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1 Effects of habitat types and within lake environmental gradients on the diversity of
2 chironomid assemblages

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Abstract

Understanding the distribution of biotic diversity across various spatial scales and environmental gradients is important from fundamental, practical and conservation biological aspects. We applied a hierarchical diversity partitioning framework to quantify the variability of sample level α - and β_1 -diversity, and environment related β_2 -diversity of benthic chironomid assemblages within and among *a priori* defined habitat types, and along the gradients of individual environmental factors in a large and shallow lake (Lake Balaton, Hungary). Taxon richness (both additive and multiplicative) and Shannon index based diversity approaches yielded highly concordant results. The α -diversity was much lower and β_1 -diversity higher than predicted by null model and both measures varied substantially among habitat types and along most individual environmental gradients. The β_2 -diversity indicated a marked variability of taxon (identified at species to genus level) pool among habitat types and higher than predicted taxon turnover along all examined environmental gradients. Moreover, the observed β_2 -diversity varied greatly among individual environmental gradients. The difference between the expected and observed β_2 -diversity values suggests that taxon turnover was most influential (in decreasing order) along the algae coverage gradient, the lake bed substratum gradient and the macrophyte coverage gradient among others. We argue that within-lake environmental heterogeneity and its effect on the taxon richness should receive more attention in biodiversity assessment and conservation. Management could benefit from the identification of within lake gradients along which taxonomic turnover maximizes.

Keywords: beta diversity, diversity partitioning, species accumulation, species richness, species turnover, within lake environmental gradient.

Introduction

Exploring patterns of biodiversity is fundamental to understand many ecological processes (Ricklefs, 2004). For instance, the framework of diversity partitioning which quantifies local (α), regional (γ) and turnover (beta) components of diversity has greatly contributed to our understanding of assembly processes in metacommunities at a variety of spatial and temporal scales (Gering et al., 2003; Crist and Veech, 2006; Anderson et al., 2011; Kraft et al., 2011). Diversity components (i.e. α , β_1 , ..., β_n) have important conservation biological implications as well as they provide fundamental information on how to allocate areas and habitats to be involved in an effective environmental management program (Gering et al., 2003; Thrush et al., 2010).

Conceptual models and empirical studies concerning biodiversity distributions of lakes focused primarily on broad scale, geographical and temporal processes (Stendera and Johnson, 2005; Ptacnik et al., 2010; Suurkuukka et al., 2012; Angeler and Drakare, 2013; Hamerlík et al., 2014). Although fine scale, microhabitat level distribution of species is widely studied in lentic organisms (e.g. Brodersen, 1995; Čerba et al., 2010; Luoto, 2012; Specziár et al., 2013; Árvai et al., 2015), the role of within lake habitats in shaping diversity patterns and their contribution to total (lake level or regional) diversity is less known (but see Flach et al., 2012; Tóth et al., 2013). Suurkuukka et al. (2012) revealed that unspecified within lake patterns included about 50% of the overall regional littoral macroinvertebrate diversity in boreal lakes. Likewise, it is largely unknown how biodiversity is distributed across specific within lake environmental gradients and/or habitat types. Partitioning within lake β -diversity for stochastic or unspecified among sample variability (i.e. β_1) and structured environment related species turnover (i.e. β_2 or higher β levels) components would yield basic information about the influence of within lake environmental heterogeneity on species diversity. By identifying environmental gradients along which the species turnover rate is the highest would facilitate focusing of conservation actions to the most important pieces of environmental heterogeneity.

In this study, we examine the response of local α -diversity and hierarchical β -diversity components expressed as taxon richness (i.e. number of taxa at species or genus level) and Shannon diversity index of benthic chironomid (Diptera, Chironomidae) assemblages to within lake environmental heterogeneity in a large and shallow lake (Lake Balaton, Hungary). Benthic chironomids is a popular model group for freshwater biomonitoring studies (Rosenberg, 1992; Wilson and Ruse, 2005; Milošević et al., 2013). Chironomid larvae have

diverse environmental optima and tolerances and relatively good dispersal ability in their winged terrestrial adult phase (Armitage, 1995). Thus according to metacommunity theory (Leibold et al., 2004; Cottenie, 2005; Beisner et al., 2006) environmental filtering (i.e. species sorting) shapes their fine scale species distribution patterns, while the role of spatial processes (i.e. dispersal limitation) become influential in their assemblage organization only at broad geographical scales (Mykrä et al., 2007; Landeiro et al., 2012; Heino, 2013a, 2013b; but see Árvai et al., 2015). Accordingly, in lakes with high environmental heterogeneity a substantial part in their species turnover could be related directly to habitat types and environmental gradients due to inter-specific separation of species optima and tolerance ranges (Rae, 2004; Puntí et al., 2009; Árvai et al., 2015). Thus not just relative abundance patterns but also species turnover rates can predictably differ among various within lake environmental gradients. To our knowledge, however, there are no studies comparing the role of species turnover along various within lake environmental gradients. Specific aims of the study are to analyse: (1) how sample level α -diversity (i.e. local taxon richness and Shannon diversity index) and among sample β_1 -diversity vary among *a priori* defined characteristic habitat types of the lake; (2) how sample level α -diversity and among sample β_1 -diversity change along the gradient of individual environmental factors (e.g. water depth, substratum type); and (3) to what extent β_2 -diversity among the habitat types and along particular environmental gradients contribute to total chironomid diversity of the lake.

Materials and methods

Study area

Balaton is the largest shallow lake (surface area: 596 km²; mean depth: 3.2 m) in Central Europe, situated at 46° 42' - 47° 04' N, 17° 15' - 18° 10' E and 104.8 m above sea level (Fig. 1). The lake is slightly alkaline (400 mg l⁻¹ of Ca²⁺ and Mg²⁺(HCO₃⁻)₂) with a decreasing trophic gradient (i.e. 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 SW to NE along its longitudinal axis (see also Istvánovics et al., 2007). Based on habitat characteristics, Lake Balaton can be divided into a little variable open water area spreading to >85% of the lake with silt substrate, largely homogeneous physico-chemical features and with no macrovegetation, and to a much heterogeneous littoral zone exhibiting marked environmental gradients along the distance

from shore, water depth, macrophyte coverage, swash exposition (i.e. the northern littoral is much less affected by wind induced waves than the southern littoral) and human impact including the establishment of artificial habitat types as well (measured ranges of environmental gradients are shown in Appendix A). Today only about 47% of the lake shore is covered by emergent macrovegetation (dominant species is reed grass *Phragmites australis*), whereas submerged macrophytes form loose and sporadic stands in the littoral zone. Significant sections (>50%) of the shore have been protected with concrete or rocks (artificial habitat covered by rocks hereafter referred to as riprap) which are generally covered by filamentous algae (mainly *Cladophora* sp.) up to 0.5 m water depth. Several large, and many small boat harbours were built along the lake for commercial and recreational purposes.

Chironomid sampling and identification

Benthic chironomid assemblages were sampled at 128 sites between 26 June and 13 July 2012 (Fig. 1). The sites were distributed across the whole lake and covered all ranges of habitat and environmental gradients (see below). Three merged Ekman grab sediment samples were taken per site (total sampled area per site: 0.036 m²), 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 corresponding to area of Ekman grab samples into plastic containers. Chironomids were separated from sediment samples alive by sugar flotation method (Anderson, 1959), and euthanized and preserved in 70% ethanol for later identification. Chironomids were digested in KOH (potassium hydroxide) to eliminate non-chitinous tissues and slide-mounted in Euparal®. Identification was performed to species or the lowest possible taxonomic level (species group to genus; for more details see Árvai et al., 2015).

Habitat assessment and environmental factors

Parallel to chironomid sampling, we measured a series of environmental factors (Appendix A) that have been found influential on the distribution of chironomids (e.g. Real et al., 2000; Rae, 2004; Free et al., 2009; Puntí et al., 2009; Tóth et al., 2012). To cover all environmental gradients in the lake, first, the position of each sampling site was characterized with six lake-scale geographical 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 shore, emergent macrophyte, submerged and floating leaved macrophytes and open water. Then, we recorded 16 local environmental factors. We measured water depth, 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 (%) were made within a circle of 3 m diameter around the origin of chironomid samples and the area of the submerged and floating leaved macrophyte stands were recorded by GPS and calculated by MapSource version 6.16.3. software (Garmin Ltd., Olathe, US, www.garmin.com). The substratum of the lake bed was inspected for percentage composition of clay (grain size ≤ 0.002 mm), silt (0.002-0.06 mm), sand (0.06-2 mm), rock (> 200 mm) and mollusc shell (5-25 mm; mainly *Dreissena polymorpha* (Pallas, 1771) and *D. bugensis* (Andrusov, 1897), and then classified into six categories: 1) silt $\geq 80\%$; 2) both silt and mollusc shells $> 20\%$; 3) both silt and sand $> 20\%$; 4) both sand and mollusc shells $> 20\%$; 5) sand $\geq 80\%$; and 6) rock = 100% (i.e. ripraps). The sediment was examined for occurrence of pure reed grass root (characteristic in some degrading reed grass stands) and fine and coarse decomposing organic matter particles and reed grass leaves and rated on a six category scale (0-5). Relative organic matter content was assessed from dry (at 50 °C for 72 hours) 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).

