



# Species diversity and abundance of plant-dwelling chironomids across hierarchical habitat and seasonal scales in the oxbow lakes of River Tisza, Hungary

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With 6 figures and 4 tables

**Abstract:** In temperate regions, plant-dwelling chironomids can be considered as cyclic colonizers that inhabit seasonally ephemeral submerged and floating-leaved macrophytes. In this study, patterns of abundance and species richness of plant-dwelling chironomids were investigated within and among stands of three macrophyte species in oxbow lakes along the River Tisza (Hungary). Chironomids colonized macrophytes rapidly and most species occupied the habitat before it had completely developed in June. Assemblage structure and abundance of particular species varied considerably between plant species, oxbow lakes and summer months in a characteristic succession from June to August indicating the presence of dynamic selection mechanisms. Abundance of most species, except *Endochironomus tendens*, total chironomid abundance, within-sample and total species diversity were highest on the submerged plant *Ceratophyllum demersum*, and most species occurred at the beginning of the colonization succession, in June. The contribution of oxbow lakes (20.3 %) and the month sampled (20.3 %) to total chironomid diversity was higher than would be expected by chance alone and the contribution of within (19.7 %) and between samples (13.5 %) to total chironomid diversity was lower than would be expected by chance alone. We conclude that regional biodiversity conservation action plans should include multiple habitats. Moreover, the significant seasonal species turnover proved the need for seasonal sampling to assess accurately the total diversity of chironomids in the system.

**Key words:** Chironomidae, cyclic colonization, diversity partitioning, balanced hierarchical sampling design, macrophytes, spatio-temporal pattern.

## Introduction

Submerged and floating-leaved macrophytes are the preferred habitat of many aquatic macroinvertebrates. Macrophytes provide living space, shelter from predators and physical disturbances, a substrate for prey (e.g. algae, bacteria, fungi, and small animals), and food for some macroinvertebrates (review in Papas 2007). The presence of macrophytes influences both macroinvertebrate diversity and abundance (Papas 2007, Żbikowski & Kobak 2007, Tarkowska-Kukuryk

2010). The composition and the abundance of plant-dwelling macroinvertebrate communities is also influenced by the architectural and chemical composition, density and structural complexity of macrophyte stands (Cheruvilil et al. 2002, Bogut et al. 2007, Cremona et al. 2008, Hinojosa-Garro et al. 2010, Matias et al. 2010, Tóth et al. 2012).

In temperate regions, submerged and floating-leaved macrophytes are present only at certain times of the year. These plants generally develop from spring to the end of the summer when they collapse

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and survive the winter mainly as seeds, root crowns or small overwintering stems at the bottom or in the sediment (Gettys et al. 2009). Macrophytes can therefore be considered a specific type of predictably ephemeral habitat (Batzer & Wissinger 1996, Wissinger 1997) that is recolonized every growing season by cyclic colonizers (*sensu* Batzer & Wissinger 1996). Cyclic colonization is a migration of organisms between permanent and ephemeral habitats (Batzer & Wissinger 1996). Different life history strategies and dispersal mechanisms may be involved in this process (review in Bilton et al. 2001). Animals, such as molluscs, crustaceans and some insect taxa, including most plant-dwelling chironomid species, may survive macrophyte-free periods in other habitats within the same aquatic system, most often in the sediment, and then occupy macrophytes when they start to develop (Drake 1982, Gilinsky 1984). Other insect taxa may overwinter in terrestrial habitats and then migrate to and disperse across macrophyte-covered aquatic habitats in spring (Moore & Lee 1991).

Although cyclic colonization usually occurs at the local scale (i.e. between the benthos and macrophytes) (review in Batzer & Wissinger 1996), insects with a flying adult stage may disperse over long distances and colonize habitats either as adults or via their deposited eggs (Danell & Sjöberg 1982, Bilton et al. 2001, Frouz et al. 2003, Solimini et al. 2003). Members of most insect taxa with an aquatic larval stage (e.g. Ephemeroptera, Trichoptera, Odonata and Chironomidae) leave the water as adults. As a result of this type of life cycle (i) each new generation will re-colonize the aquatic habitat, (ii) the flying adults may rapidly colonize new habitats, and (iii) aquatic assemblages of these taxa may change considerably over time. Therefore, in insects with flying adults, each year aquatic macrophytes may be colonised by members of both residential and neighbouring populations (Danell & Sjöberg 1982, Batzer & Wissinger 1996, Solimini et al. 2003). Between site dispersal and temporal variability may be even more dynamic in taxa with multi-voltine life histories, such as chironomids (Layton & Voshell 1991, Specziár 2008, Čerba et al. 2010).

The composition and abundance of plant-dwelling macroinvertebrate assemblages are influenced by the structure of the macrophyte stand (Cyr & Downing 1988, Cremona et al. 2008, Hansen et al. 2010, Hinojosa-Garro et al. 2010, Tóth et al. 2012) and the physical and chemical characteristics of the environment (Ali et al. 2007, Čerba et al. 2010, Tarkowska-Kukuryk 2010). There is also potential for variability of these assemblages along spatial and temporal scales (Beck-

ett et al. 1992, Marklund et al. 2001, Balci & Kennedy 2003, Strayer et al. 2003, Čerba et al. 2010). However, the relative role that different spatial and temporal factors play in structuring assemblage composition, abundance and total diversity is less known. To understand the organization of aquatic communities, spatial and temporal scales should be jointly considered (Erős & Schmera 2010). Presumably, early colonizers of ephemeral macrophytes come mainly from the local benthos (Batzer & Wissinger 1996, and references therein), but later the importance of aerial colonization from local and metacommunities increases (Danell & Sjöberg 1982, Solimini et al. 2003). Moreover, since temperate plant-dwelling macroinvertebrate communities are dynamic, and early colonization successions last for  $\leq 6$  months (Lake et al. 1989, de Szalay & Resh 2000, Solimini et al. 2003), the relative role of time (i.e. seasonality) in structuring communities is likely to be higher than in more permanent habitats (e.g. in the benthos).

