This manuscript is contextually identical with the following published paper:

Árva Diána; Tóth Mónika; Mozsár Attila; Specziár András (2017) The roles of environment, site position and seasonality in taxonomic and functional organisation of chironomid assemblages in a heterogeneous wetland, Kis-Balaton (Hungary) HYDROBIOLOGIA 787 pp. 353-373. DOI: 10.1007/s10750-016-2980-7

The original published PDF available in this website:
http://link.springer.com/article/10.1007%2Fs10750-016-2980-7

Diána Árva*, Mónika Tóth, Attila Mozsár, András Specziár

Balaton Limnological Institute, MTA Centre for Ecological Research, Klebelsberg K. str. 3., H-8237 Tihany, Hungary

*Corresponding author: Tel.: +36 87448244; email: arva.diana@okologia.mta.hu

Abstract Environmental heterogeneity plays a determinant role in structuring taxonomic and functional composition of local assemblages via various interacting processes as synthetized in the metacommunity theory. In this study we evaluate the relative roles of local environmental and landscape filters, spatial constraints and seasonality in organisation of assemblages of Chironomidae (Diptera), a diverse aquatic insect group with winged adults, in an extremely heterogeneous wetland system, Kis-Balaton, Hungary. As expected, local environmental variables explained a substantial proportion of assemblage variance mainly along sediment structure, macrophyte coverage, and decomposing plant matter gradients. Considering the narrow spatial range of the study area, pure spatial influence was unexpectedly strong, likely because of the dispersal limitation related to tall terrestrial vegetation patches and mass effect related to the uneven distribution and area of certain microhabitats and their species pools. Whereas landscape- and season-related variability proved to be low or negligible. Taxonomic and functional feeding guild (FFG) based approaches revealed the same main trends in assemblage data; however, FFGs seemed to track environmental changes more tightly. We argue for the common use of taxonomic and functional based approaches, and advise the improvement of species optima and tolerance spectra databases to expand bioassessment power.

Keywords: Bioassessment, Dispersal limitation, Environmental filtering, Functional feeding guild, Metacommunity, Optimum and tolerance.

Introduction

The relative importances of different processes, such as dispersal, colonisation, and environmental filtering in influencing distributional patterns and meta-community dynamics of organisms depend on several factors; including scale of the observation, species-specific characteristics, and environmental heterogeneity (Brown, 2007; Mykrä et al., 2007; Grönroos et al., 2013; Heino, 2013a,b). For example, decreasing relevance of dispersal limitation and in general of spatial effect can be observed from broader geographical to microhabitat scale, where environmental control becomes dominant (Cottenie, 2005; Beisner et al., 2006; Capers et al., 2009). According to their structural complexity, different types of habitats provide a variety of niches and resources and therefore influence composition and distribution of assemblages (Stewart et al., 2003). On the other hand, spatial structure of the environmental conditions itself has an influence on habitat selection and along with the dispersal ability of organisms defines the potential range of habitats they can reach (Vanormelingen et al., 2008; Capers et al., 2009). At the same time, seasonality affects all of these relationships; environment varies seasonally and determines available food sources and refuges, while life cycles of organisms define their within year occurrences and colonization patterns (García-Roger et al., 2011). Hence, it is difficult, but essential for effective biomonitoring and conservation management programs to understand these community-environment relationships.

Wetlands are productive, dynamic, and heterogeneous systems. Their ecological and practical value is manifested among others in the important role in water treatment (i.e. water quality improvement, water storage, and flood regulation), in hydrological and nutrient cycles, and in the maintenance of biotic diversity (Batzer & Wissinger, 1996; Euliss et al., 2008). Several types of wetlands are known from freshwater to marine, temporary to permanent, natural to constructed, etc. with varied habitat structure, water level fluctuation, and macrophyte coverage (Batzer & Wissinger, 1996), but universally they provide heterogeneous environment for numerous species resulting generally high local diversity (Whiles & Goldowitz, 2005; Euliss et al., 2008). Therefore, wetlands are perfect places to analyse the roles of environmental heterogeneity and its spatial and seasonal variability on the small scale distribution and meta-community organisation of aquatic organisms, and especially of those, which are characterized by relatively short life cycle, good dispersal and colonisation capacity, such as chironomids.

Chironomids (Diptera: Chironomidae) are widely distributed and abundant insects that occupy a wide-range of aquatic habitats. Thanks to their well-defined and different taxon-specific tolerances and environmental optima, chironomids have long been used as indicator organisms in recent bioassessment and paleolimnological studies (Brundin, 1958; Sæther, 1979; Gajewski et al., 2005; Milošević et al., 2013; Nicacio & Juen, 2015). In this context, proper taxonomic identification of Chironomidae could provide quite beneficial information about their environment (King & Richardson, 2002). However, several authors revealed that assessment of functional feeding groups (FFGs), which identification generally require less specified taxonomical knowledge compared to species based approaches, may promote our understanding about the relevant environmental gradients and general conditions of various ecosystems as well, but in a less laborious way (Usseglio-Polatera et al., 2000; Merrit et al., 2002; Cummins et al., 2005; Heino, 2005, 2008). Moreover, FFG based patterns are also comparable across geographical areas with different species pools, and as such may more directly facilitate the development of generalized ecological models (Heino et al., 2013). Considering the above mentioned features and the important role of Chironomidae in nutrient cycling of aquatic ecosystems (Porinchu & MacDonald, 2003), monitoring of their FFGs and the related functional diversity may be a beneficial supplementary tool for disentangling rules of natural assemblage organisation and ecosystem functioning, as well as human induced alterations. However, our knowledge about the FFG based patterns of chironomid assemblages is still scarce.

Effects of different environmental factors on the distribution of chironomids have been thoroughly studied (e.g. Mousavi, 2002; Bitušík & Svitok, 2006; Ferrington, 2008; Puntí et al., 2009; Tóth et al., 2012, 2013). We have some information about the role of spatiality in their dispersal at larger scale (Delettre et al., 1992; Delettre & Morvan, 2000) as well, but how it affects their distribution and metacommunity structure at smaller scale is hardly known. In a recent study, Árva et al. (2015a) have examined the role of local environmental conditions and spatial processes on chironomid communities within the large, shallow, and relatively homogeneous Lake Balaton. At this within lake scale, environmental filtering proved to be predominantly substantial in accordance with recent metacommunity theorems (Leibold et al., 2004; Cottenie, 2005; Beisner et al., 2006; Heino, 2013a,b), however, a significant pure spatial effect could be identified as well. At the same time, correspondingly to other studies (Suurkuukka et al., 2012; Specziár et al., 2013), we showed what a crucial role habitat heterogeneity of the relatively narrow littoral zone has in shaping total species diversity and taxon-environment relationship in a lentic environment dominated by homogeneous open water habitat (Árva et al., 2015a,b). Thus, the questions raise: how small scale metacommunity structure of chironomids forms in en bloc heterogeneous environment, such as a wetland is, and whether taxonomic and functional assemblage patterns provide the same main picture or not.

Accordingly, our objective was to investigate chironomid metacommunity structure and underlying environmental and spatial processes in a much heterogeneous environment, in Kis-Balaton, Hungary, which is a unique Ramsar and Natura 2000 (HUBF30003) wetland area. Specifically, in this study we analysed: (i) to what extent different local environmental, landscape and spatial factors and season contribute to the structural organization of chironomid assemblages examined at taxonomic and functional (FFG) basis, and distribution of individual species and FFGs; and (ii) what optima and tolerance values characterize the dominant taxa regarding the most influential environmental factors. We hypothesised the predominant role of environmental factors in the community assembly at this limited spatial scale (Mykrä et al., 2007; Heino, 2008, 2013c) and correspondingly the separation of optima and tolerance ranges of the characteristic chironomid taxa along the most influential environmental gradients (Puntí et al., 2009; Árva et al., 2015a). Since certain functional traits, which are selected by local environmental factors, may be represented by multiple taxa in the regional species pool (Heino et al., 2013), we assumed that the distribution of FFGs could be less affected by the spatial constraints and will more closely related to local environmental conditions than that of the taxa. Moreover, since both environmental conditions (i.e. food resource, refuge and physical and chemical environment) provided by different habitats and the life cycle of these multivoltine organisms related to the time of the year, we expected also some seasonal variability (phenology; Hawkins & Sedell, 1981; Heino et al., 2013) in the assemblage structure.

Material and methods

Study area

Kis-Balaton (it can be translated as “Little Lake Balaton”) evolved simultaneously with the ancient Lake Balaton about 12-15,000 years ago. On the course of time, its area and connectivity to Lake Balaton varied depending on precipitation related water level changes, along with its habitat characteristics that varied between wetland and lake status (Cserny & Nagy-Bodor, 2000). However, as part of country-wide water regulation program, most of the area of Kis-Balaton was drained in multiple steps, starting in the 19th century and accomplished in the first half of the 20th century. Finally, when Lake Balaton, which is a highly appreciated recreational water, became hypertrophic during the 1960-1980s, due to the enormous amount of nutrients got into it primarily through the River Zala, the restoration of Kis-Balaton was initiated in order to retain external nutrients and protect the water quality of Lake Balaton (Pomogyi, 1993).

As far as concerning the present situation, Kis-Balaton is a highly diverse wetland area situated at the mouth of River Zala (at ca. 46° 34’ - 46° 42’ N, 17° 07’ - 17° 16’ E. and ca. 106 m above sea level) and has ca. 147 km^2 surface area (Fig. 1). The re-established system consists of two major parts separated by sluices. The upstream part (along the River Zala; Phase I, called Lake Hídvégi) has been in operation since 1985 and it is mainly eutrophicated open water (mean depth: 80 cm) with diverse littoral macrovegetation, and has an average water retention time of 30 days. The downstream part (Phase II, including Lake Fenéki and Ingói-grove) was inundated in 1992, but its construction was completed only in 2014. Majority of this area is covered by macrophytes, dominantly by common reed grass *Phragmites australis* (Cav.) Trin ex Steud.

The Kis-Balaton wetland system is exceedingly heterogeneous with natural and semi-natural aquatic habitats, including large areas with open water, emergent, submerged and floating leaved aquatic macrovegetation, riparian vegetation, wet and inundated forests and meadows, canals either with and without currents, river habitats, ripraps, and separated borrow pits of variable succession stages, as well as extended patches of terrestrial vegetation. Most abundant submerged and floating leaved macrophytes are rigid hornwort *Ceratophyllum demersum* L., Eurasian watermilfoil *Myriophyllum spicatum* L., water chestnut *Trapa natans* L., water knotweed *Polygonum amphibium* (L.) Gray, European white water-lily *Nymphaea alba* L. and yellow water-lily *Nuphar lutea* (L.) Sm. In addition, rootless duckweed *Wolffia arrhiza* (L.) Horkel ex Wimm., common frogbit *Hydrocharis morsus-ranae* L., and water soldier *Stratiotes aloides* L. occurs in smaller patches. Extended areas of emergent macrophytes, especially in the downstream part, are composed primarily of common reed grass *P. autralis* supplemented with *Carex* (e.g. *Carex acutiformis* Ehrh., *Carex riparia* Curtis) and *Typha* species. Hydrological conditions of the system are regulated by sluices, dikes and pumping-stations, and two fish-passes provide the longitudinal permeability for fishes along the route of Lake Balaton–Kis-Balaton–Zala River within the probable long-term water level range.

Sampling design

To cover effects both from environmental variability and seasonality on chironomid assemblages with a reliable effort, we conducted a two staged sampling during 2014-2015. Moreover, in order to capture spatial effects from any constrained patterns in dispersion as well, sampling sites were dispersed not only along environmental gradients but also in space to an extent as it was feasible (Fig. 1).

First, between 23 June and 01 July, 2014 we performed an extended sampling at 79 sampling sites to obtain a comprehensive picture of the chironomid assemblages, their spatial patterns and environmental relationships across the whole system, including all the major habitat types listed in the Sampling Area section. Then, to capture seasonal variability in chironomid assemblages and their relationships with the influential environmental and spatial factors, the sampling was repeated during 29-30 September, 2014 and 21-22 April, 2015 at 32 sampling sites, representing most of the environmental heterogeneity and its spatial structure, and with adequate density of larvae, based on the results of the summer survey. Unfortunately, two of the sampling sites became dry in spring 2015 due to a faulty water regulation action, thus, sampling was insensate there.

Three parallel samples were taken from the sediment at each sampling site using Ekman grab and merged for analyses (total sampled area per site: 648 cm^2). Sediment samples were washed through a 0.25 mm mesh sieve and transported to the laboratory in a cooling box. Riprap habitats were sampled by cleaning and washing algae or moss coating and sediment from a measured rock surface being equivalent to Ekman grab samples into plastic containers. In the laboratory, chironomids were sorted from sediment alive by sugar flotation method (Anderson, 1959), euthanized, and preserved in 70% ethanol. For the identification, larvae were cleared by digestion in 10% KOH and slide-mounted in Euparal®. Identification was performed to species or the lowest possible taxonomic level according to the keys of Bíró (1981), Cranston (1982), Wiederholm (1983), Janecek (1998), Vallenduuk (1999), Sæther et al. (2000), Vallenduuk & Moller Pillot (2002) and Vallenduuk & Morozova (2005). In addition, we also recorded the number of Ceratopogonidae and Chaoboridae larvae in the samples without further taxonomic examination.

Local environmental, landscape and spatial variables

Parallel to sampling, we measured a series of local physical-, chemical- and biotic variables (Appendix A) that have been found influencing assemblage structure of chironomids in the region (Árva et al., 2015a) and elsewhere (e.g. Real et al., 2000; Rae, 2004; Free et al., 2009; Puntí et al., 2009; Tóth et al., 2012). At each sampling site, we recorded water depth, Secchi disc depth, and temperature, current, dissolved oxygen concentration, pH, and conductivity of the water close to the bottom. Emergent, submerged, and floating leaved macrophytes, filamentous algae, moss, riparian vegetation, and tree coverage (%) was estimated visually within a circle of 3 m diameter around the sampling point. The substratum of the sites was inspected for percentage compound of clay (grain size ≤0.002 mm), silt (0.002-0.06 mm), sand (0.06-2 mm), gravel (2-4 mm), rock (>200 mm), and peat. Moreover, occurrence of fine

(FOM) and coarse (COM) decomposing organic matter particles, reed and tree leaves, and woody debris (excluding leaves) in the sediment, and occurrence of dead trees at the site was rated on a six category scale (0-5). Percentage organic matter content was assessed from dry (at 50°C for 72-96 hours until constant mass was reached) samples of the upper 2 cm sediment layer according to the loss-on-ignition method at 550°C for 1 hour (LOI550; Heiri et al., 2001). Chlorophyll-a was extracted from whole water column samples by acetone method (Aminot & Rey, 2000), and then, its concentration was measured spectrophotometrically (Shimadzu UV-1601 spectrophotometer).