Statistical analysis

We ran two parallel analyses to explore the distribution of chironomid diversity in the lake. In the first, we examined how biodiversity is distributed within and among eight *a priori* distinguished habitat types. The habitat types were as follows: 1) northern reed grass stand; 2) northern reed-free littoral area; 3) offshore area without macrophyte; 4) southern reed-free littoral area; 5) southern reed grass stand; 6) small boat harbour rounded by reed grass; 7) large commercial harbour sheltered by riprap; and 8) riprap (lake side, exposed to swash). Then, samples were also classified according to their positions along the gradient of each individual environmental factor. These environmental factors were either *ab ovo* recorded at six category scales (except lake basin with four and location along the north-to-south transect of the lake with three categories) or divided to six intervals later in the data analyses. Environmental gradients measured on percentage scales were directly divided to six equal intervals. The remaining continuous factors were logarithmic transformed first and divided to

six equal intervals afterwards. Rationale of the logarithmic transformation was to decrease the weight of underrepresented extreme environmental ranges and to obtain a more balanced distribution of samples across gradient levels.

Since observed number of taxa is a function of sampling effort, thus taxon richness cannot be directly compared between samples differing in sampling effort in any respect (Gotelli and Colwell, 2001). Therefore, we examined the relationship between the sampling effort and observed taxon richness by sample- and individual based rarefaction analyses (10,000 permutations) performed with EcoSim 7.72 software (Gotelli and Entsminger 2011). Rarefied taxon richness enables to assess the adequacy of sampling effort in term of taxa detection (i.e. species accumulation curve reaches an asymptote when all taxa in the system are captured) and comparing taxon richness (γ -diversity) between groups of samples (i.e. habitat types) with unequal sample sizes (Gotelli and Colwell, 2001).

For the purpose of this study, we defined α -diversity as the taxon richness and Shannon diversity of individual sampling sites (i.e. three merged Ekman grab samples per site). Shannon diversity index (H) emphasises abundance ratios of taxa (dominant and rare taxa are weighted equally) and was calculated as $-\sum p_i (\ln p_i)$, where p_i is the proportional abundance of taxon i . We tested differences of average α -diversity among sample groups (i.e. habitat types and levels of environmental gradients) by analysis of variance (ANOVA) supplemented with Tukey HSD post hoc test in case of significant factor effect. We also investigated the pattern of α -diversity along each continuous environmental factor by using series of regression tools (results not shown for brevity), however, the only significant relationship we found was the slight decreasing tendency of taxon richness with increasing water depth and related environmental gradients (i.e. increasing distances from shore, from emergent macrophyte and from submerged and floating leaved macrophytes).

Relative contribution of local α - and two β -diversity components to total chironomid diversity (γ -diversity) was investigated based on hierarchical diversity partitioning framework, comparing observed patterns with null model distributions (Crist et al., 2003; Gering et al., 2003). We considered both additive and multiplicative approaches of taxon richness organization (Lande, 1996; Veech et al., 2002) dividing total observed diversity into the following components: $\gamma = \alpha + \beta_1 + \beta_2$ and $\gamma = \alpha \times \beta_1 \times \beta_2$, respectively, where γ is the total number of taxa identified in the system (40 taxa in this case), α is the mean number of taxa at individual sampling sites, β_1 corresponds to the variation in taxon composition among sampling sites of a particular habitat type and level of a given environmental gradient, and β_2

corresponds to variation of taxon composition among habitat types and levels of individual environmental gradients. Note that α is the same in the additive and multiplicative models, whereas the value and unit of β -diversity differs between the two models (β is unitless in the multiplicative model). While the Shannon diversity index naturally partitions into independent and additive α and β components (Jost, 2007). Observed values of α - and β -diversity components were tested against null model distributions obtained from individual based unrestricted randomizations (10,000 randomizations) in the software package PARTITION 3 (Veech and Crist, 2009). Specifically, it was tested whether the observed values of α - and particular β -diversity components significantly differed from chance. A more detailed description of the null model generation and the randomization procedure is provided by Crist et al. (2003). To evaluate the relative importance of different environmental gradients in total (γ) chironomid diversity, individual environmental gradients were ranked according to the difference ($\beta_2 \text{ observed} - \beta_2 \text{ expected}$) and ratio ($\beta_2 \text{ observed} * \beta_2 \text{ expected}^{-1}$) between the observed and expected β_2 values in additive (i.e. species richness and Shannon index) and multiplicative (i.e. species richness) diversity partitioning approaches, respectively.

Results

Chironomid assemblages and γ -diversity

Sampling of diverse array of microhabitats in Lake Balaton yielded a total of 13,804 individuals and 40 taxa (identified at species, species group and genus levels; γ -diversity of taxon richness) of chironomids belonging to three subfamilies: Tanypodinae (7 taxa), Orthocladiinae (4 taxa) and Chironominae (29 taxa). Total Shannon (γ -) diversity proved to be 2.66. Detailed list of captured taxa, their numbers of individuals and habitat uses are presented in Árvai et al. (2015). Briefly, the chironomid fauna of Lake Balaton is comprised of widely distributed taxa being characteristic for shallow, medium to high productivity, temperate standing waters. Assemblage composition varied markedly among habitat types and across environmental gradients and could be classified into four major type groups: (1) *Cladopelma virescens* (Meigen, 1818), *Chironomus balatonicus* Dévai, Wüelker & Scholl, 1983, *Tanypus kraatzi* (Kieffer, 1918), *Chironomus dorsalis* Meigen, 1818 and *Paratanytarsus* sp. were indicator taxa for the northern littoral sites and both small and large boat harbours with macrovegetation; (2) *Cricotopus reversus* Hirvenoja, 1973, *Cricotopus*

sylvestris gr. and *Orthocladius oblidens* (Walker, 1856) were characteristic at ripraps; (3) *Procladius choreus* (Meigen, 1804), *Microchironomus tener* (Kieffer, 1918) and *Tanypus punctipennis* Meigen, 1818 dominated in the offshore macrophyte-free areas; and (4) *Cladotanytarsus mancus* gr., *Cryptochironomus defectus* (Kieffer, 1913) and *Stictochironomus* sp. occurred mainly in the southern, sandy littoral.

The four singleton (*Monopelopia tenuicalcar* (Kieffer, 1918), *Endochironomus tendens* (Fabricius, 1775), *Parachironomus vitiosus* (Goetghebuer, 1921) and *Polypedilum sordens* (van der Wulp, 1875) and one doubleton taxa (*Zavreliella marmorata* (van der Wulp, 1859)) indicated the importance of rare species in the total species pool. In addition, rarefaction curves did not reach evident asymptotes, indicating that further sampling would probably yield more taxa (Fig. 2).

Sample based rarefaction curves revealed that taxon richness varied among habitat types. Taxon richness was the lowest in the offshore area with five taxa and highest in small boat harbours situated in reed grass stands with 34 taxa (Fig. 2a). The rarefaction curves of other habitat types did not separate markedly (i.e. their 95% CI ranges overlapped; note that for clarity CIs are not shown on Fig. 2) from each other. Individual based rarefaction curves supported the separation of the species poor offshore area, while the outstanding diversity of small boat harbours was not justified (Fig. 2b).

Local (α -) diversity

At the lake level, observed α -diversity of taxon richness (mean: 8.2 taxa; Fig. 3) was less than half of the predicted value (16.8 taxa) suggesting that there is a substantial non-random pattern in the distribution of chironomid taxa across sampling sites. The mean number of taxa per sampling site was significantly lower in the offshore area (3.5 ± 0.5 ; mean \pm SD) than in other habitat types, which showed similar values (7.4–11.0; means; Fig 4a). Mean taxon richness of sites also varied significantly among gradient levels in 13 of the 22 investigated environmental factors (Table 1), but no general trends were found.

Shannon α -diversity (mean: 1.38; Fig. 3) was also significantly less than the predicted value (2.34), and its patterns showed good agreement with patterns of taxon richness across habitat types (Fig. 4) and levels of environmental gradients.

Among sites variability (β_1 -diversity)

Both additive and multiplicative diversity partitioning models revealed that among sample β_1 -diversity of taxa richness was larger than expected by chance alone across habitat types and along most individual environmental gradients (Fig. 3). In addition, β_1 -diversity was also larger than expected within each habitat type (Fig. 4). Although β_1 -diversity using the Shannon index also proved to be higher than expected by chance, the result suggested a bit different picture on the relative importance of β_1 -diversity for some habitat types and particular environmental gradients than that found for taxon richness.

