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The relative importance of spatial and environmental processes in distribution of benthic chironomid larvae within a large and shallow lake

Diána Árva[1,*], Mónika Tóth[1], Hajnalka Horváth[1], Sándor A. Nagy[2], András Specziár[1]

[1]Balaton Limnological Institute, MTA Centre for Ecological Research, Klebelsberg K. u. 3., H-8237 Tihany, Hungary

[2]Department of Hydrobiology, University of Debrecen, Egyetem tér 1., H-4032 Debrecen, Hungary

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

Abstract Although chironomids are popular model organisms in ecological research and indicators of bioassessment, the relative role of dispersal and environmental filtering in their community assembly is still poorly known, especially at fine spatial scales. In this study we applied a metacommunity framework and used various statistical tools to examine the relative role of spatial and local environmental factors in distribution of benthic chironomid taxa and their assemblages in large and shallow Lake Balaton, Hungary. Contrary to present predictions on the metacommunity organization of aquatic insects with winged terrestrial adults, we found that dispersal limitation can considerably affect distribution of chironomids even at lake scale. However, we also revealed the predominant influence of environmental filtering, and strong taxa-environment relationships were observed especially along sediment type, sediment organic matter content and macrophyte coverage gradients. We account that identified reference conditions and assemblages along with specified optima and tolerances of the abundant taxa can contribute to our understanding of chironomid ecology and be utilized in shallow lake bioassessment. Further, we propose that predictive models of species-environment relationships should better take into account pure spatial structuring of local communities and species-specific variability of spatial processes and environmental control even at small spatial scales.

Keywords Chironomidae assemblages, Dispersal limitation, Environmental gradients, Indicator species, Optima and tolerances, Within lake spatial pattern.

Introduction

Most organisms are distributed non-randomly in space and the analysis of these spatial patterns is one of the most beneficial tools of ecological research and bioassessment based environmental management. For studying the spatial distribution of species and their assemblages, the metacommunity concept (Leibold et al., 2004; Logue et al., 2011) has been increasingly applied because of its comprehensive approach. This concept acknowledges that the distribution of organisms is influenced by a series of processes related to species identity, regional (dispersal and demographic stochasticity among sites) and/or local (species sorting along biotic and abiotic environmental filters) factors. In their conceptual work, Leibold et al. (2004) introduced four metacommunity perspectives accounting for local community structures depending on the relative role of stochastic, regional (i.e. dispersal) and local (i.e. environmental filtering) processes. However, development of the concept has resulted in a much more continuous approach of metacommunity organization characteristics (Gravel et al., 2006). The recent framework emphasizes the fundamental and practical importance of testing the relative role of spatial and local factors implying on the relevance of dispersal and environmental filtering processes, respectively (Logue et al., 2011), which can be dissected by recently developed statistical tools (Borcard et al., 2004; Dray et al., 2006).

Thanks to their wide distribution, huge species richness, various environmental optima and tolerances and important role in food webs, chironomids have been in the focus of aquatic ecological research for a long time (Porinchu & MacDonald, 2003; Milošević et al., 2013). In addition, chironomids have rapid generation cycle (generally from 3 weeks to few months; Porinchu & MacDonald, 2003) and relatively good dispersal and colonization capacity by their winged terrestrial adults (Armitage, 1995; Čerba et al., 2010). The above mentioned features make them one of the most popular indicators of bioassessment studies at various spatial and temporal scales (Brundin, 1958; Seather, 1979; Brodersen & Anderson, 2002; Gajewski et al., 2005; Milošević et al., 2013) and ideal model organisms for studying colonization patterns and metacommunity organization in dynamic and heterogeneous environment. However, there is a clear gap in our knowledge about the relative importance of dispersal and local environmental filtering processes in the spatial distribution of chironomids, which information is substantial for understanding their ecology and reinforce fundamentals of their bioassessment application.

Environmental factors affecting distributions of chironomids at various spatial scales have been extendedly studied in both lotic and lentic habitats (Silver et al., 2000; Mousavi, 2002;

Bitušik & Svitok, 2006; Ferrington Jr., 2008; Puntí et al., 2009; Tóth et al., 2012; Jyväsjärvi et al., 2013; Tóth et al., 2013). Nevertheless, the quantitative role of spatial (dispersal) processes in the distribution of chironomids over various spatial scales is hardly known. According to recent theories, the relative role of dispersal processes decreases from broad geographical towards fine microhabitat scale and with the increasing dispersal capacity of organisms (Cottenie, 2005; Beisner et al., 2006; Van de Meutter et al., 2007; Capers et al., 2009). Applying the metacommunity framework, Grönroos et al. (2013) and Heino (2013a,b) argued that the relative role of spatial and local environmental factors in assembly of local communities of aquatic invertebrates depend not only on the spatial scale scanned but also on species traits, especially on dispersal mode. In line with the conclusions of the above studies, it could be supposed that fine-scale (e.g. within lake) spatial distributions of chironomids are decisively determined by local environmental factors and hardly affected by pure spatial processes (i.e. dispersal limitation). However, the metacommunity framework in aquatic insects with winged adults have been applied only at medium to broad spatial scales (i.e. across drainage areas and geographical regions; Puntí et al., 2009; Grönroos et al., 2013; Heino, 2013a,b), whereas it was not tested how spatial and local environmental processes actually contribute to distribution of these organisms at small spatial scale such for instance within a lake.

In this study, we examine the relative role of spatial and various local environmental factors in the spatial distribution of benthic chironomid larvae in large and shallow Lake Balaton, Hungary. Previous investigations focused on the largely homogenous open water area of the lake and emphasised the spatio-temporal relationship between the phytoplankton production and population dynamics of the dominant chironomid species (Specziár & Bíró, 1998; Specziár & Vörös, 2001). However, considering the extended area of the lake and the high heterogeneity of its littoral and surrounding habitats, we assumed that organization of chironomid assemblages at the lake scale is influenced by various other environmental factors and complex processes likely including dispersal as well. Presumably, dispersal of adults that is largely depend on atmospheric motions (Armitage, 1995; Heino, 2013a,b) is not homogeneous over the lake area, and also dispersal capacity (i.e. colonization distance and density) may vary among species (Armitage, 1995).

Accordingly, we hypothesised that both spatial and local environmental factors have significant effect on the distribution of chironomids within Lake Balaton and the relative role of these two processes is species specific. Moreover, if spatial and local environmental processes present simultaneously, it is also important to apply the metacommunity framework when deriving species indicator values based on species-environment data for bioassessment applications. To assess these issues, we performed an extensive sampling covering entire ranges of presumed habitat types and environmental gradients over the lake within a short period of time (i.e. three weeks of sampling) and used a series of uni- and multivariate statistical tools to identify spatial and local biotic and abiotic components of assemblage and taxon level variability in chironomid data. Specific aims of this study are to analyse: (i) what relative importance spatial and local environmental factors have in structuring local chironomid communities; (ii) what environmental gradients are influential in structuring chironomid metacommunities; (iii) what groups of microhabitats (i.e. functional habitats) and related indicator taxa may be identified based on taxon-environmental relationships if spatial processes are also accounted for; and (iv) what optima and tolerances characterize the abundant taxa regarding the most influential environmental factors in Lake Balaton.

Material and methods

Study area and sampling sites

Balaton is the largest shallow lake (surface area: 596 km^2; mean depth: 3.2 m) in Central Europe, situated at 46^o 42' - 47^o 04' N, 17^o 15' - 18^o 10' E and 104.8 m above sea level. This slightly alkaline (400 mg l^{-1} of Ca^{2+} and $Mg^{2+}(HCO_3^-)_2$) lake can be divided into four basins (Keszthely, Szigliget, Szemes, Siófok) with slightly increasing mean depth (from 2.3 to 3.7 m) and decreasing mean planktonic chlorophyll-*a* concentration (from 26.6 to 9.7 µg l^{-1}, mean data of 2008-2012; Ministry of Environmental Protection and Water Management of Hungary, http://www.ktm.hu/balaton/lang_en/index.htm) from the major inflow, River Zala (Keszthely basin) toward the only outflow, Sió Canal (Siófok basin; Istvánovics et al., 2007). A majority of the lake area (>85%) is largely homogeneous open water with soft, silt sediment, little variable physico-chemical features and with no macrovegetation. The littoral zone is more heterogeneous (for ranges of some environmental variables see Appendix A). At present, only 47% of the lake shore is in a natural or semi-natural state and these sections are covered by reed grass *Phragmites australis*, dispersedly supplemented with small patches of lesser bulrush *Typha angustifolia* and common club-rush *Schoenoplactus lacustris*.
Submerged (most abundant species: perfoliate pondweed *Potamogeton perfoliatus*, sago pondweed *Potamogeton pectinatus*, Eurasian watermilfoil *Myriophyllum spicatum* and rigid hornwort *Ceratophyllum demersum*) and floating leaved (e.g. yellow water-lily *Nuphar lutea*) macrophytes occur sparsely in the littoral zone. Significant part of the lake shore has been

stabilized with rocks, and these riprap habitats are covered by filamentous algae (mainly *Cladophora* sp.) up to 0.5 m water depth. There are also several large, commercial boat harbours sheltered by ripraps from swash and many small harbours established within the reed grass stand for anglers. Since northern winds dominate in the area, northern and southern littorals are markedly different; the former has dominantly soft, silt and the latter hard, sandy sediment.

