Are macrophyte-dwelling Chironomidae (Diptera) largely opportunistic in selecting plant species?

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Abstract. In this study we evaluate how variations in taxonomic composition and physical structure of macrophyte stands affect plant-dwelling chironomid assemblages in highly variable macrophyte assemblages in two densely vegetated backwaters. By using multivariate explanatory techniques we found that similar vegetation composition did not unequivocally relate to similar chironomid assemblages, moreover the diversity of macrophyte stands did not correlate with the taxonomic diversity of chironomid assemblages in the backwaters investigated. Taxonomic composition and structural characteristics of the vegetation had little influence on the taxonomic or functional (i.e. feeding groups) composition of chironomid assemblages inhabiting them. Similarly, there are only weak relationships between the distribution of certain chironomid species or functional feeding groups and the environmental variables investigated. In general, the structure of the vegetation was more closely associated with the distribution of dominant chironomid taxa than compositional variables (i.e. density of specific macrophyte taxa). In summary, the structure of aquatic vegetation (i.e. position, size of a stand of vegetation, total plant density) and characteristics of the environment where it develops may be more important in shaping plant-dwelling chironomid assemblages than the taxonomic composition of the vegetation.

INTRODUCTION

Macro-vegetation is an important and complex habitat in aquatic ecosystems, and influences species diversity and composition of macro-invertebrate communities in several ways (Cheruvelil et al., 2002; Bogut et al., 2007; Papas, 2007; Cremona et al., 2008; Bogut et al., 2010). Aquatic macro-vegetation provides invertebrates with a living place and shelter from predation and disturbance, and a good surface for epiphytic algae, which are important food sources for aquatic animals (Papas, 2007). Several authors record that morphology of plants (Krecker, 1939; Harrod, 1964; Ali et al., 2007), the area of plant surface that is colonisable (Dvorak & Best, 1982; Cyr & Downing, 1988), seasonal changes in the pattern (Scheffer et al., 1984) or the biomass of vegetation (van den Berg et al., 1997) cause differences in the composition, density and diversity of plant-dwelling macro-invertebrate communities. Whereas others argue that the physical conditions in vegetated habitats, such as water depth (Soszka, 1975a) or velocity of flowing water (Harrod, 1964), trophic status (Pieczynska et al., 1999) and the chemical nature of the vegetation (Harrod, 1964; Cyr & Downing, 1988), and/or the quantity and quality of the available periphyton communities as a food source (Harrod, 1964; Cyr & Downing, 1988; Balci & Kennedy, 2003) could be more important in shaping the distribution of aquatic invertebrates, than the taxonomic composition of macrophyte stands.

Although there are many papers dealing with environmental influences on plant-dwelling macro-invertebrate communities, the taxonomic resolution of such studies are often limited, especially those on non-biting midges (Diptera: Chironomidae), which are commonly just classified to family or subfamily (but see e.g. Dvorak & Best, 1982; van den Berg et al., 1997). However, chironomid larvae are one of the most dominant members of plant-dwelling macro-invertebrate communities and may show a distinct preference for a certain type of substratum (Armitage et al., 1995). The preference of chironomid larvae for different substrates is reviewed by Pinder (1986), who mentions that aquatic plants are one of the most important substrates for these organisms. Other authors report a positive relationship between the distribution of macrophyte beds and the abundance, diversity and spatiotemporal distribution of chironomids (Dvorak & Best, 1982; Drake, 1983; Tokeshi & Pinder, 1985; Armitage et al., 1995). Macrophyte density and diversity, as well the percentage of a whole lake covered with vegetation influence chironomid density, taxonomic richness (i.e. number of taxa identified) and relative abundance of chironomid functional guilds both on a seasonal and long-term scale, including historic trends (Brodersen et al., 2001; Tarkowska-Kukuryk & Kornijów, 2008; Langdon et al., 2010). Chironomids avoid certain species of macrophyte and the distribution of especially their mining larvae (i.e. those living under the epidermis of leaves and stems of aquatic plants) is influenced by plant morphology (Kondo

Fig. 1. Location of the Boroszló-kerti-Holt-Tisza (BKHT) and Nagy-morotva (NAGM) backwaters in Hungary.

& Hamashima, 1992; Dvorak, 1996). In addition, seasonal changes or variations in lake trophic status or other environmental factors may have a greater effect on plant-dwelling chironomid assemblages than the structure of the vegetation (van den Berg et al., 1997; Pieczynska et al., 1999; Balci & Kennedy, 2003; Tarkowska-Kukuryk, 2006). However, it is still largely unknown, how variations in plant species composition within macrophyte stands affect chironomid assemblages at the same spatial scale.

The aim of this study was to analyse variations in chironomid assemblages living on macrophytes and determine how macrophyte assemblage structure affects the composition, abundance of the dominant species and functional feeding groups in chironomid assemblages. Unlike previous studies, the stands of vegetation were not a priory categorized based on their dominant plant species, but were treated as variable associations of different macrophyte taxa. To the best of our knowledge macrophyte-chironomid interactions have not been previously analysed using this approach. Previous studies deal mainly with chironomid assemblages associated with certain species of macrophyte (Dvorak, 1996; Balci & Kennedy, 2003; Tarkowska-Kukuryk, 2006) or different types of macrophyte stands without considering the variability in their fine-scale composition (Trivinho-Strixino et al., 2000; Tarkowska-Kukuryk & Kornijów, 2008). However, the macrophyte stands investigated were composed of dynamic mixtures of one or a few dominant and some less abundant species of plants rather than homogenous stands. We studied the association between variations in taxonomic composition and physical structure of macrophyte stands and plant-dwelling chironomid assemblages in two densely vegetated backwaters with highly variable macrophyte assemblages. Our specific objectives were: (1) to assess whether similarities among macrophyte assemblages are mirrored by similarities among chironomid assemblages, and (2) whether the diversity of chironomids increases with the diversity of macrophytes; (3) to analyse which macrophyte related environmental parameters are important in shaping chironomid assemblages; and (4) in influencing the abundance of dominant chironomid species or functional feeding groups.

MATERIAL AND METHODS

Study sites

This study was conducted on two backwaters, the Boroszló-kerti-Holt-Tisza (BKHT) and Nagy-morotva (NAGM), both located in the Upper-Tisza region, NE Hungary (Fig. 1).

The BKHT (48°05′10″N; 22°24′41″E) was artificially established during the regulation of River Tisza in the 19th century when the course of the river was straightened in order to shorten the periods of flooding and decrease the area flooded (Lászlóffy, 1982). The BKHT is a younger pond, which is connected to the River Tisza and regularly receives fresh water when the river floods. Its area is 14 ha, and it is 2.2 km long, on average 62 m wide and 1 m deep. During this investigation its shore was covered by a diversity of marshy vegetation dominated by *Typha angustifolia* L., *Schoenoplectus lacustris* (L.) Palla and *Sparganium erectum* L., and the pond was covered with patches of submerged and floating leaved macrophytes composed mainly of *Ceratophyllum demersum* L., *Trapa natans* L. and *Nymphaea alba* L., and to a smaller extent *Potamogeton lucens* L., *Potamogeton crispus* L. and *Stratiotes aloides* L.

The NAGM (48°06′46″N; 21°28′34″E) was established naturally when the river spontaneously cut across a bend. This pond-like backwater is not in direct connection with the river and receives fresh water only during extreme flooding or when it is artificially pumped from the river. Its area is 90 ha, and it is 4.4 km long, on average 205 m wide and < 1 m deep. At the time of the investigation the shore of the NAGM was covered by marshy vegetation composed of *Typha angustifolia*, *Typha latifolia* L., *Schoenoplectus lacustris*, *Phragmites australis* (Cavan.) Trin. et Stend. and *Sparganium erectum*, and the bottom was overgrown with submerged and floating leaved macrophytes, such as *Ceratophyllum demersum*, *Trapa natans*, *Hydrocharis morsus-ranae* L. *Nymphaea alba* and *Stratiotes aloides*.