Among habitat types and along environmental gradients variability (β_2 -diversity)

Based on the additive taxon richness partitioning model, β_2 -diversity was about 7.6 taxa larger than predicted across habitats indicating a marked difference in species pools among habitat types (Fig. 3a). Similarly, significant taxon turnover was revealed along all examined environmental gradients with β_2 -diversity values 4.2 to 10.5 taxa larger than expected. Difference between the expected and observed β_2 -diversity values indicated that taxon turnover was most influential (in decreasing order) along algae coverage, lake bed substratum, submerged and floating leaved macrophytes coverage, presence of reed grass root, distances from emergent macrophyte, from submerged and floating leaved macrophytes and from shore, water depth and pH gradients. Multiplicative taxon richness partitioning fully supported the above results, however, the rank of individual gradients was slightly different in term of divergence (expressed as $\beta_{2\text{observed}} * \beta_{2\text{expected}}^{-1}$) of observed from the expected β_2 -diversity (Fig. 3b). Although β_2 -diversity using the Shannon index also proved to be higher than expected by chance the result differed somewhat from the above picture (Fig. 3c). In general, taxon richness based approach related larger part of the total diversity to β levels, while diversity captured by the Shannon index was more concentrated at α level and with relatively low amount of variability related to β_2 level.

Discussion

The present study is the first to compare distribution of within lake chironomid diversity across *a priori* defined habitat types and along various individual environmental gradients. Based on an extensive sampling representing the environmental heterogeneity of Lake Balaton, we found low local taxon richness (sample level α -diversity) indicating that most of

the captured total diversity is due to β -diversity components. Sample level α -diversity accounted for only 20.5% of within lake diversity. This value is very similar to sample level macroinvertebrate α -diversity of 23% observed across the littorals of three Finnish lakes (Suurkuukka et al., 2012), but it is much higher compared to 5–8% values obtained by Stendera and Johnson (2005) for littoral macroinvertebrates across 677 Swedish lakes. However, both latter studies were based on kick-samples which cover larger effective sampling area and are with different selectivity than our Ekman grab samples. It is well known that patterns of α and β -diversities are scale dependent and therefore the definition of “local” diversity affects diversity partitioning (Matias et al., 2010; Beck et al., 2012) and the relative importance of α and hierarchical β -diversity components (Schmera and Erős, 2008). Nevertheless, lake sediment surface covered by Ekman grab can be considered as a standard sampling unit in benthic macroinvertebrate studies, and thus, generally serves as the basis for biodiversity assessment (sample level α -diversity; e.g. Free et al., 2009; Jyväsjärvi et al., 2012; Molozzi et al., 2013). By using a sampling methodology comparable to ours, Molozzi et al. (2013) found that most of macroinvertebrate diversity was related to sampling unit (43.7%; α -diversity) and among sampling unit variability (47.2%; β_1 -diversity), while only little taxon turnover occurred among regions and reservoirs in Brazil. Surprisingly, we did not find any characteristic trend in sample level α -diversity along within lake environmental gradients, except that considerably less taxa occurred in the offshore samples than in littoral sites. This result may indicate that at the lake scale different structuring processes are likely to dominate than at broad geographical scales where much longer environmental gradients act including climatic gradients (e.g. Nyman et al., 2005; Kraft et al., 2011). Compared with the results of species richness, Shannon index provided a slightly different picture and revealed the role of taxa relative abundances with giving more weight to sample level diversity.

We divided β -diversity into two components, to β_2 -diversity which is directly related to various attributes of environmental heterogeneity and to β_1 -diversity which represents unexplained among site variability. Both β components were generally larger than expected by chance alone based on either taxon richness or Shannon index. As we expected species richness varied considerably across habitat types and high β_2 -diversity indicated a significant taxon turnover along this scale. Although largest part of Lake Balaton (ca. 85% of the total lake area) is a macrophyte free offshore (open water) area, only 12.5% of the total identified chironomid taxa inhabited this habitat, and as supported by the results of the rarefaction analyses, no further taxa are likely to occur there. In addition, the relatively high ratio of α -diversity (70.6%) within the total species richness indicated that taxa distribute much more

homogeneously within this habitat type than in others. Based on the low representation of species in the offshore habitat, we suggest the better consideration of littoral habitats in monitoring and bioassessment. The outstanding role of the littoral habitat heterogeneity in the biotic diversity is also strongly supported by other macroinvertebrate groups (Muskó, 1992; Muskó et al., 2007; 2010) and fish (Specziár et al., 2013) in Lake Balaton.

Unexpectedly, we observed the highest taxon richness in small boat harbours, a modified habitat type with very small spatial extent relative to total lake area. Most of the taxa identified in the lake were present here and rarefaction analyses suggested that further taxa are likely to present. These findings seem to contradict with general knowledge on the deteriorating effect of human induced habitat alteration on biological diversity (Ehrlich, 1988; Moyle and Leidy, 1992; Dudgeon et al., 2006). The high species richness of this habitat type may be explained by its high environmental heterogeneity (i.e. diverse submerged macrophyte flora) and food richness (i.e. decomposing plant material and attached bacterial flora). It is likely that small scale habitat alterations can actually increase overall environmental heterogeneity in unstructured large lakes by establishing new habitat types. For instance, boat harbours are sheltered from swash and have high submerged vegetation coverage with very heterogeneous structure and high organic matter concentration, while ripraps provide extremely well oxygenated algae meadows with high swash disturbance. Similar microhabitats were very scarce or absent in pristine Lake Balaton. Artificial habitats (i.e. ripraps and concrete and timber constructions of boat harbours) are also important substrates for several crustacean and mollusc taxa, and thus, had a significant influence on the macroinvertebrate community of Lake Balaton (Muskó et al., 2010). Although species richness is a function of habitat area and structural complexity (Drakare et al., 2006; Thrush et al., 2010; Triantis and Sfenthourakis, 2012; Hamerlík et al., 2014) our results reflect that habitat heterogeneity is a much more influential factor in the within lake diversity of chironomid assemblages than the area of habitat types.

Substantial proportion of the observed β -diversity was related to specific attributes (i.e. local environmental factors) of among sites environmental heterogeneity in Lake Balaton. This finding is congruent with our previous results (Árva et al., 2015), which showed that optima and tolerances of chironomid species separate along some individual environmental gradients, like lake bottom algae coverage, substratum physical attributes (i.e. percentage of silt) and submerged macrophyte coverage. Moreover, Árva et al. (2015) have shown that assemblage composition is related to some environmental gradients, and assemblage structure and environmental conditions suggested substantially different habitat groups for Lake

Balaton. Present results also proved that the observed taxon turnover (i.e. β_2 -diversity) markedly varied among environmental gradients. By scaling our sampling sites along several alternative dimensions (i.e. individual factors) of environmental heterogeneity, we identified few individual environmental gradients (i.e. algae coverage, lake bed substratum, submerged and floating leaved macrophyte coverage and presence of reed grass root on the sediment surface), which explained higher proportion of overall β -diversity than did the *a priori* defined habitat types. This result suggests that the application of gradient based approaches can be useful at fine spatial scales as well, and they may yield more direct information on diversity patterns and the underlying processes than conventional diversity partitioning approaches based on hierarchical spatial units (i.e. lake area) or subjective habitat types.

The highest rates of taxon turnover were found along the algae coverage gradient, the lake bed substratum gradient and the submerged and floating leaved macrophyte coverage gradient. Coverage of algae increases towards decreasing water depth, more compact substratum (i.e. sand and rock) and less decomposed organic matter, and also coincides with higher oxygen concentration in Lake Balaton. The role of algae coverage is well known in the distribution of chironomids (Čerba et al., 2010; Tóth et al., 2013). Increasing algae coverage causes a characteristic shift in assemblage structure towards the dominance of *C. sylvestris* gr. and *C. reversus* in Lake Balaton (Árva et al., 2015). Substratum heterogeneity is an important driver of macroinvertebrate β -diversity (Stoffels et al., 2005; Ligeiro et al., 2010; Hepp et al., 2012; Suurkuukka et al., 2012), and it is well known that benthic chironomid taxa have different substratum preferences (Wolfram 1996; Fesl 2002; Rae 2004; Árva et al., 2015). In Lake Balaton, most chironomid taxa prefer soft, silty substratum and their abundances strongly decrease or they even disappear towards harder substratum such as sand and rock. Sites with sandy bottom clearly separated from other sites by their assemblages dominated by *C. mancus* gr.; *C. defectus* and *Stictochironomus* sp. While, riprap habitats with rock substratum also have individual assemblages characterised by *C. sylvestris* gr., *C. reversus* and *O. oblidens* (Árva et al., 2015). It is known that macrophytes have diverse effect on chironomid assemblages as they influence habitat structure and heterogeneity, physico-chemical properties of the water and the sediment and food conditions (e.g. Ali et al., 2007; Bogut et al., 2007). Submerged and floating leaved macrophyte coverage was most preferred by *Parachironomus varus* (Goetghebuer, 1921) and *Parachironomus* sp., while avoided by e.g. all Tanypodinae species, *C. reversus* and *O. oblidens* (Árva et al., 2015).

