<tr>
<td>Hydropsyche dinarica Marinković-Gospodnetić, 1979</td>
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<td>2 / 15</td>
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<td>Hydropsyche silvrenii Ulmer, 1906</td>
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<td>1 / 1</td>
<td>54</td>
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<td>Frequency / mean abund.</td>
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<td><strong>Coleoptera</strong></td>
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<td><em>Limnius perrisi</em> (Dufour 1843)</td>
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<td>10 / 150.3</td>
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<td><em>Elmis latreillei</em> Bedel, 1878</td>
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<td>3 / 3.7</td>
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<td>9 / 14.1</td>
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<td><em>Odeles marginata</em> cf. (Fabricius, 1798)</td>
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<td><em>Esolus angustatus</em> (P.W.J. Müller, 1821)</td>
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<td>10 / 14.7</td>
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<td>8 / 18</td>
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<td><em>Hydraena dentipes</em> Germar, 1842</td>
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<td><em>Hydraena gracilis</em> Germar, 1824</td>
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<td>5 / 6</td>
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<td><em>Hydraena saga</em> Orchymont, 1930</td>
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<td>0 / 0</td>
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<td><em>Oreodytes sanmarki</em> (Sahlberg, 1826)</td>
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<td>5 / 3.6</td>
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<td>+</td>
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<td>0 / 0</td>
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<td><em>Agabus guttatus</em> (Paykull, 1798)</td>
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<td>0 / 0</td>
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<td><em>Elodes</em> sp.</td>
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<td>0 / 0</td>
<td>21, 35</td>
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<td><em>Elmis maugetii</em> Latreille, 1798</td>
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<td>8 / 6.4</td>
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<td><em>Limnephilus truncatellus</em> (Thunberg, 1794)</td>
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Table 3. Continued

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<th>BF streams</th>
<th>Sites</th>
<th>Go catchm.</th>
<th>BFNP</th>
<th>Acid class</th>
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<td><em>Limnius volckmari</em> (Panzer, 1793)</td>
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<td>Kif</td>
<td>S&amp;W</td>
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<td><strong>Diptera, Chironomidae</strong></td>
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<td><em>Tvetenia bavarica</em> group</td>
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<td>6 / 4,7</td>
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<td>n.i.</td>
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<td>4 / 2,5</td>
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<td>n.i.</td>
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<td>n.i.</td>
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<td>n.i.</td>
<td>n.i.</td>
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<td><em>Eukiefferiella minor</em> (Edwards, 1929) / <em>E. fitkau</em> Lehmann, 1972</td>
<td>12 / 6,8</td>
<td>8 / 10,6</td>
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<td>n.i.</td>
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<td></td>
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<td>n.i.</td>
<td>n.i.</td>
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<tr>
<td>Group / species</td>
<td>Frequency / mean abund.</td>
<td>Sites</td>
<td>GO catchm.</td>
<td>BF streams</td>
<td>Acid class</td>
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<td>GO catchm.</td>
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<td><em>Stempellinella brevis</em> (Edwards, 1929) / <em>S. flavidula</em> (Edwards, 1929)</td>
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<td>5, 8, 12, 20, 22, 23, 25, 26, 27, 29, 36, 50, 54, 55, 58</td>
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<td><em>Diamesa damphi</em> (Kieffer, 1924) / <em>D. permacra</em> (Walker, 1856)</td>
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<td><em>Cricotopus tremulus</em> (Linnaeus, 1758)</td>
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<td>12, 16, 17, 18, 22, 30, 34, 40, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58</td>
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<td><em>Paratrichocladius rufiventris</em> (Meigen, 1830)</td>
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<td><em>Corynoneura lobata</em> Edwards, 1924</td>
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<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Group / species</td>
<td>Frequency / mean abund.</td>
<td>Sites</td>
<td>GO catchm.</td>
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<tr>
<td>Prodiamesa olivacea (Meigen, 1818)</td>
<td>4 / 3,8</td>
<td>1 / 16</td>
<td>45, 46, 47, 48, 55</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
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<tr>
<td>Rheocricotopus fuscipes (Kieffer, 1909)</td>
<td>4 / 2,8</td>
<td>0 / 0</td>
<td>17, 33, 45, 46</td>
<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Rheotanytarsus sp.</td>
<td>4 / 3,5</td>
<td>3 / 11,3</td>
<td>34, 40, 44, 48, 54, 56, 58</td>
<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Synorthocladius semivirens (Kieffer, 1909)</td>
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<td>29, 34, 40, 48, 49, 54</td>
<td>n.i. n.i. n.i. n.i.</td>
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<td>Thiemannimyia sp.</td>
<td>4 / 3,5</td>
<td>2 / 1</td>
<td>18, 27, 32, 42, 51, 56</td>
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<tr>
<td>Heliemiella ornaticollis (Edwards, 1929)</td>
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<td>0 / 0</td>
<td>11, 14, 29</td>
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<td>Limnophyes sp.</td>
<td>3 / 1,7</td>
<td>1 / 8</td>
<td>2, 38, 47, 55</td>
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<td>Natarsia sp.</td>
<td>3 / 1,7</td>
<td>1 / 8</td>
<td>1, 34, 40</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
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<tr>
<td>Orthocladius obumbratus group</td>
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<td>0 / 0</td>
<td>23, 29, 33</td>
<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Paracladopelma sp.</td>
<td>3 / 5,3</td>
<td>0 / 0</td>
<td>11, 14, 29</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
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<tr>
<td>Polypedilum pedestre (Meigen, 1830)</td>
<td>3 / 2,3</td>
<td>1 / 2</td>
<td>11, 36, 48, 55</td>
<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Rheocricotopus effusus (Walker, 1856)</td>
<td>3 / 5,7</td>
<td>0 / 0</td>
<td>2, 8, 18</td>
<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Cricotopus reversus Hirvenoja, 1973 / C. inter- sectus (Stæger, 1839)</td>
<td>2 / 20</td>
<td>0 / 0</td>
<td>20, 31</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
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<tr>
<td>Orthocladius rivicola group</td>
<td>2 / 1</td>
<td>0 / 0</td>
<td>22, 30</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polypedilum convictum (Walker, 1856)</td>
<td>2 / 2</td>
<td>0 / 0</td>
<td>8, 32</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
<td></td>
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<tr>
<td>Tanytarsus spp.</td>
<td>2 / 1,5</td>
<td>0 / 0</td>
<td>11, 36</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
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<tr>
<td>Krenosmittia sp.</td>
<td>1 / 1</td>
<td>0 / 0</td>
<td>17</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
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<tr>
<td>Neozavrelia sp.</td>
<td>1 / 8</td>
<td>0 / 0</td>
<td>18</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
<td></td>
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<tr>
<td>Odontomesa fulva (Kieffer, 1919)</td>
<td>1 / 1</td>
<td>1 / 4</td>
<td>47, 55</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
<td></td>
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<tr>
<td>Orthocladius frigidus (Zetterstedt, 1838)</td>
<td>1 / 4</td>
<td>1 / 1</td>
<td>44, 49</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>4</td>
<td></td>
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<tr>
<td>Paraphaenocladius pseudirritus Stenzke, 1950</td>
<td>1 / 8</td>
<td>0 / 0</td>
<td>31</td>
<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Polypedilum uncinatum (Goetghebuer, 1921)</td>
<td>1 / 1</td>
<td>1 / 1</td>
<td>22, 49</td>
<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Psectrocladius limbatellus (Holmgren, 1869) / P. sordidellus (Zetterstedt, 1838)</td>
<td>1 / 1</td>
<td>0 / 0</td>
<td>7</td>
<td>n.i. n.i. n.i. n.i.</td>
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<tr>
<td>Tvetenia discoloripes group</td>
<td>1 / 2</td>
<td>4 / 8,5</td>
<td>44, 51, 54, 56, 58</td>
<td>n.i. n.i. n.i. n.i.</td>
<td>–</td>
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</table>