Sample collection and processing

Samples were collected in August 1999 when the biomass and cover of vegetation was at their maximum, using the close-and-harvest method at 25 and 24 macrophyte covered sites at BKHT and NAGM, respectively. Sampling sites were chosen at random and were representative of all the characteristic macrophyte assemblages in the two backwaters. The units of habitat sampled were isolated using an aluminium cylinder enclosing an area of 0.5 m² and 1 or 2 m long depending on the depth of the water. The lower edge of the cylinder was sharpened in order to cut the roots of plants and enable to penetrate into the sediment ensuring complete isolation of the sample and so preventing the escape of animals. Water depth was measured inside the cylinder to determine the volume of each sample. All plants and animals were collected from the sampler using a hand-net (mesh size 0.25 mm) taking a special care not to disturb the sediment and organisms living there (Tóth et al., 1998; Nagy et al., 2001).

All samples were characterized by environmental parameters representing the size of the vegetation stand (m²), water depth (m), distance from the shore (m), distance from the nearest area of open water (m) (i.e. macrophyte free area in the pond)), vegetation cover (%) and total vegetation density (g m⁻³, in fresh weight). The size of the vegetation stand and distances from the nearest area of open water and the shore were measured in the field, while vegetation cover was estimated visually by the same person at all sites.

Samples were immediately sorted in the field. Macrophytes were determined to species level and their fresh mass measured to the nearest 1 g. Chironomid larvae were preserved in 70% ethyl-alcohol and transported to the laboratory for later identification. Chironomids were mounted on microscope slides and identified to the lowest possible taxonomic level using the keys of Bíró (1981), Cranston (1982), Wiederholm (1983), Janecek (1998), Vallenduuk (1999), Sæther et al. (2000) and Vallenduuk & Moller Pillot (2002). The nomenclature of Sæther & Spies (2004) was used. Abundance of chironomids was expressed as the number of individuals per sample volume (ind. m⁻³) and density of each species of macrophyte as plant mass per sample volume (g m⁻³).

Statistical analysis

Data on the chironomid assemblages were analyzed in terms of both taxonomic (i.e. mostly species level) and functional (i.e. feeding groups) levels. Chironomids were sorted into six guilds based on the morphology of their mouthparts, feeding behaviour and the food resource utilized according to Moog (2002). The guilds (Moog, 2002) were shredders (feeding on plant tissues and coarse particulate organic matter), grazers (feeding on epilithic algae, biofilm and partially particulate organic matter), active filter-feeders (feeding on suspended fine particulate organic matter), detritus feeders (feeding on fine particulate organic matter in the sediment), miners (feeding on leaves of aquatic plants and algae) and predators (feeding on invertebrates).

Chironomid abundance data were log(x+1) transformed for the canonical correspondence analysis (CCA) and multiple linear regression analyses (MRA), and the relative abundance data were used to calculate chironomid assemblage diversity for each sample and among samples assemblage similarities (see below). Taxonomic richness (i.e. number of taxa) data were not transformed.

Environmental data were sorted into two groups. Macrophyte assemblage data (i.e. taxonomic composition of vegetation stands) formed the first group, the "compositional" variables, and the other measured variables (size of vegetation stand, water depth, distance from the shore, distance from the nearest area of open water, vegetation cover and total vegetation density) formed the second group, the "structural" variables. Macrophytes were classified in one of seven categories as follows: *Ceratophyllum demersum*, *Hydrocharis morsus-ranae*, *Nymphaea alba*, *Potemogeton* spp. (including *P. crispus* and *P. lucens*), *Stratiotes aloides*, *Trapa natans* and emerged marshy vegetation (including *Phragmites australis*, *Schoenoplectus lacustris*, *Sparganium erectum*, *Typha angustifolia* and *T. latifolia*). Merging of some plant taxa into common groups was needed because of their low density and/or sporadic occurrence. Relative abundance data were used to calculate macrophyte assemblage diversity for each sample and among samples assemblage similarities (see below). For other analyses, macrophyte density data were log(x+1), while percentage vegetation cover data were arcsin[(x/100)^{0.5}] transformed to decrease the weight of extra high density values and to secure normality. Other environmental variables were not transformed.

Means of chironomid abundance and vegetation attribute data were compared between BKHT and NAGM using Student's t-tests, except for the percentage vegetation cover, which was compared using a Mann-Whitney U-test.

Variance in chironomid data were first analysed at the assemblage level. To explore whether similar macrophyte stands are inhabited by similar chironomid assemblages, among sample similarity matrixes of chironomid and macrophyte assemblages relative abundance data were compared using the Mantel test based on Bray-Curtis similarity measure and the PAST software package (Hammer et al., 2001). Then, to test whether higher macrophyte diversity is coupled with higher chironomid diversity, the relationship between the Shannon diversities of chironomid and macrophyte assemblages was analysed using Spearman rank correlation in Statistica 8.0 (Statsoft, Inc.).

Relationships between the taxonomic composition of chironomid assemblages and environmental variables were investigated using the CCA in CANOCO version 4.5 (ter Braak & Šmilauer, 1998). Rare chironomid taxa occurring in less than three samples were excluded from the CCA analyses. Prior to analyses environmental variables were tested for colinearity using the Pearson correlation analysis in Statistica 8.0 (StatSoft, Inc.). Among variable correlations suggested that most environmental variables, including the macrophyte abundance data, were largely independent and only the depth of the water was not included in CCA analyses of the data for BHKT because of its strong ($R > 0.5$) correlation with several other environmental variables. The relative contribution of each variable to the whole model was assessed using the forward stepwise selection procedure, and their significance tested using a Monte-Carlo permutation test and 499 permutations of the full model. Similarly, the statistical significance of the ordination axes and the whole model (i.e. including all axes) were tested using a Monte Carlo permutation test and 499 permutations. In the CCA analysis of NAGM data based on chironomid functional feeding groups, one sample clearly separated from the others and as a consequence was not included the final analysis.

Finally, the effect of type of macrophyte ("compositional" variables) and other environmental variables ("structural" variables) on specific abundant chironomid taxa and guilds, as well on chironomid taxonomic richness and total chironomid density were explored using multiple linear regression analysis (MRA) and variance partitioning method (Borcard et al., 2004). Separate MRAs were run using the two environmental variable groups (i.e. "compositional" and "structural" variables) and when both were significant the two sub-models were combined into an overall MRA model. Variable selection in the sub-models was based on the forward stepwise selection procedure and only variables with significant contributions (at $P < 0.05$)

TABLE 1. Abbreviations and values [mean, SD (standard deviation) and range] of the environmental variables associated with stands of vegetation in the Boroszló-kerti-Holt-Tisza (BKHT) and Nagy-morotva (NAGM) backwaters, Hungary. Between backwater differences in the variables were tested using paired t-test and Mann-Whitney U-test (in case of vegetation cover) and statistical differences are indicated as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Environmental variables	Abbreviation	BKHT		NAGM	
		Mean (SD)	Range	Mean (SD)	Range
Structural variables					
total vegetation density (g m^{-3})	vegdens *	846 (583)	135–2480	1368 (950)	325–4270
vegetation cover (%)	cover **	64 (28)	20–100	85 (14)	40–100
size of the sampled vegetation stand (m^2)	vegsize	56 (112)	1–550	2120 (6138)	12–30000
water depth (m)	depth	0.82 (0.40)	0.31–1.75	0.87 (0.33)	0.22–1.31
distance from the shore (m)	disshore ***	10 (11)	1–40	45 (27)	2–110
distance from the nearest area of open water (m)	disopen *	6 (8)	0–35	38 (56)	1–200
Compositional variables (Plant taxa)					
Ceratophyllum demersum L. (g m^{-3})	cer dem	770 (1144)	0–3817	972 (1794)	0–8132
Hydrocharis morsus-ranae L. (g m^{-3})	hyd mra	0	0	177 (437)	0–1895
Nymphaea alba L. (g m^{-3})	nym alb	151 (352)	0–1379	248 (557)	0–2263
Phragmites australis (Cavan.) Trin. et Stend. (g m^{-3})	phr aus	0	0	258 (1262)	0–6182
Potamogeton crispus L. (g m^{-3})	pot cri	3 (16)	0–82	0	0
Potamogeton lucens L. (g m^{-3})	pot luc	51 (172)	0–650	0	0
Schoenoplectus lacustris (L.) Palla. (g m^{-3})	sch lac	77 (389)	0–1943	0	0
Sparganium erectum L. (g m^{-3})	spa ere	524 (1891)	0–8417	0	0
Stratiotes aloides L. (g m^{-3})	str alo	607 (1272)	0–4484	592 (1202)	0–4863
Trapa natans L. (g m^{-3})	tra nat	189 (414)	0–1538	273 (455)	0–1524
Typha angustifolia L. (g m^{-3})	typ ang	268 (1085)	0–5300	183 (623)	0–2371
Typha latifolia L. (g m^{-3})	typ lat	0	0	184 (902)	0-4417

were retained. In the overall models all significant variables from the corresponding sub-models were retained. Partitioning of variation between the "compositional" and "structural" variable groups was based on adjusted R^2 values ($R^2_{adj.}$) of the three MRA models (i.e. compositional sub-model, structural sub-model and overall model) following Legendre (2008). Again, in order to avoid colinearity the depth of the water was not included in the analyses of the BHKT data. MRAs were performed in Statistica 8.0 software (StatSoft, Inc.).