Considered landscape variables encompass distances from the closest clump, shore, reed grass stand, floating leaved or submerged macrophyte meadow, and open water measured by GPS equipment. In addition, sites were classified as undisturbed and disturbed, with the latter indicating continuous or recent (i.e. within two years) habitat modifications (e.g. dredging, inundation, vegetation cutting).

Relative position of each sampling site was determined by a set of theoretical spatial variables modelling broad to fine scale spatial patterns among sampling sites by performing principal coordinates of neighbour matrices (PCNM; Borcard et al., 2004).

Statistical analyses

To analyse the distribution of chironomids, we used both taxon and FFG based approaches. Therefore, chironomid taxa were assigned to FFGs according to their feeding habits (Moog, 2002) based on the score table of IS Arrow database (Czech Hydrometeorological Institute, 2009; see Appendix B) prior to statistical analysis. FFGs presented in our samples were: shredders (SHRs), grazers (GRAs), active filter-feeders (AFILs), passive filter-feeders (PFILs), detritus feeders (DETs), miners (MINs), predators (PREs), and parasites (PARs).

We performed partial direct gradient and partial multiple second degree polynomial regression analyses (MPRA) followed by a variance partitioning approach (Cushman & McGarigal, 2002; Peres-Neto et al., 2006) to evaluate the role of local environmental, landscape and spatial factors, and season in the distribution of benthic chironomids at the assemblage (based both on taxa and FFGs), individual taxon, and FFG levels, respectively. Two separate analyses, one with the summer samples only and a second with the seasonal samples including just the relevant sites of the summer sampling, were performed for each response variable groups (i.e. assemblages of taxa, assemblages of FFGs, dominant taxa, and dominant FFGs).

Rare taxa and FFGs occurring in <2% of the samples or with <0.1% representation in the total abundance were excluded from the analyses to reduce their disproportionate effect in the multivariate statistics (Legendre & Legendre, 2012), and then abundance data were ln(x+1) transformed to improve their normality and reduce heteroscedasticity. Of explanatory variables, season and disturbance of landscape variables were re-coded into binary dummy variables (Lepš & Šmilauer, 2003). Variables measured on continuous scales and representing percentage distribution were ln(x+1) and arcsin√x transformed, respectively. Whereas, categorically scaled local environmental, pH and spatial PCNM variables were not transformed (see Appendix A). PCNM variables model the position of each sampling site relative to all the other sites, similarly as they distribute on the map (Borcard et al., 2004; Dray et al., 2006). During the procedure, a matrix of ln(x+1) transformed Euclidean distances between all pairs of sampling sites was constructed from the GPS coordinates and subjected to a principal coordinate analysis using Past version 2.17 software (Hammer et al., 2001). The procedure we applied differs somewhat from the original approach (Borcard & Legendre, 2002; Borcard et al., 2004; Dray et al., 2006), in respect of the distribution of our sampling sites. The truncation procedure (Borcard & Legendre, 2002) lost its relevance as the truncated distance (i.e. four times the largest distance between closest neighbouring sites; 9,103 m in this case) was close to the maximum distance between any two sites (13,180 m). Therefore, we did not truncate any distances; instead, based on the assumption that effect of dispersal constraints, as long as they are valid, could be cumulated at a decreasing rate with distance, we used logarithmic transformed distances for generating PCNM variables.

Assemblage level analysis: since detrended correspondence analysis (DCA) indicated relatively long gradient length in both taxon (4.14 and 4.04 in S.D. units, for summer and seasonal data respectively) and FFG (1.94 and 1.73 in S.D. units) based assemblage data, we decided to use canonical correspondence analysis (CCA) for further evaluation (Lepš & Šmilauer, 2003). Potential explanatory variables were filtered for collinearity at $r>0.7$ and subjected to a forward stepwise selection procedure (at $P<0.05$) in CCA based on Monte Carlo randomization test with 9,999 unrestricted permutations. Further, we added ln(x+1) transformed abundance data of Ceratopogonidae and Chaoboridae as supplementary variables to the CCA model in order to support the graphical interpretation of the results. Then, to partition the effects of significant variable groups on chironomid assemblages, a series of CCAs and partial CCAs were conducted (Cushman & McGarigal, 2002). DCAs and CCAs were performed using CANOCO version 4.5 software (ter Braak & Šmilauer, 2002).

Individual taxon and FFG level analyses: during the MPRA we followed basically the same methodological approach (i.e. variable selection procedure followed by variation partitioning based on the final model) as described above using STATISTICA 8.0 software (www.statsoft.com). We performed regression analyses for the most abundant chironomid taxa and FFGs occurring in ≥25 samples, and used pure and quadratic forms of the same explanatory variables as in the case of assemblages, but excluding PCNM variables with <1% eigenvalues (i.e. only PCNM1-20 were included in the primary selection procedure). This type of regression enables modelling of both linear and unimodal responses of organisms along different gradients (Legendre & Legendre, 2012). During the forward stepwise variable selection in MPRA, pure and quadratic forms of each potential explanatory variable were considered as independent variables.

In order to better understand the nature of the spatial effect, we examined the role of pure distance related dispersal limitation in the observed spatial variability of chironomid assemblages by correlating between sites assemblage similarities with the concerning geographical distances, using the non-parametric Spearman rank correlation test (i.e. Distance Decay Analysis). The spatial distance matrix of the sites was constructed by calculating geographical distances between all pairs of the sites, whereas pairwise assemblage similarities were quantified using the Bray-Curtis similarity index separately for taxon and FFG based relative abundance data.

Optima and tolerances of the abundant chironomid taxa occurring in ≥10 samples for the most influential environmental factors were assessed by weighted averaging regression method using C2 version 1.7.4 software (Juggins, 2007).

Results

Chironomid assemblages

Samplings provided altogether 12,272 individuals of 64 chironomid taxa belonging to 4 subfamilies: Tanypodinae (11), Prodiamesinae (1), Orthocladiinae (12) and Chironominae (40). The average taxon richness was 6 ranging between 0 and 25 taxa per sample. List of captured taxa and their abundances are presented in Appendix B. Most abundant taxa were *Glyptotendipes pallens*, *Chironomus plumosus* agg., *Cricotopus tremulus* gr., and *Polypedilum nubeculosum*. Of the 8 FFGs presented in the samples, detritus feeders (DETs) dominated in all seasons.

Chironomid assemblage–environmental relationships in summer

In the taxon based CCA model, local environmental, landscape, and spatial variables explained 53.7% of the total variance in the relative abundance data. First CCA axis explained 10.5% of taxon variation and correlated positively with reed grass leaves and water depth, and negatively with algae coverage and PCNM1 that reveal broader scale spatiality. The second axis (8.4%) captured mainly a depth gradient in negative association with silt and water depth and positive with algae coverage and disturbance (Fig. 2a). A large part of the variance was related only to spatial variables (23.5% as pure effect), although local environmental variables explained also considerable proportion (17.8% as pure effect and additional 9.3% as shared effect). Explanatory power of landscape variables was relatively low both as pure and shared effects (3.6% and 1.2%, respectively; Fig. 3a). Chironomid taxa scores and vectors of explanatory variables distributed quite evenly in the ordination plane, indicating a highly heterogeneous system without clearly separating habitat- and assemblage types. Ceratopogonidae, used as supplementary indicator taxa in the analysis, primarily associated with *Procladius choreus*, *Tanypus kraatzi*, and *C. plumosus* agg. dominated assemblages of mainly deeper, open water habitats with silty sediment. Whereas, Chaoboridae, the other supplementary taxa, occurred mainly in deep, vegetated areas with high amount of decomposing reed grass leaves, and other macrophyte remains on the bottom, and with very low oxygen concentration, but they did not clearly associate with any characteristic chironomid assemblages (Fig. 2a).

The FFG based CCA model explained 75.6% of the variance in the chironomid assemblages. Here, first CCA axis (37.4%) represented positive correlation with algae coverage, disturbance, and current and negative correlation with silt and water depth. Second CCA axis (22.3%) correlated positively with moss coverage and negatively with PCNM1 representing broad scale spatiality (Fig. 2b). Distribution of FFGs was affected the most by local environmental variables (36.1% as pure effect and additional 15.7% as shared effect; Fig. 3b). On the other hand, variation captured only by spatial variables proved to be also high (21% as pure effect) again, while importance of landscape variables remained small (2.8% as pure effect) in this case as well. FFGs provided a clearer grouping of habitats and associated assemblage types, compared to the taxon based analysis. Deep areas with silty sediment were predominated by PREs, DETs and AFILs, whereas algae coverage and current favoured the occurrence of SHRs, GRAs, MINs, and PARs. PFILs occurred only at a few sites and represented a clear outlier group in our dataset indicating their uniqueness in the system (Fig. 2b).

Distribution of abundant taxa and FFGs in summer

MPRA could be run with six taxa and six FFGs for the summer data. Proportion of explained variance was much less than at the assemblage level and it ranged between 17.7-60.1% for taxa, and 32.2-51.8% for FFGs (Fig. 4a). Generally, local environmental variables, especially substrate type and organic matter related variables had higher explanatory power in taxa abundance patterns than spatial and landscape variables. MPRA model proved to be less effective in the *Procladius* sp. with only 17.7% of variance, explained mainly by landscape variables (10.2% as pure effect). Spatiality per se affected notably only the distribution of *Chironomus dorsalis* (28.6% as pure effect). At FFG level, influence of local environmental variables should be highlighted, as well. However, PCNM variables captured also a remarkable proportion of variance in AFILs, DETs, and PREs (Fig. 4a).

Effect of season on assemblage level patterns

CCA revealed a very similar pattern in seasonal samples than in the summer samples only, with higher spatial and environmental resolution based either on taxa or FFGs (Figs 5a,b). Mainly due to the important contribution of local environmental, landscape, and spatial variables, the models explained again considerable 63.4% and 64.4% fractions of the total variance of chironomid abundance data based on taxa and FFGs, respectively (Figs 6a,b). However, surprisingly, seasonal variability proved to be marginal (3.3% as pure effect and additional 2.4% as shared effect) in taxon based approach, and proved to be absolutely insignificant in FFG based approach.

Effect of season on distribution of abundant taxa and FFGs

Seasonality had little influence on the distribution of individual taxa and FFGs as well (Fig. 4b). Only *Cricotopus sylvestris* gr., *C. dorsalis*, *C. plumosus* agg., and *Endochironomus albipennis* taxa, and AFILs and DETs showed some seasonality to an extent of 3.4% to 16.9% of their total abundance variability in samples. Abundances of *Cladopelma virescens*, *Cryptochironomus defectus*, *G. pallens*, *Parachironomus varus*, and GRAs, MINs, and PARs were highly influenced by local environmental and landscape variables. Like in summer samples, considerable spatial variance was observed in the distribution of *C. dorsalis* (21.2% as pure effect).

Distance decay in assemblage similarity

Correlation analysis revealed no or very little distance related variability in both taxon and FFG based assemblage composition data regarding either the detailed summer or the seasonal samples (Table 1).

Environmental optima and tolerances of abundant chironomid taxa

Optima and tolerances of dominant chironomid taxa, Chaoboridae and Ceratopogonidae regarding some influential environmental factors are presented in Fig. 7. Within the studied ranges, several chironomid taxa, especially those exhibiting higher optimum values, proved to be rather tolerant for the variability of several environmental factors. Nevertheless, some quite useful indicative patterns could also be identified. For instance, *Chironomus luridus* agg., *C. dorsalis*, and *Glyptotendipes* sp., which had the lowest tolerance limits and optima for oxygen concentration, seemed also to be capable of tolerating largest conductivity, LOI550, and highest amount of decomposing reed leaves. *C. sylvestris* gr., *P. varus*, *Dicrotendipes nervosus*, and *G. pallens* revealed highest optima for total macrophyte and algae coverage, preferred shallow water with substratum characterized by low COM and low to moderate FOM content. In addition, *P. varus* appeared mainly in harder surfaces and showed the highest optima and tolerance values for water current.

Of the two supplementary taxa, Chaoboridae larvae typically positioned at either end of the studied gradients giving some useful indication about the extremity (e.g. regarding the lower limit of oxygen and chlorophyll-a concentration, and highest values of conductivity) not being suitable for most chironomid taxa. Whereas, Ceratopogonidae showed high tolerance and intermediate optima for most environmental factor and thus proved to represent less indicative value in this respect within the studied system.

Discussion

Spatial structuring of taxa and FFGs

According to the metacommunity theory, local assemblages are structured by spatial dispersal processes of species and prevailing environmental conditions (i.e. environmental filtering) (Leibold et al., 2004; Cottenie, 2005). Importance of various landscape and local environmental factors in selecting chironomid taxa for local chironomid assemblages is quite well understood (e.g. Mousavi, 2002; Porinchu & MacDonald, 2003; Gajewski et al., 2005; Ferrington, 2008; Tóth et al., 2012; Milošević et al., 2013). However, the role of pure spatial influences (i.e. which are unrelated to local environmental conditions) and the rules of function based metacommunity assembly across heterogeneous habitats are much less known, especially at smaller spatial scale. Therefore, we investigated the contribution of different spatial, landscape, and local environmental factors, and season to the organization of assemblages of chironomid taxa and FFGs within an exceedingly heterogeneous wetland area.