**Diptera, other families**
<table>
<thead>
<tr>
<th>Group / species</th>
<th>Frequency / mean abund.</th>
<th>Sites</th>
<th>GO catchm.</th>
<th>BFNP</th>
<th>Acid class</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>GO catchm.</td>
<td>BF streams</td>
<td></td>
<td>4</td>
<td></td>
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<tr>
<td><strong>Dicranota sp.</strong></td>
<td>47 / 7.2</td>
<td>10 / 15.3</td>
<td>1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58</td>
<td>+ + n.i. n.i.</td>
<td>4</td>
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<tr>
<td><strong>Simuliidae g. sp.</strong></td>
<td>42 / 36.4</td>
<td>9 / 58.6</td>
<td>1, 2, 4, 5, 6, 7, 8, 9, 10, 12, 13, 14, 15, 16, 17, 18, 19, 20, 22, 23, 24, 25, 26, 27, 28, 30, 31, 32, 33, 34, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 49, 50, 51, 52, 53, 54, 56, 57</td>
<td>+ + n.i. n.i.</td>
<td>–</td>
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<td><strong>Eloeophila sp.</strong></td>
<td>23 / 3.6</td>
<td>7 / 2.4</td>
<td>8, 9, 13, 16, 19, 20, 21, 22, 25, 26, 27, 28, 30, 31, 32, 33, 35, 38, 39, 42, 43, 45, 47, 49, 51, 53, 54, 55, 56, 57</td>
<td>– – n.i. n.i.</td>
<td>5</td>
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<td><strong>Pedicia sp.</strong></td>
<td>17 / 2</td>
<td>2 / 1.5</td>
<td>1, 2, 6, 8, 11, 13, 22, 23, 24, 26, 29, 31, 32, 35, 43, 45, 46, 52, 56</td>
<td>– + n.i. n.i.</td>
<td>4</td>
</tr>
<tr>
<td><strong>Chelifera sp.</strong></td>
<td>16 / 3.9</td>
<td>5 / 1.4</td>
<td>2, 5, 9, 10, 11, 12, 13, 14, 20, 22, 23, 29, 34, 38, 44, 48, 49, 51, 55, 56, 57</td>
<td>– – n.i. n.i.</td>
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<td><strong>Wiedemannia sp.</strong></td>
<td>6 / 1.8</td>
<td>4 / 1.3</td>
<td>3, 5, 18, 20, 30, 34, 50, 51, 52, 54</td>
<td>– – n.i. n.i.</td>
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<td><strong>Ceratopogoninae g. sp.</strong></td>
<td>5 / 2</td>
<td>5 / 1</td>
<td>9, 19, 20, 29, 34, 50, 52, 54, 55, 56</td>
<td>– – n.i. n.i.</td>
<td>–</td>
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<tr>
<td><strong>Ibisia marginata</strong> (Fabricius, 1781)</td>
<td>2 / 2</td>
<td>5 / 30</td>
<td>23, 38, 49, 52, 54, 57, 58</td>
<td>– – n.i. n.i.</td>
<td>2</td>
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<tr>
<td><strong>Molophilus sp.</strong></td>
<td>2 / 2</td>
<td>1 / 1</td>
<td>39, 45, 55</td>
<td>– – n.i. n.i.</td>
<td>3</td>
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<tr>
<td><strong>Neolimnomyia cf. filata</strong> (Walker, 1856)</td>
<td>2 / 1.5</td>
<td>0 / 0</td>
<td>33, 47</td>
<td>– – n.i. n.i.</td>
<td>–</td>
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<tr>
<td><strong>Scleroprocta sp.</strong></td>
<td>2 / 1.5</td>
<td>0 / 0</td>
<td>22, 39</td>
<td>– – n.i. n.i.</td>
<td>–</td>
</tr>
<tr>
<td><strong>Dolichopeza albipes</strong> (Ström, 1768)</td>
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<td>0 / 0</td>
<td>7</td>
<td>– – n.i. n.i.</td>
<td>–</td>
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<tr>
<td><strong>Hemerodromia sp.</strong></td>
<td>1 / 4</td>
<td>1 / 1</td>
<td>21, 56</td>
<td>– – n.i. n.i.</td>
<td>–</td>
</tr>
<tr>
<td>Group / species</td>
<td>Frequency / mean abund.</td>
<td>Sites</td>
<td>GO catchm.</td>
<td>BF streams</td>
<td>Acid class</td>
</tr>
<tr>
<td>------------------------------</td>
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<td></td>
<td></td>
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<td>Sch</td>
<td>Kif</td>
<td>S&amp;W</td>
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<td>Chrysopilus sp. juv.</td>
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<td>0 / 0</td>
<td>2</td>
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<td>Ptychoptera sp.</td>
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<td>0 / 0</td>
<td>38</td>
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<tr>
<td>Tipula cf. varicornis Schummel, 1833</td>
<td>1 / 2</td>
<td>0 / 0</td>
<td>36</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Antocha sp.</td>
<td>0 / 0</td>
<td>1 / 6</td>
<td>58</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Berdeniella sp.</td>
<td>0 / 0</td>
<td>2 / 4</td>
<td>51, 58</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Hexatoma sp.</td>
<td>0 / 0</td>
<td>1 / 1</td>
<td>55</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Chrysops sp.</td>
<td>0 / 0</td>
<td>1 / 4</td>
<td>55</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Megaloptera</td>
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<tr>
<td>Sialis fuliginosa Pictet, 1836</td>
<td>13 / 2,4</td>
<td>4 / 2,8</td>
<td>4, 5, 7, 8, 22, 26, 27, 31, 38, 40, 45, 47, 48, 50, 55, 56, 58</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Crustacea</td>
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<tr>
<td>Gammarus fossarum Koch, 1836</td>
<td>31 / 244,1</td>
<td>5 / 232,6</td>
<td>12, 13, 14, 16, 18, 19, 20, 21, 22, 23, 24, 26, 29, 30, 31, 32, 33, 34, 35, 36, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 50, 51, 52, 56, 57</td>
<td>+</td>
<td>–</td>
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<tr>
<td>Asellus aquaticus (Linnaeus, 1758)</td>
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<td>0 / 0</td>
<td>12, 29</td>
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<td>–</td>
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<tr>
<td>Mollusca</td>
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<tr>
<td>Pisidium casertanum (Poli, 1791)</td>
<td>25 / 9</td>
<td>2 / 6,5</td>
<td>5, 8, 10, 11, 13, 15, 17, 19, 21, 22, 26, 29, 30, 32, 33, 35, 36, 37, 39, 41, 43, 45, 46, 47, 48, 55, 58</td>
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<tr>
<td>Ancylus fluviatilis Müller, 1773</td>
<td>0 / 0</td>
<td>2 / 12</td>
<td>56, 58</td>
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<td>–</td>
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<td>Tricladida</td>
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<tr>
<td>Polycelis sp.</td>
<td>12 / 12,8</td>
<td>7 / 58,4</td>
<td>12, 14, 18, 20, 22, 32, 34, 35, 38, 40, 44, 48, 49, 51, 53, 54, 56, 57, 58</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Dugesia sp.</td>
<td>4 / 26,8</td>
<td>2 / 4,5</td>
<td>3, 16, 29, 35, 52, 58</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Crenobia alpina (Dana, 1766)</td>
<td>1 / 4</td>
<td>0 / 0</td>
<td>24</td>
<td>+</td>
<td>–</td>
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</tbody>
</table>
charge 0.4 m$^3$.s$^{-1}$ (Fig. 3, Table 2). The sites covered wide altitudinal gradient, from 760 to 1095 m a.s.l., and various slope of terrain (0.4–25.6%). Water chemistry in the GO catchment was influenced by acidification and changes caused by the forest dieback and following development of forest within the area. The variability in ANC (range: −21 to 206 µmol.l$^{-1}$) was partly associated with altitude (Spearman correlation $R = −0.53$) and slightly also with the concentration of ionic Al$_i$ (0–201 µg.l$^{-1}$, $R = 0.37$). The sites were relatively variable in the concentration of total phosphorus (TP, 0.8–19.1 µg.l$^{-1}$) and, particularly, DOC (0.5–34.2 mg.l$^{-1}$), both were negatively correlated with altitude (−0.69 in TP and −0.57 in DOC).