RESULTS

Environmental conditions

Mean water depth (t-test, $t = -0.47$, $P = 0.640$) and area of the vegetation stands sampled (t-test, $t = -1.68$, $P = 0.099$) was similar (<1 m) in the two backwaters. However, other "structural" variables had significantly higher mean values in NAGM than BKHT (Table 1), reflecting that the macrophyte stands were on average larger and denser in NAGM.

In both backwaters, the areas sampled were dominated by the macrophytes *Ceratophyllum demersum* and *Stratiotes aloides*, and also by *Sparganium erectum* at BKHT. However, *Potamogeton* spp., *Schoenoplectus lacustris* and *Sparganium erectum* occurred only at BKHT and *Phragmites australis*, *Typha latifolia* and *Hydrocharis morsus-ranae* only at NAGM (Table 1; Figs 2–3). In general, the macrophyte associations were species rich and only *C. demersum* at NAGM and *N. alba* at BKHT formed monospecific stands (Figs 2–3).

In both backwaters, both "structural" and "compositional" vegetation characteristics varied markedly among the sites sampled, which provided long enough environmental gradients for vegetation-chironomid relationship analyses.

Chironomid assemblages associated with macrophytes

Altogether 34 chironomid taxa (Table 2) from three subfamilies (Tanypodinae: 6, Orthocladiinae: 1 and Chironominae: 27) were identified. Eighteen taxa occurred in both backwaters, while 12 taxa were found only at BKHT and 4 taxa only at NAGM. At BKHT three species made up more than half (56%) of the total abundance: *Polypedilum sordens* (30%), *Kiefferulus tendipediformis* (15%) and *Glyptotendipes pallens* (11%). At NAGM *Glyptotendipes cauliginellus* (14%), *Endochironomus tendens* (12%), *Chironomus luridus* gr. (10%), *Chironomus* (*Lobochironomus*) *dorsalis* (11%) and *Glyptotendipes pallens* (10%) were the most abundant species. Mean total density of chironomids was two times higher at BKHT (86 ind. m^{-3}) than NAGM (40 ind. m^{-3}), but this difference was not statistically significant (t-test, $t = 1.98$, $P = 0.054$).

Each functional feeding group (shredders, grazers, active filter-feeders, detritus feeders, miners and predators) occurred in both backwaters, of which the active filter-feeders, detritus feeders and grazers predominated (Figs 2–3).
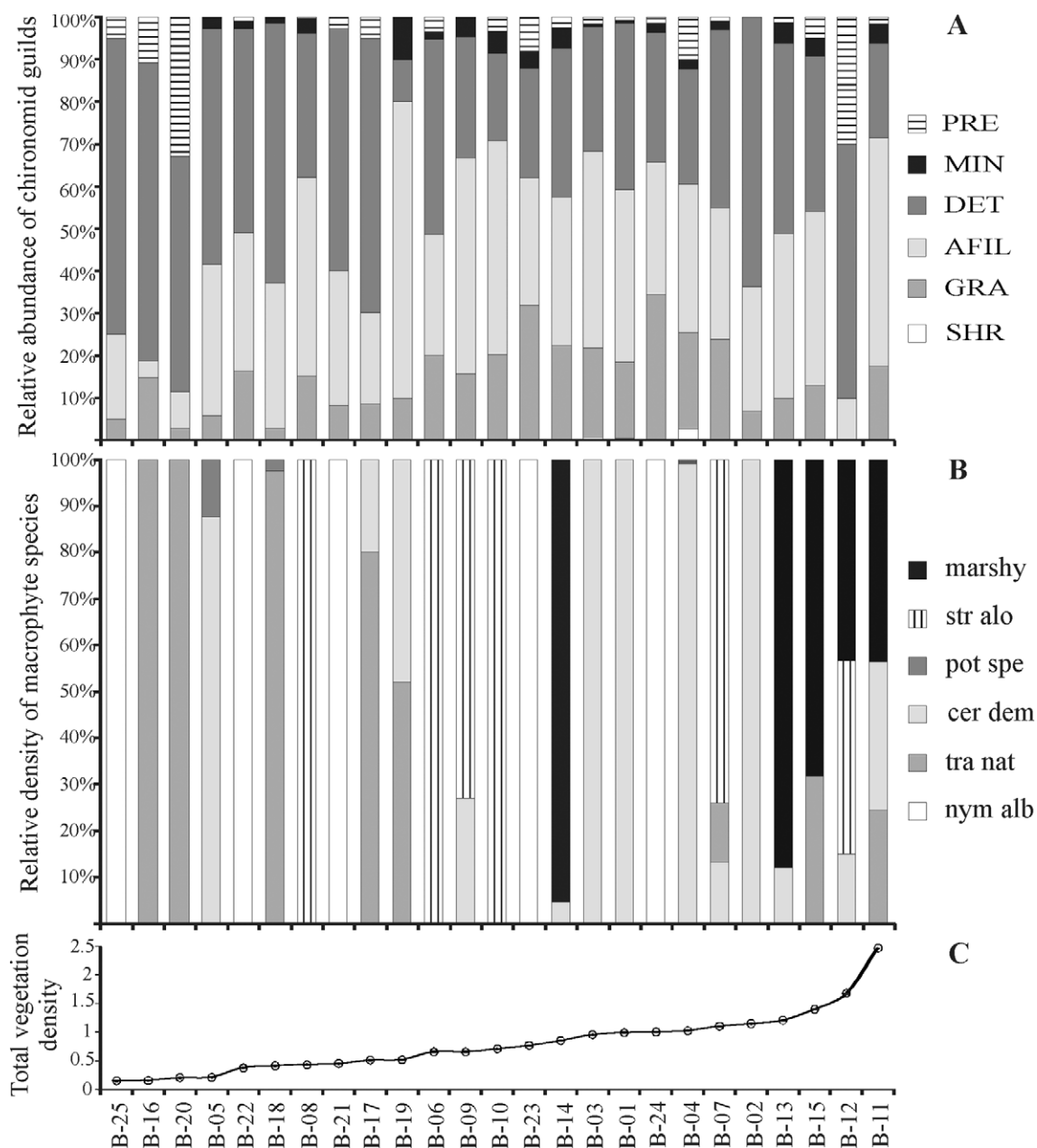
Fig. 2. Relative abundance of chironomid functional feeding guilds (A) and density of macrophyte species (B) recorded at the sites sampled in the Boroszló-kerti-Holt-Tisza (BKHT) backwater, Hungary, with the sites sampled sorted along a gradient of increasing vegetation density (kg m⁻³) (C). List of the abbreviations of plant species is given in Table 1, while abbreviations of functional feeding groups are: SHR = shredders, GRA = grazers, DET = detritus feeders, AFIL = active-filter feeders, MIN = miners and PRE = predators.

