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5 Effects of habitat types and within lake environmental gradients on the diversity of

6 chironomid assemblages

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14

15 **Abstract**

16

17 Understanding the distribution of biotic diversity across various spatial scales and  
18 environmental gradients is important from fundamental, practical and conservation biological  
19 aspects. We applied a hierarchical diversity partitioning framework to quantify the variability  
20 of sample level  $\alpha$ - and  $\beta_1$ -diversity, and environment related  $\beta_2$ -diversity of benthic  
21 chironomid assemblages within and among *a priori* defined habitat types, and along the  
22 gradients of individual environmental factors in a large and shallow lake (Lake Balaton,  
23 Hungary). Taxon richness (both additive and multiplicative) and Shannon index based  
24 diversity approaches yielded highly concordant results. The  $\alpha$ -diversity was much lower and  
25  $\beta_1$ -diversity higher than predicted by null model and both measures varied substantially  
26 among habitat types and along most individual environmental gradients. The  $\beta_2$ -diversity  
27 indicated a marked variability of taxon (identified at species to genus level) pool among  
28 habitat types and higher than predicted taxon turnover along all examined environmental  
29 gradients. Moreover, the observed  $\beta_2$ -diversity varied greatly among individual environmental  
30 gradients. The difference between the expected and observed  $\beta_2$ -diversity values suggests that  
31 taxon turnover was most influential (in decreasing order) along the algae coverage gradient,  
32 the lake bed substratum gradient and the macrophyte coverage gradient among others. We  
33 argue that within-lake environmental heterogeneity and its effect on the taxon richness should  
34 receive more attention in biodiversity assessment and conservation. Management could  
35 benefit from the identification of within lake gradients along which taxonomic turnover  
36 maximizes.

37

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

40

## 41 **Introduction**

42

43 Exploring patterns of biodiversity is fundamental to understand many ecological processes  
44 (Ricklefs, 2004). For instance, the framework of diversity partitioning which quantifies local  
45 ( $\alpha$ ), regional ( $\gamma$ ) and turnover (beta) components of diversity has greatly contributed to our  
46 understanding of assembly processes in metacommunities at a variety of spatial and temporal  
47 scales (Gering et al., 2003; Crist and Veech, 2006; Anderson et al., 2011; Kraft et al., 2011).  
48 Diversity components (i.e.  $\alpha$ ,  $\beta_1$ , ...,  $\beta_n$ ) have important conservational biological implications  
49 as well as they provide fundamental information on how to allocate areas and habitats to be  
50 involved in an effective environmental management program (Gering et al., 2003; Thrush et  
51 al., 2010).

52 Conceptual models and empirical studies concerning biodiversity distributions of lakes  
53 focused primarily on broad scale, geographical and temporal processes (Stendera and  
54 Johnson, 2005; Ptacnik et al., 2010; Suurkuukka et al., 2012; Angeler and Drakare, 2013;  
55 Hamerlík et al., 2014). Although fine scale, microhabitat level distribution of species is  
56 widely studied in lentic organisms (e.g. Brodersen, 1995; Čerba et al., 2010; Luoto, 2012;  
57 Specziár et al., 2013; Árva et al., 2015), the role of within lake habitats in shaping diversity  
58 patterns and their contribution to total (lake level or regional) diversity is less known (but see  
59 Flach et al., 2012; Tóth et al., 2013). Suurkuukka et al. (2012) revealed that unspecified  
60 within lake patterns included about 50% of the overall regional littoral macroinvertebrate  
61 diversity in boreal lakes. Likewise, it is largely unknown how biodiversity is distributed  
62 across specific within lake environmental gradients and/or habitat types. Partitioning within  
63 lake  $\beta$ -diversity for stochastic or unspecified among sample variability (i.e.  $\beta_1$ ) and structured  
64 environment related species turnover (i.e.  $\beta_2$  or higher  $\beta$  levels) components would yield basic  
65 information about the influence of within lake environmental heterogeneity on species  
66 diversity. By identifying environmental gradients along which the species turnover rate is the  
67 highest would facilitate focusing of conservation actions to the most important pieces of  
68 environmental heterogeneity.