As we expected, local environmental variables explained a substantial proportion of variance in assemblage data in Kis-Balaton. At the same time, an unexpectedly high amount of variance (13.0-25.6%) was related to pure spatial influence, especially in taxon based analysis, where its effect was even higher than the pure environmental control. In agreement with the results of Árva et al. (2015a) on the metacommunity structure of chironomids within the mainly homogeneous Lake Balaton, this finding suggests that small scale spatial processes can be more important in aquatic insects with winged adults than supposed earlier, at least in certain systems. As revealed by the results of the correlation analysis, underlying processes of the identified spatial effect could be more complex than pure distance related trends in assemblage structure. The relatively high significance of pure spatial patterning within this wetland landscape probably could be related to the joint effect of two processes; (i) limited dispersal of midge taxa and (ii) mass effect from certain habitat types with abundant stocks. Chironomids with their winged adults are considered as moderate dispersers which dispersal performances, beside the distance, are also influenced by landscape structures and winds even at very short distances (Delettre et al., 1992; Delettre & Morvan, 2000). Kis-Balaton is a diverse mixture of aquatic and terrestrial habitats with heterogeneous vegetation, including clumps and forested areas as well. This taller terrestrial vegetation, along with the patchily distributed emergent macrophyte stands, provide not just resting places for adults, but at the mean time represent dispersal barriers, and therefore cannot be ignored as essential component of population dynamics and metacommunity organisation of chironomids (Delettre et al., 1992; Delettre & Morvan, 2000). Simultaneously, the highly variable area and patchy distribution of certain microhabitat types likely support the influence of the mass effect related metacommunity patterns. Namely, species which larvae are adapted to the dominant microhabitats and thus have high larval abundances in the area have higher probability to reach new habitats in adulthood than those require more specified larval environment and thus occur sporadically and in low overall abundance (Leibold et al., 2004; Heino, 2013c).

Influences of dispersal limitation and mass effect on local assemblage structure are not distinguishable on the basis of spatial models and variation partitioning approach (Heino, 2013b) and consequently, we cannot rate their relative importance in this specific case. However, these two spatial processes act to the same direction and jointly determine the composition and abundance of potential colonizers. The outcome of the above discussed spatial processes perhaps also depends on species-specific traits, and their influence on FFGs is thus largely indirect. Moreover, since FFGs are highly redundant taxonomically, spatial processes that influence species composition of local assemblages do not necessarily alter functionality. Therefore, it is not surprising that, in accordance with our assumption, pure spatial effect was less important, while local environmental influence more pronounced in assemblage structuring of FFGs than that of the taxa.

Landscape structuring of taxa and FFGs

Landscape has an important influence on taxonomic and functional variability of local assemblages in aquatic macroinvertebrates, including chironomids, mainly at broader spatial scale (Poff, 1997; Roque et al., 2010). In this study, with a relatively narrow spatial range, landscape variables received, however, relatively little explanatory power and their influence largely overlapped with the effect of spatial and local environmental variables. We consider this result unsurprising, as sampling sites were quite close to each other and thus it was hard to relate much landscape variability to particular sites. The sole landscape variable that was retained in all of our assemblage level models (i.e. summer samples only, seasonal samples and both based either on taxa or FFGs) was the disturbance. In this area, disturbance was related to water regulation works, including the establishment of new habitats and sediment dredging. Both of these interferences configured new colonisable environments with fresh substrate, and less macrophytes and available food for chironomids than in the surrounding habitats.

Environmental control of taxa and FFGs

Direct gradient analysis (i.e. CCA) revealed that sediment structure, degree and composition of plant coverage, the amount and origin of decomposing plant material, and water depth were the most influential environmental properties in structuring chironomid assemblages on either taxonomic or functional basis. These results are highly congruent with findings of previous studies on environment-chironomid relationships in various habitats (e.g. Ali et al., 2002; Rae, 2004; Tarkowska-Kukuryk, 2014; Árva et al., 2015a). Although FFGs are defined roughly, based only on the feeding habits of chironomids, these functional traits assigned in large the same environmental variables to be influential on assemblage composition than those set by the more detailed and direct taxonomic approach. Moreover, probably because being less sensitive to spatial processes (due to a taxonomic redundancy; see above), FFGs seemed to respond more sensitively to environmental changes than assemblages of species.

In accordance with the general knowledge, sediment physical structure had a marked control on local assemblage structure in this wetland system as well. Similarly to Lake Balaton (Árva et al., 2015a) and Neusiedler See (Wolfram, 1996) the fraction of silt in the sediment had the most marked segregation power among optima of *T. kraatzi*, *C. plumosus* agg., *Procladius* sp. and *Tanypus punctipennis*, being associated with soft, silty sediment, contrary mainly to taxa associated with algae coating on stones (e.g. *P. varus*, *C. sylvestris* gr., *D. nervosus*) and other harder substrates (e.g. *C. mancus* gr.) in Kis-Balaton. The role of filamentous algae coverage on the bottom surface in itself had a remarkable explanatory power, as it was also usually associated with harder substrates, current and higher oxygen concentration; conditions which are highly divergent from the dominant environmental characteristics of this wetland area. In accordance with the results of Tarkowska-Kukuryk & Kornijow (2008) and Tarkowska-Kukuryk (2014), for example *C. sylvestris* gr., *D. nervosus*, *E. albipennis*, *Polypedilum sordens*, *G. pallens*, and *P. varus* were associated with these microhabitats. The same gradient (i.e. silty sediment vs. harder substrate, algae coverage, and current) proved to be the most important in structuring FFGs; PREs and DETs were associated with silt and MINs, SHRs, and PARs with harder substrates.

Kis-Balaton, like wetlands in general, is inhabited by a dense and productive macrophyte flora, and consequently, its nutrient cycle is largely based on the huge amount of decomposing macrophyte particles from various origins (c.f. Magee, 1993; Spieles & Mitsch, 2000), although the role of the phytoplankton is also significant in some open water sites. In accordance with these, DETs followed by AFILs proved to be predominant, indicating nutrient rich habitats and confirming the importance of FOM and periphyton as food sources. Though, in spite of that litter from different kind of plants was extremely abundant in most sites, related environmental variables (i.e. reed grass leaves, tree leaves and debris) captured little or no variance in chironomid assemblages. Moreover, SHRs which could process coarse plant matters (i.e. reed or tree leaves, COM; Cummins et al. 1989) proved to be relatively rare (likewise in Spieles & Mitsch, 2000 and Whiles & Goldowitz, 2005); actually, SHRs associated with filamentous algae, water current, and disturbed habitats where coarse decomposing plant matters hardly occur. In the light of these findings, it is highly probable that chironomid taxa receiving high scores as SHRs, may rather prefer feeding on live epiphytic algae than on coarse decomposing plant matters. Similarly, it is difficult to interpret the marked separation of PFILs in the CCA ordination space. PFILs were characteristic primarily for inundated forests with cooler water, presence of moss and dead tree parts and little or no planktonic algae (assessed as Chl-a concentration), and FOM to be filtered out.

Effect of seasonality

Seasonality had little influence on the structure of local assemblages and the distribution of individual taxa and FFGs in this study. This is seemingly surprising, since a series of environmental processes show cyclic alteration on a yearly basis. Effect of seasonality could often be observed in the structural variability of aquatic macroinvertebrate assemblages as well (Hawkins & Seddel, 1981; Šporka et al., 2006; Milošević et al., 2013; Tóth et al., 2013; but see Ali et al., 2002), but habitat heterogeneity can act as a stabilizing force even along the temporal scale and mask the effect of seasonality on local assemblages (Brown, 2007). Coincidently, we consider that a marked environmental and spatial control of local assemblages derived from the extreme habitat and landscape heterogeneity could dominate over seasonality in this wetland area. In addition, it is highly probable that, in the forward stepwise selection procedure, retained local environmental variables may cover also some seasonal patterning and thence the importance of seasonality might be underestimated.

Implications for bioassessment: taxa vs. FFGs

Beside the classic taxonomic approach, trait based or functional analyses are recently becoming increasingly popular in ecological and bioassessment studies. One of the unquestioned advantages of trait based analyses, compared to the pure taxon based approach, is that they may provide more direct answers about the functionality of assemblages and characteristic ecological processes in the studied ecosystem (Heino et al., 2013). In addition, some researchers also emphasize that this approach does not necessarily require strict species level identification of organisms (e.g. Usseglio-Polatera et al., 2000; Merrit et al., 2002; Cummins et al., 2005). However, in the case of Chironomidae, proper FFG classification is also laboursome; it requires species level identification – as far as possible – (Moog, 2002), and detailed autecological knowledge.

Of the 64 taxa presented in our samples, we found relevant FFG scoring information for only 45 taxa. This implies that much more research is needed to broaden our knowledge about the autecology of chironomids for improving function based analyses. The most important weakness of the trait based approach is, however, that behavioural traits of many taxa are highly plastic, and the function (i.e. the relevant FFG score) of a species may vary during the ontogeny, seasonally, and in relation with the particular environmental conditions (Henriques-Oliveira et al., 2003; Sanseverino & Nessimian, 2008). After all, due to their high feeding plasticity, many chironomid taxa or at least some of their life stages are considered to be omnivorous as a general rule (Moog, 2002). Since ecological plasticity and ontogenetic variability in functionality is quite usual in many animal taxa, therefore, the original concept of Root (1967) who defined functional guild as ‘a group of species that exploit the same class of environmental resources in a similar way’ has also been refined and the recent theory is that guilds (e.g. functional feeding groups) organize rather over intraspecific categories (i.e. species life stages) and not on species level as well as they are often variable in time and space (Werner & Gilliam, 1984; Cohen et al., 1993; Specziár & Rezsu, 2009). The functional feeding group approach implemented by Moog (2002) appreciates this ecological plasticity and therefore rates each taxon based on the diet, morphology of mouth parts and feeding behaviour of their third and/or fourth larval instar stages using multiple feeding guild scores to take into account their functional versatility and usual omnivory. Nevertheless, such a general categorisation can model functionality only based on average patterns, but may provide only a biased estimate at local scale. It is also problematic to include life stage specific information in such a generalized scoring table because of the lack of the appropriate information about the earlier life stages of most taxa and the environment related diet ontogeny in many cases (c.f. Specziár & Rezsu, 2009). Accordingly, in FFG based analyses classification of taxa should be based on direct ecological observations whenever it is possible and the use of such general score tables be preferably restricted to large-scale comparisons.

In this study, taxa and FFGs provided very similar results about the roles of the most important processes structuring local assemblages in the study area; although, FFG based patterns tended to be even more closely related to environmental conditions than taxon based patterns. Due to the taxonomic redundancy of functional groups, benefits of function based approaches clearly increase with the increasing spatial extent of the study and in landscapes with dispersal barriers (Heino et al., 2013). Whereas, because of the differences between the species pools of biogeographic regions, a function based approach is practically the only option for analysing assemblage-environment patterns at the largest spatial scales.

On the other hand, due to their more specified responses to a series of environmental properties, species data in many respects are highly beneficial for bioassessment. Knowledge of the environmental optima and tolerance ranges of species provide reliable chance to rate, predict and reconstruct environmental conditions of present and past aquatic ecosystems, based on information about the structure of local assemblages (Juggins & Birks, 2012). Our species optima and tolerance results suggest, however, that environmental ranges of an effective chironomid based bioassessment may be further expanded by including some other Diptera groups (e.g. Chaoboridae and Ceratopogonidae) with extreme environmental optima and tolerances.

Conclusions

In spite of the relatively small spatial extent and extreme environmental heterogeneity of the studied wetland area, we found unexpectedly high spatial influence in local chironomid assemblages. We consider that this phenomenon could be a result of dispersal limitation, caused by the heterogeneous landscape structure including tall terrestrial vegetation as well, and the mass effect, induced by the highly fragmented occurrence and variable area of certain microhabitats (i.e. specified combinations of environmental filters) and related species pools. Both processes result that local chironomid assemblages track environmental changes with a bias which also should be kept in sight in bioassessment practice. At the same time, this high heterogeneity could act as a stabilizing force considering temporal variability.

Beside the taxonomic approach, present results confirm the benefit of considering function based patterns for evaluating assemblage-environment relationships as well, especially when odds of dispersing species to reach certain habitat patches differ (e.g. in case of significant dispersal limitation and mass effect). However, we need more information on the ecological and functional traits of chironomids to be able to elucidate their responses to environmental alterations more reliably and globally. For this purpose, investigations complemented with habit traits or functional diversity and structure may be more conducing than FFG based approach alone. As we could see, both taxon and function based analyses have their benefits and weaknesses, and therefore it would be advisable to use them to supplement each other in biological assessments. On the other hand, environmental optimum and tolerance spectrum analyses also appreciably broaden our understanding about chironomid community–environment relationships and the improvement of such databases would considerably extend the potential of our bioassessment efforts.

Acknowledgements

We thank Adrienn Tóth for her assisstance in the field and Steve Juggins for providing us a free C2 license. This research was supported by the European Union and the State of Hungary, co-financed by the European Social Fund in the framework of TÁMOP-4.2.4.A/ 2-11/1-2012-0001 'National Excellence Program' and GINOP-2.3.2-15-2016-00019. The work of Mónika Tóth was also supported by the János Bolyai Research Scolarship of the Hungarian Academy of Sciences.

References

Ali, A., J. Frouz & R. J. Lobinske, 2002. Spatio-temporal effects of selected physico-chemical variables of water, algae and sediment chemistry on the larval community of nuisance Chironomidae (Diptera) in a natural and a man-made lake in central Florida. Hydrobiologia 470: 181–193.

Aminot, A. & F. Rey, 2000. Standard procedure for the dteremination of chlorophyll-a by spectroscopic methods. International Council for the Exploration of Sea, Denmark.

Anderson, R. O., 1959. A modified flotation technique for sorting bottom fauna samples. Limnology and Oceanography 4: 223–225.

Árva, D., M. Tóth, H. Horváth, S. A. Nagy & A. Specziár, 2015a. The relative importance of spatial and environmental processes in distribution of benthic chironomid larvae within a large and shallow lake. Hydrobiologia 742: 249–266.

Árva, D., A. Specziár, T. Erős & M. Tóth, 2015b. Effects of habitat types and within lake environmental gradients on the diversity of chironomid assemblages. Limnologica 53: 26–34.

Batzer, D. P. & S. A. Wissinger, 1996. Ecology of insect communities in nontidal wetlands. Annual Reviews of Entomology 41: 75–100.

Beisner, B. E., P. R. Peres-Neto, E. S. Lindström, A. Barnett & M. R. Longht, 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87: 2985–2991.

Bíró, K., 1981. A Guide for the Identification of Chironomid Larvae in Hungary. In: Felföldy, L. (ed.), Hydrobiology for Water Management Praxis, Vol. 11, VÍZDOK, Budapest: 1–229. (in Hungarian)

Bitušík, P. & M. Svitok, 2006. Structure of chironomid assemblages along environmental and geographical gradients in the Bohemian Forest lakes (Central Europe): An exploratory analysis. Biologia, Bratislava 61: 467–476.