Assemblage level effect of vegetation on chironomids

Chironomid and macrophyte assemblage data correlated in the BKHT (Mantel test, $R = 0.322$, $P < 0.001$), but not in the NAGM ($R = -0.004$, $P = 0.499$) suggesting that similar chironomid assemblages do not necessarily associate with similar vegetation even within a small system. Moreover, the taxonomic diversity of chironomid assemblages did not correlate with the diversity of macrophyte associations at BKHT (Spearman rank correlation, $R = 0.119$, $P = 0.057$) or NAGM ($R = 0.073$, $P = 0.730$).

CCA also did not reveal any unequivocal relationship between vegetation attributes and chironomid assemblage composition either at a taxonomic or functional level. Only one of the four CCA analyses (i.e. species/functional feeding group × two backwaters) had significant explanatory power, but only in the overall model (i.e. all axes) and not for any single axis (Fig. 4).

For BKHT, the CCA resulted in a statistically significant overall model explaining 60.6% of the total variance in the data but none of the derived ordination axes were significant. The first two CCA ordination axes explained 44.1% of the relation in the species-environment data and 26.7% of the variance in species data (Fig. 4). Forward selection procedure resulted in three significant "compo-
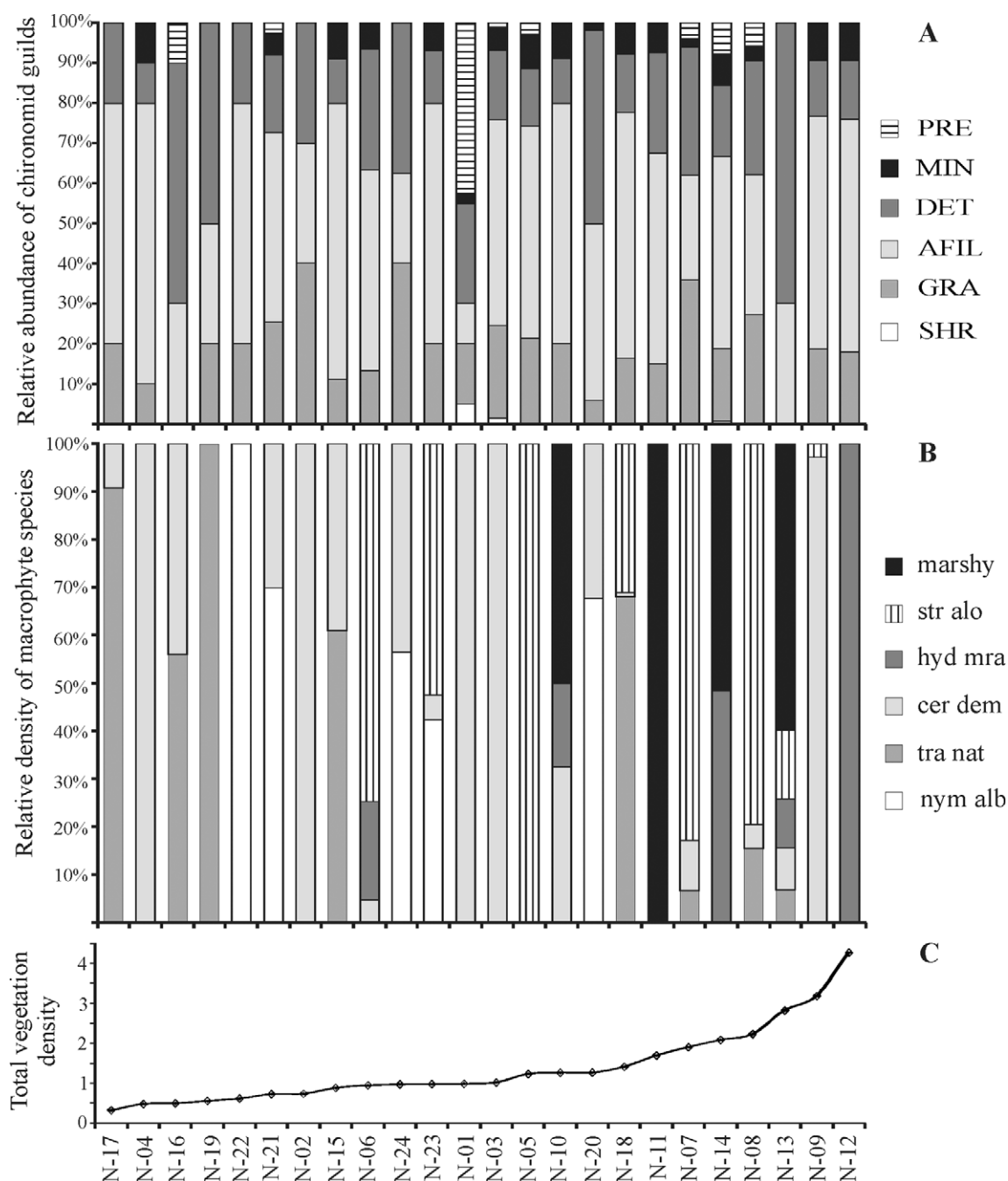
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Fig. 3. Relative abundance of chironomid functional feeding guilds (A) and density of macrophyte species (B) in the Nagy-morotva (NAGM) backwater, Hungary with the sites sample sorted along a gradient of increasing vegetation density (kg m⁻³) (C). List of the abbreviations of plant species is given in Table 1, while the abbreviations of functional feeding groups are SHR = shredders, GRA = grazers, DET = detritus feeders, AFIL = active-filter feeders, MIN = miners and PRE = predators.

sitional" variables, the densities of *N. alba*, *S. aloides* and *T. natans* (Table 3). These three variables, together with total vegetation density and vegetation cover were associated mainly with the first axis. Vegetation stands dominated by floating-leaved *T. natans* and *N. alba* are located on the right side of the diagram and associated with *Chironomus* spp. and *Cladopelma virescens* that feed mainly on detritus. The second axis correlated mostly with *Potamogeton* spp., marshy vegetation and distance from the nearest area of open water, and the position of *Procladius* sp., *Chironomus annularius* agg. and *Glyptotendipes*

viridis suggest a possible relationship with these variables. However, most of the chironomid taxa are positioned in the centre of the graph, suggesting that their occurrence was not significantly influenced by vegetation characteristics.

For NAGM, the CCA explained 55.6% of the total variation in the data, and the first two axes explained 39.3% of the relation in the species-environment data and 21.8% of the variance in species data, however, even the whole model was not significant (Fig. 5). Forward selection procedure indicated only one significant variable, the

TABLE 2. List of chironomid taxa, their abbreviations and abundances (ind m^{-3}) recorded in the Boroszló-kerti-Holt-Tisza (BKHT) and Nagy-morotva (NAGM) backwaters, Hungary. Between backwater differences in the examined variables were tested with paired t-test and statistical differences are indicated as follows:* $P < 0.05$, ** $P < 0.01$.