The aim of this study was to analyse the distributional patterns of plant-dwelling chironomid assemblages in oxbow lakes, densely covered by macrophytes, in the River Tisza system. Specifically, we were interested in (1) to what extent differences between plant species, oxbow lake and season (sampling month) contribute to the variability in chironomid species richness, relative and absolute abundance, and (2) how total chironomid diversity ( $\gamma$ ) partitions across additive  $\alpha$  (within-sample), hierarchical spatial (i.e. between samples, plants and oxbow lakes) and temporal (between months)  $\beta$  components. To quantify the relative role of each explanatory variable we performed balanced hierarchical sampling across three plant species, three oxbow lakes and three months with three replicates of each sampling block. Largely monospecific stands of the three most widely distributed plant species in the region were investigated: European white water lily *Nymphaea alba* L. which has undivided, broad floating leaves; submerged rigid hornwort *Ceratophyllum demersum* L. which has complex, finely dissected architecture; water chestnut *Trapa natans* L. which has both submerged and floating leaves.

We hypothesized that (i) different plant species will be colonized by different chironomid assemblages, and those with more robust plant architecture (i.e. *N. alba* and *T. natans*) may be preferred by miners, whereas those species with a large total plant surface (i.e. *C. demersum* and *T. natans*) would support high larval abundance, while those species with a complex plant architecture (i.e. *C. demersum* and *T. natans*)

may support high species richness. We also hypothesized that (ii) species richness will increase with oxbow lake size (i.e. HHT > BKHT > HAG) according to the species area relationship (e.g. Williams 1943, Adler et al. 2005, Matias et al. 2010), (iii) species richness will increase in time due to the prolonged arrival of new colonizers from metacommunities, and (iv) due to the cyclic availability of macrophytes as habitat for chironomids and the short colonization period available, each assemblage metric will vary between oxbow lakes and sampling months.

## Material and methods

### Study area

This study was conducted on three oxbow lakes, Boroszlókerti-Holt-Tisza (BKHT), Hordódi-Holt-Tisza (HHT) and Három-ágú (HAG), on the River Tisza, Hungary (Fig. 1). A large number of oxbow lakes of variable sizes, trophic states and utilization (conservation area, fishery, recreation) are located along the regulated channel of River Tisza. These habitats have been established either naturally or artificially as a result

of channel straightening, and they maintain diverse aquatic ecosystems and several of them are protected biodiversity conservation areas.

BKHT is located in the Upper Tisza region (48° 05' 10" N; 22° 24' 41" E). The channel was cut through in the 19<sup>th</sup> century during the regulation of the River Tisza which aimed to shorten the flood periods of the river and to decrease flooded areas. Today BKHT is in direct connection with the river and regularly receives fresh water during floods. It has an area of 14 ha and an average depth of 1 m. During the study its shore was covered by diverse marshy vegetation dominated by *Glyceria maxima* (Hartm.) Holmb., *Typha angustifolia* L., *Schoenoplectus lacustris* (L.) Palla, *Sparganium erectum* L. and *Carex* spp., while the water surface was covered with patches of submerged and floating-leaved macrophytes composed mainly of *C. demersum*, *T. natans* and *N. alba*, and to a smaller extent *Potamogeton lucens* L., *Potamogeton crispus* L., *Nuphar lutea* (L.) and *Stratiotes aloides* L.

Lakes HHT and HAG are relatively isolated within the man-made Kisköre Reservoir in the Middle Tisza region. Both HHT and HAG are strictly protected because they form part of a bird reserve and are preserved in their semi-natural state. HHT (47° 39' 01" N; 20° 44' 42" E) was cut off during the regulation of the river in the second part of the 19<sup>th</sup> century. It has an area of 37 ha and average depth is 1.2 m. In the last few years, accelerated sedimentation has resulted in a rapid decrease in its maximum depth from 5–8 m to <3 m. This change sup-



**Fig. 1.** Location of the investigated oxbow lakes, Boroszlókerti-Holt-Tisza (BKHT), Hordódi-Holt-Tisza (HHT) and Három-ágú (HAG) of the River Tisza, Hungary.

**Table 1.** Hydrological and limnological characteristics of the studied oxbow lakes, Boroszló-kerti-Holt-Tisza (BKHT), Hordódi-Holt-Tisza (HHT) and Három-ágú (HAG) of River Tisza, Hungary.

	BKHT	HHT	HAG
Surface area (ha)	14.0	37.0	11.8
Maximum depth (m)	4.2	3.0	1.7
Mean depth (m)	1.0	1.2	0.9
Annual water level fluctuation (m)	1.3	0.6	0.5
Macrophyte coverage (%)			
June	60	55	60
July	75	60	75
August	75	70	85
Water temperature (°C)			
June	23.8	22.9	24.0
July	24.1	23.5	25.2
August	26.7	25.4	26.8
pH			
June	7.9	7.5	7.3
July	7.2	7.0	7.6
August	7.3	7.2	8.1
Dissolved oxygen (mg l <sup>-1</sup> )			
June	8.2	7.5	7.8
July	6.6	7.9	7.6
August	7	7.3	8.1
P and N concentration in the water (mg l <sup>-1</sup> )			
Dissolved orthophosphate	<0.01	–	–
Total P	0.062	–	–
Inorganic N	0.043	–	–
Organic N	0.449	–	–

ported the development of macrophytes, which have covered the greater part of HHT. During the study, the shore was covered mainly by *T. angustifolia*, *G. maxima* and *S. erectum*. At the same time, the pond area was strongly overgrown by stands of *T. natans*, *C. demersum*, *Myriophyllum spicatum* L. and *N. alba*, supplemented by small patches of *P. lucens* and *Salvinia natans* (L.). Lake HAG (47° 39' 29" N; 20° 44' 45" E) was established naturally by the spontaneous cut of a river bend. Its area is 11.8 ha and on average the lake is 0.9 m deep. The shore of this oxbow lake is covered by diverse marshy vegetation dominated by *Phragmites australis* (Cavan.) Trin. et Steud., *T. angustifolia*, *G. maxima* and *S. erectum*, while in the water *T. natans*, *N. alba*, *C. demersum*, *M. spicatum* and *P. lucens* were the most abundant plants.

Physico-chemical characteristics of the BKHT, HHT and HAG are summarized in Table 1.

## Sampling

A balanced hierarchical sampling design was used. Three parallel samples were taken from the monospecific stands of *C. demersum*, *N. alba* and *T. natans* in BKHT, HHT and HAG each month from June (i.e. the start of development of macrophytes) to August (i.e. the onset of decomposition of macrophytes) in summer 2008. The total number of samples was 81 (three samples × three plant species × three oxbow lakes × three months).