Significant proportion of the total diversity was unexplained β_1 -diversity indicating an aggregated species distribution, which is independent on the structuring effect of the habitat

or environmental gradients captured by particular higher β levels. Unlike in relative abundance based approaches (Cushman and McGarigal, 2002; Peres-Neto et al., 2006), we do not have an appropriate statistical tool that enables decomposing overall β -diversity in means of taxonomic richness or Shannon index into multiple parallel components related to series of environmental stressors (only the effect of hierarchical factors can be tested). This is a problem because environmental gradients generally are not independent from each other, and therefore, their effects can overlap. For example, we found that algae coverage tended to increase towards harder lake bed substratum (i.e. sand and rock) and to decrease with increasing water depth. Consequently, (1) β_2 -diversity related to a specific environmental gradient will include both the pure and shared effects of the concerning environmental factor and these two effects are not separable, (2) independent effects of all concurrent environmental factors that are not included in the analysis (i.e. as the factor that specifies β_2 -diversity level) will be displayed as β_1 -diversity. Therefore, in order to understand organization of biotic diversity more completely, we suggest examining the distribution of diversity in alternative hierarchical sampling designs (i.e. spatial scale vs. various direct environmental gradients). Dispersal limitation is another potential mechanism influencing β -diversity especially at broader geographical scales (Palmer et al., 1996; Thrush et al., 2010; Logue et al., 2011). The relevance of dispersal limitation was also indicated in Lake Balaton using direct gradient analysis based on relative abundance data (Árva et al., 2015). However, regarding true diversity measures (i.e. species richness and Shannon index), to our knowledge, there is no appropriate statistical tool that could enable dissecting the effect of dispersal limitation from overall β -diversity. Consequently, the independent effect of dispersal limitation in site-to-site species turnover will also be included in β_1 -diversity.

From a conservation biological point of view, direct gradient based diversity partitioning could be beneficial and supplement the traditional approach based on pure spatial hierarchy of samples (e.g. sample, lake-area, lake, geographical region; Gering et al., 2003; Stendera and Johnson, 2005) especially at finer spatial scales like for example within a lake. Assemblage level conservation needs assessing which habitats support most species (α -diversity) and which dimensions of environmental heterogeneity support the highest species turnover (i.e. β -diversity). While at broad geographical scales taxon turnover is much dependent on habitat connectivity and dispersal processes, at finer spatial scale the role of environmental filtering becomes more dominant. Our results suggest that for maintaining diverse macroinvertebrate assemblages care should be taken to maintain a diversity of natural environmental gradients,

besides protecting the most natural habitat types, because environmental gradients play a critical role in shaping taxon turnover.

In conclusion, our analyses prove the high importance of non-random β -diversity components which are related to various within lake environmental gradients in shaping the total taxon richness and Shannon diversity of chironomids. We argue that within-lake heterogeneity and its effect on true diversity measures should receive more attention in biodiversity assessment even in studies analysing diversity patterns and underlying mechanisms at broad spatial scales (e.g. ecoregion and biographical region). The comprehensive information on how biotic diversity is structured across multiple scales and how taxon turnover rate varies among different within-lake environmental gradients could be used to identify the appropriate area for conservation.

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References

- Ali, M.M., Mageed, A.A., Heikal, M., 2007. Importance of aquatic macrophyte for invertebrate diversity in large subtropical reservoir. *Limnologia* 37, 155–169.
- Anderson, R.O., 1959. A modified flotation technique for sorting bottom fauna samples. *Limnol. Oceanogr.* 4, 223–225.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Cornita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28.
- Angeler, D.G., Drakare, S., 2013. Tracing alpha, beta, and gamma diversity responses to environmental change in boreal lakes. *Oecologia* 172, 1191–1202.

- 473 Armitage, P.D., 1995. Behaviour and ecology of adults, in: Armitage, P.D., Cranston, P.S.,
474 Pinder, L.C.V. (Eds.), *The Chironomidae: Biology and ecology of non-biting midges*.
475 Chapman and Hall, London, pp. 194–224.
- 476 Árvai, D., Tóth, M., Horváth, H., Nagy, S.A., Specziár, A., 2015. The relative importance of
477 spatial and environmental processes in distribution of benthic chironomid larvae within
478 a large and shallow lake. *Hydrobiologia* 742, 249–266.
- 479 Beck, J., Holloway, J.D., Vun Khen, C., Kitching, I.J., 2012. Diversity partitioning confirms
480 the importance of beta components in tropical rainforest Lepidoptera. *Am. Nat.* 180,
481 E64–E74.
- 482 Beisner, B.E., Peres-Neto, P.R., Lindström, E.S., Barnett, A., Longht, M.R., 2006. The role of
483 environmental and spatial processes in structuring lake communities from bacteria to
484 fish. *Ecology* 87, 2985–2991.
- 485 Bogut, I., Vidaković, J., Palijan, G., Čerba, D., 2007. Benthic macroinvertebrates associated
486 with four species of macrophytes. *Biologia (Bratislava)* 62, 600–606.
- 487 Brodersen, K.P., 1995. The effect of wind exposure and filamentous algae on the distribution
488 of surf zone macroinvertebrates in Lake Esrom, Denmark. *Hydrobiologia* 297, 131–148.
- 489 Čerba, D., Mihaljević, Z., Vidaković, J., 2010. Colonisation of temporary macrophyte
490 substratum by midges (Chironomidae: Diptera). *Ann. Limnol. – Int. J. Lim.* 46, 181–
491 190.
- 492 Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community
493 dynamics. *Ecol. Lett.* 8, 1175–1182.
- 494 Crist, T.O., Veech, J.A., 2006. Additive partitioning of rarefaction curves and species-area
495 relationships: unifying α -, β - and γ -diversity with sample size and habitat area. *Ecol.*
496 *Lett.* 9, 923–932.
- 497 Crist, T.O., Veech, J.A., Summerville, K.S., Gering, J.C., 2003. Partitioning species diversity
498 across landscapes and regions: a hierarchical analysis of α , β and γ diversity. *Am. Nat.*
499 162, 734–743.
- 500 Cushman, S.A., McGarigal, K., 2002. Hierarchical, multi-scale decomposition of species-
501 environment relationships. *Landscape Ecol.* 17, 637–646.
- 502 Drakare, S., Lennon, J.J., Hillebrand, H., 2006. The imprint of the geographical, evolutionary
503 and ecological context on species-area relationships. *Ecol. Lett.* 9, 215–227.
- 504 Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C.,
505 Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006.

- 506 Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol.*
507 *Rev.* 81, 163-182.
- 508 Ehrlich, P.R., 1988. The loss of diversity, in: Wilson, E.O (Ed.), *Biodiversity*. National
509 Academy Press, Washington, D.C., pp. 21-26.
- 510 Fesl, C., 2002. Biodiversity and resource use of larval chironomids in relation to
511 environmental factors in a large river. *Freshw. Biol.* 47, 1065–1087.
- 512 Flach, P.Z.S., Ozorio, C.P., Melo, A.S., 2012. Alpha and beta components of diversity of
513 freshwater nematodes at different spatial scales in subtropical coastal lakes. *Fund. Appl.*
514 *Limnol.* 180, 249-258.
- 515 Free, G., Solimini, A.G., Rossaro, B., Marziali, L., Giacchini, R., Paracchini, B., Ghiani, M.,
516 Vaccaro, S., Gawlik, B.M., Fresner, R., Santner, G., Schönhuber, M., Cardoso, A.C.,
517 2009. Modelling lake macroinvertebrate species in the shallow sublittoral: relative roles
518 of habitat, lake morphology, aquatic chemistry and sediment composition.
519 *Hydrobiologia* 633, 123–136.
- 520 Gering, J.C., Crist, T.O., Veech, J.A., 2003. Additive partitioning of species diversity across
521 multiple spatial scales: implication for regional conservation of biodiversity. *Conserv.*
522 *Biol.* 17, 488–499.
- 523 Gotelli, N.J., Entsminger, G.L., 2011. *EcoSim: Null Models Software for Ecology*, Version 7.
524 Acquired Intelligence Inc. and Kesey-Bear, Jericho, VT 05465. Available at:
525 <http://www.garyentsminger.com/ecosim/index.htm> (accessed 18 November 2014).
- 526 Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the
527 measurement and comparison of species richness. *Ecol. Lett.* 4, 379-391.
- 528 Hamerlík, L., Svitok, M., Novíkmec, M., Očadlík, M., Bitušík, P., 2014. Local, among-site,
529 and regional diversity patterns of benthic macroinvertebrates in high altitude
530 waterbodies: do ponds differ from lakes? *Hydrobiologia* 723, 41-52.
- 531 Heino, J., 2013a. Environmental heterogeneity, dispersal mode, and co-occurrence in stream
532 macroinvertebrates. *Ecol. Evol.* 3, 344–355.
- 533 Heino, J., 2013b. Does dispersal ability affect the relative importance of environmental
534 control and spatial structuring of littoral macroinvertebrate communities? *Oecologia*
535 171, 971–980.
- 536 Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss of ignition as a method for estimating organic
537 and carbon content in sediments: reproducibility and comparability of results. *J.*
538 *Paleolimnol.* 25, 101–110.