Main gradients in species data were associated with stream size (average stream width, depth, and flow velocity) and acidic conditions (ANC, pH, and Al$_i$) linked with altitude (Fig. 7). Water conductivity and substrate (phi and CPOM) were partly independent on them as

**Fig. 5.** Species richness of the GO catchment and BF streams modelled by rarefaction curves. The transparent area around a curve represents 95% confidence interval.

**Fig. 6.** Relation of species abundance, and pH and Al$_i$ at the GO catchment. Different size of circles shows ANC.
they can differ in streams of similar size and acid conditions (Fig. 7). Conductivity represented mainly the concentrations of cations (Ca, Na, K, and less Mg), Cl, and TP, because it was strongly (R>0.60) correlated with them. Average velocity (significantly correlated (R>0.65) with stream width and discharge), pH (correlated with ANC, R = 0.87), and slope (correlated with altitude, R = 0.81) explained 25.2% of variability in species data (Table 7).

![Diagram of variables significantly fitted into the ordination of samples of the GO catchment. The size and colour of the symbols are proportional to the measured values of the variables, while the contour lines indicate their fit into the ordination. Phi value decreases with increasing roughness of bed substrate.]

Fig. 7. The NMDS ordination diagrams showing variables significantly fitted into the ordination of samples of the GO catchment. The size and colour of the symbols are proportional to the measured values of the variables, while the contour lines indicate their fit into the ordination. Phi value decreases with increasing roughness of bed substrate.
Table 4. List of species reported by Schöll (1987) and Kifinger et al. (2004) from the GO catchment not found in our study.