Taxon	Abbreviation	BKHT		NAGM	
		Mean (SD)	Range	Mean (SD)	Range
Tanypus kraatzi (Kieffer, 1912)	Tpu kra	0.38 (1.31)	0–5	0.76 (3.24)	0–15.79
Procladius sp.	Pro spe	0.71 (2.04)	0–7.5	0	0
Anatopynia plumipes (Fries, 1823)	Ana plu	0	0	0.29 (1.03)	0–4.35
Ablabesmyia longistyla Fittkau, 1962	Abl lon	0.37 (1.32)	0–5.71	0	0
Ablabesmyia monilis (Linnaeus, 1758)	Abl mon	0.19 (0.96)	0–4.82	0	0
Ablabesmyia phatta (Egger, 1863)	Abl pha	0.19 (0.97)	0–4.88	0.18 (0.89)	0–4.35
Cricotopus sylvestris gr.	Cri syl	1.08 (3.27)	0–14.28	0.62 (1.69)	0–5.31
Chironomus (*Camptochironomus*) sp.	Chi spe	0	0	1.22 (3.10)	0–12.5
Chironomus annularius agg.	Chi ann	0.89 (2.48)	0–10	1.97 (3.16)	0–9.09
Chironomus luridus gr.	Chi lur *	0	0	4.05 (7.54)	0–31.58
Chironomus nuditarsis Keyl, 1961	Chi nut	0.15 (0.77)	0–3.85	0	0
Chironomus plumosus agg.	Chi plu	1.26 (3.06)	0–12.12	0.65 (1.80)	0–7.69
Chironomus riparius agg.	Chi rip *	1.95 (3.39)	0–12.19	0	0
Chironomus dorsalis Meigen, 1818	Chi dor **	0.13 (0.67)	0–3.33	4.41 (6.92)	0–21.05
Cladopelma virescens (Meigen, 1818)	Cla vir *	2.23 (3.76)	0–14.81	0	0
Dicrotendipes lobiger (Kieffer, 1921)	Dic lob	0.1 (0.5)	0–2.5	0.65 (1.42)	0–5.26
Dicrotendipes nervosus (Staeger, 1839)	Dic ner **	1.61 (2.60)	0–7.32	0	0
Dicrotendipes tritomus (Kieffer, 1916)	Dic tri	0.45 (1.41)	0–5.71	0.14 (0.48)	0–1.83
Endochironomus albipennis (Meigen, 1830)	Ech alb	0	0	1.77 (7.19)	0–35.40
Endochironomus tendens (Fabricius, 1775)	Ech ten	4.46 (8.88)	0–40	3.64 (9.01)	0–34.34
Glyptotendipes viridis (Macquart, 1834)	Gly vir	3.18 (8.36)	0–29.79	0.36 (1.15)	0–5.26
Glyptotendipes cauliginellus (Kieffer, 1913)	Gly cgi	4.78 (7.59)	0–29.27	6.49 (11.39)	0–36.84
Glyptotendipes pallens (Meigen, 1804)	Gly pal	9.05 (20.16)	0–80	4.43 (9.60)	0–42.10
Kiefferulus tendipediformis (Goetghebuer, 1921)	Kie ten **	12.88 (16.49)	0–52.05	0.36 (1.26)	0–5.26
Parachironomus arcuatus gr.	Pch arc	2.65 (5.18)	0–19.51	0.67 (1.38)	0–4.08
Phaenopsectra flavipes (Meigen, 1818)	Pha fla	3.31 (7.09)	0–34.04	1.89 (4.95)	0–21.92
Polypedilum sordens (van der Wulp, 1874)	Pol sor	27.21 (61.56)	0–275	2.52 (5.07)	0–23
Polypedilum nubeculosum (Meigen, 1804)	Pol nub *	1.94 (4.68)	0–19.23	0	0
Polypedilum cultellatum Goetghebuer, 1931	Pol cul	0.45 (1.77)	0–8.51	0.73 (1.65)	0–5.48
Synendotendipes dispar gr.	Syn dis	1.20 (2.66)	0–11.11	2.66 (8.30)	0–31.58
Zavreliella marmorata (van der Wulp, 1858)	Zav mar	0.11 (0.55)	0–2.74	0	0
Micropsectra atrofasciata agg.	Mic atr	0.11 (0.55)	0–2.74	0	0
Paratanytarsus sp.	Pta spe *	1.16 (2.73)	0–10.71	0	0
Tanytarsus sp.	Tan spe	2.15 (5.73)	0–19.17	0	0
Total density of chironomids		86.35 (105.38)	2.38–407.14	40.49 (43.18)	1.85–210.53
Number of taxa		30		22	

depth of the water (Table 3), which correlated most with the density of the chironomid *Endochironomus albipennis*. The only other chironomid taxa positioned distantly from the centre of the graph is *Chironomus plumosus* agg., suggesting some relationship with *C. demersum* and *T. natans* densities, as well with the distance from an area of open water, vegetation cover and distance from the shore.

CCA ordinations did not reveal any significant relationships between vegetation attributes and functional feeding group based chironomid assemblages in either backwater (Table 3, Figs 4–5).

MRA revealed that the taxon richness of the chironomid assemblage is correlated positively with vegetation density and negatively with distance from an open area of water at BKHT, but it did not correlate with any vegetation attribute at NAGM (Table 4, Fig. 6). Total density of chironomids correlated positively with vegetation density and negatively with *N. alba* at BKHT. Again, no correlation was found in the data for NAGM (Table 4, Fig. 6).

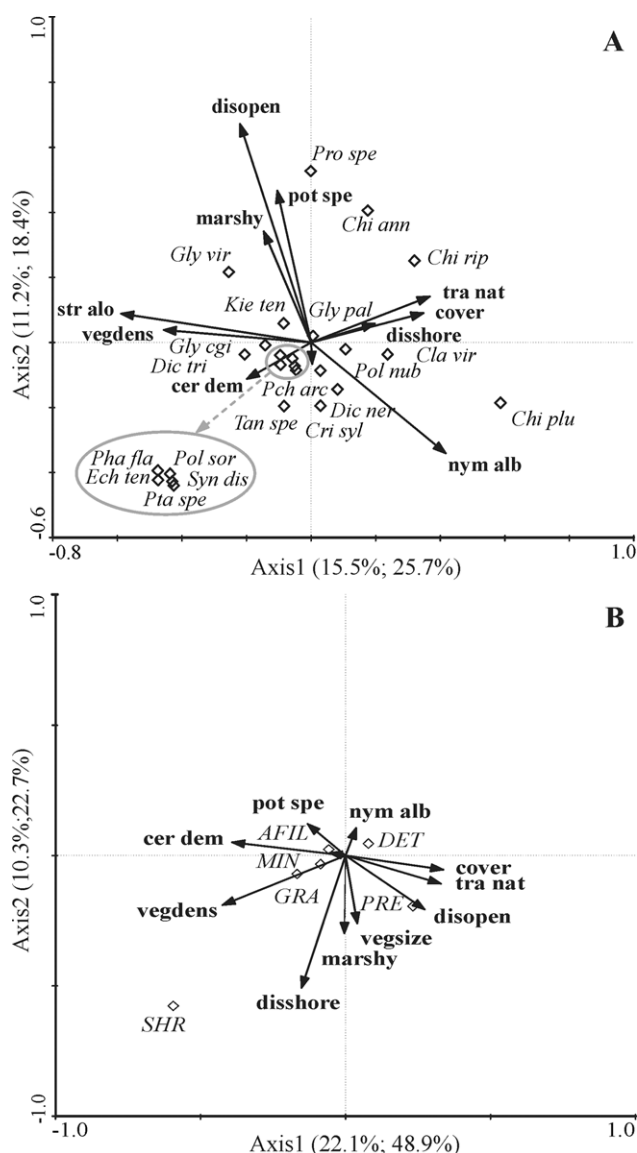| Variable	Cumulative eigenvalues	P	Variable	Cumulative eigenvalues	P
chironomid species × variables			chironomid guilds × variables		
BKHT					
nym alb	**0.17**	**0.012**	cover	0.02	0.188
str alo	**0.33**	**0.012**	cer dem	0.03	0.276
marshy	0.46	0.092	disshore	0.05	0.112
vegdens	0.57	0.070	disopen	0.07	0.106
tra nat	**0.71**	**0.030**	tra nat	0.08	0.296
cover	0.83	0.064	vegdens	0.09	0.382
disshore	0.95	0.056	vegsize	0.09	0.536
vegsize	1.06	0.096	marshy	0.10	0.626
pot spe	1.13	0.402	str alo	0.11	0.400
disopen	1.23	0.078	pot spe	0.11	0.624
cer dem	1.29	0.482	nym alb	0.11	0.870
NAGM					
depth	**0.21**	**0.020**	tra nat	0.02	0.162
tra nat	0.39	0.078	depth	0.03	0.278
str alo	0.56	0.072	cover	0.04	0.400
disopen	0.73	0.084	disshore	0.05	0.480
hyd mra	0.85	0.322	disopen	0.05	0.472
cer dem	0.96	0.364	nym alb	0.07	0.268
nym alb	1.07	0.398	vegsize	0.08	0.346
vegsize	1.15	0.688	vegdens	0.08	0.578
cover	1.25	0.478	marshy	0.09	0.354
vegdens	1.33	0.648	str alo	0.10	0.488
disshore	1.43	0.562	hyd mra	0.11	0.676
marshy	1.52	0.554	cer dem	0.11	0.910

Fig. 4. Canonical correspondence analysis (CCA) plots depicting the relationships between vegetation stand attributes and chironomid assemblages in Boroszló-kerti-Holt-Tisza (BKHT) based on chironomid taxa (A) and functional feeding groups (B). Percentage variances represented by axes are indicated in brackets (of species data; of species-vegetation relation) after the axis name. Lists of abbreviations of environmental variables and chironomid taxa are given in Table 1–2, while abbreviations of functional feeding groups are SHR = shredders, GRA = grazers, DET = detritus feeders, AFIL = active-filter feeders, MIN = miners and PRE = predators. Note that, only the CCA shown in plot A is significant ($F = 1.82$, $P = 0.004$), and none of the individual axes have statistically significant explanatory power; for clarity some variables close to the centre of the graph do not have a legend.