In order to capture the longest possible length of the major environmental gradients, we sampled 128 sites distributed across the four basins and characteristic habitat types of the lake (Fig. 1), between 26. June and 13. July 2012. Examined habitats included offshore area (along the longitudinal axis of the lake), natural-like littoral habitat transects from the riparian edge of the reed grass stand towards the macrophyte-free inshore area (typically one to three sites within the reed grass stand, one in the edge of the reed grass stand and the open water, and at 50 and 200 m distances from the reed grass stand; Fig. 1), small boat harbours situated within the reed grass stand, stands of the most characteristic submerged and floating leaved macrophytes, and modified littoral areas, large sailing-vessel and ship harbours, ripraps and nearby littoral areas. Samplings covered both the northern and southern littorals.

Chironomid survey

At each sampling site, three sediment samples were taken using an Ekman grab and merged for analyses (total sampled area per site: 0.036 m^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 algal 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 samples alive by sugar flotation method (Anderson, 1959), euthanized and preserved in 70% ethanol for later identification. Chironomids were cleared by digestion in 10% KOH (potassium hydroxide) and slide-mounted in Euparal®. Identification was performed to species or the lowest possible taxonomic level according the keys of Bíró (1981), Cranston (1982), Wiederholm (1983), Janecek (1998), Vallenduuk (1999), Sæther et al. (2000) and Vallenduuk & Moller Pillot (2002).

Local environmental variables

We measured a number of local physical-, chemical- and biotic variables (Appendix A) that have been found influencing abundance and assemblage structure of chironomids (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, temperature and redox potential of the uppermost sediment layer, and dissolved oxygen, pH and conductivity of the water close to the bottom. Visual estimates of emergent (dominantly reed grass), submerged and floating leaved macrophytes and filamentous algae (*Cladophora* sp.) coverage (%) was made within a circle of 3 m diameter around the origin of chironomid samples and the area of the submerged and floating leaved macrophyte stand was recorded by GPS and calculated by MapSource version 6.16.3. software (Garmin Ltd., www.garmin.com). The substratum of the lake bed was inspected for percent occurrence of clay, silt, sand, rock, mollusc shells and pure reed grass root (characteristic in some degrading reed grass stands), and the sediment was examined for the occurrence of fine and coarse particle decomposing plant material and leaves of reed grass and rated on a six category scale (0-5). Additional sediment samples were taken for laboratory analyses. Chlorophyll-*a* was extracted from the upper 2 cm sediment layer by hot methanol method (Iwamura et al., 1970) and measured spectrophotometrically (Shimadzu UV-1601 spectrophotometer). Percentage organic matter content was assessed from dry (at 50 ^{o}C for 72 hours) samples of the upper 2 cm sediment layer according to the loss-on-ignition method at 550 ^{o}C for 1 hour (LOI550; Heiri et al., 2001).

Spatial variables

We established two sets of spatial variables (Appendix A). First, to model directional environmental gradients of the lake, position of each sampling site was characterized with lake-scale geographical (LSG) variables including lake basin (i.e. Keszthely-, Szigliget-, Szemes- and Siófok-basins), location along the north-to-south transect of the lake (i.e. northern littoral, offshore and southern littoral), and distances from the closest shore, reed grass stand, floating leaved or submerged macrophyte meadow and open water. Second, to capture remaining spatial pattern in the chironomid data not described by the local environmental and LSG variables, we composed a set of theoretical variables modelling broad to fine scale spatial patterns among sampling sites by performing principal coordinates of neighbour matrices (PCNM) analysis based on GPS coordinates of sampling sites (Borcard et al., 2004; Dray et al., 2006) using Past version 2.17 software (Hammer et al., 2001). This method practically models position of each sampling site relative to all the other sites similarly as they distribute on the map by means of artificial PCNM variables. During this procedure a matrix of Euclidean distances between all pairs of sampling sites was constructed from the GPS coordinates and truncated at a threshold value of 6 km corresponding to the largest minimum distance between neighbouring sites (i.e. offshore to littoral distance).

Distances >6 km were replaced with an arbitrary large value of 24 km equal to four times the threshold distance (Borcard & Legendre, 2002). Then, a principal coordinate analysis of the truncated distance matrix was performed and the derived principal coordinate functions with positive eigenvalues (in total 76 functions were obtained) were retained as PCNM variables (Borcard et al., 2004).

Statistical analyses

Aims (i) and (ii): 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 spatial (i.e. LSG and PCNM variables) and local environmental factors in within lake distribution of benthic chironomids at the assemblage and individual taxon levels, respectively.

Extremely rare taxa with <0.1% representation in the total abundance or occurring in <5% of the samples were excluded to reduce their disproportionate effect in the multivariate analyses (Legendre & Legendre, 2012). For analyses, chironomid abundance data were $\ln(x+1)$ transformed to improve their normality and reduce heteroscedasticity. Of LSG variables, lake basin and location along the north-to-south transect were treated as categorical factors and re-coded into binary dummy variables (Lepš & Šmilauer, 2003), whereas others were $\ln(x+1)$ transformed. Local environmental variables measured on continuous scales (including variables representing percentage distribution) were transformed depending on their scale of measurement. However, PCNM variables and local environmental variables which scaled categorically were not transformed (see Appendix A).

Because a detrended correspondence analysis (DCA) indicated relatively long gradient length (4.11 in standard deviation units) in our data, we chose canonical correspondence analysis (CCA) for further analyses (Lepš & Šmilauer, 2003). Potential explanatory variables (i.e. LSG, PCNM and local environmental variables) were filtered for collinearity at $r>0.7$ and subjected to a forward stepwise selection procedure (at $P<0.05$) based on Monte Carlo randomization test with 9,999 unrestricted permutations. This selection resulted in two LSG, 13 PCNM and 16 local environmental variables for the final overall CCA model (Appendix A). Finally, a series of CCA and partial CCAs were conducted to partition the effects of significant variable groups on chironomid assemblages (Cushman & McGarigal, 2002). DCA and CCA analyses were performed using CANOCO version 4.5 software (ter Braak & Šmilauer, 2002).

At the individual taxon level, we followed the same approach (i.e. variable selection procedure followed by variation partitioning based on the final model) and used the same explanatory variables as described above, but by applying MPRA including pure and quadratic form of each explanatory variable. 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. We performed regression analyses for the most abundant chironomid taxa occurring in ≥25 samples by using STATISTICA 8.0 software (www.statsoft.com).

Aim (iii): a k-means cluster analysis was performed to obtain ecologically relevant groups of sites based on their scores along the first three CCA axes by using STATISTICA 8.0 software (www.statsoft.com). Clustering sampling sites into four groups gave the best interpretable results. Differences in the environmental conditions between the four sample-groups were analysed by Kruskal-Wallis ANOVA followed by Mann-Whitney pairwise post hoc test. The most characteristic taxa for each sample group were identified with the indicator value method using IndVal 2.0 software (Dufrêne & Legendre, 1997; http://old.biodiversite.wallonie.be/outils/indval/). This method calculates an indicator value (IV) that may range between 0 and 100 for each taxon by defined groups of samples and tests its significance by Monte Carlo permutations (9,999 permutations in this case).

Aim (iv): optima and tolerances of the abundant chironomid taxa regarding the influential environmental factors were assessed by weighted averaging regression method applied widely in ecological (Puntí et al., 2009) and especially in palaeoecological studies (Brodersen & Anderson, 2002) using C2 version 1.7.4 software (Juggins, 2007; http://www.staff.ncl.ac.uk/staff/stephen.juggins/software/C2Home.htm). Optima and tolerances were calculated for taxa occurring in ≥10 samples and only for environmental factors which measured on continuous scales.

Results

Chironomidae assemblages

Altogether 13,804 specimens of 40 taxa were identified from 3 subfamilies: Tanypodinae (7), Orthocladiinae (4) and Chironominae (29) (Appendix B). The average taxon richness was 8 with a range of 2 to 22 taxa per sample. Most abundant taxa were *Cladotanytarsus mancus* gr., *Polypedilum nubeculosum*, *Chironomus balatonicus*, *Chironomus dorsalis*, *Cricotopus sylvestris* gr. and *Procladius choreus*.

Components of assemblage level variance

The overall CCA model based on all significant and non-collinear LSG, PCNM and environmental variables explained 61.9% (eigenvalue: 1.546) of the total variance (eigenvalue: 2.496) in the chironomid relative abundance data. First CCA axis explained 15.9% of taxon variation and represented gradients of substrate type from hard (i.e. rock and sand) to soft (i.e. silt) and oxygen concentration, as well as captured some broad spatial structure described by PCNM1 and PCNM3 and distance from the shore (Fig. 2). Second CCA axis explained 12.1% of variance in chironomid data and represented a gradient of organic matter; it correlated positively with LOI550, submerged macrophyte coverage and amount of reed leaves on the sediment, and negatively with the oxygen concentration, pH and of LSG variables with distances from the reed-grass stand and shore. Third CCA axis explained 8.3% of variance in chironomid data and emphasized the difference between rock (i.e. riprap habitats) and sandy substrates (i.e. southern littoral zone).