- 539 Hepp, U.L., Landeiro, V.L., Melo, A.S., 2012. Experimental assessment of the effects of
540 environmental factors and longitudinal position on alpha and beta diversities of aquatic
541 insects in a neotropical stream. *Int. Rev. Hydrobiol.* 97, 157-167.
- 542 Istvánovics, V., Clement, A., Somlyódy, L., Specziár, A., Tóth, L.G.-, Padisák, J., 2007.
543 Updating water quality targets for shallow Lake Balaton (Hungary), recovering from
544 eutrophication. *Hydrobiologia* 581, 305–318.
- 545 Jost, L., 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88,
546 2427-2439.
- 547 Jyväsjärvi, J., Aroviita, J., Hämäläinen, H., 2012. Performance of profundal
548 macroinvertebrate assessment in boreal lakes depends on lake depth. *Fund. Appl.*
549 *Limnol.* 180, 91-100.
- 550 Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen,
551 J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone,
552 A.L., Inouye, B.D., Harrison, S.P., Myers, J. A., 2011. Disentangling the drivers of β
553 diversity along latitudinal and elevational gradients. *Science* 333, 1755-1758.
- 554 Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple
555 communities. *Oikos* 76, 5-13.
- 556 Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.M.O., Magnusson, W.E., 2012. The roles of
557 dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera)
558 assemblages. *Freshw. Biol.* 57, 1554–1564.
- 559 Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt,
560 R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzales, A., 2004. The
561 metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7,
562 601–613.
- 563 Ligeiro, R., Melo, A.S., Callisto, M., 2010. Spatial scale and the diversity of
564 macroinvertebrates in a Neotropical catchment. *Freshw. Biol.* 55, 424-435.
- 565 Logue, J.B., Mouquet, N., Peter, H., Hillebrand, H., Declerck, P., Flohre, A., Gantner, S.,
566 Gülzow, N., Hörtnagl, P., Meier, S., Pecceu, B., 2011. Empirical approaches to
567 metacommunities: a review and comparison with theory. *Trends Ecol. Evol.* 26, 482–
568 491.
- 569 Luoto, T.P., 2012. Spatial uniformity in depth optima of midges: evidence from sedentary
570 archives of shallow Alpine and boreal lakes. *J. Limnol.* 71, 228–232.

- 571 Matias, M.G., Underwood, A.J., Hochuli, D.F., Coleman, R.A., 2010. Independent effects of
572 patch size and structural complexity on diversity of benthic macroinvertebrates. *Ecology*
573 91, 1908–1915.
- 574 Milošević, D., Simić, V., Stojković, M., Čerba, D., Mančev, D., Petrović, A., Paunović, M.,
575 2013. Spatio-temporal pattern of the Chironomidae community: toward the use of non-
576 biting midges in bioassessment programs. *Aquat. Ecol.* 47, 37–55.
- 577 Molozzi, J., Hepp, L.U., Callisto, M., 2013. The additive partitioning of macroinvertebrate
578 diversity in tropical reservoirs. *Mar. Freshw. Res.* 64, 609–617.
- 579 Moyle, P.B., Leidy, R.A., 1992. Loss of biodiversity in aquatic ecosystems: evidence from
580 fish faunas, in: Fiedler, P.L., Jain, S.K. (Eds.), *Conservation Biology*. Chapman and
581 Hall, New York, pp. 127–169.
- 582 Muskó, I.B., 1992. Amphipoda species found in Lake Balaton since 1897. *Miscnea. Zool.*
583 *Hung.* 7, 59–64.
- 584 Muskó, I.B., Balogh, C., Tóth, Á.P, Varga, É., Lakatos, G., 2007. Differential response of
585 invasive malacostracan species to lake level fluctuations. *Hydrobiologia* 590, 65–74.
- 586 Muskó, I.B., Balogh, C., Tóth, Á.P, Varga, É., Lakatos, G., 2010. Effects of water level
587 fluctuations on littoral macroinvertebrates (Lake Balaton, Hungary). *Acta. Biol. Debr.*
588 *Suppl. Oecol. Hung.* 21, 15–29.
- 589 Mykrä, H., Heino, J., Muotka, T., 2007. Scale-related patterns in the spatial and
590 environmental components of stream macroinvertebrate assemblage variation. *Global*
591 *Ecol. Biogeogr.* 16, 149–159.
- 592 Nyman, M., Korhola, A., Brooks, S.J., 2005. The distribution and diversity of Chironomidae
593 (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes.
594 *Global Ecol. Biogeogr.* 14, 137–153.
- 595 Palmer, M., Allan, J.D., Butman, C.A., 1996. Dispersal as a regional process affecting the
596 local dynamics of marine and stream benthic invertebrates. *Trends Ecol. Evol.* 11, 322–
597 326.
- 598 Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species
599 data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625.
- 600 Ptacnik, R., Andersen, T., Brettum, P., Lepistö, L., Willén, E., 2010. Regional species pool
601 controls community saturation in lake phytoplankton. *P. Roy. Soc. B* 277, 3755–3764.
- 602 Puntí, T., Rieradevall, M., Prat, N., 2009. Environmental factors, spatial variation and specific
603 requirements of Chironomidae in Mediterranean reference streams. *J. N. Am. Benthol.*
604 *Soc.* 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., Rieradevall, M., Prat, N., 2000. *Chironomus* species (Diptera: Chironomidae) in the profundal benthos of Spanish reservoirs and lakes: factors affecting distribution patterns. *Freshw. Biol.* 43, 1–18.
- Ricklefs, R.E., 2004. A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* 7, 1–15.
- Rosenberg, D.M., 1992. Freshwater Biomonitoring and Chironomidae. *Netherlands J. Aquat. Ecol.* 26, 101–121.
- Schmera, D., Erős, T., 2008. Linking scale and diversity partitioning in comparing species diversity of caddisflies in riffle and pool habitats. *Fund. Appl. Limnol.* 172, 205–215.
- Specziár, A., György, Á.I., Erős, T., 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. *J. Fish Biol.* 82, 840–855.
- Stendera, S.E.S., Johnson, R.K., 2005. Additive partitioning of aquatic invertebrate species diversity across multiple spatial scales. *Freshw. Biol.* 50, 1360–1375.
- Stoffels, R.J., Clarke, K.R., Closs, G.P., 2005. Spatial scale and benthic community organisation in the littoral zones of large oligotrophic lakes: potential for cross-scale interactions. *Freshw. Biol.* 50, 1131–1145.
- Suurkuukka, H., Meissner, K.K., Muotka, T., 2012. Species turnover in lake littorals: spatial and temporal variation of benthic macroinvertebrate diversity and community composition. *Divers. Distrib.* 18, 931–941.
- Thrush, S.F., Hewitt, J.E., Cummings, V.J., Norkko, A., Chiantore, M., 2010. β -diversity and species accumulation in Antarctic coastal benthos: influence of habitat, distance and productivity on ecological connectivity. *PLoS ONE* 5, e11899.
- Tóth, M., Móra, A., Kiss, B., Dévai, Gy., Specziár, A., 2012. Are macrophyte-dwelling Chironomidae (Diptera) largely opportunistic in selecting plant species? *Eur. J. Entomol.* 109, 247–260.
- Tóth, M., Árvai, D., Nagy, S.A., Specziár, A., 2013. Species diversity and abundance of plant-dwelling chironomids across hierarchical habitat and seasonal scales in the oxbow lakes of River Tisza, Hungary. *Fund. Appl. Limnol.* 182, 309–321.
- Triantis, K.A., Sfethourakis, S., 2012. Island biogeography is not a single-variable discipline: the small island effect debate. *Divers. Distrib.* 18, 92–96.