Taxonomic and functional level influence of vegetation on chironomids

Out of the nine most abundant chironomid taxa, seven showed some correlation with vegetation attributes at BKHT. The relative contribution of pure "structural" (18–38%) and pure "compositional" variables (12–53%) to multiple linear regression models depended on the chironomid taxa, and the explanatory power of overall regression models (i.e. including affects of pure "compositional" and pure "structural" variables as well their shared effect) ranged between 10–28%, while a larger part of the variance (38–77%) in the data for BKHT remained unexplained. In contrast, only "structural" variables in the significant multiple regression models for the three guilds had significant explanatory power (23–32%) (Table 4, Fig. 6). In the NAGM data only a significant vegetation effect was for *G. cauliginellus* and *G. pallens*, and the guild of predators (Table 4, Fig. 6).

In general, the results of the MRA indicated that pure "compositional" variables had only a minor influence ($R^2_{adj.} \leq 0.3$) on densities of chironomid taxa and functional groups, except for the *C. riparius* agg. ($R^2_{adj.} =$ 0.534, $P < 0.001$) at BKHT and *G. pallens* ($R^2_{adj.} = 0.372$, $P < 0.003$) at NAGM. Although, pure "structural" variables had a greater influence on chironomids their significant contribution was also limited to certain chironomid taxa/guilds and restricted mainly to BKHT (Table 4, Fig. 6). Shared effect of "structural" and "compositional" variables proved to be significant for *E. tendens* ($R^2_{adj.} =$
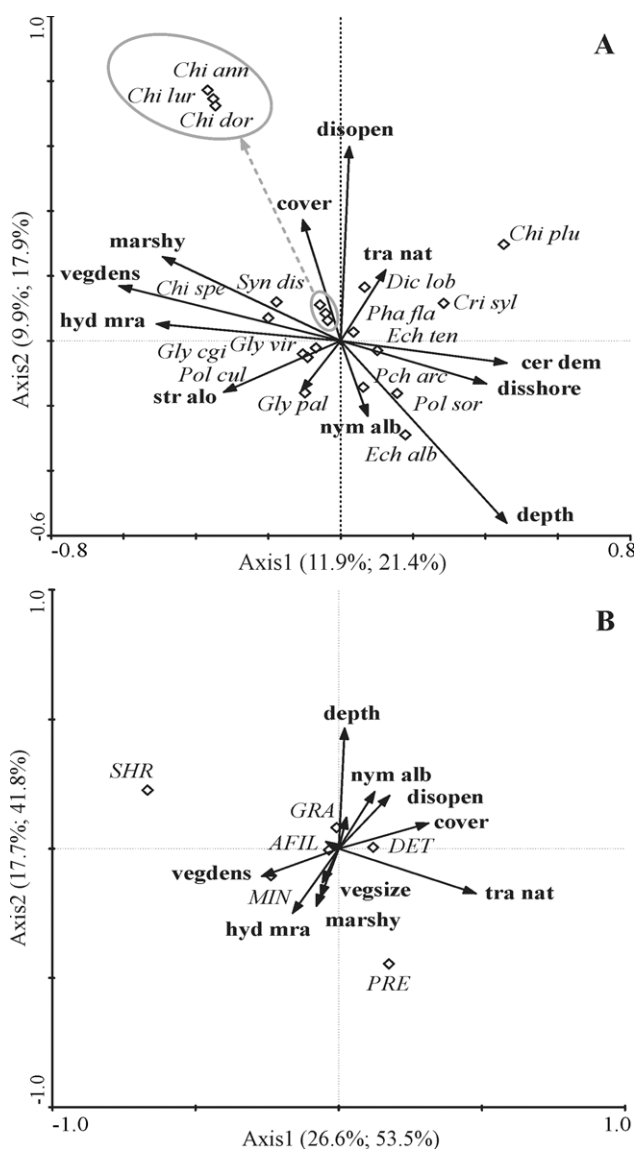
Fig. 5. Canonical correspondence analysis (CCA) plots depicting the relationships between vegetation stand attributes and chironomid assemblages in Nagy-morotva (NAGM) based on chironomid taxa (A) and functional feeding groups (B). Percentage variances represented by axes are indicated in brackets (of species data; of species-vegetation relation) after the axis name. Lists of abbreviations of environmental variables and chironomid taxa are given in Table 1–2, while abbreviations of functional feeding groups are SHR = shredders, GRA = grazers, DET = detritus feeders, AFIL = active-filter feeders, MIN = miners and PRE = predators. Note that in the CCA shown in plot B one outlying site is not included (explained in the text); for clarity some variables very close to the centre of the graph do not have a legend.

0.453, $P < 0.001$), *G. cauliginellus* ($R^2_{adj.} = 0.429$, $P < 0.005$), *K. tendipediformis* ($R^2_{adj.} = 0.622$, $P < 0.001$) and *P. sordens* ($R^2_{adj.} = 0.464$, $P < 0.001$) at BKHT, and *G. cauliginellus* ($R^2_{adj.} = 0.358$, $P < 0.005$) at NAGM (Fig. 6).

Of the "compositional" variables mainly densities of floating leaved macrophyte species had significant explanatory values for the density of chironomid taxa, except

C. riparius agg., which correlated with both the densities of *Potamogeton* spp. and *C. demersum*. *S. aloides* correlated positively with *E. tendes* (ß = 0.47, $P < 0.05$), *G. cauliginellus* (ß = 0.53, $P < 0.01$), and *P. flavipes* (ß = 0.35, $P = 0.07$), and negatively with *C. riparius* agg. (ß = –0.51, $P < 0.01$) in BKHT, while *N. alba* correlated negatively with *C. riparius* agg. (ß = –0.66, $P < 0.01$), *K. tendipediformis* (ß = –0.41, $P < 0.01$) and *P. sordens* (ß = –0.39, $P < 0.05$) at BKHT. *T natans* correlated negatively with *K. tendipediformis* (ß = –0.37, $P < 0.05$) at BKHT and with *G. pallens* (ß = –0.35, $P < 0.05$) at NAGM; while, *H. morsus-ranae* correlated positively with *G. cauliginellus* (ß = 0.48, $P < 0.05$) and *G. pallens* (ß = 0.5, $P < 0.01$) at NAGM (Table 4).

Of the "structural" variables total vegetation density correlated positively with the density of *E. tendes* (ß = 0.41, $P < 0.05$), *G. cauliginellus* (ß = 0.56, $P < 0.01$), *G. pallens* (ß = 0.71, $P < 0.001$), *K. tendipediformis* (ß = 0.51, $P < 0.01$) and *P. sordens* (ß = 0.66, $P < 0.01$) at BKHT, and the density of *G. cauliginellus* (ß = 0.60, $P < 0.002$) at NAGM. The density of *G. pallens* and *P. sordens* both correlated negatively (ß = –0.36, $P < 0.05$; ß = –0.50, $P < 0.01$, respectively) with the distance from open water at BKHT, while the distance from the lakeshore correlated negatively with that of *K. tendipediformis* (ß = –0.55, $P < 0.01$) at BKHT and positively with predator guild (ß = 0.62, $P < 0.01$) at NAGM. Miners (ß = –0.51, $P < 0.01$), in particular *E. tendes* (ß = –0.53, $P < 0.01$), correlated negatively with vegetation cover at BKHT (Table 4).