Local environmental variables explained 45.4%, LSG variables 12.7% and PCNM variables 29.1% of total variance in chironomid assemblage data (Fig. 3). However, the shared effect of local environmental and spatial (i.e. both LSG and PCNM) variables was relatively high (21.8%) suggesting a marked spatiality in the local environmental conditions as well. Retained LSG variables (i.e. distances from reed-grass stand and shore) modelled variance related to inshore towards offshore patterns, but had little individual effect (2.2%) compared to PCNM (13.5%) and local environmental (23.6%) variables. Local environmental effects could be divided into three components: 1) substrate type (25.0%, including shared effect), 2) plant material (26.7%) and 3) chemical properties (14.3%). The influence of water chemistry on chironomid assemblages was highly overlapped by the effects of substrate type and plant material. Live (i.e. macrophytes) and decomposing plant material had approximately equal influence on the variability of chironomid assemblages.

Components of individual taxon level variance

At the individual taxon level, local environmental condition had generally higher explanatory power in abundance patterns of benthic chironomids than spatial variables (i.e. LSG and PCNM variables; Table 1, Fig. 4). *C. sylvestris* gr., *C. balatonicus*, *C. virescens* and *Microtendipes chloris* agg. proved to be especially sensitive to local environmental factors and were hardly influenced by spatiality. Local environmental factors also captured a large proportion of variance in the abundance of *P. choreus* and *C. mancus* gr., but in high overlap with spatial factors. Spatial processes clearly predominated in the distribution of *C. defectus*, *P. nubeculosum* and *Stictochironomus* sp. and the considerable proportion of purely PCNM related variance indicated the presence of dispersal limitation in these taxa.

Functional habitats and their indicator taxa

Based mainly on the type (i.e. silt, sand and rock) and organic matter content of the substrate, the CCA indicated the separation of sites into four (functional) habitat types and associated chironomid assemblages. This grouping of sites was supported by k-means clustering (Fig. 5) as follows: 1) northern littoral sites and boat harbours with macrophytes; 2) ripraps; 3) offshore and northern littoral sites without macrophytes; and 4) southern littoral sites (for distribution of site groups in the lake see Fig. 1). Environmental conditions and indicator taxa of these habitat types are presented in Tables 2 and 3, respectively. Briefly, group 1 sites were mainly covered by macrophytes, had silt sediment with high organic matter content, low to medium oxygen concentration and redox potential. These sites were indicated by ten taxa including *Cladopelma virescens*, *C. balatonicus*, *Tanypus kraatzi*, *C. dorsalis* and *Paratanytarsus* sp. Group 2 sites represented shallow riprap habitats (rock: 100%) covered by *Cladophora* sp. algae, had high oxygen concentration and redox potential. Indicator taxa for these sites were *Cricotopus reversus*, *C. sylvestris* gr. and *Orthocladius oblidens*. Group 3 sites were in the offshore area and in the macrophyte free parts of the northern littoral, generally had silt sediment, moderate organic matter content, medium to high oxygen concentration and low to medium redox potential. Indicator taxa of this site group were *P. choreus*, *Microchironomus tener* and *Tanypus punctipennis*. Group 4 sites had sandy sediment, low amount of decomposing organic matter, medium to high oxygen concentration and medium redox potential. Indicator taxa of this site group were *C. mancus* gr., *Cryptochironomus defectus* and *Stictochironomus* sp.

Optima and tolerances of chironomid taxa

The optima and tolerances of taxa occurred in >10 samples are shown for some important factors in Fig. 6. Indicator taxa of site group 1, *T. kraatzi*, *Paratanytarsus* sp. and *C. dorsalis* had high optima for silt, LOI550 and emerged and submerged macrophyte coverage, and relatively low for dissolved oxygen and redox potential. It is not surprising that indicator taxa of ripraps (site group 2: *C. reversus*, *C. sylvestris* gr. and *O. oblidens*) and offshore habitats (site group 3: *P. choreus*, *M. tener* and *T. punctipennis*) were found at the opposite ends of some optima diagrams. *C. reversus*, *C. sylvestris* gr. and *O. oblidens* were restricted to shallow water, with high oxygen concentration, redox potential, algae coverage and low percentage of silt, while *P. choreus*, *M. tener* and *T. punctipennis* preferred deep water with silt sediment, moderate oxygen concentration and redox potential and low algae coverage. Indicator taxa of site group 4, *C. mancus* gr., *C. defectus* and *Stictochironomus* sp., preferred shallow water and sandy sediment, had medium optima for redox potential and emerged and submerged macrophyte coverage, and low optima for LOI550 and algae coverage. Regarding pH, *T. kraatzi* had the lowest, whereas *C. mancus* gr. the highest optima. Tolerance values varied considerably across taxa and environmental factors. For instance, regarding water depth, LOI550, algae, emergent and submerged macrophyte coverage highest tolerances were observed in taxa with high optima, whereas regarding silt, taxa with medium optima were the most tolerant.

Discussion

Relative role of spatial processes and environmental filtering

Metacommunity theory assumes that local assemblages are structured by a series of spatial processes related to the migration of species among neighbouring sites and by local environmental control, and the relative role of these two types of processes changes with the spatial scale and varies among taxonomic groups (Leibold et al., 2004; Cottenie, 2005). At small-scale (i.e. within a lake) and in organisms with relatively good dispersal capacity, such as chironomids with winged adults, recent theorems predict overwhelming role of local environmental filtering and consider that spatial processes may have only marginal importance (Leibold et al., 2004; Cottenie, 2005; Beisner et al., 2006; Heino, 2013a,b). Our results show some divergence from these theories. We could prove the predominant role of local environmental filtering at assemblage level and in several individual taxa. However, we also revealed that a substantial part of the non-random spatial patterning in the within lake distribution of chironomids was unrelated to environmental conditions and 13.5% of the total and 21.8% of the explained variance of relative abundance data purely related to PCNM variables. Moreover, in line with the conclusion of other studies (Pandit et al., 2009; Verberk et al., 2010), our results reinforce the inter-specific variability of the relative role of these two type of processes (i.e. spatial and environmental).

We consider that LSG variables in a metacommunity context captured both some coarse scale within lake environmental patterns and spatiality related to dispersal. Distances from the shore and emergent macrophyte stand represent coarse patterns of the obvious littoral to offshore habitat gradient with increasing water depth, decreasing macrophyte abundance and sediment organic matter content, etc. On the other hand, distance from the shore correlates with the distance of nearby aquatic habitats serving potential species pools for colonization. Distance from these sites may play a crucial role because it filters the species that are able to reach and colonize particular lake sites (Patrick & Swan, 2011). However, LSG variables purely explained only minor proportion (2.2%) of the total variance in the relative abundance data and most of the variance they captured was also explained by local environmental and PCNM variables.

Pure spatial (PCNM related) pattern in metacommunities is a strong indicator of uneven dispersal of organisms among sites (Borcard et al., 2004; Cottenie, 2005). Chironomids with winged adults are considered as medium to good dispersers, although their dispersal over longer distances depends on atmospherical motions and dispersal potential of particular species can also be highly variable due to behavioural and habitat factors (Armitage, 1995; Heino, 2013a,b). Specziár and Vörös (2001) and Specziár (2008) showed that *C. balatonicus*, which is an abundant large-bodied species in Lake Balaton, has high dispersal capacity and can very densely colonize extended lake areas within one generation time when food condition (i.e. production of planktonic algae) becomes favourable. However, distributions of other smaller-bodied open water species (*P. choreus*, *T. punctipennis* and *M. tener*) had substantial purely PCNM related variance indicating dispersal limitation even at lake scale. Similarly, littoral taxa proved to be highly variable in their relative sensitivity to spatial and environmental filtering processes. Although inter-specific variability of the influence of spatial processes seems to be evident in chironomids the underlying mechanisms are not ascertained yet. Dispersal capacity of an organism depends on its mobility and abundance and distribution of species pools (Palmer et al., 1996; Shurin et al., 2000; Heino, 2013b). Since adults of open water species may hatch over extended lake area and thus may have larger and more evenly dispersed stock of potential colonizers than species restricted to relatively small and separated microhabitat patches in the littoral of Lake Balaton. Consequently, lesser spatial effect could be supposed in the former group. However, our results did not unequivocally support this hypothesis. Based on observations on variety of aquatic organisms, Pandit et al. (2009) and Verberk et al. (2010) argued that habitat generalists are governed mainly by spatial (dispersal) processes and habitat specialist are governed mainly by environmental control. However, we could not unequivocally classify individual chironomid taxa into such categories and thus could not test this hypothesis.

The high ratio of shared effect between environmental and PCNM and LSG variables indicates that environmental conditions have a considerable spatial structure in the lake as well. This environmental patterning includes a littoral to open water gradient and the marked difference between northern and southern littorals. Previous studies also reported a consistent longitudinal gradient in the open water chironomid assemblages related to the abundance trend of planktonic algae (Specziár & Bíró, 1998; Specziár & Vörös, 2001). However, in the present study, the more pronounced effects of the littoral and the littoral to open water gradients likely outcompeted the weak longitudinal trend in the statistical analyses, and neither chlorophyll-*a* concentration, nor lake basin (LSG variable group) were retained in the final model.