<table>
<thead>
<tr>
<th>Group / species</th>
<th>Schöll 1987</th>
<th>Kifinger et al. 2004</th>
<th>acid class</th>
</tr>
</thead>
<tbody>
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<td><strong>Crustacea</strong></td>
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</tr>
<tr>
<td>Niphargus sp.</td>
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<td></td>
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<tr>
<td><strong>Ephemeroptera</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ephemera ignita Poda, 1761</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leptophlebia marginata (Linnaeus, 1767)</td>
<td>+</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Leptophlebia vespertina (Linnaeus, 1758)</td>
<td>+</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td><strong>Odonata</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aeshna cyanea (Müller, 1764)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pyrrhosoma nympha (Sulzer, 1776)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Plecoptera</strong></td>
<td></td>
<td></td>
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<tr>
<td>Amphinemura standfussi (Ris, 1902)</td>
<td>+</td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Capnia vidua Klapálek, 1904</td>
<td>+</td>
<td>+</td>
<td>3</td>
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<tr>
<td>Leuctra autumnalis Aubert, 1948</td>
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<tr>
<td>Leuctra digitata Kempny, 1899</td>
<td>+</td>
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<td>3</td>
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<tr>
<td>Leuctra handlirschi Kempny, 1898</td>
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<tr>
<td>Leuctra pseudosignifera Aubert, 1954</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Leuctra rauscheri Aubert, 1957</td>
<td>+</td>
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<td>4</td>
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<tr>
<td>Nemoura cambrica Stephens, 1836</td>
<td>+</td>
<td>+</td>
<td>5</td>
</tr>
<tr>
<td>Nemoura mortoni Ris, 1902</td>
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<td>Protonemura montana Kimmins, 1941</td>
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<td>Protonemura nitida (Pictet, 1935)</td>
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<td>Protonemura risi (Jacobson &amp; Bianchi, 1905)</td>
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<tr>
<td>Siphonoperla montana (Pictet, 1841)</td>
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<td><strong>Heteroptera</strong></td>
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</tr>
<tr>
<td>Gerris sp.</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Trichoptera</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acrophyllax zerberus Brauer, 1867</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adicella reducta (McLachlan, 1865)</td>
<td>+</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Beraea pullata (Curtis, 1834)</td>
<td>+</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Ecclisopteryx guttulata (Pictet, 1834)</td>
<td>+</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Glossosoma intermedium (Klapálek, 1892)</td>
<td>+</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Limnephilus centralis Curtis, 1834</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lype phaeopa (Stephens, 1836)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Notidobia ciliaris (Linnaeus, 1761)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parachiona picicornis (Pictet, 1834)</td>
<td>+</td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Philopotomus montanus (Donovan, 1813)</td>
<td>+</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Polycentropus flavomaculatus (Pictet, 1834)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudosilopteryx zimmeri (McLachlan, 1876)</td>
<td>+</td>
<td>+</td>
<td>4</td>
</tr>
<tr>
<td>Psilopteryx psorosa (Kolenati, 1860)</td>
<td>+</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Wormaldia triangulifera McLachlan, 1878</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Coleoptera</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deronectes platynotus (Germar, 1834)</td>
<td>+</td>
<td>+</td>
<td>3</td>
</tr>
<tr>
<td>Elmis rietscheli Steffan, 1958</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydroporus nigrita (Fabricius, 1792)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oulimmius tuberculatus (P. W. J. Müller, 1806)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Platambus maculatus (Linnaeus, 1758)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Diptera</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atherix ibis (Fabricus, 1798)</td>
<td>+</td>
<td></td>
<td>3</td>
</tr>
</tbody>
</table>
Other significant factors, i.e. CPOM, conductivity, Al, and average depth explained up to 2% of variability in species data (Table 7).

The diagram of species best fitted to NMDS ordination (Fig. 8) emphasized mainly species of mid-altitude and near neutral conditions of larger streams. They included mainly common rhithral species, the stoneflies *Amphinemura sulcicollis*, *Leuctra inermis* Gr., and *Protonemura austriaca/intricata*, and running water beetles *Elmis rioloides* and *Limnius perrisi*. Small brooks had usually lower species richness (Table 6) and their assemblages are likely a subset of those at more species-rich sites. Only few species were characteristic for small streams with low pH and higher Al (Fig. 8): *Nemoura cinerea*, *Agabus guttatus*, and

<table>
<thead>
<tr>
<th>Group</th>
<th>GO catchment</th>
<th>BF streams</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ephemeroptera</td>
<td>16</td>
<td>15</td>
<td>16</td>
</tr>
<tr>
<td>Plecoptera</td>
<td>22</td>
<td>17</td>
<td>24</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>37</td>
<td>38</td>
<td>45</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>15</td>
<td>9</td>
<td>16</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>55</td>
<td>31</td>
<td>55</td>
</tr>
<tr>
<td>Diptera (except Chironomidae)</td>
<td>16</td>
<td>14</td>
<td>20</td>
</tr>
<tr>
<td>Megaloptera</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Crustacea</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Mollusca</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Tricladida</td>
<td>3</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Species</td>
<td>168 (153.2±1.8)</td>
<td>130</td>
<td>184</td>
</tr>
<tr>
<td>Individuals</td>
<td>30,354</td>
<td>10,328</td>
<td>40,682</td>
</tr>
</tbody>
</table>

**Table 5.** Number of species found in different macroinvertebrate groups in the GO catchment and BF streams. Rarefied number of species for the GO catchment is in the brackets.