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

75 diverse environmental optima and tolerances and relatively good dispersal ability in their  
76 winged terrestrial adult phase (Armitage, 1995). Thus according to metacommunity theory  
77 (Leibold et al., 2004; Cottenie, 2005; Beisner et al., 2006) environmental filtering (i.e. species  
78 sorting) shapes their fine scale species distribution patterns, while the role of spatial processes  
79 (i.e. dispersal limitation) become influential in their assemblage organization only at broad  
80 geographical scales (Mykrä et al., 2007; Landeiro et al., 2012; Heino, 2013a, 2013b; but see  
81 Árvá et al., 2015). Accordingly, in lakes with high environmental heterogeneity a substantial  
82 part in their species turnover could be related directly to habitat types and environmental  
83 gradients due to inter-specific separation of species optima and tolerance ranges (Rae, 2004;  
84 Puntí et al., 2009; Árvá et al., 2015). Thus not just relative abundance patterns but also  
85 species turnover rates can predictably differ among various within lake environmental  
86 gradients. To our knowledge, however, there are no studies comparing the role of species  
87 turnover along various within lake environmental gradients. Specific aims of the study are to  
88 analyse: (1) how sample level  $\alpha$ -diversity (i.e. local taxon richness and Shannon diversity  
89 index) and among sample  $\beta_1$ -diversity vary among *a priori* defined characteristic habitat types  
90 of the lake; (2) how sample level  $\alpha$ -diversity and among sample  $\beta_1$ -diversity change along the  
91 gradient of individual environmental factors (e.g. water depth, substratum type); and (3) to  
92 what extent  $\beta_2$ -diversity among the habitat types and along particular environmental gradients  
93 contribute to total chironomid diversity of the lake.

94

## 95 **Materials and methods**

96

### 97 *Study area*

98

99 Balaton is the largest shallow lake (surface area: 596 km<sup>2</sup>; mean depth: 3.2 m) in Central  
100 Europe, situated at 46° 42' - 47° 04' N, 17° 15' - 18° 10' E and 104.8 m above sea level (Fig.  
101 1). The lake is slightly alkaline (400 mg l<sup>-1</sup> of Ca<sup>2+</sup> and Mg<sup>2+</sup>(HCO<sub>3</sub><sup>-</sup>)<sub>2</sub>) with a decreasing  
102 trophic gradient (i.e. chlorophyll-a concentration from 26.6 to 9.7 µg l<sup>-1</sup>, mean data of 2008-  
103 2012; Ministry of Environmental Protection and Water Management of Hungary,  
104 [http://www.ktm.hu/balaton/lang\\_en/index.htm](http://www.ktm.hu/balaton/lang_en/index.htm)) from SW to NE along its longitudinal axis  
105 (see also Istvánovics et al., 2007). Based on habitat characteristics, Lake Balaton can be  
106 divided into a little variable open water area spreading to >85% of the lake with silt substrate,  
107 largely homogeneous physico-chemical features and with no macrovegetation, and to a much  
108 heterogeneous littoral zone exhibiting marked environmental gradients along the distance

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

119

#### 120 *Chironomid sampling and identification*

121

122 Benthic chironomid assemblages were sampled at 128 sites between 26 June and 13 July  
123 2012 (Fig. 1). The sites were distributed across the whole lake and covered all ranges of  
124 habitat and environmental gradients (see below). Three merged Ekman grab sediment samples  
125 were taken per site (total sampled area per site: 0.036 m<sup>2</sup>), washed through a 0.25 mm mesh  
126 sieve and transported to the laboratory in a cooling box. Riprap habitats were sampled by  
127 cleaning and washing algal coating and sediment from a measured rock surface corresponding  
128 to area of Ekman grab samples into plastic containers. Chironomids were separated from  
129 sediment samples alive by sugar flotation method (Anderson, 1959), and euthanized and  
130 preserved in 70% ethanol for later identification. Chironomids were digested in KOH  
131 (potassium hydroxide) to eliminate non-chitinous tissues and slide-mounted in Euparal<sup>®</sup>.  
132 Identification was performed to species or the lowest possible taxonomic level (species group  
133 to genus; for more details see Árvai et al., 2015).