- 639 Veech, J.A., Crist, T.O., 2009. PARTITION: software for hierarchical partitioning of species
640 diversity, version 3.0. Available at: <http://www.users.muohio.edu/cristto/partition.htm>
641 (accessed 18 November 2014).
- 642 Veech, J.A., Wildi, O., Ewald, K.C., 2002. Additive partitioning of plant species diversity in
643 an agricultural mosaic landscape. *Landscape Ecol.* 15, 219-227.
- 644 Wilson, R.S., Ruse, L.P., 2005. A guide to the identification of genera of chironomid pupal
645 exuviae occurring in Britain and Ireland (including common genera from northern
646 Europe) and their use in monitoring lotic and lentic fresh waters. *Freshwater Biological*
647 *Association, Special publication No. 13, Ambleside, Cumbria, 176 p.*
- 648 Wolfram, G., 1996. Distribution and production of chironomids (Diptera, Chironomidae) in a
649 shallow, alkaline lake (Neusiedler See, Austria). *Hydrobiologia* 318, 103-115.
- 650

Figure captions

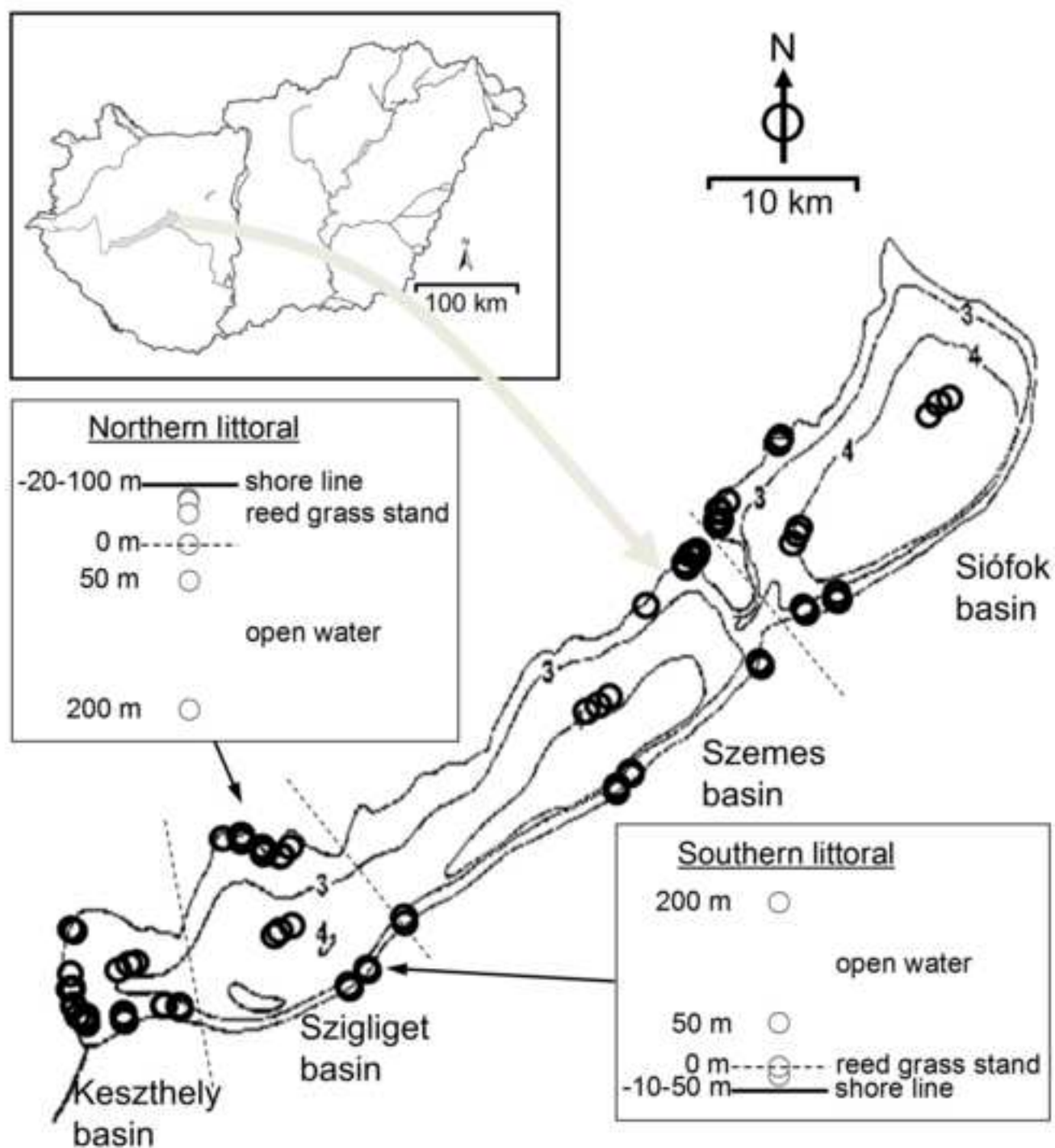
Fig. 1. Distribution of sampling sites in Lake Balaton, Hungary. Examined habitats included offshore area, natural-like littoral habitat transects from the riparian edge of the reed grass stand towards the macrophyte-free inshore area (typically one to three sites within the reed grass stand, one in the edge of the reed grass stand and the open water, and at 50 and 200 m distances from the reed grass stand; examples of typical northern littoral and southern littoral transects are presented), 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. The small map of Hungary in the upper left corner indicates the location of Lake Balaton.

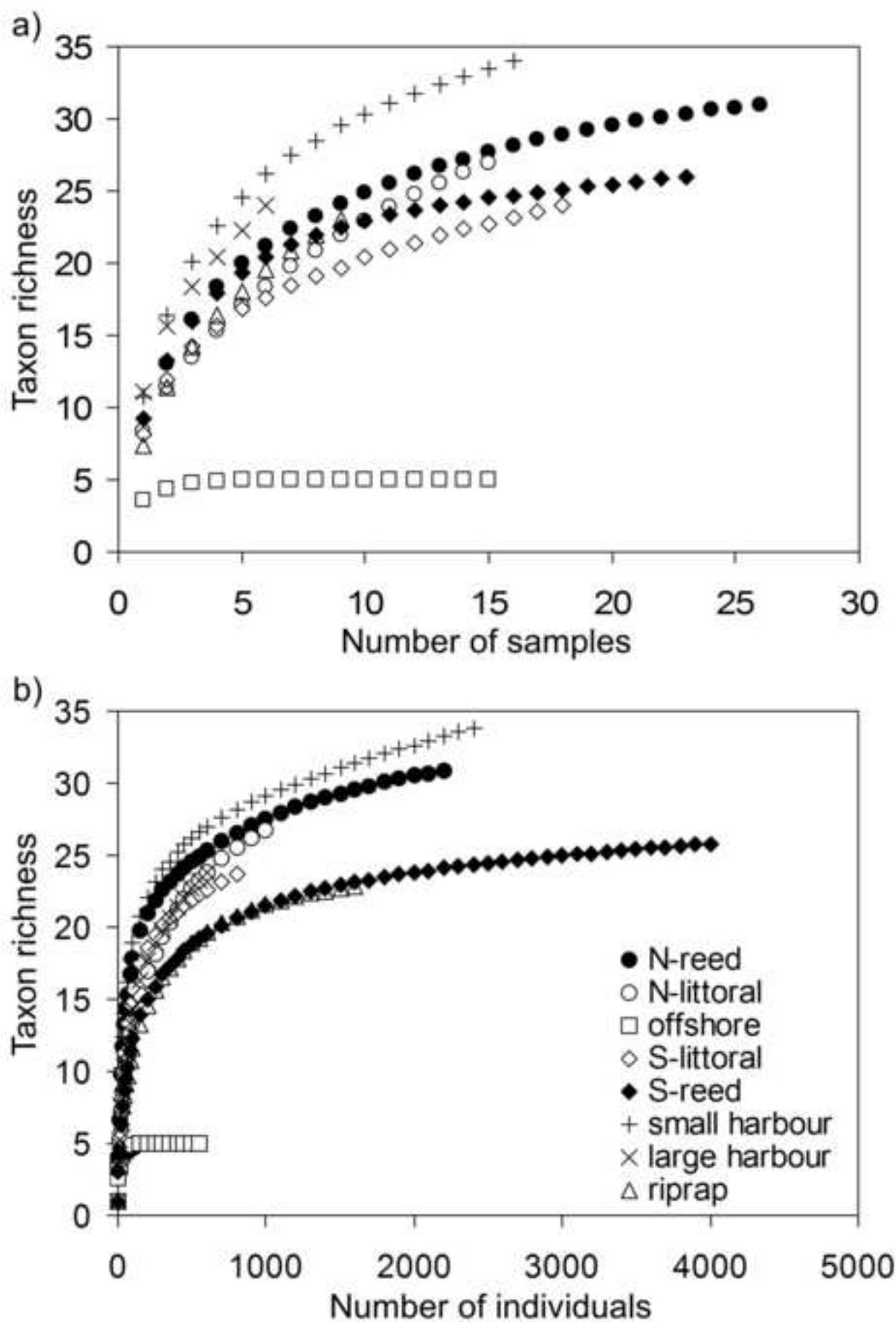
Fig. 2. Rarefied number of taxa of sediment-dwelling chironomids as a function of number of samples (a) and number of individuals (b) by habitat types in Lake Balaton, Hungary.