**Fig. 8.** Ordination diagram of species in the GO catchment. Only species with frequency, >2 and fit >0.4 are displayed and the font size is proportional to the square root of their total abundance.
Table 6. Spearman correlations of species richness, abundance and acid class of the GO sites with environmental variables. Significant correlations are in bold (p<0.001)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Species richness</th>
<th>Total abundance</th>
<th>Acid class – abundance</th>
<th>Acid class – dominance</th>
<th>Acid class – weighted average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude</td>
<td>-0.29</td>
<td>-0.30</td>
<td>0.36</td>
<td>0.23</td>
<td>0.29</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.34</td>
<td>-0.21</td>
<td>0.27</td>
<td>0.13</td>
<td>0.09</td>
</tr>
<tr>
<td>pH</td>
<td>0.34</td>
<td><strong>0.67</strong></td>
<td>-0.53</td>
<td>-0.63</td>
<td>-0.72</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.05</td>
<td>0.27</td>
<td>-0.22</td>
<td>-0.20</td>
<td>-0.39</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.23</td>
<td>0.19</td>
<td>-0.01</td>
<td>-0.01</td>
<td>-0.10</td>
</tr>
<tr>
<td>O₂</td>
<td>0.14</td>
<td>0.06</td>
<td>-0.11</td>
<td>-0.24</td>
<td>-0.07</td>
</tr>
<tr>
<td>O₂ saturation</td>
<td>0.11</td>
<td>-0.06</td>
<td>0.08</td>
<td>0.00</td>
<td>0.20</td>
</tr>
<tr>
<td>DOC</td>
<td>0.15</td>
<td>0.01</td>
<td>0.14</td>
<td>0.31</td>
<td>0.18</td>
</tr>
<tr>
<td>TN</td>
<td>-0.11</td>
<td>-0.01</td>
<td>-0.24</td>
<td>-0.04</td>
<td>-0.08</td>
</tr>
<tr>
<td>TP</td>
<td>0.33</td>
<td>0.42</td>
<td>-0.22</td>
<td>-0.12</td>
<td>-0.24</td>
</tr>
<tr>
<td>ANC</td>
<td>0.33</td>
<td><strong>0.61</strong></td>
<td>-0.46</td>
<td>-0.56</td>
<td>-0.68</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>-0.07</td>
<td>0.14</td>
<td>-0.28</td>
<td>-0.22</td>
<td>-0.44</td>
</tr>
<tr>
<td>SO₄²⁻</td>
<td>0.17</td>
<td>0.12</td>
<td>-0.01</td>
<td>-0.17</td>
<td>-0.18</td>
</tr>
<tr>
<td>Na⁺</td>
<td>0.26</td>
<td>0.42</td>
<td>-0.36</td>
<td>-0.29</td>
<td>-0.48</td>
</tr>
<tr>
<td>K⁺</td>
<td>-0.09</td>
<td>0.20</td>
<td>-0.21</td>
<td>-0.20</td>
<td>-0.44</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>0.21</td>
<td>0.35</td>
<td>-0.28</td>
<td>-0.25</td>
<td>-0.43</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>0.06</td>
<td>0.20</td>
<td>-0.21</td>
<td>-0.08</td>
<td>-0.18</td>
</tr>
<tr>
<td>Al³⁺</td>
<td>-0.26</td>
<td><strong>0.53</strong></td>
<td>0.44</td>
<td><strong>0.49</strong></td>
<td><strong>0.52</strong></td>
</tr>
<tr>
<td>Discharge</td>
<td><strong>0.50</strong></td>
<td>0.25</td>
<td>-0.33</td>
<td>-0.20</td>
<td>0.02</td>
</tr>
<tr>
<td>Pools proportion</td>
<td>-0.25</td>
<td>-0.10</td>
<td>0.20</td>
<td>0.19</td>
<td>0.12</td>
</tr>
<tr>
<td>Max. velocity</td>
<td>0.36</td>
<td>0.16</td>
<td>-0.14</td>
<td>-0.09</td>
<td>0.08</td>
</tr>
<tr>
<td>Average velocity</td>
<td>0.42</td>
<td>0.24</td>
<td>-0.33</td>
<td>-0.26</td>
<td>0.00</td>
</tr>
<tr>
<td>Max. depth</td>
<td>0.29</td>
<td>0.12</td>
<td>-0.11</td>
<td>0.00</td>
<td>0.21</td>
</tr>
<tr>
<td>Average depth</td>
<td>0.28</td>
<td>0.12</td>
<td>-0.11</td>
<td>0.06</td>
<td>0.22</td>
</tr>
<tr>
<td>Average width</td>
<td>0.41</td>
<td>0.24</td>
<td>-0.11</td>
<td>-0.12</td>
<td>0.12</td>
</tr>
<tr>
<td>Phi</td>
<td>-0.15</td>
<td>0.06</td>
<td>-0.10</td>
<td>-0.04</td>
<td>-0.20</td>
</tr>
<tr>
<td>Macrophytes</td>
<td>-0.11</td>
<td>-0.14</td>
<td>0.09</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>Wood</td>
<td>-0.15</td>
<td>-0.24</td>
<td>0.11</td>
<td>0.05</td>
<td>0.17</td>
</tr>
<tr>
<td>CPOM</td>
<td>-0.52</td>
<td>-0.18</td>
<td>0.21</td>
<td>0.02</td>
<td>-0.13</td>
</tr>
<tr>
<td>FPOM</td>
<td>0.10</td>
<td>-0.01</td>
<td>0.16</td>
<td>0.16</td>
<td>0.02</td>
</tr>
<tr>
<td>Species richness</td>
<td>–</td>
<td><strong>0.61</strong></td>
<td>-0.40</td>
<td>-0.47</td>
<td>-0.21</td>
</tr>
<tr>
<td>Total abundance</td>
<td>0.61</td>
<td>–</td>
<td>-0.50</td>
<td><strong>0.57</strong></td>
<td><strong>0.55</strong></td>
</tr>
</tbody>
</table>

*Plectrocnemia geniculata* were classified as tolerant species adapted to strong acidity (Table 3). Small, but less acidic streams were inhabited by crenobiont *Agapetus fuscipes* sensitive to acidity. *Gammarus fossarum* was abundant at slightly acidic sites with high proportion of CPOM in the bed substrate (cf. Figs. 7, 8).

Based on maximum sensitivity of bioindicators, most of sites belonged to acid class 2, predominantly neutral to episodically weakly acidic streams, however, with almost two times more streams of acid classes 3 and 4 in assessment based on dominance than abundance classes (Fig. 9). Based on all classified species (weighted average), most streams were classified as periodically critically acidic (acid class 3). However, considerable number of
sites fell into periodically strongly acidic and permanently very acidic (acid classes 4 and 5) (Fig. 9) indicating strong biotic changes caused by acidification. Relation of acid class with water acidity measured at the sites was very weak in the acid class based on abundance classes (Table 6), showing very wide extent of pH and mainly ANC at the sites of acid class 2 (Fig. 10). The strongest relation was found in the acid class based on weighted average which significantly correlated with water pH and ANC (R = −0.72), and Al (R = 0.52) (Table 6, Fig. 10). Acid class of sites were not correlated with stream size or any habitat property, and, importantly, neither with altitude nor slope (Table 6).

**BF streams**

Main gradients in species data were associated with altitude, terrain topography (slope) closely linked with substrate roughness (phi) and share of pools, and water pH (Fig. 11). The composition of macroinvertebrate assemblages significantly changed from steep sites with boulder-stony substrate and dominating riffles to low-slope sites with finer substratum and equal share of riffles and pools (samples arranged from right to left in the diagrams, Fig. 11). Most influential variable in db-RDA was phi (strongly negatively correlated with slope and macrophytes cover, R<−0.65) which explained 18.1% variability in species data. Water conductivity (significantly correlated with pH and altitude, R = 0.67 and −0.72) explained 9.1% variability in species data (Table 7).