134

#### 135 *Habitat assessment and environmental factors*

136

137 Parallel to chironomid sampling, we measured a series of environmental factors (Appendix  
138 A) that have been found influential on the distribution of chironomids (e.g. Real et al., 2000;  
139 Rae, 2004; Free et al., 2009; Puntí et al., 2009; Tóth et al., 2012). To cover all environmental  
140 gradients in the lake, first, the position of each sampling site was characterized with six lake-  
141 scale geographical variables including lake basin (i.e. Keszthely-, Szigliget-, Szemes- and  
142 Siófok-basins), location along the north-to-south transect of the lake (i.e. northern littoral,

143 offshore and southern littoral) and distances from shore, emergent macrophyte, submerged  
144 and floating leaved macrophytes and open water. Then, we recorded 16 local environmental  
145 factors. We measured water depth, redox potential of the uppermost sediment layer, and  
146 dissolved oxygen, pH and conductivity of the water close to the bottom. Visual estimates of  
147 emergent (dominantly reed grass), submerged and floating leaved macrophytes and  
148 filamentous algae (*Cladophora* sp.) coverage (%) were made within a circle of 3 m diameter  
149 around the origin of chironomid samples and the area of the submerged and floating leaved  
150 macrophyte stands were recorded by GPS and calculated by MapSource version 6.16.3.  
151 software (Garmin Ltd., Olathe, US, www.garmin.com). The substratum of the lake bed was  
152 inspected for percentage composition of clay (grain size  $\leq 0.002$  mm), silt (0.002-0.06 mm),  
153 sand (0.06-2 mm), rock ( $>200$  mm) and mollusc shell (5-25 mm; mainly *Dreissena*  
154 *polymorpha* (Pallas, 1771) and *D. bugensis* (Andrusov, 1897), and then classified into six  
155 categories: 1) silt  $\geq 80\%$ ; 2) both silt and mollusc shells  $> 20\%$ ; 3) both silt and sand  $> 20\%$ ;  
156 4) both sand and mollusc shells  $> 20\%$ ; 5) sand  $\geq 80\%$ ; and 6) rock = 100% (i.e. ripraps). The  
157 sediment was examined for occurrence of pure reed grass root (characteristic in some  
158 degrading reed grass stands) and fine and coarse decomposing organic matter particles and  
159 reed grass leaves and rated on a six category scale (0-5). Relative organic matter content was  
160 assessed from dry (at 50 °C for 72 hours) samples of the upper 2 cm sediment layer according  
161 to the loss-on-ignition method at 550 °C for 1 hour (LOI550; Heiri et al., 2001).

162

### 163 *Statistical analysis*

164

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

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

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

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

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

210 corresponds to variation of taxon composition among habitat types and levels of individual  
211 environmental gradients. Note that  $\alpha$  is the same in the additive and multiplicative models,  
212 whereas the value and unit of  $\beta$ -diversity differs between the two models ( $\beta$  is unitless in the  
213 multiplicative model). While the Shannon diversity index naturally partitions into  
214 independent and additive  $\alpha$  and  $\beta$  components (Jost, 2007). Observed values of  $\alpha$ - and  $\beta$ -  
215 diversity components were tested against null model distributions obtained from individual  
216 based unrestricted randomizations (10,000 randomizations) in the software package  
217 PARTITION 3 (Veech and Crist, 2009). Specifically, it was tested whether the observed  
218 values of  $\alpha$ - and particular  $\beta$ -diversity components significantly differed from chance. A more  
219 detailed description of the null model generation and the randomization procedure is provided  
220 by Crist et al. (2003). To evaluate the relative importance of different environmental gradients  
221 in total ( $\gamma$ ) chironomid diversity, individual environmental gradients were ranked according to  
222 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  
223 expected  $\beta_2$  values in additive (i.e. species richness and Shannon index) and multiplicative  
224 (i.e. species richness) diversity partitioning approaches, respectively.