Borcard, D. & P. Legendre, 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrix. Ecological Modelling 153: 51–68.

Borcard, D., P. Legendre, C. Avois-Jacquet & H. Toumisto, 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85: 1826–1832.

Brown, B. L., 2007. Habitat heterogeneity and disturbance influence patterns of community temporal variability in a small temperate stream. Hydrobiologia 586: 93–106.

Brundin, L., 1958. The bottom faunistical lake type system and its application to the southern hemisphere. Moreover a theory of glacial erosion as a factor of productivity in lakes and oceans. Verhandlungen der Internationalen Vereinigung für Limnologie 13: 288–297.

Capers, R. S., R. Selsky & G. J. Bugbee, 2009. The relative importance of local conditions and regional processes in structuring aquatic plant communities. Freshwater Biology 55: 952–966.

Cohen, J. E., R. A. Beaver, S. H. Cousins, D. L. DeAngelis, L. Goldwasser, K. L. Heong, R. D. Holt, A. J. Kohn, J. H. Lawton, N. Martinez, R. O'Malley, L. M. Page, B. C. Patten, S. L. Pimm, G. A. Polis, M. Rejm´anek, T. W. Schoener, K. Schoenly, W. G. Sprules, J.

M. Teal, R. E. Ulanowicz, P. H. Warren, H. M. Wilbur & P. Yodzis, 1993. Improving food webs. Ecology 74: 252–258.

Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8: 1175–1182.

Cranston, P. S., 1982. A key to the Larvae of the British Orthocladiinae (Chironominae). Freshwater Biological Association Scientific Publication 45, The Freshwater Biological Association, Ambleside.

Cserny, T. & E. Nagy-Bodor, 2000. Limnogeological investigations on Lake Balaton. In: Gierlowski-Kordesch, E. & K. Kelts (eds), Lake basins through space and time. AAPG Studies in Geology 46: 605-618.

Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry & W. B. Taliaferro, 1989. Shredders and riparian vegetation. BioScience 39: 24–30.

Cummins, K. W., R. W. Merritt & P. C. N. Andrade, 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. Studies on Neotropical Fauna and Environment 40: 69–89.

Cushman, S. A. & K. McGarigal, 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology 17: 637–646.

Czech Hydrometeorological Institute, 2009. Arrow: assessment and reference reports of water monitoring (Czech approach). Online database, Prague. http://hydro.chmi.cz/isarrow/index.php?lng=eng (accessed July 2015).

Delettre, Y. R. & N. Morvan, 2000. Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. Freshwater Biology 44: 399–411.

Delettre, Y., P. Tréhen & P. Grootaert, 1992. Space heterogeneity, space use and short range dispersal in Diptera: A case study. Landscape Ecology 6: 175–181.

Dray, S., P. Legendre & P. R. Peres-Neto, 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrix (PCNM). Ecological Modellling 196: 483–493.

Euliss, N. H., L. M. Smith, D. A. Wilcox & B. A. Browne, 2008. Linking ecosystem processes with wetland management goals: charting a course for a sustainable future. Wetlands 28: 553–562.

Ferrington, L. C. Jr., 2008. Global diversity of non-biting midges (Chironomidae; Insecta-Diptera) in freshwater. Hydrobiologia 595: 444–455.

Free, G., A. G. Solimini, B. Rossaro, L. Marziali, R. Giacchini, B. Paracchini, M. Ghiani, S. Vaccaro, B. M. Gawlik, R. Fresner, G. Santner, M. Schönhuber & A. C. Cardoso, 2009. Modelling lake macroinvertebrate species in the shallow sublittoral: relative roles of habitat, lake morphology, aquatic chemistry and sediment composition. Hydrobiologia 633: 123–136.

Gajewski, K., G. Bouchard, S. E. Wilson, J. Kurek & L. C. Cwynar, 2005. Distribution of Chironomidae (Insecta: Diptera) head capsules in recent sediments of Canadian Arctic lakes. Hydrobiologia 549: 131–143.

García-Roger, E. M., M. M. Sánchez-Montoya, R- Gómez, M. L. Suárez, M. R. Vidal-Abarca, J. Latron, M. Rieradevall & N. Prat, 2011. Do seasonal changes in habitat features influence aquatic macroinvertebrate assemblages in perennial versus temporary Mediterranean streams? Aquatic Sciences 73: 567–579.

Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen & L. M. Bini, 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. Ecology and Evolution 3: 4473–4487.

Hammer, Ø., D. A. T. Harper & P. D. Ryan, 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 1–9.

Hawkins, C. P. & J. R. Sedell, 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. Ecology 62: 387–397.

Heino, J., 2005. Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. Freshwater Biology 50: 1578–1587.

Heino, J., 2008. Patterns of functional biodiversity and function-environment relationships in lake littoral macroinvertebrates. Limnology and Oceanography 53: 1446–1455.

Heino, J., 2013a. Environmental heterogeneity, dispersal mode, and co-occurrence in stream macroinvertebrates. Ecology and Evolution 3: 344–355.

Heino, J., 2013b. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? Oecologia 171: 971–980.

Heino, J., 2013c. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. Biological Reviews 88: 166–178.

Heino, J, D. Schmera & T. Erős, 2013. A macroecological perspective of trait patterns in stream communities. Freshwater Biology 58: 1539–1555.

Heiri, O, A. F. Lotter & G. Lemcke, 2001. Loss of ignition as a method for estimating organic and carbon content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25: 101–110.

Henriques-Oliveira, A. L., J. L. Nessimian & L. F. M. Dorvillé, 2003. Feeding habits of chironomid larvae (Insecta: Diptera) from a stream in the Floresta da Tijuca, Rio de Janeiro, Brazil. Brazilian Journal of Biology 63: 269–281.

Janecek, B. F. R., 1998. Diptera: Chironomidae (Zuckmücken). Bestimmung von 4. Larvenstadien mitteleuropäischer Gattungen und österreichischer Arten. In: Moog, O. (ed.), Fauna Aquatica Austriaca V. Universität für Bodenkultur, Wien: 1–117.

Juggins, S., 2007. C2 Version 1.5 User guide. Software for ecological and palaeoecological data analysis and visualisation. Newcastle University, Newcastle upon Tyne, UK. http://www.staff.ncl.ac.uk/staff/stephen.juggins/software/C2Home.htm

Juggins, S. & H. J. B. Birks, 2012. Quantitative environmental reconstructions from biological data. In: Birks, H. J. B., A. F. Lotter, S. Juggins & J. P. Smol, (eds), Tracking environmental changes using lake sediment. Developments in Paleoenvironmental Research 5. Springer, Dordrecht: 431–494.

King, R. S. & C. J. Richardson, 2002. Evaluating subsampling approaches and macroinvertebrate taxonomic resolution for wetland bioassessment. Journal of the North American Benthological Society 21: 150–171.

Legendre, P. & L. Legendre, 2012. Numerical ecology. Elsevier, Amsterdam.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau & A. Gonzales, 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601–613.

Lepš, J. & P. Šmilauer, 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, New York.

Magee, P. A., 1993. 13.3.14. Detrital accumulation and processing in wetlands. Waterfowl Management Handbook, Paper 20.

Merrit, R. W., K. W. Cummins, M. B. Berg, J. A. Novak, M. J. Higgins, K. J. Wessel & J. L. Lessard, 2002. Development and application of a macroinvertebrate functional-group approach in the bioassessment of remnant river oxbows in southwest Florida. Journal of the North American Benthological Society 21: 290–310.

Milošević, D., V. Simić, M. Stojković, D. Čerba, D. Mančev, A. Petrović & M. Paunović, 2013. Spatio-temporal pattern of the Chironomidae community: toward the use of non-biting midges in bioassessment programs. Aquatic Ecology 47: 37–55.

Moog, O. (ed.), 2002. Fauna Aquatica Austriaca. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Vienna.

Mousavi, S. K., 2002. Boreal chironomid communities and their relations to environmental factors – the impact of lake depth, size and acidity. Boreal Environment Research 7: 63–75.

Mykrä, H., J. Heino & T. Muotka, 2007. Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. Global Ecology and Biogeography 16: 149–159.

Nicacio, G. & L. Juen, 2015. Chironomids as indicators in freshwater ecosystems: an assessment of the literature. Insect Conservation and Diversity 8: 393–403.

Peres-Neto, P. R., P. Legendre, S. Dray & D. Borcard, 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87: 2614–2625.

Poff, N. L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16: 391–409.

Pomogyi, P., 1993. Nutrient retention by the Kis-Balaton Water Protection System. Hydrobiologia 251: 309–320.

Porinchu, D. F. & G. M. MacDonald, 2003. The use and application of freshwater midges (Chironomidae: Insecta: Diptera) in geographical research. Progress in Physical Geography 27: 378–422.

Puntí, T., M. Rieradevall & N. Prat, 2009. Environmental factors, spatial variation and specific requirements of Chironomidae in Mediterranean reference streams. Journal of the North American Benthological Society 28: 247–265.

Rae, J. G., 2004. The colonization response of lotic chironomid larvae to substrate size and heterogeneity. Hydrobiologia 524: 115–124.

Real, M., M. Rieradevall & N. Prat, 2000. *Chironomus* species (Diptera: Chironomidae) in the profundal benthos of Spanish reservoirs and lakes: factors affecting distribution patterns. Freshwater Biology 43: 1–18.

Root, R. B., 1967. The niche exploitation pattern of the blue-grey gnatcatcher. Ecological Monographs 37: 317–350.

Roque, F. O., T. Siqueira, L. M. Bini, M. C. Ribeiro, L. R. Tambosi, G. Ciocheti & S. Trivinho-Strixino, 2010. Untangling associations between chironomid taxa in Neotropical streams using local and landscape filters. Freshwater Biology 55: 847–865.

Sæther, O. A., 1979. Chironomid communities as water quality indicators. Holarctic Ecology 2: 65–74.

Sæther, O. A., P. Ashe & D. A. Murray, 2000. A.6. Family Chironomidae. In: Papp, L. & B. Darvas (eds), Contribution to a Manual of Palearctic Diptera. Appendix. Science Herald, Budapest: 113–334.

Sanseverino, A. M. & J. L. Nessimian, 2008. The food of larval Chironomidae (Insecta, Diptera) in submerged litter in a forest stream of the Atlantic Forest (Rio de Janeiro, Brazil). Acta Limnologica Brasiliensia 20: 15–20.

Specziár, A. & E. T.-Rezsu, 2009. Feeding guilds and food resource partitioning in a lake fish assemblage: an ontogenetic approach. Journal of Fish Biology 75: 247-267.

Specziár, A., Á. I. György & T. Erős, 2013. Within-lake distribution patterns of fish assemblages: the relative role of spatial, temporal and random environmental factors in assessing fish assemblages using gillnets in a large and shallow temperate lake. Journal of Fish Biology 82: 840–855.

Spieles, D. J. & W. J. Mitsch, 2000. Macroinvertebrate community structure in high- and low-nutrient constructed wetlands. Wetlands 20: 716–729.

Šporka, F., H. E. Vlek, E. Bulánková & I. Krno, 2006. Influence of seasonal variation on bioassessment of streams using macroinvertebrates. Hydrobiologia 566: 543–555.

Stewart, T. W., T. L. Shumaker & T. A. Radzio, 2003. Linear and nonlinear effects of habitat structure on composition and abundance in the macroinvertebrate community of a large river. The American Midland Naturalist 149: 293–305.

Suurkuukka, H., K. K. Meissner & T. Muotka, 2012. Species turnover in lake littorals: spatial and temporal variation of benthic macroinvertebrate diversity and community composition. Diversity and Distributions 18: 931–941.

Tarkowska-Kukuryk, M., 2014. Spatial distribution of epiphytic chironomid larvae in a shallow macrophyte-dominated lake: effect of macrophyte species and food resources. Limnology 15: 141–153.

Tarkowska-Kukuryk, M. & R. Kornijów, 2008. Influence of spatial distribution of submerged macrophytes on Chironomidae assemblages in shallow lakes. Polish Journal of Ecology 56: 569–579.

ter Braak, C. J. F. & P. Šmilauer, 2002. CANOCO reference manual and CanoDraw for Windows user’s guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York.

Tóth, M., A. Móra, B. Kiss, Gy. Dévai & A. Specziár, 2012. Are macrophyte-dwelling Chironomidae (Diptera) largely opportonustic in selecting plant species? European Journal of Entomology 109: 247–260.

Tóth, M., D. Árva, S. A. Nagy & A. Specziár, 2013. Species diversity and abundance of plant-dwelling chironomids across hierarchical habitat and seasonal scales in the oxbow lakes of River Tisza, Hungary. Fundamental and Applied Limnology 182: 309–321.

Usseglio-Polatera, P., M. Bournaud, P. Richoux & H. Tachet, 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. Freshwater Biology 43: 175–205.

Vallenduuk, H. J., 1999. Key to the Larvae of *Glyptotendipes* Kieffer (Diptera, Chironomidae) in Western Europe. Privately published, Lelystad.

Vallenduuk, H. J. & H. K. M. Moller Pillot, 2002. Key to the larvae of *Chironomus* in Western Europe. Privately published, Lelystad.

Vallenduuk, H.J. & E. Morozova 2005: Cryptochironomus. An identification key to the larvae and pupal exuviae in Europe. Lauterbornia 55: 1–22.

Vanormelingen, P., K. Cottenie, E. Michels, K. Muylaert, W. Vyverman & L. De Meester, 2008. The relative importance of dispersal and local processes in structuring phytoplankton communities in a set of highly interconnected ponds. Freshwater Biology 53: 2170–2183.

Werner, E. E. & J. F. Gilliam, 1984. The ontogenetic niche and species interactions in sizestructured populations. Annual Reviews of Ecology and Systematics 15: 393–425.

Whiles, M. R. & B. S. Goldowitz, 2005. Macroinvertebrate communities in central Platte River wetlands: patterns across a hydrologic gradient. Wetlands 25: 462–472.

Wiederholm, T., 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. Entomologica Scandinavica Supplement 19: 1–457.