Equivolume (0.018 m<sup>3</sup>) samples were collected near the water surface amongst the densest, monospecific macrophyte stands using a Plexiglas box sampler (length × width × height: 30 × 30 × 20 cm). The open sampler was gently submerged into the water and closed, simultaneously cutting all the plants within and preventing the escape of animals. Sampled water and plants were washed through a 0.25 mm mesh sieve, and then the remaining samples (plants and epiphytic animals) were transferred to plastic containers and carried to the laboratory in cooling bags.

Samples were sorted in the laboratory within 24 hours of sampling. The dry mass of sampled macrophytes was measured after desiccation (60 °C, 48 h). Chironomid larvae were preserved in 70 % ethyl-alcohol, mounted on microscopic slides and identified to the lowest possible taxonomic level according to keys of Bíró (1981), Cranston (1982), Wiederholm (1983), Vallenduuk (1999) and Vallenduuk & Moller Pillot (2002). The nomenclature of Sæther & Spies (2011) was applied. Abundance (A) of chironomids was expressed as the number of individuals per kg dry mass of macrophytes.

## Statistical analysis

The relationship of relative chironomid abundance (%) with plant species, oxbow lake and sampling month were investigated by redundancy analysis (RDA) using CANOCO version 4.5 (ter Braak & Šmilauer 2002). RDA was chosen because a preliminary detrended correspondence analysis (DCA) indicated a relatively short gradient length ( $\leq 3.22$  in standard deviation units, see Lepš & Šmilauer 2003). Relative abundance data were  $\arcsin(x^{0.5})$  transformed prior to analyses. Rare chironomid species (i.e. <0.5 % of the total number of larvae collected) were excluded from the analysis. Explanatory variables (plant species, oxbow lake and sampling month) were re-coded into binary dummy variables (Lepš & Šmilauer 2003). First, a preliminary overall RDA model was built, which included all potential explanatory variables (Lepš & Šmilauer 2003). The relative contribution of each variable to the model was assessed by using the forward stepwise selection procedure, and their significance was tested by a Monte-Carlo permutation test with 9,999 permutations under the full model. On the basis of this selection procedure, five (*T. natans*, June, BKHT, *C. demersum*, HHT) dummy variables proved to be significant ( $p < 0.05$ ) and one (July) marginally significant ( $p = 0.055$ ). These six variables were retained in the final RDA model. Note that due to collinearity, the dummy variables *N. alba*, HAG and August were used only as supplementary variables. Statistical significance of ordination axes and the whole model were tested using a Monte Carlo permutation test with 9,999 permutations. Next, a series of RDAs and partial RDAs were conducted to partition the effects of plant species, oxbow lake and sampling month on chironomid assemblage composition (Cushman & McGarigal 2002).

Chironomid abundance and within-sample species richness data were analysed using general linear models in Statistica 8.0 (StatSoft, Inc.). For statistical analyses, abundance data were  $\log_{10}(x+1)$  transformed. Effects of plant species, oxbow lake and sampling month on assemblage composition were evaluated using multivariate analysis of variance (MANOVA) under a full factorial design (i.e. including all variations of factor interactions), followed by univariate analyses of variance (ANOVA) by chironomid species also under a full factorial design and completed with a Tukey HSD post hoc test for significant pure

factor effects. Rare species (i.e. <0.5% of the total number of larvae collected) were grouped into a common category called other chironomids. Thus, MANOVA was based on abundance data of 17 common species and the group of other chironomids.

Between sample variance in chironomid abundance and species richness (all species considered; untransformed data) was investigated using three way (i.e. plant species, oxbow lake, sampling month) ANOVA under a full factorial design followed by a Tukey HSD post hoc test for significant pure factor effects. Evaluation of abundance and species richness data was completed using variance component analysis (VCA). This analysis was used to quantify the relative contribution of the plant species, oxbow lake and sampling month (each handled as random-effects factors) and their second and third degree interactions to between sample variability. Since the data was distributed symmetrically, the ANOVA method (expected MS, MS type I; full factorial design) was used for the VCA (Searle et al. 1992).

To examine the relationship between the sampling effort and the observed species richness, sample-based rarefaction (10,000 permutations) was performed with EcoSim 7.72 software (Gotelli & Entsminger 2011).

Since larger samples tend to include more species (Crist & Veech 2006), prior to diversity partitioning, the independence of within-sample species richness to deviations in sample size was examined. In the present study, the volume of water sampled was constant. However, the occurrence and abundance of plant-dwelling chironomids is more closely related to the density of macrophytes than to the volume of the water and therefore, chironomid abundance is expressed as per unit plant mass or plant surface area sampled (e.g. Strayer et al. 2003, Čerba et al. 2010, Tarkowska-Kukuryk 2010, Tóth et al. 2012). For species richness estimates, however, the problem is that the amount of macrophytes sampled cannot generally be standardized (due to practical constraints) and species richness data cannot simply be divided by the effective sample size (i.e. sampled plant mass). Since the density of macrophytes varied between the equivolume samples, we tested (1) whether this deviation was associated with spatial and seasonal factors (i.e. plant species, oxbow lake and sampling month), and (2) whether within-sample species richness ( $\alpha_{\text{samples}}$ ) depended upon macrophyte density. Macrophyte density proved to vary between plant species and was highest for *T. natans* stands (three way main effect ANOVA,  $F_{2,74} = 17.12$ ,  $p < 0.001$ ; Tukey HSD post hoc test  $p < 0.05$ ), but not between seasons and oxbow lakes (three way main effect ANOVA,  $F_{2,74} = 1.39-3.03$ ,  $p = 0.255-0.054$ , respectively). However, since species richness in each sample ( $\alpha$ ) did not correlate with density of macrophytes (Pearson's correlation,  $df = 79$ ,  $r = 0.074$ ,  $p = 0.408$ ), no adjustment for sample size (i.e. plant mass sampled) was needed.