225

## 226 **Results**

227

### 228 *Chironomid assemblages and $\gamma$ -diversity*

229

230 Sampling of diverse array of microhabitats in Lake Balaton yielded a total of 13,804  
231 individuals and 40 taxa (identified at species, species group and genus levels;  $\gamma$ -diversity of  
232 taxon richness) of chironomids belonging to three subfamilies: Tanypodinae (7 taxa),  
233 Orthocladiinae (4 taxa) and Chironominae (29 taxa). Total Shannon ( $\gamma$ -) diversity proved to be  
234 2.66. Detailed list of captured taxa, their numbers of individuals and habitat uses are  
235 presented in Árvai et al. (2015). Briefly, the chironomid fauna of Lake Balaton is comprised of  
236 widely distributed taxa being characteristic for shallow, medium to high productivity,  
237 temperate standing waters. Assemblage composition varied markedly among habitat types  
238 and across environmental gradients and could be classified into four major type groups: (1)  
239 *Cladopelma virescens* (Meigen, 1818), *Chironomus balatonicus* Dévai, Wüelker & Scholl,  
240 1983, *Tanytus kraatzi* (Kieffer, 1918), *Chironomus dorsalis* Meigen, 1818 and  
241 *Paratanytarsus* sp. were indicator taxa for the northern littoral sites and both small and large  
242 boat harbours with macrovegetation; (2) *Cricotopus reversus* Hirvenoja, 1973, *Cricotopus*



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

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

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

261

#### 262 *Local ( $\alpha$ -) diversity*

263

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

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

274

#### 275 *Among sites variability ( $\beta_1$ -diversity)*

276

277 Both additive and multiplicative diversity partitioning models revealed that among sample  
278  $\beta_1$ -diversity of taxa richness was larger than expected by chance alone across habitat types  
279 and along most individual environmental gradients (Fig. 3). In addition,  $\beta_1$ -diversity was also  
280 larger than expected within each habitat type (Fig. 4). Although  $\beta_1$ -diversity using the  
281 Shannon index also proved to be higher than expected by chance, the result suggested a bit  
282 different picture on the relative importance of  $\beta_1$ -diversity for some habitat types and  
283 particular environmental gradients than that found for taxon richness.

284

285 *Among habitat types and along environmental gradients variability ( $\beta_2$ -diversity)*

286

287 Based on the additive taxon richness partitioning model,  $\beta_2$ -diversity was about 7.6 taxa  
288 larger than predicted across habitats indicating a marked difference in species pools among  
289 habitat types (Fig. 3a). Similarly, significant taxon turnover was revealed along all examined  
290 environmental gradients with  $\beta_2$ -diversity values 4.2 to 10.5 taxa larger than expected.  
291 Difference between the expected and observed  $\beta_2$ -diversity values indicated that taxon  
292 turnover was most influential (in decreasing order) along algae coverage, lake bed substratum,  
293 submerged and floating leaved macrophytes coverage, presence of reed grass root, distances  
294 from emergent macrophyte, from submerged and floating leaved macrophytes and from  
295 shore, water depth and pH gradients. Multiplicative taxon richness partitioning fully  
296 supported the above results, however, the rank of individual gradients was slightly different in  
297 term of divergence (expressed as  $\beta_{2\text{observed}} * \beta_{2\text{expected}}^{-1}$ ) of observed from the expected  $\beta_2$ -  
298 diversity (Fig. 3b). Although  $\beta_2$ -diversity using the Shannon index also proved to be higher  
299 than expected by chance the result differed somewhat from the above picture (Fig. 3c). In  
300 general, taxon richness based approach related larger part of the total diversity to  $\beta$  levels,  
301 while diversity captured by the Shannon index was more concentrated at  $\alpha$  level and with  
302 relatively low amount of variability related to  $\beta_2$  level.