DISCUSSION

It is well-known that the compositions of macro-invertebrate communities living on macrophytes differ from those living in other habitats, like sediment or decomposing organic matter; and a similar pattern is recorded for the composition of chironomid assemblages (e.g. Soszka, 1975a; Pinder, 1986). In addition, macro-invertebrate assemblages vary among macrophyte beds mainly in relation to the heterogeneity of the environment, plant architecture, plant species composition and vegetation density (reviewed by Papas, 2007). Therefore, it is logical to assume that (1) particular chironomid assemblages are associated with particular types of vegetation, (2) vegetation pattern should be more important in shaping the distribution of chironomids living in this habitat than those associated with other substrates (i.e. benthic species), and (3) that the relationships between chironomid assemblages and the vegetation may be more obvious in terms of functional groups than species of chironomids (e.g. Erős et al., 2009 and references cited therein). In contrast, in this study, there was no relationship between the spatial distributions of chironomid species or functional feeding groups and characteristics of macrophyte stands over wide structural and compositional gradients. Moreover plant-dwelling chironomids seemed to be highly opportunistic in terms of the plant taxa they were associated with in the aquatic systems studied.

TABLE 4. Multiple linear regression models of the relationships between chironomid species richness, total abundance of chironomids, and abundance of dominant taxa and functional feeding groups (GRA = grazers, AFIL = active filter-feeders, DET = detritus feeders, MIN = miners, PRE = predators), and the attributes of the vegetation in the Boroszló-kerti-Holt-Tisza (BKHT) and Nagy-morotva (NAGM) backwaters, Hungary. Explanatory variables in the structural and compositional submodels were selected using the forward stepwise method (at $P < 0.05$) and only significant variables were included in the overall model ("+" indicates positive, "–" negative and "ns" non significant relationship). For lists of abbreviations see Tables 1–2.

	Compositional submodel	Structural submodel	Overall model		
			df	F	P
BKHT					
taxon richness	+vegdens; –disopen	ns	2,22	6.79	<0.005
total density	+vegdens	–nym alb	2,22	9.06	<0.001
Chi rip	ns	+pot spe; –str alo; –nym alb; –cer dem	4,20	7.89	<0.001
Cla vir	ns	ns	–	–	ns
Ech ten	–cover; + vegdens	+str alo	3,21	7.62	<0.001
Gly cgi	+vegdens	+str alo	2,22	10.04	<0.001
Gly pal	+vegdens; –disopen	ns	2,22	8.23	<0.002
Kie ten	–disshore; +vegdens	–nym alb; –tra nat	4,20	10.86	<0.001
Pch arc	ns	ns	–	–	ns
Pha fla	ns	+str alo	3,21	3.46	<0.034
Pol sor	+vegdens; –disopen	–nym alb	3,21	7.92	<0.001
GRA	–disopen; +vegdens	ns	2,22	6.60	<0.005
AFIL	ns	ns	–	–	ns
DET	–vegdens	ns	1,23	8.93	<0.006
MIN	–cover	ns	1,23	8.28	<0.008
PRE	ns	ns	–	–	ns
NAGM					
taxon richness	ns	ns	–	–	ns
total density	ns	ns	–	–	ns
Chi lur	ns	ns	–	–	ns
Chi dor	ns	ns	–	–	ns
Ech alb	ns	ns	–	–	ns
Ech ten	ns	ns	–	–	ns
Gly cgi	+vegdens	+hyd mra	2,21	7.43	<0.004
Gly pal	ns	+hyd mra; –tra nat	2,21	7.81	<0.003
Pha fla	ns	ns	–	–	ns
Pol sor	ns	ns	–	–	ns
GRA	ns	ns	–	–	ns
AFIL	ns	ns	–	–	ns
DET	ns	ns	–	–	ns
MIN	ns	ns	–	–	ns
PRE	+disshore; –depth	ns	2,21	8.35	<0.002

Similar chironomid assemblages did not unequivocally relate to similar vegetation compositions in the two backwaters. Moreover, the taxonomic diversity of chironomid assemblages did not correlate with the diversity of macrophyte stands in the investigated habitats. This is surprising because of the great variety in the morphology and taxonomic composition of the macrophyte taxa occurring at BKHT and NAGM, and several other authors (e.g. Ali et al., 2007; Papas, 2007; Tessier et al., 2008) record a positive correlation between the diversity of macro-invertebrate communities and heterogeneity of aquatic macro-vegetation. Similarly, there are positive correlations recorded between plant and arthropod species compositions in terrestrial environments (e.g. Schaffers et

al., 2008). In our study, the CCAs indicated that taxonomic composition and structural characteristics of the vegetation had little influence on the taxonomic or functional (i.e. feeding groups) composition of the chironomid assemblages inhabiting them.

Similarly, CCAs did not reveal any significant relationships just some weak trends between the distribution of certain chironomid species and functional feeding groups, and environmental variables. For instance, at BKHT detritivore midge taxa (e.g. *C. annularius* agg., *C. riparius* agg., *C. plumosus* agg., *C. virescens*) were associated mainly with macrophytes with floating leaves (*Trapa natans* and *Nymphaea alba*) and with relatively high vegetation cover (77–78%), while the miner chiro-
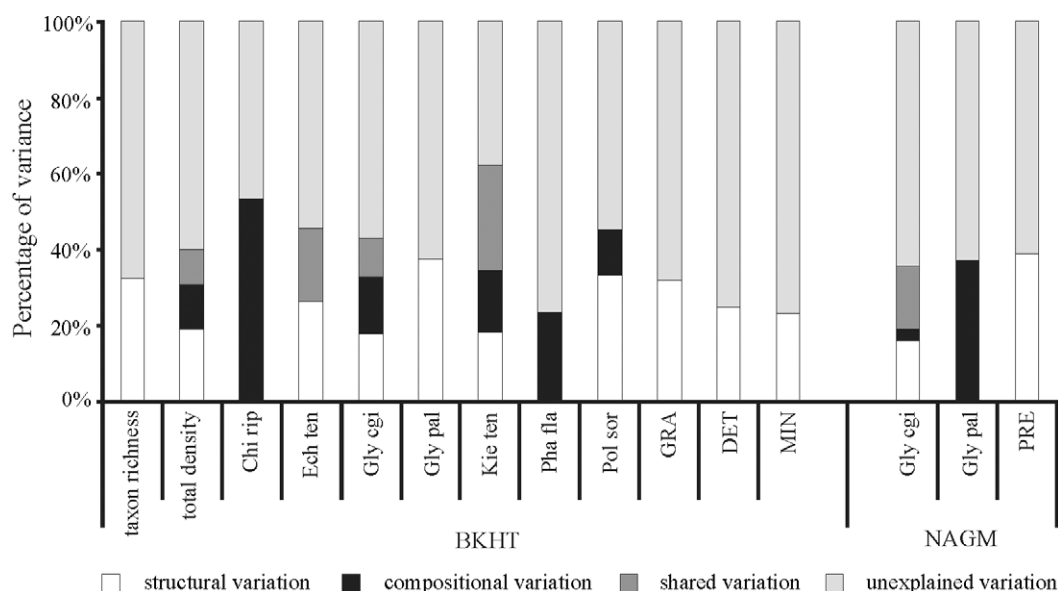
Fig. 6. Percentage of the variation of various aspects of the chironomid assemblages studied accounted for by "structural" and "compositional" components of the macrophyte vegetation in the Boroszló-kerti-Holt-Tisza (BKHT) and Nagy-morotva (NAGM) backwaters, Hungary. Only variables having a significant contribution in pure "structural" and "compositional" multiple linear regression models were included in the overall model. Variables included in specific models are presented in Table 4. List of the abbreviations for chironomid taxa is given in Table 2, while abbreviations of functional feeding groups are: GRA = grazers, DET = detritus feeders, MIN = miners and PRE = predators.

nomid, *G. viridis,* was associated primarily with marshy vegetation. At NAGM there was a weak positive relationship between the distribution of *E. albipennis* and the depth of the water, as previously reported (Moller Pillot, 2009).