Wolfram, G., 1996. Distribution and production of chironomids (Diptera, Chironomidae) in a shallow, alkaline lake (Neusiedler See, Austria). Hydrobiologia 318: 103–115

Figure captions

Fig. 1 Location of Lake Balaton watershed system in Hungary (A), position of Kis-Balaton wetland area within the system (B) and map of Kis-Balaton showing the distribution of sampling sites (C). Note, that Kis-Balaton is a highly divers wetland area including different terrestrial habitats (not differentiated on the map) with very variable ranges as well. Examined aquatic habitats included most characteristic habitat types such as open water areas, stands of emergent, submerged and floating leaved macrophytes, riparian vegetation, wet and inundated forests and meadows, artificial canals either with or without currents, river habitats, ripraps and separated borrow pits of variable succession stages.

Fig. 2 Canonical correspondence analysis plots along the first and second canonical axes (CA) describing the relationship between the abundance data of chironomid taxa (a) and chironomid feeding guilds (b) and forward selected (at $P < 0.05$) local environmental, landscape and spatial variables in Kis-Balaton (Hungary), based on the detailed summer survey with 79 sampling sites. Percentage variances represented by axes are indicated in brackets (of taxa data; of taxa-explanatory variables relation) after the axis name. Scale factors for biplotting are given in the upper right corners of the graphs. Explanatory variables with highest correlation (*r* values are given in brackets) by axes are indicated. Chironomid taxa and guilds (filled circles) as well as explanatory variables (arrows) with scores close to the centre of the graph and thus with less effect on the general picture are not specified in order to keep readability. Scores of supplementary assemblage members Chaoboridae (Chaob) and Ceratopogonidae (Cerato) were also added to the plot (empty circles).

Explanatory variable, taxa and feeding guild names abbreviations are explained in Appendixes A and B, respectively.

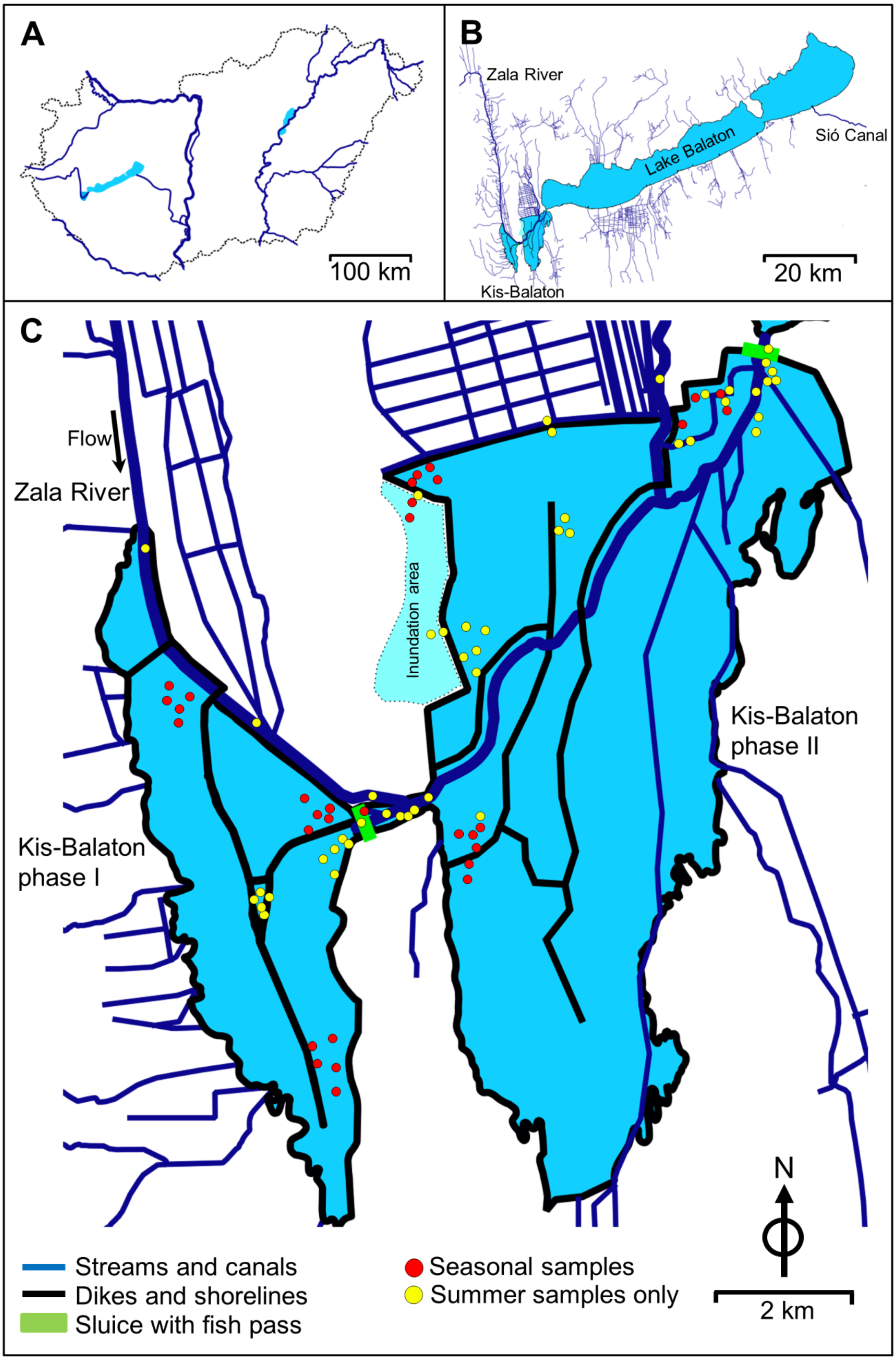
Fig. 3 Result of the variation partitioning of the influence of local environmental, landscape (Landsc.) and spatial variables on the abundance of chironomid taxa (a) and chironomid feeding guilds (b) in Kis-Balaton (Hungary), based on the detailed summer survey with 79 sampling sites. The area of each rectangular cell is proportional to the variance accounted for by that component. Significant local environmental variables are listed along with their proportional pure and total effects (in brackets). Abbreviations of specified local environmental variables are explained in Appendix A.

Fig. 4 Result of the multiple second degree polynomial regression analyses based variation partitioning showing the relative influence of local environmental, landscape and spatial factors (a; detailed summer survey with 79 sampling sites) and also season (b; seasonal surveys of 32 selected sampling sites) on the abundance of individual chironomid taxa and feeding guilds in Kis-Balaton, Hungary. Taxa and feeding guild names abbreviations are explained in Appendix B.

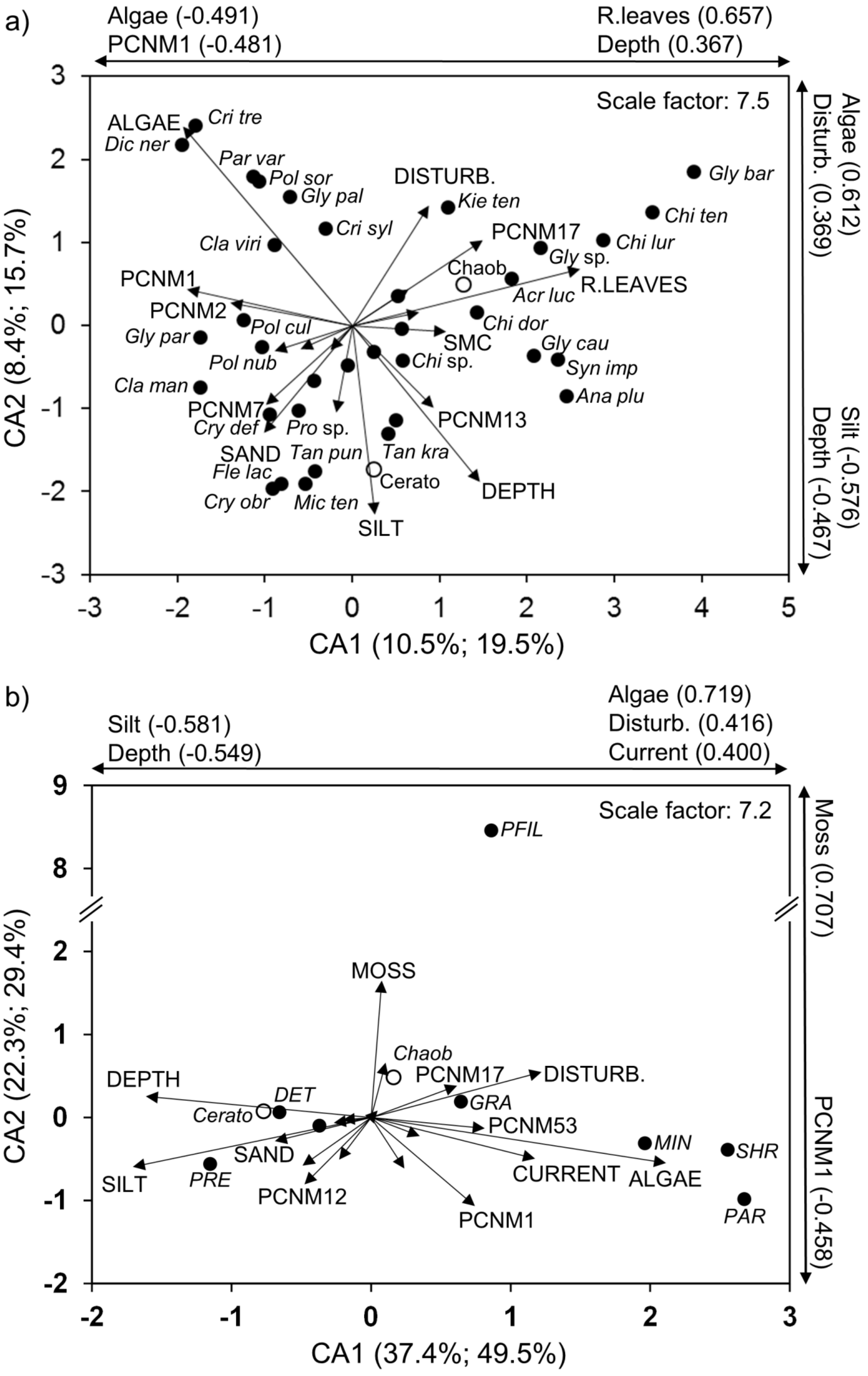
Fig. 5 Canonical correspondence analysis plots along the first and second canonical axes (CA) describing the relationship between the abundance data of chironomid taxa (a) and chironomid feeding guilds (b) and forward selected (at $P < 0.05$) seasonal, local environmental, landscape and spatial variables in Kis-Balaton (Hungary), based on seasonal surveys of 32 selected sampling sites. Percentage variances represented by axes are indicated in brackets (of taxa data; of taxa-explanatory variables relation) after the axis name. Scale factors for biplotting are given in the upper right corners of the graphs. Explanatory variables with highest correlation (*r* values are given in brackets) by axes are indicated. Chironomid taxa and guilds (filled circles) as well as explanatory variables (arrows) with scores close to the centre of the graph, and thus with less effect on the general picture are not specified in order to keep readability. Scores of supplementary assemblage members Chaoboridae (Chaob) and Ceratopogonidae (Cerato) were also added to the plot (empty circles). Explanatory variable, taxa and feeding guild names abbreviations are explained in Appendixes A and B, respectively.

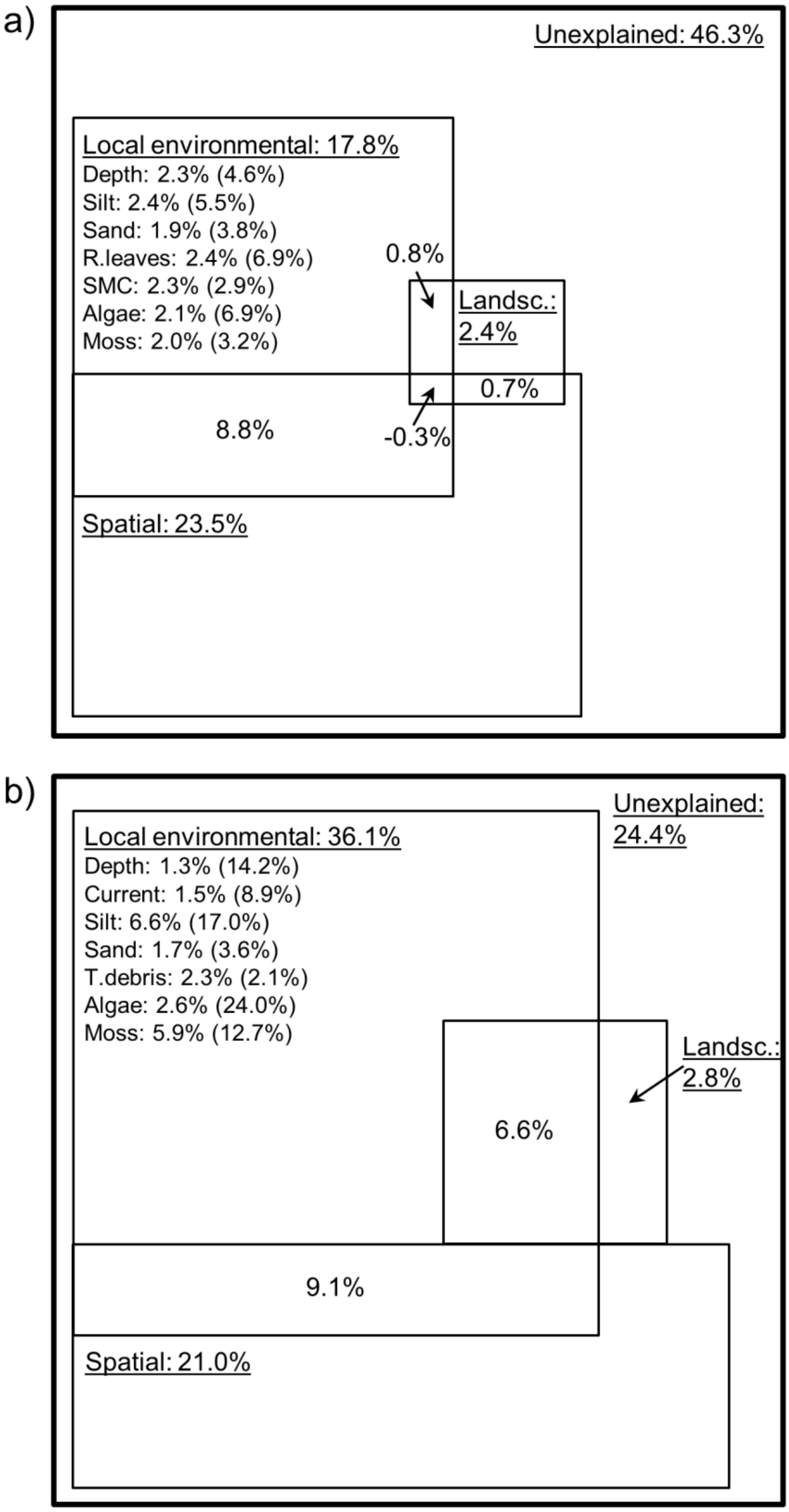
Fig. 6 Result of the variation partitioning of the influence of seasonal, local environmental (Local env.) and landscape (Landsc.), and spatial variables on the abundance of chironomid taxa (a) and chironomid feeding guilds (b) in Kis-Balaton (Hungary), based on seasonal surveys of 32 selected sampling sites. The area of each rectangular cell is proportional to the variance accounted for by that component. Significant local environmental and landscape variables (only for Fig. 5a) are listed along with their proportional pure and total effects (in brackets). Abbreviations of specified local environmental and landscape variables are explained in Appendix A.