As within lake distribution of chironomid assemblages is governed by both environmental control and dispersal limitation (e.g. distance among sites, weather conditions, species pool and behaviour of adults; Armitage, 1995), a comprehensive metacommunity framework seems to have better conceptual responsibility than pure niche based models even at this spatial scale (Leibold et al., 2004). However, Balaton is a relatively large lake, and consequently the question arises whether spatial processes still have relevance in smaller lakes (i.e. <10 km^2 lake area) or ponds. Further challenge could be specifying underlying spatial (dispersal) processes and their relative importance in structuring chironomid metacommunities over various spatial scales. For instance, there is a clear gap in our knowledge to what extent species-specific mobility and drifting by wind contributes to dispersion of chironomid species across different spatial scales and various landscapes, and whether this inter-specific differences could be related to specific morphological, life-history or functional (i.e. food and habitat preference) traits.

Environmental filters and bioindication value of chironomid assemblages

Environmental control is one of the strongest ecological regulator theorems in community ecology (Chase & Leibold, 2003) and explored species-environment relationships also underlie bioassessment applications (Brundin, 1958; Seather, 1979; Brodersen & Anderson, 2002). In Lake Balaton, we identified number of relatively long environmental gradients and revealed that the optima and tolerances of individual chironomid taxa distributed quite evenly along them supporting the significance of environmental filtering. Of environmental factors, physical attributes of the sediment and the occurrence of different plant materials (i.e. algae, macrophytes, and their decomposing particles) received high explanatory power, whereas water chemistry had lower individual influence on chironomid assemblages. The effect of chemical factors (i.e. dissolved oxygen concentration, pH and conductivity of the water and redox potential of the sediment) greatly overlapped with the effect of sediment and plants. A substrate gradient from silt to sand and the presence of rock affect the distribution of burrowing and tube building larvae and larvae living on the sediment surface (Wolfram, 1996; Rae, 2004). Moreover, physical characteristic of the sediment usually correlates with other environmental factors affecting chironomid assemblage structure (Ruse, 1994; Rae, 2013). In Lake Balaton, sand and especially rock substrates coincide with swash, low amount of decomposing organic matter and high oxygen concentration. The ratio of silt in the sediment provided one of the best separations of taxa optima. For instance, *T. kraatzi*, *P. varus*, *T. punctipennis*, *C. balatonicus* and *P. choreus* showed the highest preference whereas *O. oblidens*, *C. reversus*, *C. mancus* gr. and *Stictochironomus* sp. the highest avoidance of silt. Likewise larvae of *T. punctipennis* and *Chironomus* gr. *plumosus*, which group *C. balatonicus* belongs to, were found to associate with muddy substrate in Neusiedler See (Wolfram, 1996). On the other hand, *P. choreus* did not show a clear sediment preference there. The preference of *C. mancus* gr. for sandy sediment is widely approved as well as the two other indicator species of the southern littoral in Lake Balaton, the *C. defectus* and *Stictochironomus* sp. are usually associated with sand or other compact sediments (Wolfram, 1996; Na & Bae, 2010). The particular importance of algae, macrophytes and decomposing plant material in structuring chironomid assemblages is also well known. Plants provide chironomids with substrate and specific environmental conditions, while their decomposing parts offer directly (live tissues or detritus) and indirectly (via bacteria and fungi growing on detritus) food sources (Tokeshi & Pinder, 1985; Papas, 2007; Čerba et al., 2010). *Cladophora* sp. algae coating on the substrate was tolerated only by few of the abundant taxa and among them *C. reversus*, *O. oblidens* and *M. chloris* agg. had the highest optima and thus probably represent the highest indicative value for bioassessments. Most abundant taxa in Lake Balaton showed low optima but relatively high tolerance for macrophytes. Dense emergent vegetation was most preferred and tolerated by *T. kratzii* and *C. viridulum*. Whereas *P. varus* and *C. mancus* gr. were two good benthic indicator taxa of dense submerged macrophyte stands in the silty northern and sandy southern littorals, respectively. Present results are in good agreement with other information on the habitat preference of the above taxa as their occurrences are usually associated with algal coating on the substrate surface or with macrophytes (Čerba et al., 2010; Tóth et al., 2012, 2013). Moreover, *Cricotopus* species require plant surfaces free of sediment as increasing amounts of sedimented particles reduces the availability of the periphyton (Čerba et al., 2010; Tarkowska-Kukuryk, 2010) which criterion is best met in swashed riprap habitats in Lake Balaton. The amount of particulate organic matter was found to affect the distribution of chironomids even at very fine microhabitat scale (Ruse, 1994; Ali et al., 2002; Syrovátka et al., 2009). Although they are important food resources, decomposing organic matters usually produce unfavourable chemical environment for most macroinvertebrates in standing waters (Carpenter & Lodge, 1986; Porinchu & MacDonald, 2003; Papas, 2007). The highest LOI550 values were measured at the riparian edge of dense reed-grass stands along the northern littoral, where the dissolved oxygen concentration and the redox potential were the lowest. These specific circumstances were best tolerated by *T. kraatzi* and *Tanytarsus* and *Paratanytarsus* species.

Based mainly on physical characteristics of the sediment, and density of macrophytes and decomposing plant materials four site groups and associated chironomid assemblages could be separated. These habitat types and related chironomid assemblages provided ecologically meaningful primary reference conditions for this lake. The four habitat types are (1) northern macrophyted littoral and sheltered boat harbours with silt sediment and high LOI550, (2) ripraps (rocks) with algal coating, (3) open water with silt sediment and low LOI550, and (4) southern littoral with sand sediment and low LOI550. Indicator species analysis also supported this habitat classification. Our results prove the presence of a consequent north to south natural habitat and associated chironomid assemblage gradients in the lake, which is mainly related to the effect of dominant northern winds in the region. However, human induced changes were also obviously recognizable. The building of ripraps to stabilize large parts of the lake shore and to provide sheltered areas for boats, resulted in the establishment of a new habitat type (site group 2) and specific chironomid assemblages (indicator taxa: *C. reversus*, *C. sylvestris* gr. and *O. oblidens*). While, benthic chironomid assemblages of the sheltered boat harbours were similar to natural assemblages of the macrophyted northern littoral. The establishment of these two new habitats (i.e. ripraps and boat harbours) also affects consistent patterns of the northern and southern littorals. All ripraps, either locate in the northern or southern littorals, clustered to the habitat group 2. Whereas boat harbours enable for assemblages characterized originally only the northern littoral (group 1) to locate also in the southern littoral (originally belonging exclusively to group 4).

Water depth is an important predictor of chironomid assemblage attributes in many studies (e.g. Verneaux & Aleya, 1998; Ali et al., 2002; Luoto, 2012) and depth optima of several species prove to be consequent across broad spatial scales (Luoto, 2012). However, in this study, the water depth tightly correlated with several potential LSG and local environmental factors and thus was excluded from CCA and MPRA analyses. Optima and tolerances of taxa are clearly separated along this gradient in Lake Balaton as well. Most obviously *C. balatonicus*, *T. punctipennis*, *M. tener* and *P. choreus* as the most abundant open water species separate from the other taxa along this gradient. However, since most environmental factors scale with water depth (e.g. sediment characteristics, oxygen concentration, macrovegetation, composition and production of benthic algae, temperature and fish assemblages) it is very difficult to disentangle the individual effect of water depth on chironomid and other macroinvebrate communities (Real et al., 2000; Wilson & Gajewski, 2004). Therefore, water depth itself has probably little indicative value in chironomid based bioassessment in shallow lake habitats (Brodersen & Quinlan, 2006; but see Luoto, 2012).

Conclusions

We found a clear support that within lake local chironomid assemblages are structured according to metacommunity principles and both spatial processes and environmental filtering have strong relevance at fine spatial scale as well. Moreover, assembly of within lake chironomid metacommunities is further complicated by a marked inter-specific variability in the relative role of spatial and environmental processes. Accordingly, we propose that predictive models of species-environment relationships should better take into account pure spatial structuring of local assemblages even at lake scale. Disentangling the underlying reasons of dispersal limitation and its inter-specific variability is clearly one of the most critical problems in this respect. In addition, since the relative role of spatial and environmental processes depends on the spatial scale and taxa examined, we argue that the reliability of predictive bioassessment models can also vary among regions and habitats, if they do not consider spatial processes as well. Future challenges thus also include to explore to what extent disregarded spatial processes may bias conclusions of monitoring studies depending on the assemblage metric (i.e. relative abundance, presence-absence) and taxonomic and/or functional resolution used.

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Table 1 Summary results of multiple second degree polynomial regression models for abundant chironomid taxa in Lake Balaton, Hungary. The relative contribution of spatial and local environmental variable groups to the total variance is shown on Figure 4. Note that pure and quadratic forms of each explanatory variable entered the forward stepwise variable selection procedure as independent variables. Abbreviations for explanatory variables are explained in Appendix A.