The diagram with the species best fitted to this ordination (Fig. 12) showed a numerous group of species associated with the middle part of the gradient (moderately-slope streams with stony substrate) including mainly common and abundant rhithral species (*Elmis rioloides*, *Esolus angustatus*, *Protonemura austriaca*/*intricata*, *Amphinemura sulcicollis*, *Polycelis* sp., etc.) and some species with narrower habitat requirements being sensitive to organic pollution and higher temperatures (*Hydropsyche tenuis*, *Rhyacopherla tristis*, *Rhi-throgena hercynia*). Low-slope gravel streams were preferred by *Nigrobaetis muticus*, *Anomalopterygella chauviniana*, *Orthocladius rubicundus* Gr., and *Elmis maugetii*. The second gradient showed the variability associated with the altitude and water pH. Sites at higher altitudes had lower pH, although its range was not wide (from 5.9 to 7.1). Species as-

<table>
<thead>
<tr>
<th>Variables</th>
<th>R²adj</th>
<th>Explained variability (%)</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GO catchment</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average velocity</td>
<td>0.10360</td>
<td>10.36</td>
<td>6.4322</td>
<td>0.002</td>
</tr>
<tr>
<td>pH</td>
<td>0.19916</td>
<td>9.566</td>
<td>6.4886</td>
<td>0.002</td>
</tr>
<tr>
<td>Slope</td>
<td>0.25170</td>
<td>5.254</td>
<td>4.1594</td>
<td>0.002</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.27212</td>
<td>2.042</td>
<td>2.2349</td>
<td>0.004</td>
</tr>
<tr>
<td>CPOM</td>
<td>0.29163</td>
<td>1.951</td>
<td>2.1839</td>
<td>0.002</td>
</tr>
<tr>
<td>Al_i</td>
<td>0.31388</td>
<td>2.225</td>
<td>2.3620</td>
<td>0.004</td>
</tr>
<tr>
<td>Average depth</td>
<td>0.32879</td>
<td>1.491</td>
<td>1.9111</td>
<td>0.008</td>
</tr>
<tr>
<td>&lt;All variables&gt;</td>
<td>0.34795</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>BF streams</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phi</td>
<td>0.18121</td>
<td>18.12</td>
<td>2.9918</td>
<td>0.006</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.27181</td>
<td>9.06</td>
<td>1.9954</td>
<td>0.020</td>
</tr>
<tr>
<td>&lt;All variables&gt;</td>
<td>0.50624</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**Fig. 9.** Acid classes of the sites in the GO catchment calculated by three different methods. Sites are sorted by pH and ANC. Acid classes: 2 – predominantly neutral to episodically weakly acidic streams, 3 – periodically critically acidic streams, 4 – periodically strongly acidic streams, and 5 – permanently very acidic streams.
sociated with higher altitude included species able to inhabit periodically acidic waters, such as *Rhyacophila praemorsa*, *R. glareosa*, *Ameletus inopinatus*, *Heterotrissocladius marcidus* (Table 3). All of them are pollution sensitive, with very low saprobic index (Moog 2002, Graf et al. 2008, Zahradková et al. 2009).

Acid classes of sites calculated by three different methods showed fairly different results. The acid classes based on abundance classes showed half and half streams belonging to acid class 1 and acid class 2, whereas the acid classes based on dominance classified all sites as acid class 2 (Fig. 10). The strictest method, based on weighted average, classified all sites as acid class 3, except for Große Ohe 3 belonging to acid class 4 (Fig. 10).

**Discussion**

The two sets of data included in this study cover the variability in stream types and their environmental attributes, as well as main patterns in macroinvertebrate diversity in the BFNP. The BF streams contain “the largest” streams in the area with sampling sites located near the border of the BFNP, i.e. at the lower altitude of the monitored stream biodiversity (Fig. 2). The main outcome of this study is to provide the data on the array of species relevant for future systematic monitoring focusing on altitudinal shifts in species distribution and variability in the assemblages relevant for planning of the monitoring design. The GO catchment represents a typical example of stream network common at the area, i.e. steep, richly branching network with diverse forest in the catchment (Figs. 1, 2), being a model system for stream biodiversity monitoring in the Bohemian Forest. Sampling sites were located evenly within the catchment and their Strahler’s orders proportionally correspond to real distribution of Strahler’s orders within the catchment (cf. Fig. 1). Thus, data on key ecological gradients and diversity patterns found in the GO catchment are aimed to provide a detailed insight into the structuring of macroinvertebrate assemblages on the local scale.

**Fig. 10.** Relation of acid classes of the sites in the GO catchment calculated by three different methods with pH and ANC.
Species richness and abundance of macroinvertebrates and their relation to acidification

The BF streams provide heterogeneous environment for variety of rhiiral species resulting in higher alpha diversity and abundance of macroinvertebrates than in the GO catchment (Fig. 4), where alpha diversity is positively related to the stream size (i.e. significantly correlates with water discharge, average velocity, and stream width). Higher gamma diversity found in the GO catchment (168 species compared to 130 species in the BF streams) is attributable not only to three times more individuals examined, but mainly to higher environmental variability among sites resulting in higher beta diversity. Rarefied species richness is 153.2±1.8 species found for 10,328 individuals examined in the GO catchment comparing to 130 species in the BF streams (Fig. 5). Within the GO catchment, species richness (and total abundance) is not related to altitude, but rather to stream type and amount of CPOM (Table 6). Likewise, main gradient in species composition of assemblages is related to stream type – stream size and flow velocity (Fig. 7). It emphasizes the necessity to include sufficient number of replicates of same stream types in the altitudinal transects studied in the monitoring of stream biodiversity. Sampling sites added on side branches from 700 to 900 m a.s.l. (see Fig. 2) differing from a stream type of a main stream in each transect, are well-supported.