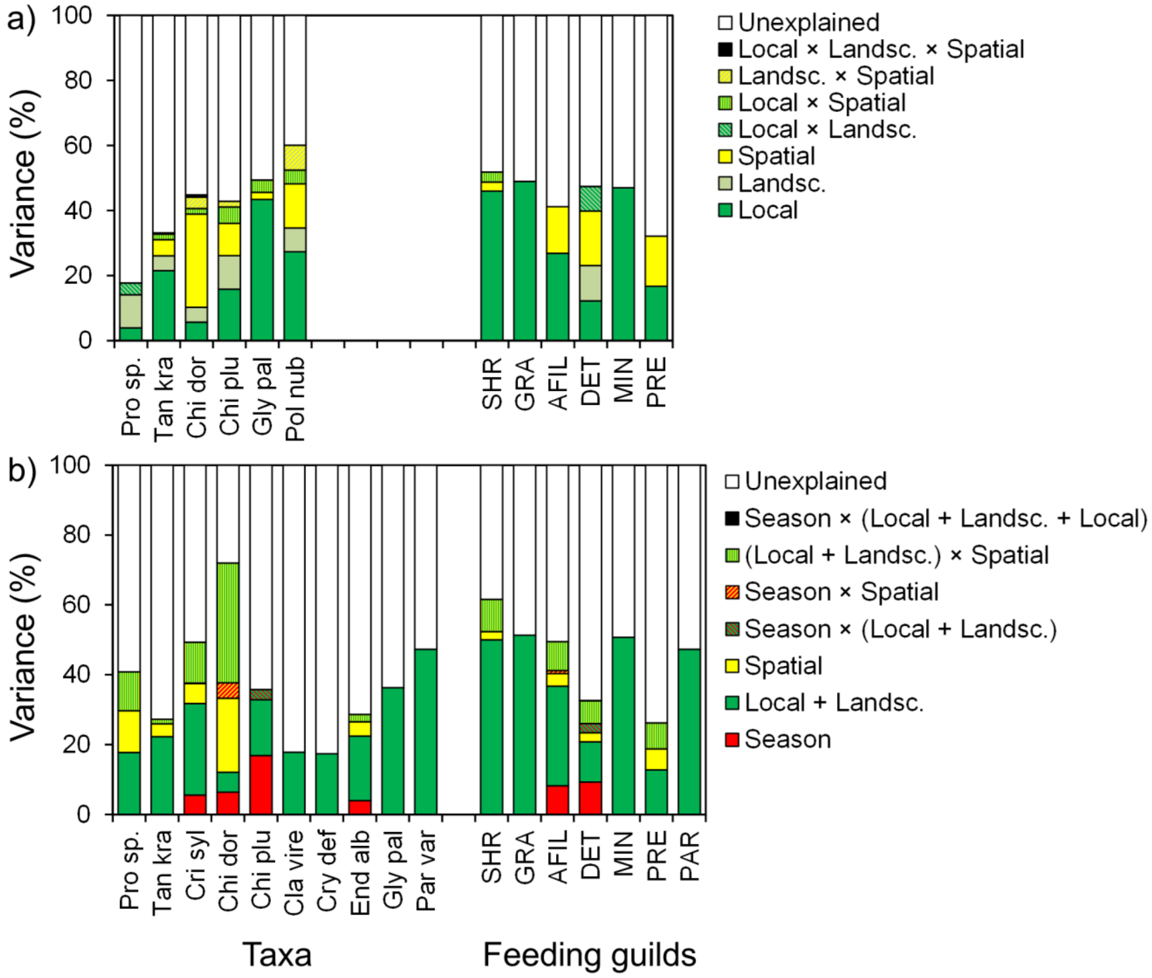
Fig. 7 Optima and tolerance ranges of individual chironomid taxa regarding some influential environmental factors such as: water depth (a); water current (b); dissolved oxygen in the water (c); conductivity (Cond) of the water (d); percent silt in the sediment (e); percent sand in the sediment (f); amount of coarse decomposing organic matter particles (COM) on the sediment surface (g); amount of fine decomposing organic matter particles (FOM) on the sediment surface (h); loss-on-ignition of the sediment (LOI550; i); percent total macrophyte coverage (TMC; j); percent algae coverage (k); and chlorophyll-a concentration in the water (Chl-a; l) in Kis-Balaton, Hungary. For reference, optima and tolerance ranges of Chaoboridae (Chaob) and Ceratopogonidae (Cerato) were also indicated. Note that estimated tolerance ranges were cut at the edge of the studied ranges of particular gradients. Taxa names abbreviations are explained in Appendix B.


A
100 km
B
Zala River
Lake Balaton
Sió Canal
Kis-Balaton
20 km
C
Flow
Zala River
Inundation area
Kis-Balaton phase II
Kis-Balaton phase I
N
2 km
Streams and canals
Dikes and shorelines
Sluice with fish pass
Seasonal samples
Summer samples only

935

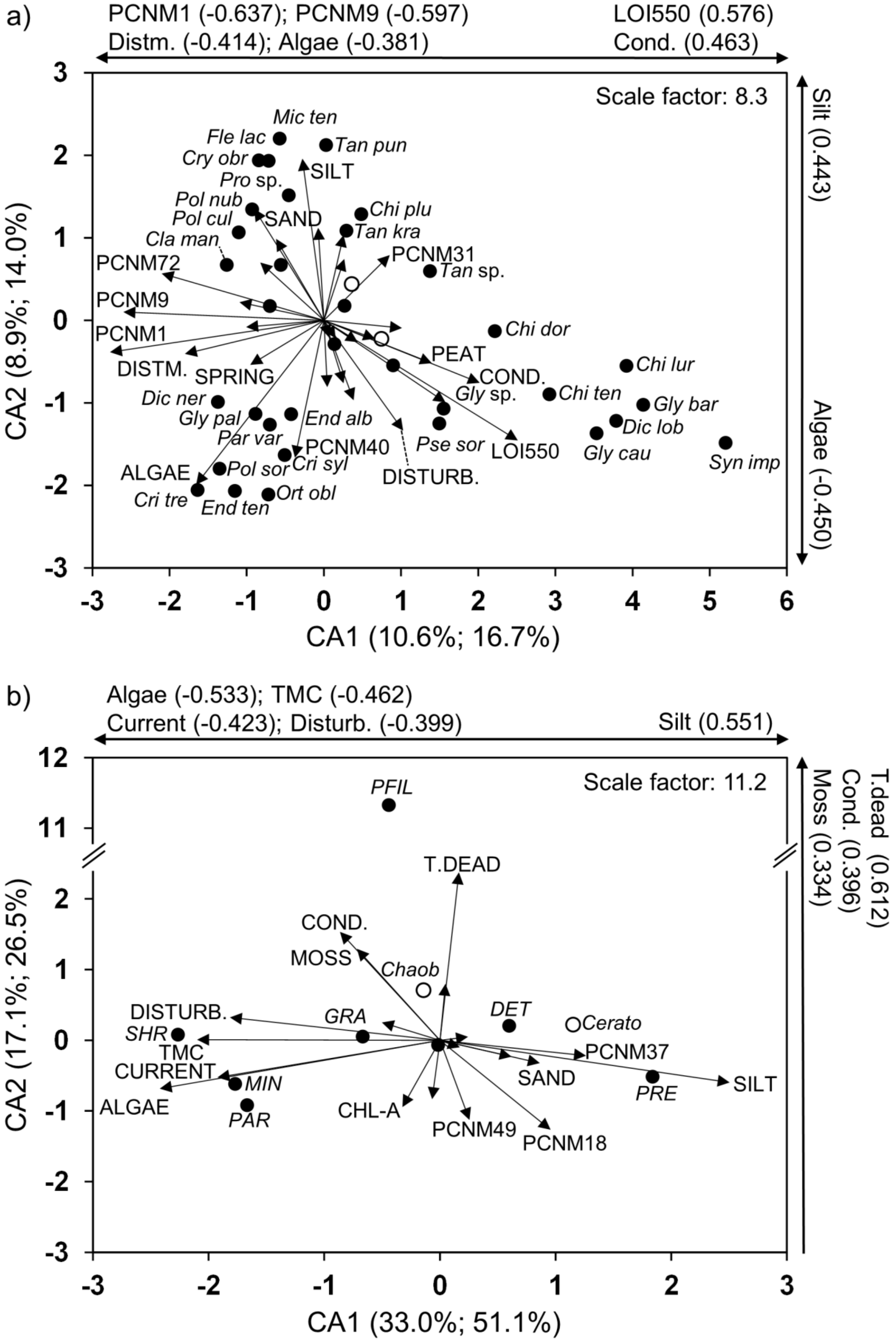

a)
Algae (-0.491)
PCNM1 (-0.481)
R.leaves (0.657)
Depth (0.367)
Scale factor: 7.5
Algae (0.612)
Disturb. (0.369)
Silt (-0.576)
Depth (-0.467)
ALGAE
Cri tre
Dic ner
Par var
Pol sor
Gly pal
Cri syl
Cla viri
DISTURB.
Kie ten
PCNM17
Gly bar
Chi ten
Chi lur
Gly sp.
Chaob
Acr luc
R.LEAVES
PCNM1
PCNM2
Pol cul
Gly par
Pol nub
Chi dor
SMC
Gly cau
Chi sp.
Syn imp
Cla man
Ana plu
PCNM7
Cry def
Pro sp.
PCNM13
SAND
Tan pun
Tan kra
Fle lac
Cerato
DEPTH
Cry obr
Mic ten
SILT
3
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3
4
5
CA2 (8.4%; 15.7%)
CA1 (10.5%; 19.5%)
b)
Silt (-0.581)
Depth (-0.549)
Algae (0.719)
Disturb. (0.416)
Current (0.400)
Scale factor: 7.2
Moss (0.707)
PCNM1 (-0.458)
PFIL
MOSS
Chaob
PCNM17
DISTURB.
DEPTH
DET
GRA
Cerato
PCNM53
MIN
SHR
SAND
CURRENT
ALGAE
SILT
PRE
PCNM12
PCNM1
PAR
9
8
2
1
0
-1
-2
-2
-1
0
1
2
3
CA2 (22.3%; 29.4%)
CA1 (37.4%; 49.5%)


a)
Unexplained: 46.3%
Local environmental: 17.8%
Depth: 2.3% (4.6%)
Silt: 2.4% (5.5%)
Sand: 1.9% (3.8%)
R.leaves: 2.4% (6.9%)
SMC: 2.3% (2.9%)
Algae: 2.1% (6.9%)
Moss: 2.0% (3.2%)
0.8%
Landsc.: 2.4%
0.7%
8.8%
-0.3%
Spatial: 23.5%
b)
Unexplained: 24.4%
Local environmental: 36.1%
Depth: 1.3% (14.2%)
Current: 1.5% (8.9%)
Silt: 6.6% (17.0%)
Sand: 1.7% (3.6%)
T.debris: 2.3% (2.1%)
Algae: 2.6% (24.0%)
Moss: 5.9% (12.7%)
Landsc.: 2.8%
6.6%
9.1%
Spatial: 21.0%