303

## 304 **Discussion**

305

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

310 the captured total diversity is due to  $\beta$ -diversity components. Sample level  $\alpha$ -diversity  
311 accounted for only 20.5% of within lake diversity. This value is very similar to sample level  
312 macroinvertebrate  $\alpha$ -diversity of 23% observed across the littorals of three Finnish lakes  
313 (Suurkuukka et al., 2012), but it is much higher compared to 5–8% values obtained by  
314 Stendera and Johnson (2005) for littoral macroinvertebrates across 677 Swedish lakes.  
315 However, both latter studies were based on kick-samples which cover larger effective  
316 sampling area and are with different selectivity than our Ekman grab samples. It is well  
317 known that patterns of  $\alpha$  and  $\beta$ -diversities are scale dependent and therefore the definition of  
318 “local” diversity affects diversity partitioning (Matias et al., 2010; Beck et al., 2012) and the  
319 relative importance of  $\alpha$  and hierarchical  $\beta$ -diversity components (Schmera and Erős, 2008).  
320 Nevertheless, lake sediment surface covered by Ekman grab can be considered as a standard  
321 sampling unit in benthic macroinvertebrate studies, and thus, generally serves as the basis for  
322 biodiversity assessment (sample level  $\alpha$ -diversity; e.g. Free et al., 2009; Jyväsjärvi et al.,  
323 2012; Molozzi et al., 2013). By using a sampling methodology comparable to ours, Molozzi  
324 et al. (2013) found that most of macroinvertebrate diversity was related to sampling unit  
325 (43.7%;  $\alpha$ -diversity) and among sampling unit variability (47.2%;  $\beta_1$ -diversity), while only  
326 little taxon turnover occurred among regions and reservoirs in Brazil. Surprisingly, we did not  
327 find any characteristic trend in sample level  $\alpha$ -diversity along within lake environmental  
328 gradients, except that considerably less taxa occurred in the offshore samples than in littoral  
329 sites. This result may indicate that at the lake scale different structuring processes are likely to  
330 dominate than at broad geographical scales where much longer environmental gradients act  
331 including climatic gradients (e.g. Nyman et al., 2005; Kraft et al., 2011). Compared with the  
332 results of species richness, Shannon index provided a slightly different picture and revealed  
333 the role of taxa relative abundances with giving more weight to sample level diversity.

334 We divided  $\beta$ -diversity into two components, to  $\beta_2$ -diversity which is directly related to  
335 various attributes of environmental heterogeneity and to  $\beta_1$ -diversity which represents  
336 unexplained among site variability. Both  $\beta$  components were generally larger than expected  
337 by chance alone based on either taxon richness or Shannon index. As we expected species  
338 richness varied considerably across habitat types and high  $\beta_2$ -diversity indicated a significant  
339 taxon turnover along this scale. Although largest part of Lake Balaton (ca. 85% of the total  
340 lake area) is a macrophyte free offshore (open water) area, only 12.5% of the total identified  
341 chironomid taxa inhabited this habitat, and as supported by the results of the rarefaction  
342 analyses, no further taxa are likely to occur there. In addition, the relatively high ratio of  $\alpha$ -  
343 diversity (70.6%) within the total species richness indicated that taxa distribute much more

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

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

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

378 Balaton. Present results also proved that the observed taxon turnover (i.e.  $\beta_2$ -diversity)  
379 markedly varied among environmental gradients. By scaling our sampling sites along several  
380 alternative dimensions (i.e. individual factors) of environmental heterogeneity, we identified  
381 few individual environmental gradients (i.e. algae coverage, lake bed substratum, submerged  
382 and floating leaved macrophyte coverage and presence of reed grass root on the sediment  
383 surface), which explained higher proportion of overall  $\beta$ -diversity than did the *a priori*  
384 defined habitat types. This result suggests that the application of gradient based approaches  
385 can be useful at fine spatial scales as well, and they may yield more direct information on  
386 diversity patterns and the underlying processes than conventional diversity partitioning  
387 approaches based on hierarchical spatial units (i.e. lake area) or subjective habitat types.