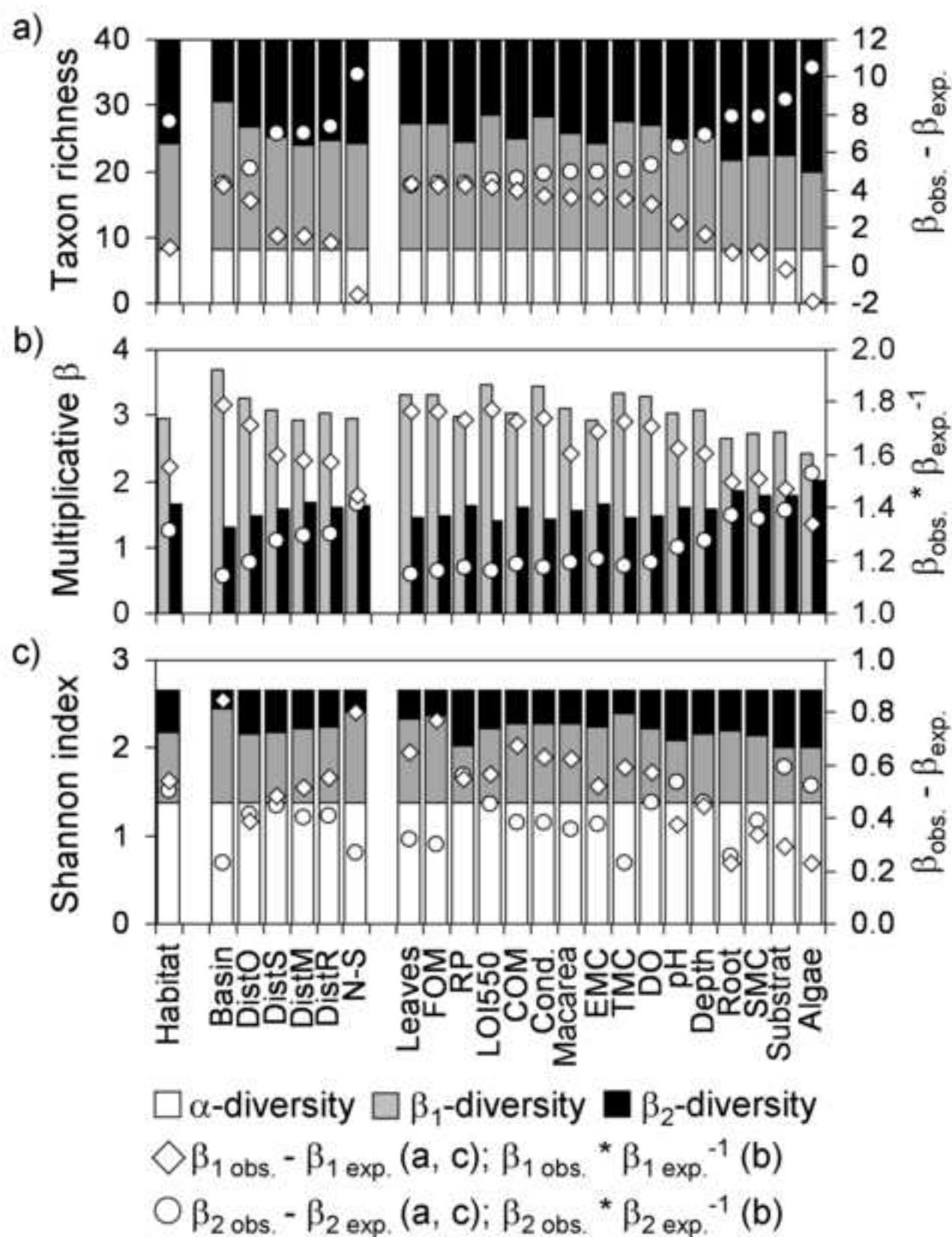
Fig. 3. Additive (a) and multiplicative (b) partitioning of taxon richness and additive partitioning of Shannon index (c) of sediment-dwelling chironomids by habitat type, indirect spatial (i.e. lake-scale geographical variables) and direct environmental gradients in Lake Balaton (Hungary) at two hierarchical sampling scales: sample (α and β_1) and environmental gradient (β_2 ; habitat type, environmental gradients). The relative importance of each individual gradient in chironomid diversity was characterized by the difference and ratio between the observed and expected β_2 -diversity in the additive and multiplicative approaches, respectively. Note that in the multiplicative model of taxon richness β -diversity components are unitless. Note also that since all habitat type and gradient based analyses were performed on the same 128 samples, α - and γ -diversities are constant in both additive and multiplicative taxon richness models (8.2 and 40 taxa, respectively; α -diversity is not plotted on Fig. 3b), and therefore, the product of multiplicative β_1 and β_2 is constant (4.9) as well. Abbreviations of spatial and environmental variables are explained in Appendix A.

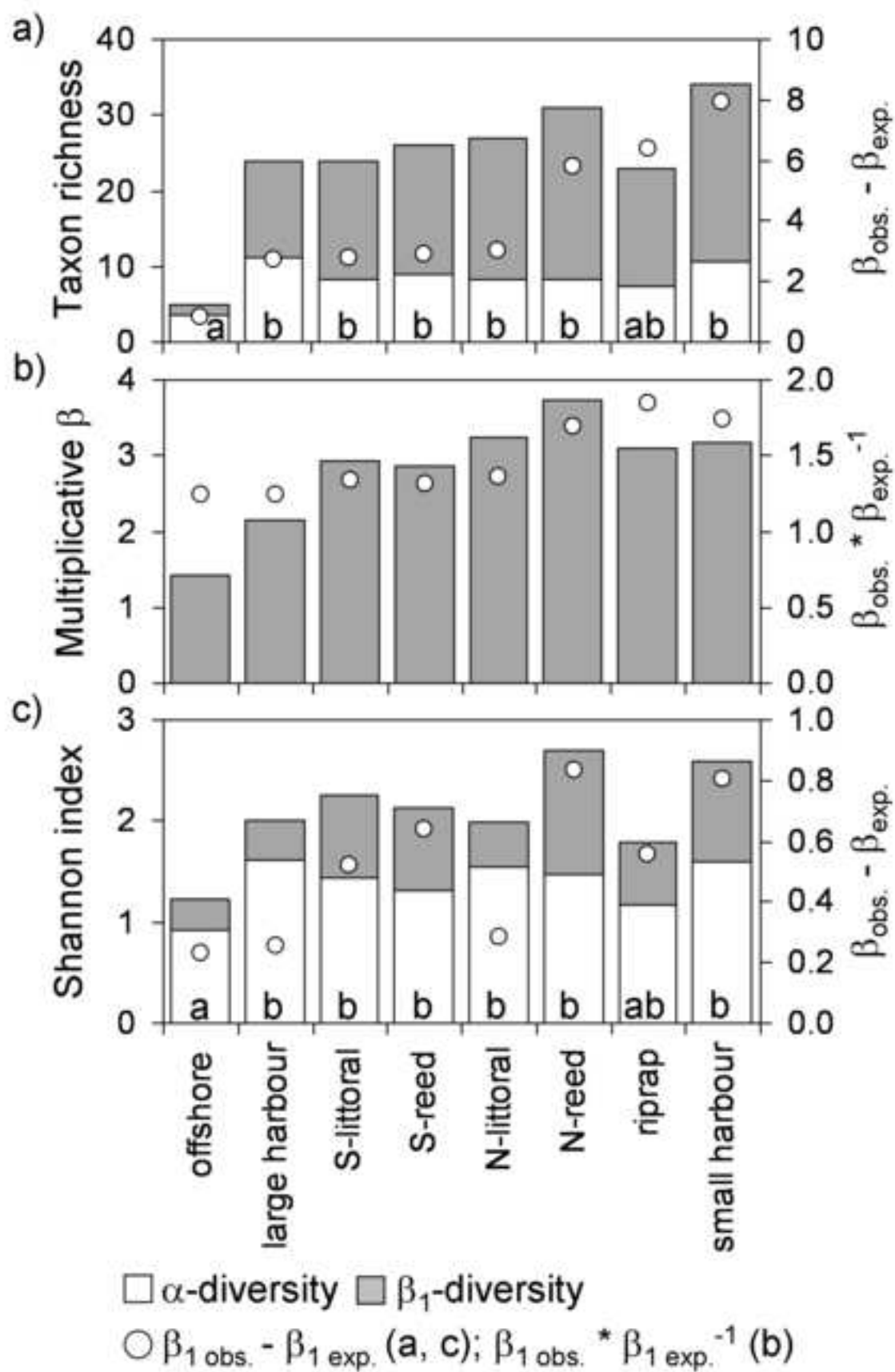
Fig. 4. Additive (a) and multiplicative (b) partitioning of taxon richness and additive partitioning of Shannon index (c) of sediment-dwelling chironomids by habitat types in Lake Balaton (Hungary) at the sample scale (α and β_1). The relative importance of among sample β_1 -diversity in each individual habitat type was characterized by the difference and ratio

684 between the observed and expected β_1 -diversities in the additive and multiplicative
685 approaches, respectively. Note that α has the same value in additive and multiplicative taxon
686 richness models, and thus, it is not plotted on Fig. 4b. Note also that in the multiplicative
687 model of taxon richness β -diversity components are unitless. The α -diversity varied
688 significantly among habitat types (ANOVA, $df=7,12$, $P<0.001$) and statistically homogenous
689 groups (Tukey HSD post hoc test, $P<0.05$) are indicated by lettering on Fig. 4a and 4c.
690









1 **Table 1**

2 Results of the ANOVA statistics comparing mean sample level species richness (α -diversity) of sediment-dwelling chironomids among ranges
 3 (classes 1 to 6, except lake basin and north to south transect which had 4 and 3 classes, respectively) of lake-scale geographical and direct
 4 environmental gradients in Lake Balaton, Hungary. In case of significant main effect, mean sample level species richness of classes were
 5 compared with Tukey HSD *post-hoc* test and statistically homogenous groups (at $P < 0.05$) are indicated by lettering. Abbreviations of spatial and
 6 environmental variables are explained in Appendix A.