	No. of PCNM variables, including pure and quadratic forms	Lake-scale geographical variables	Environmental variables in the model	$R^2_{adj.}$	df	*F*	*P*
Procladius choreus	2	distr.	(pH)^2, (cond.)^2, silt, (silt)^2, EMC	0.590	8, 119	23.9	<0.001
Tanypus kraatzi	4	-	DO, (DO)^2, (SMC)^2, FMC	0.587	8, 119	23.6	<0.001
Tanypus punctipennis	8	dists.	silt, (LOI550)^2, (SMC)^2	0.542	12, 115	13.5	<0.001
Cricotopus sylvestris gr.	1	-	(RP)^2, cond., sand, (sand)^2, rock, (LOI550)^2, SMC, FMC, (FMC)^2	0.647	10, 117	24.3	<0.001
Chironomus balatonicus	4	-	(pH)^2, (RP)^2, cond., sand, rock, root, LOI550, (LOI550)^2, (FMC)^2	0.712	13, 114	25.2	<0.001
Chironomus dorsalis	3	distr., (distr.)^2	(DO)^2, RP, (RP)^2, silt	0.476	9, 118	13.8	<0.001
Cladopelma virescens	-	-	DO, (DO)^2, FMC, macarea, (macarea)^2, (FOM)^2, COM, (COM)^2, leaves	0.532	9, 118	17.0	<0.001
Cladotanytarsus mancus gr.	1	dists.	sand, (sand)^2	0.561	4, 123	41.6	<0.001
Cryptochironomus defectus	4	-	RP, sand	0.498	6, 121	22.0	<0.001
Dicrotendipes nervosus	4	dists.	cond., (SMC)^2	0.349	7, 120	10.7	<0.001
Microchironomus tener	3	dists.	(silt)^2, algae, LOI550	0.451	7, 120	15.9	<0.001
Microtendipes chloris agg.	-	-	(rock)^2, (root)^2, (algae)^2, COM	0.265	4, 123	12.5	<0.001
Polypedilum nubeculosum	4	(distr.)^2, dists., (dists.)^2	(RP)^2, (LOI550)^2	0.464	9, 118	13.2	<0.001
Stictochironomus sp.	4	dists.	sand, algae	0.567	7, 120	24.8	<0.001

PCNM = spatial variables derived from principal coordinate analysis of neighbouring matrix.

Table 2 Median, minimum and maximum values of the main explanatory variables for the four site groups established by k-means clustering from constrained canonical correspondence analysis site scores based on spatial and environmental variables versus relative chironomid abundance data in Lake Balaton, Hungary. Differences in the environmental conditions between the four sample groups were tested by Kruskal-Wallis ANOVA (K-W). Median values without any common letter in their markings are statistically different according to Mann-Whitney pairwise post hoc test (P<0.05). Abbreviations for explanatory variables are explained in Appendix A.

	Group 1 (38 sites)			Group 2 (8 sites)			Group 3 (34 sites)			Group 4 (48 sites)			K-W	
	median	min.	max.	median	min.	max.	median	min.	max.	median	min.	max.	$H_{df=3}$	P
Distr. (m)	1^{a}	0	1000	100^{b}	3	400	245^{b}	1	5500	2^{a}	0	500	49.2	<0.001
Distm. (m)	5^{a}	0	200	5^{a}	1	50	270^{b}	0	5500	15^{a}	0	450	31.2	<0.001
Disto. (m)	20^{b}	0	129	0^{ab}	0	50	0^{a}	0	50	0^{a}	0	100	27.6	<0.001
Dists. (m)	38^{b}	0	190	1^{a}	0	1	303^{d}	5	5500	54^{c}	0	380	50.1	<0.001
Depth (m)	0.7^{c}	0.1	2.3	0.1^{a}	0.0	0.2	2.3^{d}	0.3	4.5	0.6^{b}	0.1	2.2	64.1	<0.001
T (^{o}C)	25.4^{b}	18.8	27.4	28.0^{bc}	19.7	29.8	22.9^{a}	21.6	27.1	26.5^{c}	19.4	33.3	20.5	<0.001
pH	7.2^{a}	5.6	8.2	7.4^{ab}	6.7	7.9	7.8^{b}	6.7	8.4	7.7^{b}	6.5	9.0	25.2	<0.001
DO (mg l^{-1})	8.9^{a}	3.6	14.1	15.5^{b}	9.6	17.0	12.9^{b}	11.1	16.1	14.4^{b}	6.7	20.6	67.7	<0.001
RP (mV)	36^{a}	-67	149	319^{c}	289	365	137^{b}	-48	184	90^{b}	-15	279	42.9	<0.001
Cond. (µS cm^{-1})	847^{c}	760	914	832^{abc}	784	858	841^{b}	806	868	814^{a}	634	864	25.2	<0.001
Clay (%)	0	0	0	0	0	0	0	0	50	0	0	0	2.8	0.429
Silt (%)	100^{d}	20	100	0^{a}	0	0	100^{c}	0	100	10^{b}	0	70	96.9	<0.001
Sand (%)	0^{a}	0	60	0^{a}	0	0	0^{a}	0	0	90^{b}	30	100	114	<0.001
Moll. (%)	0^{a}	0	80	0^{a}	0	0	0^{b}	0	60	0^{a}	0	40	12.4	0.006
Rock (%)	0^{a}	0	0	100^{b}	100	100	0^{a}	0	10	0^{a}	0	20	103.4	<0.001
Root (classes 0-5)	0^{a}	0	3	0^{ab}	0	0	0^{d}	0	5	0^{b}	0	5	12.6	0.006
Algae (%)	0^{a}	0	80	50^{b}	30	100	0^{a}	0	0	0^{a}	0	100	45.8	<0.001
EMC (%)	8^{c}	0	100	0^{ab}	0	0	0^{a}	0	30	0^{bc}	0	80	21.9	<0.001
SMC (%)	0^{a}	0	100	0^{a}	0	0	0^{a}	0	30	0^{a}	0	90	8	0.046
FMC (%)	0	0	80	0	0	0	0	0	0	0	0	30	5	0.175

TMC (%)	55^{c}	0	100	0^{a0}	0	0	0^{a0}	0	60	30^{b}	0	95	46,4	<0.001
Macarea (m^2)	0	0	2000	0	0	0	0	0	500	0	0	5000	10.4	0.016
Chl-a (µg g sediment dwt^{-1})	51^{b}	9	1195	427^{c}	99	1078	17^{a}	1	744	17^{a}	2	104	47.9	<0.001
LOI550 (%)	16^{c}	4	81	19^{c}	8	45	8^{b}	5	27	1^{a}	1	26	88.1	<0.001
FOM (classes 0-5)	0^{c}	0	5	0^{ab}	0	0	0^{b}	0	1	0^{a}	0	1	24.9	<0.001
COM (classes 0-5)	0^{b}	0	5	0^{a}	0	0	0^{a}	0	2	0^{a}	0	2	23.1	<0.001
Leaves (classes 0-5)	2^{b}	0	5	0^{a}	0	0	0^{a}	0	2	0^{a}	0	5	32.9	<0.001

Table 3 Indicator values (IV) of chironomid taxa and their statistical tests (based on 9999 permutations of data) for the four site groups established by k-means clustering from constrained canonical correspondence analysis site scores based on spatial and environmental variables versus relative chironomid abundance data in Lake Balaton, Hungary. Group 1: northern littoral sites and boat harbours with soft sediment and macrophytes; group 2: ripraps; group 3: offshore and northern littoral sites with soft sediment and without macrophytes; and group 4: southern littoral sites with sandy sediment (for a more detailed description of environmental conditions see Table 2).

	Taxa	IV	t	Rank	P
Group 1	*Cladopelma virescens*	62.1	6.09	9	P<0.05
	Chironomus balatonicus	58.8	6.19	4	P<0.05
	Tanypus kraatzi	56.6	8.21	3	P<0.05
	Chironomus dorsalis	44.6	3.42	126	P<0.05
	Paratanytarsus sp.	33.4	3.83	103	P<0.05
	Parachironomus varus	31.4	4.85	40	P<0.05
	Tanytarsus sp.	30.5	3.29	152	P<0.05
	Cladopelma viridulum	21.1	2.27	395	P<0.05
	Guttipelopia guttipennis	21.1	3.58	127	P<0.05
	Dicrotendipes lobiger	18.4	3.06	177	P<0.05
Group 2	*Cricotopus reversus*	86.2	13.46	1	P<0.05
	Cricotopus sylvestris gr.	85.5	9.72	1	P<0.05
	Orthocladius oblidens	59.4	10.33	1	P<0.05
Group 3	*Procladius choreus*	68.8	8.71	1	P<0.05
	Microchironomus tener	62.7	7.13	4	P<0.05
	Tanypus punctipennis	38.4	4.00	82	P<0.05
Group 4	*Cladotanytarsus mancus* gr.	72.0	6.07	4	P<0.05
	Cryptochironomus defectus	42.8	3.84	66	P<0.05
	Stictochironomus sp.	38.1	4.85	41	P<0.05

t = the result of a t-test computing the weighted distance between randomized IV values and the observed value; Rank = the rank of the observed IV value among the decreasing ordered randomized value distribution (9999 permutations; as the observed value is always added to the randomized set, the minimum is 1).