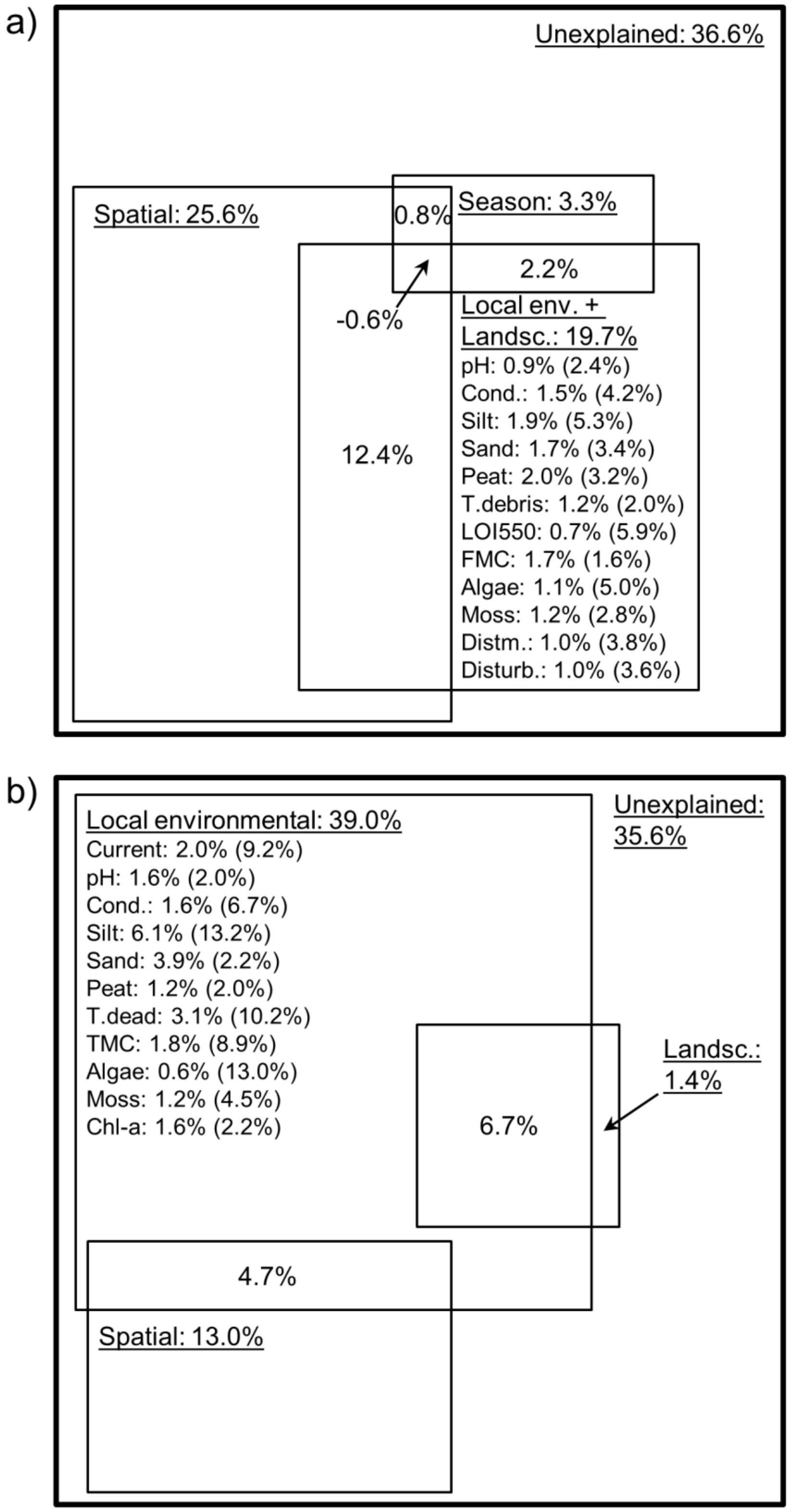

a)
Variance (%)
0
20
40
60
80
100
Pro sp.
Tan kra
Chi dor
Chi plu
Gly pal
Pol nub
SHR
GRA
AFIL
DET
MIN
PRE
Unexplained
Local × Landsc. × Spatial
Landsc. × Spatial
Local × Spatial
Local × Landsc.
Spatial
Landsc.
Local
b)
Pro sp.
Tan kra
Cri syl
Chi dor
Chi plu
Cla vire
Cry def
End alb
Gly pal
Par var
SHR
GRA
AFIL
DET
MIN
PRE
PAR
Unexplained
Season × (Local + Landsc. + Local)
(Local + Landsc.) × Spatial
Season × Spatial
Season × (Local + Landsc.)
Spatial
Local + Landsc.
Season
Taxa
Feeding guilds

940

941



a)
PCNM1 (-0.637); PCNM9 (-0.597)
Distm. (-0.414); Algae (-0.381)
LOI550 (0.576)
Cond. (0.463)
Scale factor: 8.3
Silt (0.443)
Algae (-0.450)
CA2 (8.9%; 14.0%)
CA1 (10.6%; 16.7%)
Mic ten
Fle lac
Tan pun
Cry obr
SILT
Pro sp.
Pol nub
Chi plu
Pol cul
SAND
Tan kra
Cla man
PCNM31
PCNM72
Tan sp.
PCNM9
Chi dor
PCNM1
PEAT
DISTM.
SPRING
COND.
Chi lur
Gly sp.
Chi ten
Dic ner
Gly bar
Gly pal
End alb
Dic lob
Par var
Pse sor
PCNM40
LOI550
Gly cau
Syn imp
ALGAE
Pol sor
Cri syl
DISTURB.
Cri tre
End ten
Ort obl
3
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3
4
5
6
b)
Algae (-0.533); TMC (-0.462)
Current (-0.423); Disturb. (-0.399)
Silt (0.551)
Scale factor: 11.2
T.dead (0.612)
Cond. (0.396)
Moss (0.334)
CA2 (17.1%; 26.5%)
CA1 (33.0%; 51.1%)
PFIL
T.DEAD
COND.
MOSS
Chaob
DISTURB.
GRA
DET
Cerato
SHR
TMC
PCNM37
CURRENT
SAND
MIN
SILT
PRE
ALGAE
PAR
CHL-A
PCNM49
PCNM18
12
11
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3


a)
Unexplained: 36.6%
Spatial: 25.6%
0.8%
Season: 3.3%
2.2%
-0.6%
Local env. +
Landsc.: 19.7%
pH: 0.9% (2.4%)
Cond.: 1.5% (4.2%)
Silt: 1.9% (5.3%)
Sand: 1.7% (3.4%)
12.4%
Peat: 2.0% (3.2%)
T.debris: 1.2% (2.0%)
LOI550: 0.7% (5.9%)
FMC: 1.7% (1.6%)
Algae: 1.1% (5.0%)
Moss: 1.2% (2.8%)
Distm.: 1.0% (3.8%)
Disturb.: 1.0% (3.6%)
b)
Local environmental: 39.0%
Current: 2.0% (9.2%)
pH: 1.6% (2.0%)
Cond.: 1.6% (6.7%)
Silt: 6.1% (13.2%)
Sand: 3.9% (2.2%)
Peat: 1.2% (2.0%)
T.dead: 3.1% (10.2%)
TMC: 1.8% (8.9%)
Algae: 0.6% (13.0%)
Moss: 1.2% (4.5%)
Chl-a: 1.6% (2.2%)
Unexplained:
35.6%
Landsc.:
1.4%
6.7%
4.7%
Spatial: 13.0%

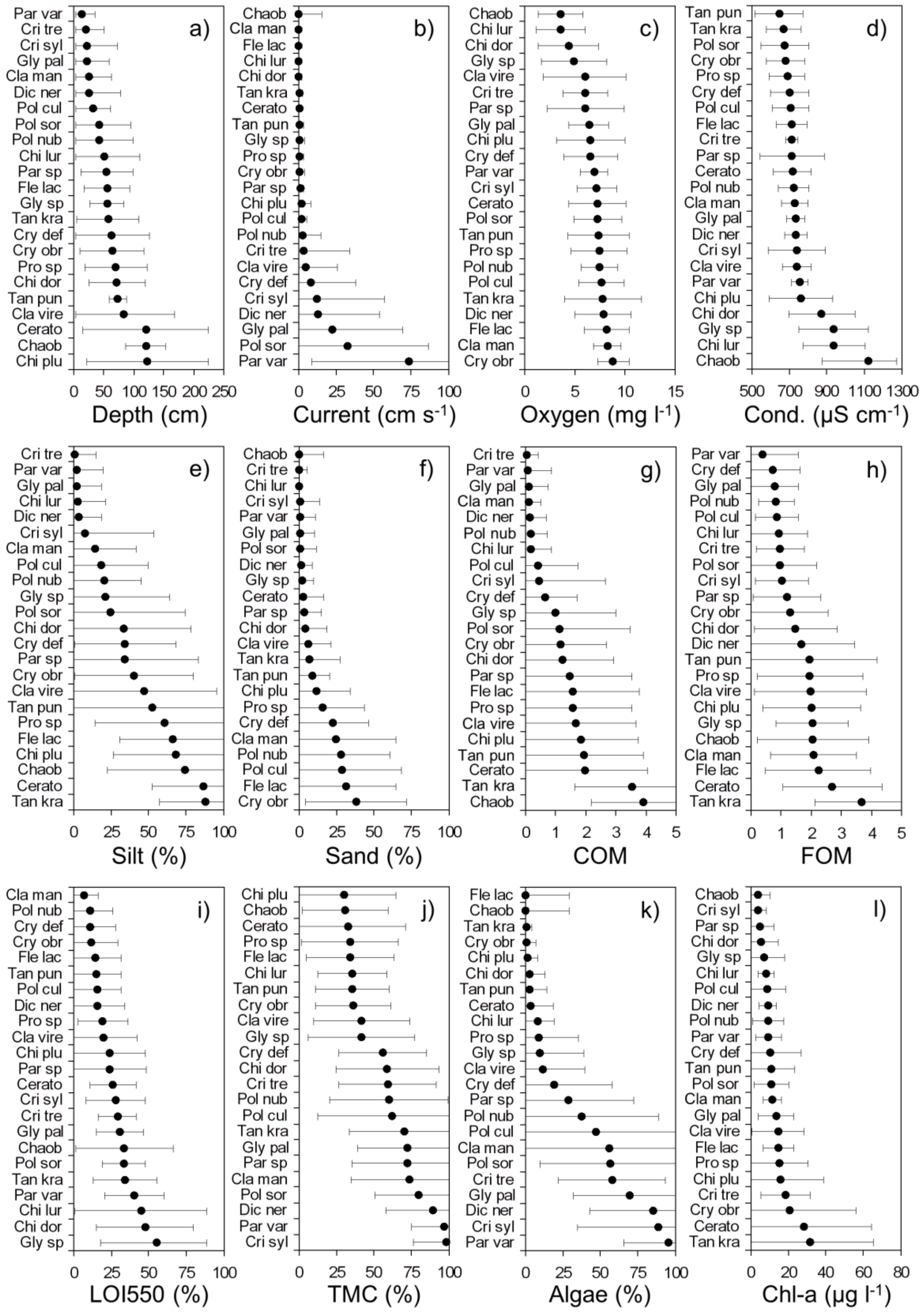

a)
Par var
Cri tre
Cri syl
Gly pal
Cla man
Dic ner
Pol cul
Pol sor
Pol nub
Chi lur
Par sp
Fle lac
Gly sp
Tan kra
Cry def
Cry obr
Pro sp
Chi dor
Tan pun
Cla vire
Cerato
Chaob
Chi plu
0 50 100 150 200 250
Depth (cm)
b)
Chaob
Cla man
Fle lac
Chi lur
Chi dor
Tan kra
Cerato
Tan pun
Gly sp
Pro sp
Cry obr
Par sp
Chi plu
Pol cul
Pol nub
Cri tre
Cla vire
Cry def
Cri syl
Dic ner
Gly pal
Pol sor
Par var
0 25 50 75 100
Current (cm s^{-1})
c)
Chaob
Chi lur
Chi dor
Gly sp
Cla vire
Cri tre
Par sp
Gly pal
Chi plu
Cry def
Par var
Cri syl
Cerato
Pol sor
Tan pun
Pro sp
Pol nub
Pol cul
Tan kra
Dic ner
Fle lac
Cla man
Cry obr
0 5 10 15
Oxygen (mg l^{-1})
d)
Tan pun
Tan kra
Pol sor
Cry obr
Pro sp
Cry def
Pol cul
Fle lac
Cri tre
Par sp
Cerato
Pol nub
Cla man
Gly pal
Dic ner
Cri syl
Cla vire
Par var
Chi plu
Chi dor
Gly sp
Chi lur
Chaob
500 700 900 1100 1300
Cond. (µS cm^{-1})
e)
Cri tre
Par var
Gly pal
Chi lur
Dic ner
Cri syl
Cla man
Pol cul
Pol nub
Gly sp
Pol sor
Chi dor
Cry def
Par sp
Cry obr
Cla vire
Tan pun
Pro sp
Fle lac
Chi plu
Chaob
Cerato
Tan kra
0 25 50 75 100
Silt (%)
f)
Chaob
Cri tre
Chi lur
Cri syl
Par var
Gly pal
Pol sor
Dic ner
Gly sp
Cerato
Par sp
Chi dor
Cla vire
Tan kra
Tan pun
Chi plu
Pro sp
Cry def
Cla man
Pol nub
Pol cul
Fle lac
Cry obr
0 25 50 75 100
Sand (%)
g)
Cri tre
Par var
Gly pal
Cla man
Dic ner
Pol nub
Chi lur
Pol cul
Cri syl
Cry def
Gly sp
Pol sor
Cry obr
Chi dor
Par sp
Fle lac
Pro sp
Cla vire
Chi plu
Tan pun
Cerato
Tan kra
Chaob
0 1 2 3 4 5
COM
h)
Par var
Cry def
Gly pal
Pol nub
Pol cul
Chi lur
Cri tre
Pol sor
Cri syl
Par sp
Cry obr
Chi dor
Dic ner
Tan pun
Pro sp
Cla vire
Chi plu
Gly sp
Chaob
Cla man
Fle lac
Cerato
Tan kra
0 1 2 3 4 5
FOM
i)
Cla man
Pol nub
Cry def
Cry obr
Fle lac
Tan pun
Pol cul
Dic ner
Pro sp
Cla vire
Chi plu
Par sp
Cerato
Cri syl
Cri tre
Gly pal
Chaob
Pol sor
Tan kra
Par var
Chi lur
Chi dor
Gly sp
0 25 50 75 100
LOI550 (%)
j)
Chi plu
Chaob
Cerato
Pro sp
Fle lac
Chi lur
Tan pun
Cry obr
Cla vire
Gly sp
Cry def
Chi dor
Cri tre
Pol nub
Pol cul
Tan kra
Gly pal
Par sp
Cla man
Pol sor
Dic ner
Par var
Cri syl
0 25 50 75 100
TMC (%)
k)
Fle lac
Chaob
Tan kra
Cry obr
Chi plu
Chi dor
Tan pun
Cerato
Chi lur
Pro sp
Gly sp
Cla vire
Cry def
Par sp
Pol nub
Pol cul
Cla man
Pol sor
Cri tre
Gly pal
Dic ner
Cri syl
Par var
0 25 50 75 100
Algae (%)
l)
Chaob
Cri syl
Par sp
Chi dor
Gly sp
Chi lur
Pol cul
Dic ner
Pol nub
Par var
Cry def
Tan pun
Pol sor
Cla man
Gly pal
Cla vire
Fle lac
Pro sp
Chi plu
Cri tre
Cry obr
Cerato
Tan kra
0 20 40 60 80
Chl-a (µg l^{-1})

Table 1 Spearman rank correlation (r) of between sites Bray-Curtis taxonomic and functional feeding gruild (FFG) based assemblage similarities with geographical distances for summer and seasonal samples in Kis-Balaton wetland, Hungary.

	r	df	P
Summer samples, taxon based	-0,076	3079	P<0.05
Summer samples, FFG based	0,009	3079	ns
Seasonal samples, summer data, taxon based	-0,027	494	ns
Seasonal samples, summer data, FFG based	0,054	494	ns
Seasonal samples, autumn data, taxon based	-0,201	494	P<0.05
Seasonal samples, autumn data, FFG based	-0,058	494	ns
Seasonal samples, spring data, taxon based	-0,332	433	P<0.05
Seasonal samples, spring data, FFG based	-0,057	433	ns

Appendix A Seasonal, local environmental, landscape and spatial variables used to model variability of chironomid assemblages in Kis-Balaton (Hungary), their abbreviations used in figures, classification, variable type, type of transformation for multivariate analyses, median, minimum and maximum values.