Environmental gradient	ANOVA			Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
	F	df _{numerator} , df _{denominator}	P	mean \pm SD	mean \pm SD	mean \pm SD	mean \pm SD	mean \pm SD	mean \pm SD
Lake-scale geographical variables									
Basin	1.2	3,124	0.326	8.6 \pm 3.7	7.2 \pm 3.5	8.9 \pm 3.2	8.0 \pm 5.3		
N-S	14.9	2,125	<0.001	8.8 \pm 4.2 ^b	3.5 \pm 0.5 ^a	8.9 \pm 3.2 ^b			
DistR	7.0	5,122	<0.001	8.9 \pm 3.8 ^b	9.9 \pm 3.5 ^b	9.6 \pm 3.6 ^b	7.6 \pm 3.9 ^b	9.0 \pm 3.1 ^b	3.5 \pm 0.5 ^a
DistM	6.9	5,122	<0.001	9.2 \pm 4.0 ^b	8.7 \pm 3.5 ^b	8.6 \pm 4.6 ^b	8.6 \pm 2.8 ^b	5.3 \pm 3.5 ^{ab}	3.5 \pm 0.5 ^a
DistO	3.0	5,122	0.015	7.7 \pm 3.8 ^{ab}	4.0 \pm 2.0 ^a	9.2 \pm 3.4 ^{ab}	10.5 \pm 2.3 ^b	9.7 \pm 4.7 ^b	9.2 \pm 3.2 ^{ab}
DistS	6.4	5,122	<0.001	8.9 \pm 4.8 ^b	8.5 \pm 3.7 ^b	9.6 \pm 3.7 ^b	8.4 \pm 3.6 ^b	8.3 \pm 2.7 ^{ab}	3.5 \pm 0.5 ^a
Local environmental variables									
Depth	5.8	5,122	<0.001	7.6 \pm 3.5 ^b	9.5 \pm 3.7 ^b	9.5 \pm 4.7 ^b	8.9 \pm 3.4 ^b	7.4 \pm 4.1 ^{ab}	3.6 \pm 0.5 ^a
pH	1.8	5,122	0.122	8.0 \pm 1.4	7.3 \pm 3.1	10.5 \pm 4.7	8.2 \pm 3.6	7.4 \pm 3.8	8.0 \pm 3.1
DO	3.7	5,122	0.004	8.1 \pm 2.9 ^{ab}	8.0 \pm 3.1 ^{ab}	10.7 \pm 5.1 ^b	10.5 \pm 4.1 ^b	7.2 \pm 3.5 ^a	7.6 \pm 2.9 ^a
RP	3.5	5,122	0.005	4.0 \pm 0.0 ^{ab}	9.3 \pm 2.5 ^{ab}	9.6 \pm 2.5 ^b	9.6 \pm 3.9 ^b	7.4 \pm 4.2 ^{ab}	5.9 \pm 3.5 ^a

Cond.	2.3	5,122	0.046	11.5±4.2 ^a	7.4±3.6 ^a	7.4±3.8 ^a	9.0±3.4 ^a	7.7±3.9 ^a	11.3±6.0 ^a
Substrat	2.2	5,122	0.054	8.4±4.6	8.8±5.1	11.8±1.5	6.3±3.5	8.0±3.0	6.6±3.5
Root	0.6	5,122	0.721	8.3±4.1	8.8±2.9	10.2±3.1	6.5±2.9	6.5±4.1	6.5±4.1
Algae	0.5	5,122	0.783	8.4±4.0	8.6±4.6	8.0±1.4	7.8±3.0	5.5±2.1	6.0±1.4
EMC	0.4	5,122	0.851	8.2±4.2	7.8±3.1	10.0±2.4	7.8±3.1	9.2±4.9	6.5±3.5
SMC	2.6	5,122	0.027	8.0±3.8 ^a	6.3±3.0 ^{ab}	10.5±3.5 ^{ab}	9.0±4.6 ^{ab}	7.4±2.7 ^{ab}	12.9±4.7 ^b
TMC	1.6	5,122	0.159	7.6±4.0	8.9±2.2	8.2±3.4	7.8±3.5	9.1±3.9	10.8±4.9
Macarea	3.9	5,122	0.003	7.6±3.6 ^a	5.7±2.4 ^{ab}	10.5±5.5 ^{ab}	9.7±3.8 ^{ab}	10.9±2.2 ^b	12.0±5.7 ^{ab}
LOI550	0.6	5,122	0.674	8.3±3.0	9.4±3.2	7.6±4.3	9.1±4.7	8.4±4.1	8.3±4.1
FOM	2.8	3,124	0.044	7.8±3.7 ^a	10.1±5.7 ^a	12.7±1.2 ^a	-	-	9.2±2.2 ^a
COM	6.3	5,122	<0.001	7.7±3.5 ^a	10.0±3.1 ^{ab}	11.0±5.6 ^{abc}	16.0±4.2 ^{bc}	22.0±0.0 ^c	8.3±4.6 ^{ab}
Leaves	0.8	5,122	0.546	7.9±4.2	7.8±2.8	9.1±4.0	11.2±3.0	8.9±3.5	8.5±3.5

1 **Appendix A**

2 Within lake environmental gradients considered in this study, their abbreviations and units, and true ranges by resource classes of continuous
 3 variables in Lake Balaton, Hungary.

Within lake gradient	Abbreviation	Unit	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Habitat type	Habitat	8 classes	see table foot note ¹					
Lake-scale geographical variables								
Lake Basin	Basin	4 classes ²	Keszthely	Szigliget	Szemes	Siófok		
North to south transect	N-S	3 classes	northern littoral	offshore	southern littoral			
Distance from emergent macrophyte	DistR	(m)	0-3	3-17	17-73	73-311	311-1308	1308-5500
Distance from submerged and floating leaved macrophytes	DistM	(m)	0-3	3-17	17-73	73-311	311-1308	1308-5500
Distance from open water	DistO	(m)	0-1	1-4	4-10	10-25	25-57	57-129
Distance from shore	DistS	(m)	0-3	3-17	17-73	73-311	311-1308	1308-5500
Local environmental variables								
Water depth	Depth	(m)	0.0-0.4	0.4-0.8	0.8-1.4	1.4-2.1	2.1-3.2	3.2-4.5
pH	pH	-	5.6-6.1	6.1-6.6	6.6-7.1	7.1-7.7	7.7-8.3	8.3-9.0
Dissolved oxygen	DO	(mg l ⁻¹)	3.6-5.0	5.0-6.7	6.7-9.0	9.0-11.9	11.9-15.7	15.7-20.6

Redox potential	RP	(mV)	-67--49	-49--20	-20-24	24-93	93-199	199-365
Conductivity	Cond.	(mS cm ⁻¹)	755-779	779-805	805-831	831-858	858-885	885-914
Lake bed substratum	Substrat	6 classes	silt ≥ 80%	both silt and mollusc shells > 20%	both silt and sand > 20%	both sand and mollusc shells > 20%	sand ≥ 80	rock = 100% (i.e. ripraps)
Reed grass root	Root	6 classes ³	no					high
Algae coverage	Algae	(%)	0.0-16.7	16.7-33.3	33.3-50.0	50.0-66.7	66.7-83.3	83.3-100.0
Emergent macrophyte coverage	EMC	(%)	0.0-16.7	16.7-33.3	33.3-50.0	50.0-66.7	66.7-83.3	83.3-100.0
Submerged and floating leaved macrophyte coverage	SMC	(%)	0.0-16.7	16.7-33.3	33.3-50.0	50.0-66.7	66.7-83.3	83.3-100.0
Total macrophyte coverage	TMC	(%)	0.0-16.7	16.7-33.3	33.3-50.0	50.0-66.7	66.7-83.3	83.3-100.0
Area of submerged and floating leaved macrophyte stand	Macarea	(m ²)	0-3	3-16	16-70	70-291	291-1208	1208-5000
Loss-on-ignition at 550 °C	LOI550	(%)	0.7-2.2	2.2-5.2	5.2-10.8	10.8-21.5	21.5-42.0	42.0-81.1
Fine (≤1 mm) decomposing organic matter particles	FOM	6 classes ³	no					high
Coarse (>1 mm) decomposing organic matter particles	COM	6 classes ³	no					high
Reed grass leaves	Leaves	6 classes ³	no					high

¹ Habitat type classes: 1) northern reed grass stands; 2) northern reed-free littoral zone; 3) offshore area without macrophyte; 4) southern reed-free littoral zone; 5) southern reed grass stands; 6) small boat harbours rounded by reed grass; 7) large commercial harbours sheltered by ripraps; and 8) ripraps.

² Lake basin classes correspond to the four basins of Lake Balaton from the major inflow River Zala to the only outflow Sió Canal (see also Fig. 1).

³ Samples were classified into six subjective categories ranging between zero and the highest observed resource level.