More specific analyses based on MRA and aiming to explore relationships between chironomids and the attributes of stands of vegetation also did not reveal any strong relationships. In general, some significant relationships were found in the BKHT data, but these trends were not found in the NAGM data. Taxon richness of chironomids correlated positively with vegetation density and negatively with distance from the nearest area of open water in the BKHT data, but did not correlate with any of the variables in the NAGM data. The latter result accords with the findings of Balci & Kennedy (2003) who also did not find differences in the taxon richness of chironomids in various types of vegetation. It is even more interesting that the total density of chironomids was not unequivocally associated with any parameter in any of the stands of vegetation investigated. Although it correlated positively with vegetation density and negatively with the density of *N. alba* at BKHT, however it was not correlated with any of the parameters at NAGM. In addition the literature on this topic is contradictory. Cremona et al. (2008) records greater abundances and biomasses of macro-invertebrates on submerged than on emergent and floating leaved macrophytes, which accords with some other studies (e.g., Dvorak & Best, 1982; Cattaneo et al., 1998), however there are a number of contrary observations (e.g., Soszka et al., 1975a, b; Cyr & Downing, 1988; Pieczynska et al., 1999; Bogut et al., 2007).

In general, the explanatory power of the "structural" variables of vegetation as determinants of the distribution of dominant chironomid taxa was greater than that of "compositional" variables. However, the results are contradictory as *Glyptotendipes cauliginellus* was the only chironomid whose distribution followed similar trends in the two backwaters. Its density correlated positively with vegetation density at both backwaters and positively with the density of the floating leaved *S. aloides* at BKHT and *H. morsus-ranae* at NAGM. It should be noted, however, that *H. morsus-ranae* occurred only at NAGM and in association with *S. aloides* and marshy vegetation. Therefore, *H. morsus-ranae* may indicate the features of the vegetation stands it dominates rather than it being an important living place for *G. cauliginellus*. This is supported by the report that the larvae of miners like *G. cauliginellus* primarily mine the old tissues of leaves and stems of *S. aloides* and emergent marshy macrophytes (e.g. *Typha*, *Sparganium*, *Phragmites* and *Glyceria* species) (Koperski, 1998; Tarkowska-Kukuryk, 2006; Moller Pillot, 2009).

Like the present findings there are reports of strong relationships between the abundance and distribution of herbivorous insects and the structural complexity, density and spatial pattern (patch size and isolation) of the vegetation in terrestrial environments (e.g. Langelotto & Denno, 2004; Crist et al., 2006; Obermaier et al., 2008; Randlkofer et al., 2009). In terrestrial systems density, height and fragmentation of the vegetation seem to be the most important at the habitat level and at the individual plant level it is mainly plant height that has a strong positive influence on herbivore distribution and oviposition (Crist et al., 2006; Obermaier et al., 2008; Randlkofer et

al., 2009). However, in other cases plant species composition and structural features of the vegetation have an important influence on the community structure of insects (e.g. Crist et al., 2006; Schaffers et al., 2008). For example, Schaffers et al. (2008) compare the species composition of seven functional groups of arthropods with plant species composition, vegetation structure, flower richness, landscape composition and environmental data and demonstrate a stronger relation between the species composition of arthropod and plant communities than with vegetation structure and environmental conditions.

In our study, as in some previous studies (e.g. Dvorak & Best, 1982; Cattaneo et al., 1998; Strayer et al., 2003), the distribution of chironomids was most closely associated with total density of macrophytes. Vegetation cover and distance from the nearest area of open water, as well the presence of floating leaved macrophytes (such as *Trapa natans* and *Nymphaea alba*) negatively influenced the abundance of some chironomids (e.g. *C. riparius* agg., *E. tendens*, *K. tendipediformis*, *P. sordens*, *G. pallens*). Similar observations are reported by Marklund et al. (2001), who investigated the distribution and diel migration of macro-invertebrates in dense beds of *Chara*. They found that total abundance of macro-invertebrates is higher at the edge of macrophyte stands than in the innermost parts, even during daytime and in spite of predation pressure. Similarly, several authors suggest that too dense a stand of macrophytes with a high percentage vegetation cover could alter the physico-chemical features of the underlying environment and make it unfavourable for invertebrates (e.g. Cheruvelil et al., 2002; Papas, 2007). Moreover, certain plant species (e.g. *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Chara* spp.) secrete antialgal-compounds, which limit the growth of epiphytic algae (Ervin & Wetzel, 2003). Since the epiphyton is a very important food source for aquatic macro-invertebrates (e.g. Cattaneo et al., 1998; Balci & Kennedy, 2003; Papas, 2007; Bogut et al., 2010) these chemicals could also indirectly influence the distribution and density of macro-invertebrates (like chironomids).

Chironomids differ from each other in their feeding habits and although it is difficult to classify some of the species into well defined guilds since the guild to which they are assigned depends on the life stage and what food resource is available (Armitage et al., 1995; Moog, 2002). In this study six functional feeding groups were identified of which active filter-feeders, detritus feeders and grazers were the most abundant, while shredders, miners and predators occurred in smaller numbers. However, their distribution was not influenced either by the structure or taxonomic composition of the vegetation. In contrast, Cremona et al. (2008) report a clear relationship between the architecture of the vegetation and the density of various macro-invertebrate guilds. These authors suggest that detritivores and predators prefer macrophytes with a complex structure, while grazers choose chiefly simple structured vegetation. The most likely explanation of the latter observation is that simple structured macrophytes allow more light to penetrate thus favouring the growth of periphyton and so provide more food for grazers (Cremona et al., 2008; Tessier et al., 2008). However, the taxonomic resolution used in the above paper is low (i.e. chironomids were only classified to subfamily level), which might bias the results.

Present analyses identified only weak relationships between the aquatic vegetation and their chironomid fauna, however, the high level of inconsistencies in the results suggest that even these relationships should be viewed with caution and further analyses are needed to establish their validity. The most obvious discrepancy is that majority of the significant relationships were only for BKHT, with the exception of the chironomid *Glyptotendipes cauliginellus* (discussed above). Different characteristics of the two backwaters may explain most of the above differences in their macrophyte-chironomid relationships (Ali et al., 2002). Namely, BKHT was established relatively recently and is at an early stage of succession while NAGM is at a later stage of succession, the transition between pond and marsh. The macrophyte stands at NAGM were considerably larger and denser than those at BKHT, which indicates that dense vegetation may negatively influence algal production, oxygen concentration at night and as a consequence the density and productivity of macro-invertebrates (Cheruvelil et al., 2002; Papas, 2007; Cremona et al., 2008) (see above). In some parts of NAGM the density of macro-vegetation was probably above this critical level. Therefore, it is likely that the relationship between chironomids and macrophytes is not linear over the entire vegetation density scale, but hump-shaped when high vegetation densities are included. This assumption is supported by the lower abundance (around half compared to BKHT) of chironomids at NAGM.

In several earlier publications other factors than habitat type and plant morphology or architecture are said to significantly affect the composition of macro-invertebrate communities and the distribution of certain invertebrates (Papas, 2007). The factors cited are the trophic state of a lake (Pieczynska et al., 1999; Bogut et al., 2007, 2010), depth of the water (Ali et al., 2002; Bogut et al., 2007, 2010; Engels & Cwynar, 2011), nutrient content (Bogut et al., 2010), availability of epiphytic food (Marklund et al., 2001; Ali et al., 2002; Balci & Kennedy, 2003; Cremona et al., 2008; Bogut et al., 2010; Hansen et al., 2010) and water chemistry (Cattaneo et al., 1998). Since some species of chironomid develop very rapidly and their development time may vary among habitats (e.g. Armitage et al., 1995; van den Berg et al., 1997; Tarkowska-Kukuryk, 2006) seasonality may also influence the trends in chironomid assemblages observed along habitat gradients, even if all samples are collected from all the sites within a short period of time. However, in the present study there is no evidence of the life cycle of any chironomid differing in the two backwaters.

In conclusion, present results demonstrate that macrophyte-chironomid associations are organized in a complex way as there is no simple relationship between the structure of chironomid assemblages and the taxo-

nomic composition of the vegetation with which they are associated. It is suggested that the structure (i.e. position, stand size, total density) of aquatic vegetation and the characteristics of the environment where it develops may be more important in shaping plant-dwelling chironomid assemblages than the taxonomic composition of the vegetation.

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