	Abbreviation	Variable group	Variable type	Transformation	Median	Min.	Max.
Spring (dummy)	Spring	season	dummy	-	-	-	-
Summer (dummy) *	Summer	season	dummy	-	-	-	-
Autumn (dummy)	Autumn	season	dummy	-	-	-	-
Water depth (cm)	Depth	local environmental	quantitative	ln(x+1)	70	0	450
Current (cm s^{-1})	Current	local environmental	quantitative	ln(x+1)	0	0	120
Water temperature (°C) *	T	local environmental	quantitative	ln(x+1)	18.9	6.1	28.4
pH	pH	local environmental	quantitative	-	8.3	6.6	10.2
Dissolved oxygen (mg l^{-1})	Oxygen	local environmental	quantitative	ln(x+1)	6.9	1	22.4
Secchi depth (cm)	Secchi	local environmental	quantitative	ln(x+1)	37	0	200
Conductivity (µS cm^{-1})	Cond.	local environmental	quantitative	ln(x+1)	725	348	1441
Clay (≤ 0.002 mm; %)	Clay	local environmental	quantitative	arcsin(0.01x)$^{0.5}$	0	0	100
Silt (0.002-0.06 mm; %)	Silt	local environmental	quantitative	arcsin(0.01x)$^{0.5}$	55	0	100
Sand (0.06-2 mm; %)	Sand	local environmental	quantitative	arcsin(0.01x)$^{0.5}$	0	0	100
Gravel (2-4 mm; %)	Gravel	local environmental	quantitative	arcsin(0.01x)$^{0.5}$	0	0	90
Rock (> 200 mm; %) *	Rock	local environmental	quantitative	arcsin(0.01x)$^{0.5}$	0	0	100
Peat (%)	Peat	local environmental	quantitative	arcsin(0.01x)$^{0.5}$	0	0	100
Reed grass leaves (classes 0-5)	R.leaves	local environmental	cathegorical (semiquantitative)	-	0	0	5
Coarse (>1 mm) decomposing organic matter particles (classes 0-5)	COM	local environmental	cathegorical (semiquantitative)	-	1	0	5
Fine (≤ 1mm) decomposing organic matter particles (classes 0-5)	FOM	local environmental	cathegorical (semiquantitative)	-	1	0	5
Tree leaves (classes 0-5)	T.leaves	local environmental	cathegorical (semiquantitative)	-	0	0	5
Tree debris (classes 0-5)	T.debris	local environmental	cathegorical	-	0	0	5

Dead tree parts (classes 0-5)	T.dead	local environmental	cathegorical (semiquantitative)	-	0	0	5
Loss-on-ignition at 550 °C (%)	LOI550	local environmental	quantitative	ln(x+1)	27.6	0	92.2
Total macrophyte coverage (%)	TMC	local environmental	quantitative	$\arcsin(0.01x)^{0.5}$	50	0	100
Emergent macrophyte coverage (%)	EMC	local environmental	quantitative	$\arcsin(0.01x)^{0.5}$	0	0	90
Submerged macrophyte coverage (%)	SMC	local environmental	quantitative	$\arcsin(0.01x)^{0.5}$	0	0	100
Floating leaved macrophyte coverage (%)	FMC	local environmental	quantitative	$\arcsin(0.01x)^{0.5}$	0	0	100
Algae coverage (%)	Algae	local environmental	quantitative	$\arcsin(0.01x)^{0.5}$	0	0	100
Moss coverage (%)	Moss	local environmental	quantitative	$\arcsin(0.01x)^{0.5}$	0	0	100
Tree coverage (%)	Tree	local environmental	quantitative	$\arcsin(0.01x)^{0.5}$	0	0	50
Riparian vegetation coverage (%)	Riparian	local environmental	quantitative	$\arcsin(0.01x)^{0.5}$	0	0	20
Water chlorophyll-a concentration (mg l^{-1})	Chl-a	local environmental	quantitative	ln(x+1)	13.4	0	230.6
Distance from the nearest reed stand (m)	Distr.	landscape	quantitative	ln(x+1)	10	0	250
Distance from the nearest macrophyte stand (m)	Distm.	landscape	quantitative	ln(x+1)	0	0	1000
Distance from the nearest open water (m)	Disto.	landscape	quantitative	ln(x+1)	0	0	1000
Distance from the shore (m) *	Dists.	landscape	quantitative	ln(x+1)	10	0	300
Distance from the nearest clump (m) *	Distc.	landscape	quantitative	ln(x+1)	15	0	300
Disturbance	Disturb.	landscape	binary	ln(x+1)	-	-	-
PCNM 1-78	PCNM	spatial	quantitative	-	-	-	-

*Variables discarded due to collinearity.
PCNM = spatial variables derived from principal coordinate analysis of neighbouring matrix.

Appendix B List of chironomid taxa, their abbreviations used in figures, numbers of individuals collected (N), relative abundance (A%), frequency of occurrence (FO%) and feeding guild scores (Moog, 2002) according to the score table of IS Arrow database (Czech Hydrometeorological Institute, 2009) in samples of Kis-Balaton, Hungary.

					Feeding group scores								
	Abbreviation	N	A%	FO%	SHR	GRA	AFIL	PFIL	DET	MIN	XYL	PRE	PAR
Tanypodinae													
Ablabesmyia longistyla Fittkau, 1962	Abl long	3	0.02	1.4	0	0	0	0	2	0	0	8	0
Ablabesmyia monilis (Linnaeus 1758)	Abl mon	4	0.03	1.4	0	0	0	0	2	0	0	8	0
Ablabesmyia phatta (Egger, 1864)	Abl pha	2	0.02	1.4	0	0	0	0	2	0	0	8	0
Anatopynia plumipes (Fries 1823)	Ana plu	8	0.07	3.6	0	0	0	0	1	0	0	9	0
Clinotanypus pinguis (Loew 1861)	Cli pin	2	0.02	0.7	0	0	0	0	1	0	0	9	0
Guttipelopia guttipennis (van der Wulp, 1861)	Gut gut	21	0.17	2.9	0	0	0	0	0	0	0	10	0
Monopelopia tenuicalcar (Kieffer, 1918)	Mon ten	3	0.02	0.7	0	0	0	0	0	0	0	10	0
Procladius (Holotanypus) sp. (Meigen, 1804)	Pro sp	584	4.76	46.4	0	0	0	0	4	0	0	6	0
Tanypus (Tanypus) kraatzi (Kieffer, 1912)	Tan kra	241	1.96	29.7	0	0	0	0	7	0	0	3	0
Tanypus (Tanypus) punctipennis Meigen, 1818	Tan pun	92	0.75	9.4	0	0	0	0	7	0	0	3	0
Zavrelimyia sp.	Zav sp	2	0.02	0.7	0	0	0	0	0	0	0	10	0
Prodiamesinae													
Prodiamesa olivacea (Meigen 1818)	Pro oli	8	0.07	0.7	0	0	1	0	9	0	0	0	0
Orthocladiinae													
Acricotopus lucens (Zetterstedt 1850)	Acr luc	7	0.06	2.9	0	0	0	0	10	0	0	0	0
Corynoneura scutellata Winnertz 1846	Cor scu	1	0.01	0.7	0	7	0	0	3	0	0	0	0
Cricotopus (Cricotopus) albiforceps (Kieffer 1916)	Cri alb	2	0.02	0.7	0	8	0	0	2	0	0	0	0
Cricotopus (Cricotopus) bicinctus (Meigen 1818)	Cri bic	606	4.94	1.4	1	6	0	0	3	0	0	0	0
Cricotopus (Cricotopus) flavocinctus (Kieffer 1924)	Cri fla	15	0.12	2.2	0	8	0	0	2	0	0	0	0
Cricotopus (Cricotopus) tremulus gr.	Cri tre	1175	9.57	15.9	1	7	0	0	2	0	0	0	0
Cricotopus (Cricotopus) trifascia Edwards 1929	Cri tri	4	0.03	0.7	1	6	0	0	3	0	0	0	0
Cricotopus (Isocladius) sylvestris gr.	Cri syl	644	5.25	28.3	2	6	0	0	1	1	0	0	0
Orthocladius (Orthocladius) oblidens (Walker, 1856)	Ort obl	5	0.04	2.2	0	4	0	0	6	0	0	0	0
Paralimnophyes longiseta (Thienemann 1919)	Par lon	1	0.01	0.7	0	0	0	0	0	0	0	0	0
Psectrocladius (Allopsectrocladius) obvius (Walker 1856)	Pse obv	1	0.01	0.7	5	0	0	0	5	0	0	0	0

Psectrocladius sordidellus gr.	Pse sor	48	0.39	7.2	5	0	0	0	5	0	0	0	0
Chironominae													
Chironomus (Lobochironomus) dorsalis Meigen, 1818	Chi dor	646	5.26	41.3	0	0	1	0	9	0	0	0	0
Chironomus (Chironomus) luridus agg.	Chi lur	112	0.91	8.7	0	3	0	3	4	0	0	0	0
Chironomus (Chironomus) plumosus agg.	Chi plu	1199	9.77	58.7	0	0	4	0	6	0	0	0	0
Chironomus sp.	Chi sp	32	0.26	15.2	0	0	4	0	6	0	0	0	0
Chironomus (Chironomus) tentans Fabricius 1805	Chi ten	314	2.56	7.2	1	0	3	0	6	0	0	0	0
Cladopelma virecens (Meigen, 1818)	Cla vire	226	1.84	26.8	0	1	0	0	8	0	0	1	0
Cladopelma viridulum (Linnaeus, 1767)	Cla viri	8	0.07	2.2	0	1	0	0	8	0	0	1	0
Cladotanytarsus mancus gr.	Cla man	376	3.06	17.4	0	4	4	0	2	0	0	0	0
Cryptochironomus (Cryptochironomus) defectus (Kieffer, 1913)	Cry def	118	0.96	26.8	0	0	0	0	4	0	0	6	0
Cryptochironomus (Cryptochironomus) obreptans (Walker 1856)	Cry obr	62	0.51	13.8	0	0	0	0	4	0	0	6	0
Demeijerea rufipes (Linnaeus 1761)	Dem ruf	1	0.01	0.7	0	0	0	0	0	0	0	0	10
Dicrotendipes lobiger (Kieffer, 1921)	Dic lob	18	0.15	5.1	0	4	3	0	3	0	0	0	0
Dicrotendipes nervosus (Staeger, 1839)	Dic ner	331	2.70	18.1	0	4	3	0	3	0	0	0	0
Dicrotendipes notatus (Meigen 1818)	Dic not	4	0.03	1.4	0	4	3	0	3	0	0	0	0
Dicrotendipes pulsus (Walker 1856)	Dic pul	1	0.01	0.7	0	0	0	0	0	0	0	0	0
Endochironomus albipennis (Meigen 1830)	End alb	253	2.06	21.7	0	2	6	0	1	1	0	0	0
Endochironomus tendens (Fabricius, 1775)	End ten	43	0.35	6.5	0	1	7	0	1	1	0	0	0
Fleuria lacustris Kieffer, 1924	Fle lac	78	0.64	15.2	0	0	0	0	10	0	0	0	0
Glyptotendipes (Glyptotendipes) barbipes (Staeger 1839)	Gly bar	572	4.66	5.1	0	0	2	0	8	0	0	0	0
Glyptotendipes (Glyptotendipes) cauliginellus (Kieffer 1913)	Gly cau	17	0.14	4.3	0	2	6	0	1	1	0	0	0
Glyptotendipes (Caulochironomus) imbecillis (Walker 1856)	Gly imb	1	0.01	0.7	0	0	0	0	0	0	0	0	0
Glyptotendipes (Glyptotendipes) pallens (Meigen 1804)	Gly pal	1483	12.08	41.3	0	2	6	0	1	1	0	0	0
Glyptotendipes (Glyptotendipes) paripes (Edwards 1929)	Gly par	116	0.95	10.9	0	2	3	0	5	0	0	0	0
Glyptotendipes sp.	Gly sp	88	0.72	15.9	0	2	6	0	1	1	0	0	0
Kiefferulus (Kiefferulus) tendipediformis (Goetghebuer, 1921)	Kie ten	47	0.38	3.6	0	0	2	0	8	0	0	0	0
Lipiniella moderata Kalugina 1970	Lip mod	1	0.01	0.7	0	0	0	0	0	0	0	0	0
Microchironomus tener (Kieffer, 1918)	Mic ten	19	0.15	10.1	0	0	0	0	10	0	0	0	0
Micropsectra atrofasciata (Kieffer 1911)	Mic atr	1	0.01	0.7	0	2	1	0	7	0	0	0	0

Microtendipes chloris agg.	Mic chl	11	0.09	2.9	0	1	2	0	7	0	0	0	0
Parachironomus varus (Goetghebuer, 1921)	Par var	711	5.79	26.8	0	0	0	0	0	0	0	0	10
Paratanytarsus sp.	Par sp	98	0.80	23.2	0	4	3	0	3	0	0	0	0
Phaenopsectra flavipes (Meigen 1818)	Pha fla	1	0.01	0.7	0	4	2	0	4	0	0	0	0
Polypedilum cf. *cultellatum*	Pol cul	131	1.07	16.7	0	1	1	0	8	0	0	0	0
Polypedilum (Polypedilum) nubeculosum (Meigen, 1804)	Pol nub	1017	8.29	29.0	0	1	1	0	8	0	0	0	0
Polypedilum (Pentapedilum) sordens (van der Wulp, 1875)	Pol sor	262	2.13	19.6	0	2	6	0	2	0	0	0	0
Stictochironomus sp.	Sti sp	1	0.01	0.7	0	0	2	0	8	0	0	0	0
Synendotendipes impar gr.	Syn imp	31	0.25	6.5	0	2	6	0	1	1	0	0	0
Tanytarsus sp.	Tan sp	361	2.94	13.8	0	3	1	0	6	0	0	0	0
Xenochironomus xenolabis (Kieffer 1916)	Xen xen	1	0.01	0.7	0	0	0	0	0	0	0	0	10
Zavreliella marmorata (van der Wulp 1859)	Zav mar	1	0.01	0.7	0	0	0	0	10	0	0	0	0
Total		12272											

Abbreviations for feeding guilds: SHR, shredder; GRA, grazer; AFIL, active filter-feeder; PFIL, passive filter-feeder; DET, detritus feeder; MIN, miner; XYL, xylophagous; PRE, predator; PAR, parasite.