Figure captions

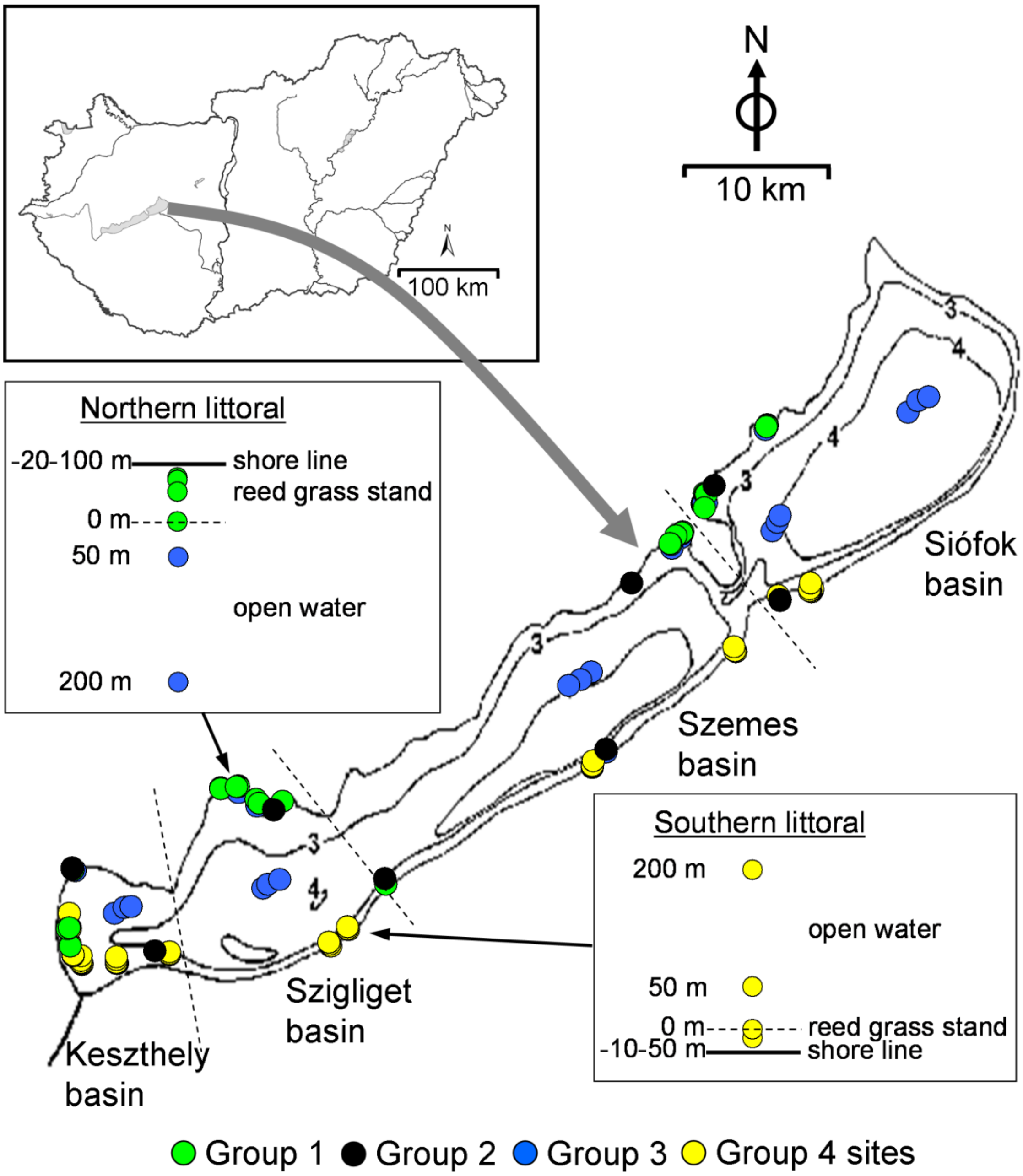

Fig. 1 Distribution of sampling sites in Lake Balaton, Hungary. Sampling sites clustered to four groups according to the *k*-means method based on their full model canonical correspondence analysis scores are differentiated by colouring: 1) northern littoral sites and boat harbours with soft sediment and macrophytes; 2) ripraps; 3) offshore and northern littoral sites with soft sediment and without macrophytes; and 4) southern littoral sites with sandy sediment. The small map of Hungary in the upper left corner indicates the location of Lake Balaton.

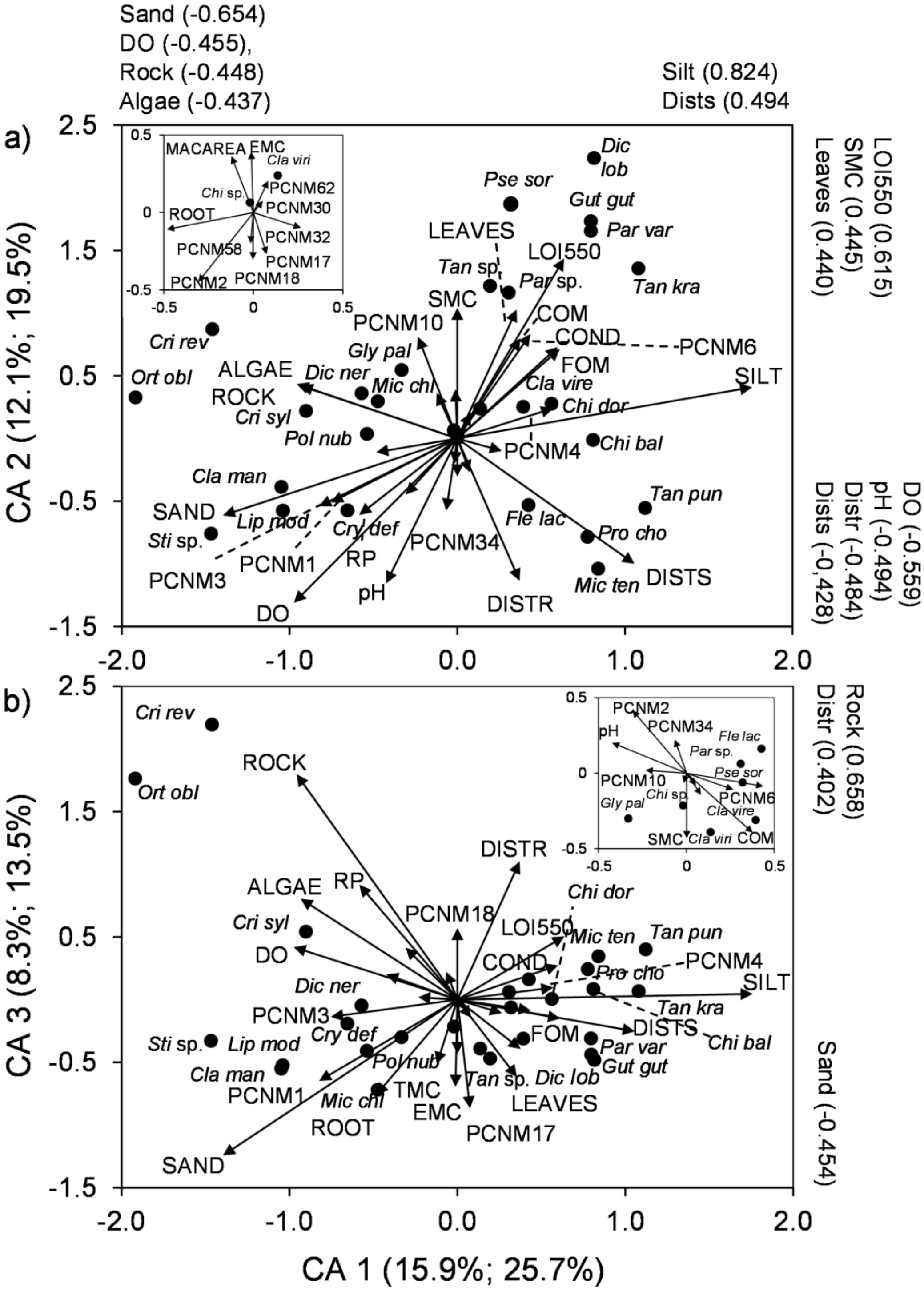

Fig. 2 Canonical correspondence analysis plot along the first and second (a) and first and third (b) canonical axes (CA) describing the relationship between the abundance data of chironomid taxa and forward selected (at $P < 0.05$) spatial and local environmental variables in Lake Balaton, Hungary. Percentage variances represented by axes are indicated in brackets (of taxa data; of taxa-explanatory variables relation) after the axis name. Scale factor for biplotting was 2.6. Explanatory variables with highest correlation (*r* values are given in

brackets) by axes are indicated. Chironomid taxa and explanatory variables with scores close to the centre of the graph are clarified on the small graph in the upper left and right corners. Explanatory variable and taxa names abbreviations are explained in Appendixes A and B, respectively.