Consequently, distribution of total chironomid diversity ( $\gamma$  diversity) in the hierarchical habitat levels (i.e. sample, plant species and oxbow lake) and the sampling month was investigated based on an additive diversity partitioning approach (Crist et al. 2003, Gering et al. 2003). According to the hierarchical sampling design, total observed diversity was divided into the following:  $\gamma = \alpha_{\text{samples}} + \beta_{\text{samples}} + \beta_{\text{plants}} + \beta_{\text{oxbow lakes}} + \beta_{\text{months}}$ , where  $\gamma$  is the total number of species identified in the system,  $\alpha_{\text{sample}}$  is the mean species richness of all samples, and  $\beta_{\text{samples}}$ ,  $\beta_{\text{plants}}$ ,  $\beta_{\text{oxbow lakes}}$  and  $\beta_{\text{months}}$  correspond to the average diversity among sampling units of the four investigated sampling levels, namely, between samples, plant species, oxbow lakes and sampling months, respectively. Observed values of  $\alpha$  and  $\beta$  di-

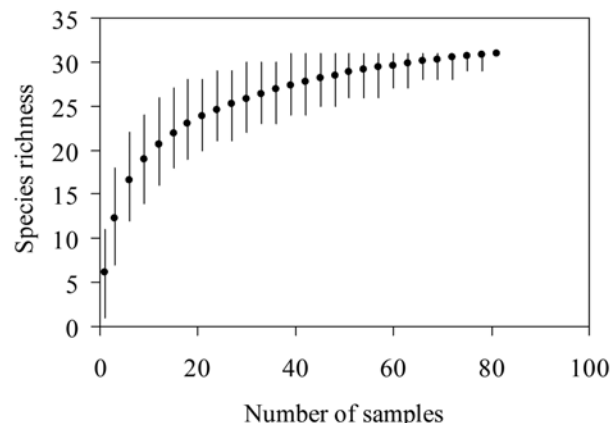
versity components were tested against the null model distribution obtained from an individual based unrestricted randomization (10,000 randomizations) in PARTITION 3 (Veech & Crist 2009). Specifically, it was tested whether the observed values of particular  $\alpha$  and  $\beta$  diversity components significantly differed from chance. A more detailed description of the null model generation and the randomization procedure can be found in Crist et al. (2003).

## Results

### Community structure

Altogether 3088 individuals of 31 chironomid taxa from three subfamilies (four Tanypodinae, four Orthocladiinae and 23 Chironominae) were recorded. Four species, *Paratanytarsus* sp. (27.2%), *Dicrotendipes lobiger* (Kieffer) (17.0%), *Dicrotendipes tritonus* (Kieffer) (11.8%) and *Endochironomus tendens* (Fabricius) (9.6%) dominated the plant-dwelling chironomid community, comprising 65.5% of the total abundance. Rare species were not numerous; there were two singletons and three doubletons in the samples (Table 2). The rarefied species richness curve shows moderate evidence of approaching an asymptote (Fig. 2) suggesting that the total species pool could include a few more species ( $\gamma$  diversity). The number of species per sample varied between 1–14 (mean  $\pm$  SD:  $6.1 \pm 2.9$ ;  $\alpha_{\text{samples}}$ ), and the total abundance of larvae varied between 1–168 ( $38 \pm 35$ ) individuals per sample and 113–17387 ( $2358 \pm 3634$ ) individuals  $\text{kg}^{-1}$  plant dry mass.

Redundancy analysis (full model:  $F = 8.93$ ,  $p < 0.001$ ) and variation partitioning showed that plant species, oxbow lake and sampling month accounted for 23.9%, 8.5% and 9.6% of the variance in the rela-



**Fig. 2.** Rarefied species richness ( $\pm$  95% CI) of plant-dwelling chironomids as a function of number of samples in the oxbow lakes of the River Tisza, Hungary.

**Table 2.** List of plant-dwelling chironomid species, the abbreviations used in tables and figures, numbers of individuals collected (N), frequency of occurrence in samples (FO%) and relative abundance (A%) in the oxbow lakes of the River Tisza, Hungary.

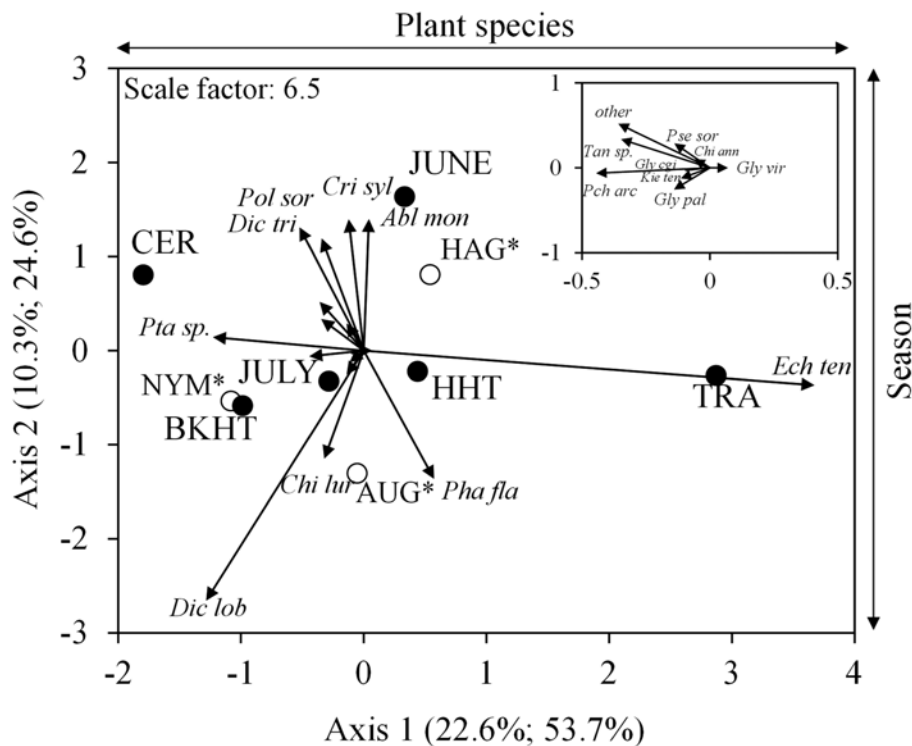
Species name	Abbreviation	N	FO%	A%
<b>Tanypodinae</b>				
<i>Ablabesmyia longistyla</i> Fittkau 1962	Abl lon	2	2.5	0.1
<i>Ablabesmyia monilis</i> (Linnaeus 1758)	Abl mon	87	25.9	2.8
<i>Ablabesmyia phatta</i> (Egger 1863)	Abl pha	10	8.6	0.3
<i>Monopelopia tenuicalcar</i> (Kieffer 1918)	Mon ten	1	1.2	0.0
<b>Orthoclaadiinae</b>				
<i>Acricotopus lucens</i> (Zetterstedt 1850)	Acr luc	2	2.5	0.1
<i>Cricotopus sylvestris</i> gr.	Cri syl	83	34.6	3.1
<i>Cricotopus</i> sp.	Cri sp.	10	8.6	0.4
<i>Psectrocladius sordidellus</i> gr.	Pse sor	60	34.6	2.3
<b>Chironominae</b>				
<i>Chironomus (Camptochironomus)</i> sp.	CCh sp.	6	1.2	0.2
<i>Chironomus annularius</i> agg.	Chi ann	24	1.2	0.8
<i>Chironomus luridus</i> agg.	Chi lur	143	32.1	3.7
<i>Dicrotendipes lobiger</i> (Kieffer 1921)	Dic lob	523	60.5	17.0
<i>Dicrotendipes nervosus</i> (Stæger 1839)	Dic ner	2	2.5	0.1
<i>Dicrotendipes tritonus</i> (Kieffer 1916)	Dic tri	316	49.4	11.8
<i>Einfeldia pagana</i> (Meigen 1838)	Ein pag	9	3.7	0.3
<i>Endochironomus albipennis</i> (Meigen 1830)	Ech alb	10	9.9	0.4
<i>Endochironomus tendens</i> (Fabricius 1775)	Ech ten	500	50.6	9.6
<i>Glyptotendipes caulicola</i> (Kieffer 1913)	Gly cco	3	2.5	0.1
<i>Glyptotendipes cauliginellus</i> (Kieffer 1913)	Gly cgi	55	13.6	1.7
<i>Glyptotendipes pallens</i> (Meigen 1804)	Gly pal	19	18.5	0.6
<i>Glyptotendipes viridis</i> (Macquart 1834)	Gly vir	24	9.9	0.7
<i>Kiefferulus tendipediformis</i> (Goetghebuer 1921)	Kie ten	21	6.2	1.1
<i>Parachironomus arcuatus</i> gr.	Pch arc	63	30.9	1.9
<i>Phaenopsectra flavipes</i> (Meigen 1818)	Pha fla	86	32.1	2.2
<i>Polypedilum cultellatum</i> Goetghebuer 1931	Pol cul	13	6.2	0.5
<i>Polypedilum sordens</i> (van der Wulp 1874)	Pol sor	138	48.1	5.8
<i>Synendotendipes dispar</i> gr.	Syn dis	10	6.2	0.3
<i>Synendotendipes lepidus</i> (Meigen 1830)	Syn lep	7	2.5	0.2
<i>Zavreliella marmorata</i> (van der Wulp 1858)	Zav mar	1	1.2	0.0
<i>Paratanytarsus</i> sp.	Pta sp.	719	74.1	27.2
<i>Tanytarsus</i> sp.	Tan sp.	141	27.2	4.8
Total chironomids		3088		
Number of species		31		