Species richness of macroinvertebrates is significantly related to water pH and toxic Al concentrations in acidic streams (e.g. Guerold et al. 2000, Baldigo et al. 2009, Traister et al. 2013), although the relation cannot be apparent in naturally acidic streams (Dangles et al. 2004). In the GO catchment, species richness is, surprisingly, not influenced by stream acidity (pH, ANC or Al) or altitude which is aligned with the effects of acidification in the region. The GO catchment has been without any doubts affected by the acidification since the mid-1980s (Schöll 1987, LfW 1999, Alewell et al. 2001, Kifinger et al. 2004, Schauburg

Fig. 11. The NMDS ordination diagrams showing variables significantly fitted into the ordination of BF streams species data. The size and colour of the symbols are proportional to the measured values of the variables, while the contour lines indicate their fit into the ordination. Phi value decreases with increasing roughness of bed substrate.
et al. 2010). Acid sensitive fish and macroinvertebrates (particularly mayflies and *Gammarus fossarum*) died out locally and their absence and/or low abundance and species-richness were documented especially at higher altitudes of the BFNP (Schöll 1987, 1989). The long-term acidification monitoring documented gradual increase of species richness along with increasing pH and decreasing difference between minimal and maximal annual pH in Große Ohe and Vorderer Schachtenbach (Schaumburg et al. 2010). In contrast, this gradual recovery leading to relatively advanced phase of recovery in the late-1990 was followed by pronounced deterioration of water chemistry due to forest dieback in the catchments of Seebach and Hinterer Schachtenbach (Schaumburg et al. 2010). Nevertheless, last data available to us (after 2005) indicate overall positive trends (LFU 2015) and we can assume that macroinvertebrates studied by our study refer to much more developed phase of recovery. Therefore, acidity seems to be recently not so strong environmental filter to structure species richness within environmentally heterogeneous stream network of Große Ohe.

Total abundance of macroinvertebrates, unlike their species richness, is significantly related to ANC, pH and Al\textsubscript{i} (Fig. 6). The relation is non-linear, abundance is low up to pH about 5.5 and then steeply increases being highest at sites with high ANC. Likewise, abundance is variable, related to ANC, in Al\textsubscript{i} concentration from 0 to 53 µg.l\textsuperscript{-1}, and dramatically decreases in Al\textsubscript{i}>53. It clearly demonstrates persisting effect of Al toxicity on macroinvertebrates. The highest Al\textsubscript{i} concentration, extremal within our dataset, is 201 µg.l\textsuperscript{-1} in “Tiefe Seige 1” (TISE1, nr. 3) which has the lowest macroinvertebrate abundance (42). It is comparable with strongly acidified streams with extreme hydrochemistry (pH 4–4.7 and Al\textsubscript{i} between 0.2 and 2.0 mg.l\textsuperscript{-1}) in the Czech Republic (Horecký et al. 2006, 2013), which are inhabited only by extremely acid-tolerant species (*Leuctra nigra*, *Nemurella pictetii*, *Plectrocnemia conspersa*, and *Corynoneura* spp.) (Horecký et al. 2006).

![Fig. 12. Ordination diagram of species in the BF streams. Only species with frequency >2 and fit >0.6 are displayed and the font size is proportional to the square root of their total abundance.](image-url)
Community composition of macroinvertebrates: important gradients and acid status of streams

The main compositional gradient in species data in the BF streams, which are environmentally relatively similar each other, is aligned with substrate roughness (Fig. 11). Composition of macroinvertebrate assemblages differs from sloping Kleiner Regen and Hirschbach above Frauenau drinkwater reservoir and Sagwasser (streams with large stones dominating in bed substrate) to low-sloping Große Ohe near Riedlhütte (fine gravel-dominated substrate) (Fig. 11). Substrate roughness explains 18% of variability in species data. Water conductivity, second significant factor explaining 9% of variability in species data, likely express the difference in water quality among catchments resulting from different bedrock and land cover. Composition of macroinvertebrate assemblages is, naturally, more complex in the GO catchment. Most important factors shaping macroinvertebrate assemblages are average flow velocity and water pH which represent two main independent gradients in species data (Fig. 7). The remaining five significant factors (slope, water conductivity, CPOM, Al, and average stream depth) determine local environmental conditions in different parts of the network. Macroinvertebrates are influenced by local catchment properties, such as local terrain topography determining morphology of streams, forest structure influencing the amount of CPOM in streams, and also water chemistry. The significant effect of water conductivity can be interpreted as possible influence of nutrients, cations, and Cl, because these are significantly correlated with conductivity. Detailed insight to the role of local influences, catchment properties as well as spatial structuring on the macroinvertebrate assemblages within the GO network require further study.

Composition of macroinvertebrate assemblages in the Bohemian Forest streams have been studied mainly to describe and assess the effect of acidification (Růžičková et al. 1998, Alewell et al. 2001, Fríčová et al. 2007, Svobodová et al. 2012, LfU 2015). Acidification monitoring, which gathered extensive species data since the early 1980s, has been concentrated primarily on evaluation of species richness and acid status of streams, and their temporal changes (e.g. Schäumburg et al. 2010, LfU 2015). Acid status assessment is based on maximum sensitivity of bioindicators, i.e. species are cumulatively added from acid sensitive to acid very resistant till the threshold is reached (Braukmann & Biss 2004). In the 1980s, acid status of streams in the Bavarian Forest ranged from permanently very acidic (acid class 5 – Rachelsee inlets) and periodically strongly acidic (acid class 4 – Markungsgraben, Seebach, Große Ohe, and Sagwasser) to periodically critically acidic streams (acid class 3 – Vorderer Schachtenbach, Hinterer Schachtenbach, Hirschbach, and Kleiner Regen) (LfU 2015). Recently (2005–2013), acid status of most streams reached class 2 (predominantly neutral to episodically weakly acidic) or even class 1 (continuously neutral streams) in the case of Hirschbach and Sagwasser (LfU 2015). Only Rachel see inlets remained under strong acid stress (acid class 4).

Evaluation of our data using the same method (i.e. scoring of species with maximal sensitivity, when threshold based on sum of abundance classes of scoring species is 4) shows same results in the above-mentioned streams (Fig. 9). Of all GO and BF streams, six streams reach even the status of continuously non-acidic streams and most streams belong to acid class 2 (Fig. 9), including streams of various acidity (from pH 4.6 and negative ANC to pH 6.8 and positive ANC). Thus, the acid class of streams is not related to pH and ANC measured directly in the field (Table 6, Fig. 10), which suggests that this assessment overestimates acid sensitive species. It is caused by quite permissive threshold, which can be reached by two species of acid class 2 with abundance class 2 (from 2 to 20 individuals according to Alfl et al. 1992), it means in fact by four specimens, irrespective of the rest of specimens in the
sample. Thus, we calculated the acid class based on two other methods, scoring of species with maximal sensitivity with threshold based on species dominance (recommended method by Braukmann & Biss 2004) and by average acid class based on all scoring species in the sample (weighted average). The results are much better related to pH and ANC (Table 6, Fig. 10) and show the relation of the assemblage to the acidity from different perspectives.