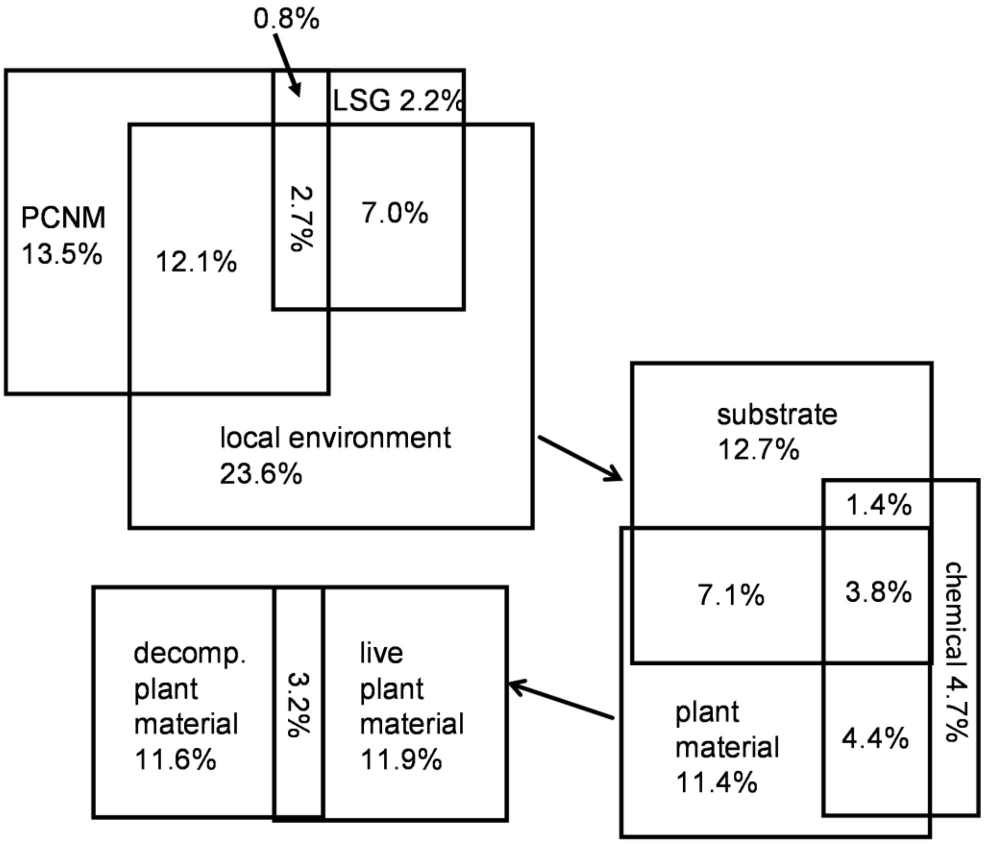

Fig. 3 Result of the variation partitioning of the influence of spatial and local environmental factors on the abundance of chironomid taxa in Lake Balaton, Hungary. The area of each rectangular cell is proportional to the variance accounted for by that component. The total explained variance proportion was 61.9%. The list of significant individual spatial and local environmental variables and their grouping is presented in Appendix A. PCNM = spatial variables derived from principal coordinate analysis of neighbouring matrix; LSG = lake-scale geographical variables; decomp. plant material = decomposing plant material.

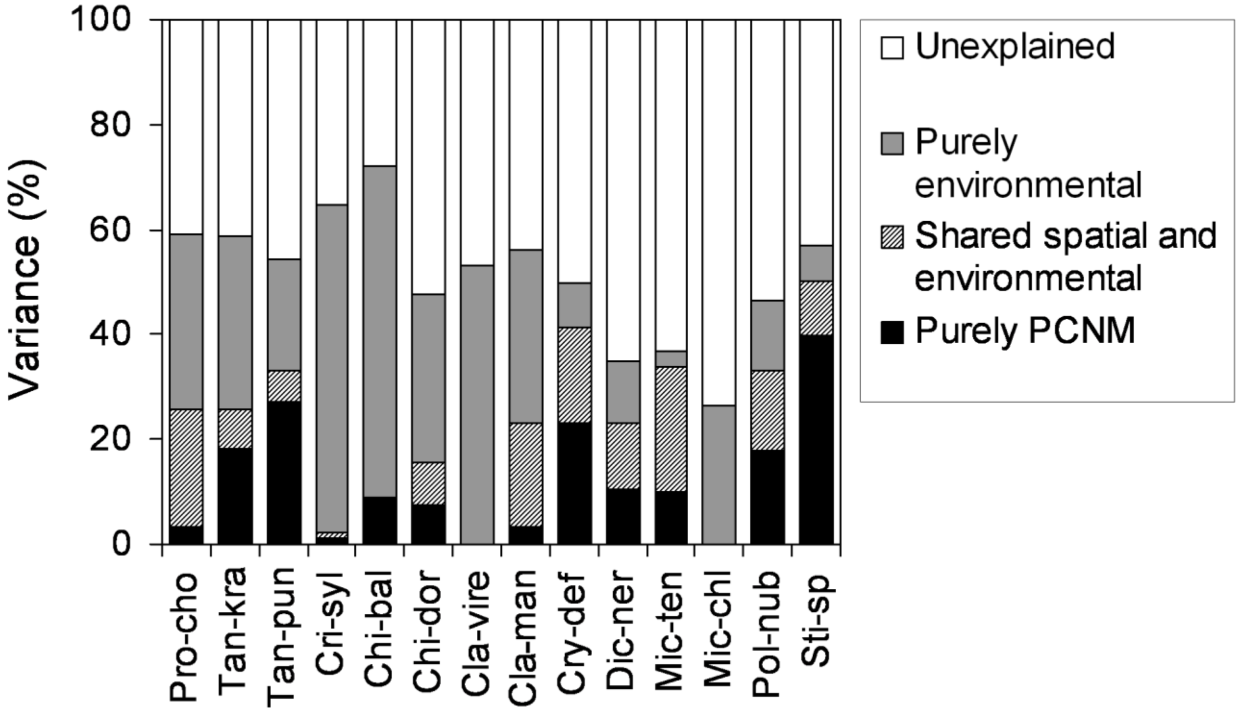

Fig. 4 Result of the variation partitioning showing the relative influence of spatial and local environmental factors on the abundance of individual chironomid taxa in Lake Balaton, Hungary. The effect of lake-scale geographical (LSG) variables is included in shared spatial and environmental variance proportion (see discussion). Taxa names abbreviations are explained in Appendix B. PCNM = spatial variables derived from principal coordinate analysis of neighbouring matrix.

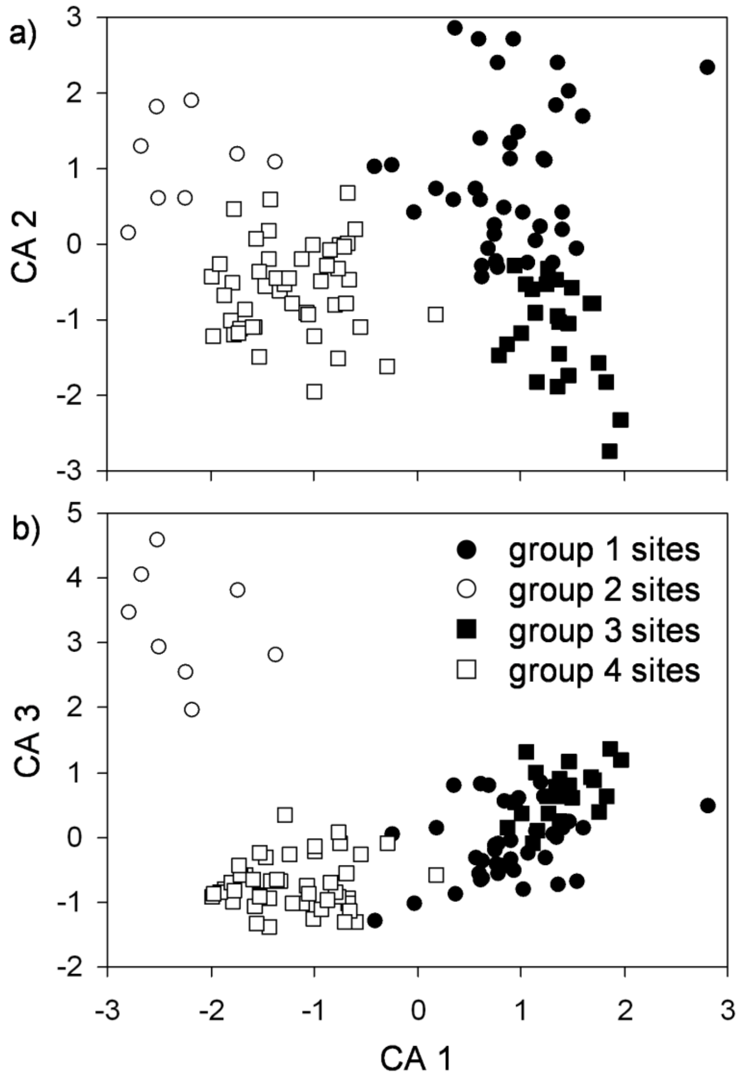

Fig. 5 Canonical correspondence analysis plot of sampling sites along the first and second (a) and first and third (b) canonical axes (CA) describing the relationship between the abundance data of chironomid taxa and forward selected (at $P < 0.05$) spatial and local environmental variables in Lake Balaton, Hungary. Sampling sites were clustered to four groups by *k*-means method as follows: 1) northern littoral sites and boat harbours with soft sediment and macrophytes; 2) ripraps; 3) offshore and northern littoral sites with soft sediment and without macrophytes; and 4) southern littoral sites with sandy sediment. Environmental characteristics and indicator taxa of the site groups are presented in Table 2 and 3, respectively.