tive abundance data, respectively; while 58% of the variance remained unexplained. The first axis of the ordination (22.6% of the total variance) represented the plant species “gradient”; the high relative abundance of *E. tendens* was clearly associated with *T. nantans* and that of the *Paratanytarsus* sp. with *C. demersum*. The second axis (10.3%) mainly captured the seasonal variability and indicated a shift in time from June assemblages, characterised by *Ablabesmyia monilis* (L.), *Cricotopus sylvestris* gr., *D. tritonus*, and *Polypedilum sordens* (van der Wulp), towards July–August assemblages, which had higher relative

abundance of *Chironomus luridus* agg., *D. lobiger* and *Phaenopsectra flavipes* (Meigen) (Fig. 3). The third axis (4.8%, not shown here) mainly captured the between oxbow lake variability and indicated the weak association of *Paratanytarsus* sp. with HAG and the association of other (rare) species with BKHT.

### Patterns of abundance

Results of the MANOVA showed that all three investigated factors (i.e. plant species, oxbow lake and sampling month) as well as all possible combinations of



**Fig. 3.** Redundancy analysis (RDA) plot describing the relationship between relative abundance data (%) of plant-dwelling chironomids (arrows) and dummy coded explanatory variables (filled circles), plant species, oxbow lake and sampling month in oxbow lakes of the River Tisza, Hungary. Percentage variances represented by axes are indicated in brackets (of species data; of species-explanatory variables relation) after the axis name. Scale factor for biplotting and characteristic environmental gradients represented by the axes are also indicated. Chironomid species with scores close to the centre of the graph are clarified on the small graph in the upper right corner. Explanatory variables marked with “\*” were handled as supplementary variables (empty circles) and were not included in the RDA model (due to collinearity). Abbreviations of chironomid species names are given in Table 1, while abbreviations of explanatory variables are as follows: CER – *Ceratophyllum demersum*; NYM – *Nymphaea alba*; TRA. – *Trapa natans*; BKHT – Boroszló-kerti-Holt-Tisza; HHT – Hordódi-Holt-Tisza; HAG – Három-ágú; AUG – August.

**Table 3.** Results of assemblage level MANOVA based on  $\log_{10}(x+1)$  transformed abundance data of plant-dwelling chironomids along three predictor factors (plant species, oxbow lake and sampling month) and their interactions in the oxbow lakes of the River Tisza, Hungary.

	Wilks' $\lambda$	F	df <sub>effect</sub>	df <sub>error</sub>	p
Intercept	0.034	58.42	18	37	<0.001
Plant	0.038	8.52	36	74	<0.001
Oxbow lake	0.094	4.64	36	74	<0.001
Month	0.050	7.16	36	74	<0.001
Plant × oxbow lake	0.060	2.15	72	148	<0.001
Plant × month	0.138	1.34	72	148	0.068
Oxbow lake × month	0.069	2.00	72	148	<0.001
Plant × oxbow lake × month	0.017	1.46	144	286	0.004

their interactions, except the plant species × sampling month, had a significant effect on chironomid assemblage abundance and structure (Table 3).