Acid class assessment based on the dominance emphasizes the contribution of moderately acid sensitive species scoring many streams to acid class 2, the rest being acid class 3 (with 2 exceptions). However, 31 of 43 streams classified as acid class 2 were scored by the only species, i.e. the remaining scoring species together do not reach the threshold of 10%. The most important species is Gammarus fossarum (scoring in 17 streams), following by Baetis alpinus, Leuctra alpina, Isoperla goertzi/rivulorum/silesica, and Philopotamus ludificatus. The remaining 12 streams (especially six largest BF streams and Große Ohe) showed diverse array of (medium) acid sensitive species scoring to the acid class 2. Acid status of streams based on weighted average is shifted more to acidic streams, because the assemblages are mostly composed of individuals of acid classes 3 and 4 (cf. Table 4). This assessment better recognises assemblages under strong acid stress, i.e. those dominated by acid-tolerant or eurytopic species, such as stoneflies Brachyptera seticornis, Nemoura cinerea, Nemurella pictetii, Protonemura auberti, Leuctra nigra, and caddisflies, Plectrocnemia conspersa, Chaetopteryx villosa, which are not accompanied by moderately sensitive species.

Weak point of this method can be the proportion of unclassified species in each sample, similarly as the definition of threshold in the method based on maximum sensitivity of bioindicators. Importantly, acid status of sites (assessed by all methods) is not related to altitude, stream size or any habitat feature (Table 6). It indicates that macroinvertebrates are influenced by a mosaic of local conditions within the catchment offering local refugia in different parts of the network and different altitude, which is advantageous for biotic recovery.

**Comparison with literature data**

Our data include about a third of species recorded by Schulte & Weinzierl (1990; Ephemeroptera, Plecoptera, Trichoptera, Coleoptera) and Pittsch (1994; Trichoptera, Odonata, Crustacea) from the entire Bavarian Forest, including the area of the BFNP. Schulte & Weinzierl (1990) found 289 species, 101 of them were found in our study, and Pittsch (1994) found 111 species of Trichoptera, 44 of them were found in our study. Putting aside obvious differences in the sampling methods and more habitat types covered by these two studies, we can conclude that they recorded almost all species found in our study (Table 3) including also Ephemeroptera (Ecdyonurus venosus, Nigrobaetis niger) and acid sensitive Trichoptera (e.g. Agapetus fuscipes, Glossosoma conformis) not found in the core zone of the BFNP in the period of strong acidification (Schöll 1987; Kifinger et al. 2004). This indicates that acid sensitive species had some refugia outside the area impacted by acidification in that time, which could later help them to colonise recovering habitats. On the other hand, many acid sensitive or moderately sensitive species, which are very common and abundant in the Bohemian Forest (including the Czech part of the mountains), are recently still missing in the GO catchment and also in many BF streams. They are, for instance, stoneflies Perla marginata and Dinocras cephalotes, and mayflies Ephemerida danica, Centroptilum lutulom, Torleya major, Paraleptophlebia submarginata (e.g. Landa & Soldán 1989, Soldán 1996).

Roughly direct comparison is possible in the GO catchment, where Schöll (1987) and Kifinger et al. (2004) studied 14 sites covering the entire catchment in the period of strong acidification in the 1980 and after the forest dieback in 2001–2002. Total number of species...
recorded by us, 113 species, is comparable with 106 species recorded by these two studies. We found most of species recorded by them, 51 species of 82 species recorded by Schöll (1987) and 54 species of 72 species recorded by Kifinger et al. (2004). Most of the species not recorded by us are not reliably distinguishable in larval stage (Nemoura cambrica, Leuctra handlirschi, L. rauscheri, L. pseudosignifera, Wormaldia triangulifera), thus, can be included at higher taxonomic levels in our data, or cannot be captured by spring sampling (mainly stoneflies with emergence in summer and autumn, Leuctra autumnalis, L. digitata, Protonemura montana, P. nittida, and the mayfly Ephemera ignita) (Table 4). More important difference is that our data do not include numerous crenophilic and crenobiont species, such as Parachiona picicornis, Beraea pullata, Psiloteryx psorosa, Adicella reducta, etc., which indicates that we do not cover the whole (relatively high) beta diversity even by 48 sites within the GO catchment. Very small headwaters and springbrooks can harbour unique fauna highly contrasting to the surrounding rithral streams (Hubáčková et al. 2016) and, thus, they, despite their low alpha diversity, can considerably contribute to biodiversity at the network scale (Meyer et al. 2007, Clarke et al. 2008, Finn et al. 2011).

Importantly, we found distinctly higher species richness of Ephemeroptera, Coleoptera and Diptera (Table 3) which can be interpreted as a sign of colonisation of recovering streams. Moreover, we recorded five species classified as acid sensitive (preferring continuously neutral streams according to Braukmann & Biss 2004) not recorded by the two compared studies, which, however, occur rarely (mayflies Habroleptoides confusa and Ephemera mucronata, caddisflies Agapetus fuscipes and Glossosoma conformis, and the isopod Asellus aquaticus). Only two acid sensitive species, the mayfly Ephemera ignita and the caddisfly Allogamus auricollis, are known from the GO catchment in the period of strong acidification. Remarkable number of species (12) not recorded by Schöll (1987) and Kifinger et al. (2004) are moderately acid sensitive (preferring predominantly neutral to episodically weakly acidic conditions), e.g. Habrophlebia lauta, Rhithrogena iridina/picteti, Rhithrogena loyolaea, Anomalopterygella chauviniana, Hydraena dentipes, and Ibisia marginata. The most abundant moderately acid sensitive species, the amphipod Gammarus fossarum, referred as absent at the higher altitudes by Schöll (1987), is frequent and locally very abundant at our studied sites, but avoiding the highest altitudes. In total, Schöll (1987) and Kifinger et al. (2004) found same number of acid tolerant and resistant species (classes 3–5) as our study (58 and 56 species, respectively), but they found only 13 species of the classes 1 and 2 comparing to 27 species found by us (see Table 3, 4). Moreover, moderately acid sensitive species are recently much more frequent, for example Gammarus fossarum and mayflies (except for B. alpinus) were found only in 2 of 14 localities in the 1980s (Schöll 1987). Thus, the comparison with literature data suggests that recent macroinvertebrate assemblages are more diversified and dissimilar to those described by Schöll (1987) and Kifinger et al. (2004).

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