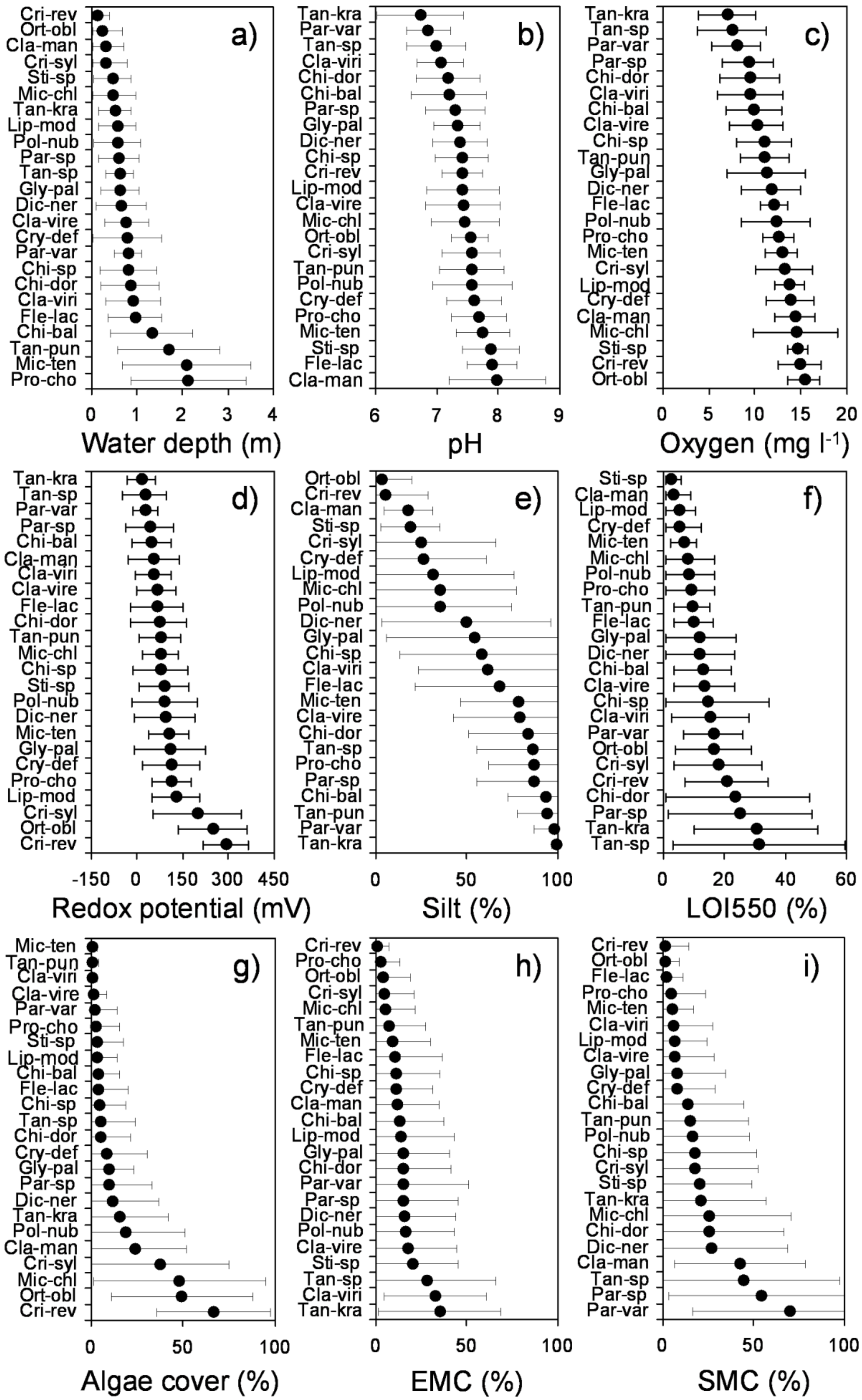
Cri-rev
Ort-obl
Cla-man
Cri-syl
Sti-sp
Mic-chl
Tan-kra
Lip-mod
Pol-nub
Par-sp
Tan-sp
Gly-pal
Dic-ner
Cla-vire
Cry-def
Par-var
Chi-sp
Chi-dor
Cla-viri
Fle-lac
Chi-bal
Tan-pun
Mic-ten
Pro-cho
a)
0 1 2 3 4
Water depth (m)
Tan-kra
Par-var
Tan-sp
Cla-viri
Chi-dor
Chi-bal
Par-sp
Gly-pal
Dic-ner
Chi-sp
Cri-rev
Lip-mod
Cla-vire
Mic-chl
Ort-obl
Cri-syl
Tan-pun
Pol-nub
Cry-def
Pro-cho
Mic-ten
Sti-sp
Fle-lac
Cla-man
b)
6 7 8 9
pH
Tan-kra
Tan-sp
Par-var
Par-sp
Chi-dor
Cla-viri
Chi-bal
Cla-vire
Chi-sp
Tan-pun
Gly-pal
Dic-ner
Fle-lac
Pol-nub
Pro-cho
Mic-ten
Cri-syl
Lip-mod
Cry-def
Cla-man
Mic-chl
Sti-sp
Cri-rev
Ort-obl
c)
0 5 10 15 20
Oxygen (mg l-1)
Tan-kra
Tan-sp
Par-var
Par-sp
Chi-bal
Cla-man
Cla-viri
Cla-vire
Fle-lac
Chi-dor
Tan-pun
Mic-chl
Chi-sp
Sti-sp
Pol-nub
Dic-ner
Mic-ten
Gly-pal
Cry-def
Pro-cho
Lip-mod
Cri-syl
Ort-obl
Cri-rev
d)
-150 0 150 300 450
Redox potential (mV)
Ort-obl
Cri-rev
Cla-man
Sti-sp
Cri-syl
Cry-def
Lip-mod
Mic-chl
Pol-nub
Dic-ner
Gly-pal
Chi-sp
Cla-viri
Fle-lac
Mic-ten
Cla-vire
Chi-dor
Tan-sp
Pro-cho
Par-sp
Chi-bal
Tan-pun
Par-var
Tan-kra
e)
0 50 100
Silt (%)
Sti-sp
Cla-man
Lip-mod
Cry-def
Mic-ten
Mic-chl
Pol-nub
Pro-cho
Tan-pun
Fle-lac
Gly-pal
Dic-ner
Chi-bal
Cla-vire
Chi-sp
Cla-viri
Par-var
Ort-obl
Cri-syl
Cri-rev
Chi-dor
Par-sp
Tan-kra
Tan-sp
f)
0 20 40 60
LOI550 (%)
Mic-ten
Tan-pun
Cla-viri
Cla-vire
Par-var
Pro-cho
Sti-sp
Lip-mod
Chi-bal
Fle-lac
Chi-sp
Tan-sp
Chi-dor
Cry-def
Gly-pal
Par-sp
Dic-ner
Tan-kra
Pol-nub
Cla-man
Cri-syl
Mic-chl
Ort-obl
Cri-rev
g)
0 50 100
Algae cover (%)
Cri-rev
Pro-cho
Ort-obl
Cri-syl
Mic-chl
Tan-pun
Mic-ten
Fle-lac
Chi-sp
Cry-def
Cla-man
Chi-bal
Lip-mod
Gly-pal
Chi-dor
Par-var
Par-sp
Dic-ner
Pol-nub
Cla-vire
Sti-sp
Tan-sp
Cla-viri
Tan-kra
h)
0 50 100
EMC (%)
Cri-rev
Ort-obl
Fle-lac
Pro-cho
Mic-ten
Cla-viri
Lip-mod
Cla-vire
Gly-pal
Cry-def
Chi-bal
Tan-pun
Pol-nub
Chi-sp
Cri-syl
Sti-sp
Tan-kra
Mic-chl
Chi-dor
Dic-ner
Cla-man
Tan-sp
Par-sp
Par-var
i)
0 50 100
SMC (%)

Fig. 6 Optima and tolerances of individual chironomid taxa regarding some influential environmental factors (a: water depth; b: pH; c: dissolved oxygen in the water; d: redox potential of the sediment surface; e: percent silt in the sediment; f: loss-on-ignition of the sediment – LOI550; g: algae coverage; h: percent emerged macrophyte coverage – EMC; i: percent submerged macrophyte coverage - SMC) in Lake Balaton, Hungary. Taxa names abbreviations are explained in Appendix B. Note that estimated tolerance ranges were cut at the edge of the studied ranges of particular gradients.