Univariate ANOVAs indicated that abundance of most chironomid species (11 out of the 17 tested) and the total abundance of larvae varied between plant

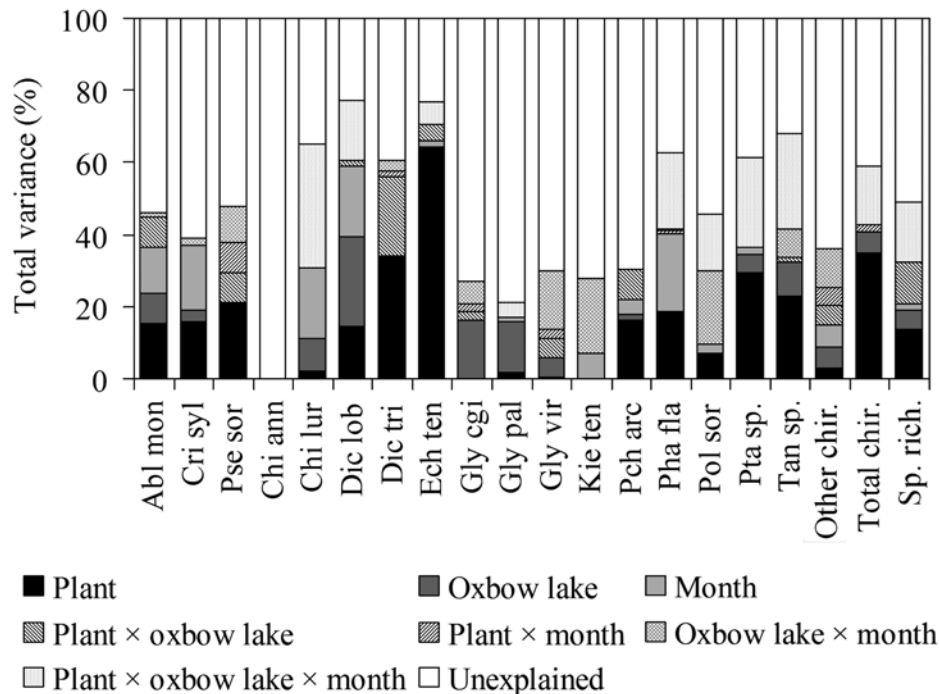
species. Generally, chironomids were most abundant on *C. demersum*, except *E. tendens* which occurred in highest number on *T. natans*. Between oxbow lakes variance was important in eight chironomid species and six of these reached their highest abundance in BKHT. *Ablabesmyia monilis* and *Tanytarsus* sp. were

**Table 4.** Results (*p*-values) of ANOVAs performed on  $\log_{10}(x+1)$  transformed abundance data of abundant plant-dwelling chironomid species, other chironomids and total chironomids, as well for species number along three predictor factors (plant species, oxbow lake and sampling month) and their interactions in the oxbow lakes of the River Tisza, Hungary. Results of the Tukey HDS post hoc tests are reported for significant factor effects by indicating significantly different variable levels (at  $p < 0.05$ ) with different lettering starting with “a” denoting the lowest value.

Variable	Significance of the effect ( $df_{\text{effect}}$ , $df_{\text{error}}$ )						Post hoc test results ( $p < 0.05$ )										
	Intercept	Plant	Oxbow lake	Month	Plant × oxbow lake	Plant × month	Oxbow lake × month	Plant × oxbow lake × month	Plant	Oxbow lake	Month	Plant × Oxbow lake	Plant × Month	Oxbow lake × Month			
Abl mon	(1, 54)	(2, 54)	(2, 54)	(2, 54)	(4, 54)	(4, 54)	(4, 54)	(8, 54)	Cer.	Nym.	Tra.	BKHT	HHT	HAG	June	July	August
	<0.001	<0.001	0.003	0.001	0.071	0.486	0.362	0.510	b	a	a	a	b	b	b	ab	a
Cri syl	<0.001	0.002	0.133	0.001	0.891	0.633	0.506	0.785	b	a	a	a	b	b	b	ab	a
Pse sor	<0.001	<0.001	0.365	0.550	0.092	0.084	0.055	0.647	b	a	a	a	b	b	b	ab	a
Chi ann	0.322	0.375	0.375	0.375	0.416	0.416	0.416	0.447									
Chi lur	<0.001	0.275	<0.001	<0.001	0.018	0.755	0.025	0.001					b	a	a	b	b
Dic lob	<0.001	<0.001	<0.001	<0.001	0.007	0.267	0.032	0.005	c	b	a	c	b	a	a	b	b
Dic tri	<0.001	<0.001	0.563	0.136	0.001	0.379	0.298	0.731	b	a	a	a	b	a	a	b	b
Ech ten	<0.001	<0.001	0.122	0.086	0.010	0.159	0.462	0.090	a	a	b	b	a	a	a	b	b
Gly cgi	0.001	0.904	0.002	0.374	0.764	0.782	0.456	0.994				b	a	a	a		
Gly pal	<0.001	0.359	0.012	0.974	0.388	0.722	0.946	0.344				b	a	a	a		
Gly vir	0.002	0.188	0.007	0.075	0.309	0.494	0.045	0.805				b	ab	a	a		
Kie ten	0.027	0.997	0.059	0.009	0.810	1.000	0.026	0.917							a	b	a
Pch arc	<0.001	0.001	0.078	0.151	0.112	0.821	0.483	0.528	b	b	a	b	a	a	a	a	b
Pha fla	<0.001	<0.001	0.194	<0.001	0.112	0.031	0.037	0.015	b	b	a	b	a	a	a	a	b
Pol sor	<0.001	0.017	0.010	0.005	0.166	0.367	0.001	0.086	b	a	ab	b	a	ab	b	ab	a
Pta sp.	<0.001	<0.001	0.103	0.122	0.754	0.072	0.279	0.009	b	a	a	b	a	ab	b	ab	a
Tan sp.	<0.001	<0.001	<0.001	0.144	0.008	0.100	0.001	0.003	c	b	a	a	a	b	b	ab	a
Other chironomids	<0.001	0.067	0.012	0.010	0.474	0.492	0.179	0.997				b	ab	b	b	ab	a
Total chironomids	<0.001	<0.001	0.072	0.650	0.814	0.044	0.680	0.042	b	a	a	b	ab	b	b	ab	a
Species richness ( $\alpha$ )	<0.001	<0.001	0.005	0.705	0.006	0.820	0.418	0.068	b	a	a	b	ab	a	a		

Abbreviations of chironomid species names are given in Table 1. Cer. – *Ceratophyllum demersum*; Nym. – *Nymphaea alba*; Tra. – *Trapa natans*; BKHT – Boroszló-kerti-Holt-Tisza; HHT – Hordódi-Holt-Tisza; HAG – Három-ágú.





**Fig. 4.** Partitioning effects of plant species, oxbow lake and sampling month, and their interactions on the variability of abundance and species richness of plant-dwelling chironomids in the oxbow lakes of the River Tisza, Hungary. Abbreviations of chironomid species names are given in Table 1. Other chir. – other chironomids; Total chir. – total chironomids; Sp. rich. – species richness.

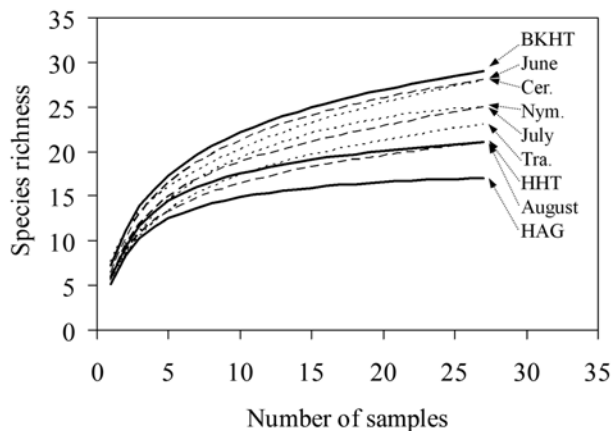
more abundant in HHT and HAG. Sampling month was responsible for variations of larval abundance in seven species, but the temporal dynamics of these species were diverse (Table 4).

According to the VCA, plant species accounted for  $\geq 10\%$  of the total variance in the abundance of 10 chironomid species, especially that of *D. tritonus* (33.6%) and *E. tendens* (64.3%), as well as in the total chironomid abundance (34.7%). Oxbow lake explained  $\geq 10\%$  of the total variance in the abundance of *D. lobiger*, *Glyptotendipes cauliginellus* (Kieffer) and *Glyptotendipes pallens* (Meigen), whereas sampling month explained  $\geq 10\%$  of the total variance in the abundance of *A. monilis*, *Cricotopus sylvestris* gr., *Chironomus luridus* agg., *D. lobiger* and *P. flavipes*. Specific factor interactions also proved to be important in some chironomid species. The total explained variance ranged between zero (*Chironomus annularius* agg.) and 77.4% (*D. lobiger*), with a mean of 46.2 ( $\pm 21.6\%$ , SD) at the species level, and it was 59.1% for the total chironomid abundance (Fig. 4).

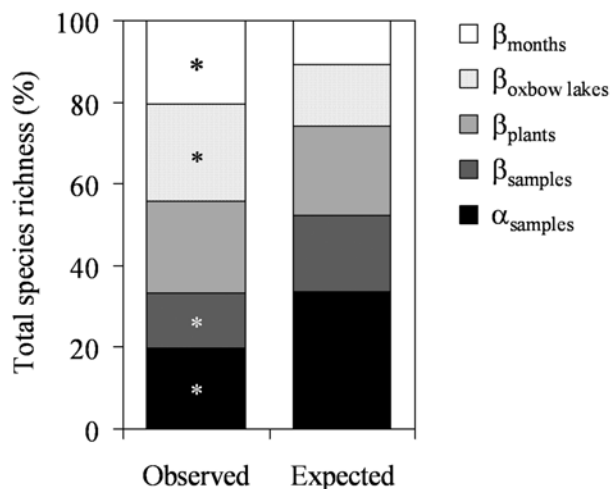
#### Patterns of species diversity

Mean species number per sample varied with plant species, oxbow lake and their interaction, but not between sampling months. On average, *C. demersum* samples were more species rich than *N. alba* and *T. natans* samples, and mean number of species was higher in BKHT than in HAG (Table 3). According to the results of the VCA, 5.2% of the variance of species richness in samples could be attributed to the sole effect of oxbow lake, 13.8% to the sole effect of plant species and 11.6% to the shared effect of these two factors (Fig. 4).

Total species richness also varied along habitat and seasonal scales. Most species were found in *C. demersum* stands (28 species), in BKHT (29 species) and in June (28 species), while fewest species occurred in *T. natans* stands (23 species), in HAG (17 species) and in August (21 species) (Fig. 5). The number of common species was moderate across all plant species (21 species, 67.7%), oxbow lakes (15 species; 48.4%) and sampling months (19 species, 61.3%).



**Fig. 5.** Rarefied number of species of plant-dwelling chironomids as a function of number of samples by plant species (dotted lines), oxbow lakes (continuous lines) and sampling month (broken lines) in the oxbow lakes of the River Tisza, Hungary. Cer. – *Ceratophyllum demersum*; Nym. – *Nymphaea alba*; Tra. – *Trapa natans*; BKHT – Boroszló-kerti-Holt-Tisza; HHT – Hordódi-Holt-Tisza; HAG – Három-ágú.



**Fig. 6.** Relative contribution of additive  $\alpha$  and  $\beta$  diversity components to the total observed species richness of plant-dwelling chironomid community in the oxbow lakes of the River Tisza (Hungary) at four hierarchical sampling scales: sample, plant species, oxbow lake and sampling month. Significant deviations from the randomization based null pattern are denoted with asterisks.

Species diversity significantly differed from that predicted by the null model. Results of diversity partitioning suggested that higher diversity was associated with habitat (oxbow lake) and season than assumed, and species diversity of small-scale habitat patches was relatively low. Namely,  $\alpha_{\text{samples}}$  (19.7%;  $p < 0.001$ ) and  $\beta_{\text{samples}}$  (13.5%;  $p < 0.001$ ) were lower and  $\beta_{\text{oxbow lakes}}$  (23.9%;  $p < 0.001$ ) and  $\beta_{\text{months}}$  (20.3%;  $p < 0.001$ )

were higher than expected by the chance alone, while  $\beta_{\text{plants}}$  (22.6%;  $p = 0.183$ ) did not differ from its expected value (Fig. 6).

## Discussion

In temperate regions, plant-dwelling chironomids act as cyclic colonizers as they inhabit seasonally ephemeral aquatic macrophytes. In the oxbow lakes of River Tisza colonization was rapid and most species occupied the habitat before it had completely developed in June. Assemblage structure and abundance of species varied considerably between plant species and oxbow lakes and temporally, suggesting the presence of dynamic selection mechanisms and succession. The contribution of oxbow lakes and sampling months  $\beta$  components to the total ( $\gamma$ ) chironomid diversity was higher than would be expected by chance alone. However, observed patterns did not fully match with the hypotheses of the present study.

Relative abundance of chironomids (i.e. percent composition of the assemblage) varied mainly across plant species and the RDA reflected the strong association of *E. tendens*-dominated assemblages with *T. natans* contrary to the predominance of *Paratanytarsus* sp. in *C. demersum* and *N. alba* stands. Since larvae of *Paratanytarsus* sp. are epiphytic collector-filterers, their high abundance may indicate a rich periphyton or phytoplankton (Čerba et al. 2010). This taxon dominated in BKHT. Larvae of *E. tendens* often mine into soft or damaged leaves and stems of macrophytes (Moller Pillot 2009). The bulbous buoyancy stems and floating leaves of *T. natans* could provide particularly good conditions for plant-miners (Kondo & Hamashima 1992).

The role of plant species associations and degree of dissection of their leaves in structuring macrophyte-dwelling invertebrate assemblages is antinomic (e.g. Cyr & Downing 1988, and references therein). Many researchers argue that environmental conditions, food resource, habitat heterogeneity (i.e. complexity, size and density of plant patches) and, in particular, the total colonisable plant surface area might play a more important role in structuring macroinvertebrate assemblages than which macrophytes they inhabit (Cyr & Downing 1988, Lalonde & Downing 1992, Pieczyńska et al. 1999, Tarkowska-Kukuryk & Kornijów 2008). A previous investigation on taxonomically heterogeneous plant stands in the same oxbow system of the River Tisza supported the latter suggestion for structuring chironomid communities (Tóth et al. 2012).

Our observations based on highly monospecific macrophyte stands agree with this idea, which emphasizes the strong influence of the architectural complexity of plants (e.g. Krecker 1939, Cheruvelil et al. 2002, Hansen et al. 2010, Hinojosa-Garro et al. 2010). Relative abundance, abundance of most chironomid species, total chironomid abundance, sample level  $\alpha$  and total species richness all varied between plant species. Generally, most of these metrics reached their highest values in the stands of *C. demersum*, which is a submerged macrophyte with highly complex, finely dissected architecture. Due to its more complex architecture (i.e. having both submerged and floating leaves), it might be supposed that *T. natans* would have higher species richness and total larval abundance than *N. alba*, which has only simple floating leaves, but this was not the case. In fact, species richness was higher in *N. alba* stands than in *T. natans*. Our results agree with those of Cremona et al. (2008) who found significantly higher macroinvertebrate abundance on submerged than on floating-leaved macrophytes.

Although total chironomid abundance was the same between oxbow lakes, the species in each of the three oxbow lakes differed notably and only 48.4% of species occurred in all three. This result indicates significant species turnover over at this scale. Based on the RDA, chironomid assemblages of HHT and HAG were more similar to each other than to that of BKHT. This pattern reflects the relative position of these oxbow lakes, as HHT and HAG lie close to each other while BKHT is about 270 km upstream. Since HHT and HAG are located in the centre of a large man-made reservoir (Kisköre Reservoir), which provides a diverse set of aquatic habitats for chironomids, a more diverse secondary metacommunity colonization might be expected than BKHT as it is more isolated from other lentic habitats. However, the results contradict this hypothesis. Most species, and especially the rare species, occurred in BKHT, and also, the  $\alpha$  diversity (i.e. mean species richness of samples) was highest in this oxbow lake. This pattern also contradicts the general species area relationship (e.g. Williams 1943, McArthur & Wilson 1963, Adler et al. 2005, Matias et al. 2010), which suggest the highest number of species would be expected from HHT as its surface area is more than 2.5 times larger than BKHT and HAG. Differences in the species pools were most likely related to differences in environmental conditions (water chemistry, food resource and predation) of the three oxbow lakes. However, for a better understanding of the roles that habitat size, complexity and other environmental factors play in cyclic colonization

of chironomid species, controlled experiments using artificial substrates of different levels of complexity and periphyton quality are required.

Since many chironomid species have multivoltine life cycles and specific environmental needs, considerable seasonal succession was apparent in the assemblages. Such variability is especially likely in assemblages inhabiting habitats experiencing rapid change (Beckett et al. 1992, Balci & Kennedy 2003, Čerba et al. 2010). In our study *C. sylvestris* was initially at high abundance but declined as the season progressed. Other studies have found similar trends as *Cricotopus* species require plant surfaces free of sediment as increasing amounts of sedimented particles reduces the availability of the periphyton and causes a rapid decline in the abundance of these non-mining phytophages (Balci & Kennedy 2003, Čerba et al. 2010, Tarkowska-Kukuryk 2010).

As expected, time (i.e. sampling month) had a strong effect on total species richness. However, in contrary to the null hypothesis, neither the species richness nor the total abundance of larvae increased with time. In fact, total species richness decreased notably from June to August, and 90% of species were represented in the June samples. This indicates rapid colonization of macrophytes by chironomids from the benthos. Our data did not provide clear evidence on the role of metacommunity colonizers. Since only three new species appeared after June, the relatively high species turnover through time was due to environmental filtering and differences in phenology, than to prolonged colonization from metacommunities. Čerba et al. (2010) identified three main colonization events during the three months of *M. spicatum* stands, which were mostly from local populations. However, there was a characteristic succession of chironomid assemblages during the vegetation season. These patterns suggest that change in habitat quality was strongly selective and resulted in the decrease in chironomid species and the observed succession of larval assemblages. Unfortunately, we do not have data to characterize these mechanisms. Based on other studies, chironomids can be considered as early colonizers (Layton & Voshell 1991) that then are strongly affected by other invertebrate groups (Lake et al. 1989). However, since only species richness and not the total abundance of larvae decreased during the vegetation period, it is likely that species-specific selection mechanisms operated rather than group-specific mechanisms. A further interesting finding is that the  $\alpha$  diversity (i.e. mean species richness of samples) remained stable throughout

the study. This, together with strongly decreasing total species richness, resulted in the convergence of chironomid assemblages at small spatial scale (i.e. between samples) in time.

In conclusion, diversity partitioning showed that there is a notable species turnover between oxbow lakes and through time in the backwater system of the River Tisza. Between oxbow lakes variability suggests differences in both the species pool of potential colonizers and the environmental characteristics of the habitats. Considering the high species turnover across oxbow lakes, regional biodiversity conservation projects should include multiple habitats and in particular the species rich BKHT should receive a high priority. Significant seasonal species turnover highlights the limitations of single surveys and proves the necessity of seasonal sampling to assess the total chironomid diversity of this system.

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