388 The highest rates of taxon turnover were found along the algae coverage gradient, the lake  
389 bed substratum gradient and the submerged and floating leaved macrophyte coverage  
390 gradient. Coverage of algae increases towards decreasing water depth, more compact  
391 substratum (i.e. sand and rock) and less decomposed organic matter, and also coincides with  
392 higher oxygen concentration in Lake Balaton. The role of algae coverage is well known in the  
393 distribution of chironomids (Čerba et al., 2010; Tóth et al., 2013). Increasing algae coverage  
394 causes a characteristic shift in assemblage structure towards the dominance of *C. sylvestris* gr.  
395 and *C. reversus* in Lake Balaton (Árva et al., 2015). Substratum heterogeneity is an important  
396 driver of macroinvertebrate  $\beta$ -diversity (Stoffels et al., 2005; Ligeiro et al., 2010; Hepp et al.,  
397 2012; Suurkuukka et al., 2012), and it is well known that benthic chironomid taxa have  
398 different substratum preferences (Wolfram 1996; Fesl 2002; Rae 2004; Árva et al., 2015). In  
399 Lake Balaton, most chironomid taxa prefer soft, silty substratum and their abundances  
400 strongly decrease or they even disappear towards harder substratum such as sand and rock.  
401 Sites with sandy bottom clearly separated from other sites by their assemblages dominated by  
402 *C. mancus* gr.; *C. defectus* and *Stictochironomus* sp. While, riprap habitats with rock  
403 substratum also have individual assemblages characterised by *C. sylvestris* gr., *C. reversus*  
404 and *O. oblidens* (Árva et al., 2015). It is known that macrophytes have diverse effect on  
405 chironomid assemblages as they influence habitat structure and heterogeneity, physico-  
406 chemical properties of the water and the sediment and food conditions (e.g. Ali et al., 2007;  
407 Bogut et al., 2007). Submerged and floating leaved macrophyte coverage was most preferred  
408 by *Parachironomus varus* (Goetghebuer, 1921) and *Parachironomus* sp., while avoided by  
409 e.g. all Tanypodinae species, *C. reversus* and *O. oblidens* (Árva et al., 2015).

410 Significant proportion of the total diversity was unexplained  $\beta_1$ -diversity indicating an  
411 aggregated species distribution, which is independent on the structuring effect of the habitat

412 or environmental gradients captured by particular higher  $\beta$  levels. Unlike in relative  
413 abundance based approaches (Cushman and McGarigal, 2002; Peres-Neto et al., 2006), we do  
414 not have an appropriate statistical tool that enables decomposing overall  $\beta$ -diversity in means  
415 of taxonomic richness or Shannon index into multiple parallel components related to series of  
416 environmental stressors (only the effect of hierarchical factors can be tested). This is a  
417 problem because environmental gradients generally are not independent from each other, and  
418 therefore, their effects can overlap. For example, we found that algae coverage tended to  
419 increase towards harder lake bed substratum (i.e. sand and rock) and to decrease with  
420 increasing water depth. Consequently, (1)  $\beta_2$ -diversity related to a specific environmental  
421 gradient will include both the pure and shared effects of the concerning environmental factor  
422 and these two effects are not separable, (2) independent effects of all concurrent  
423 environmental factors that are not included in the analysis (i.e. as the factor that specifies  $\beta_2$ -  
424 diversity level) will be displayed as  $\beta_1$ -diversity. Therefore, in order to understand  
425 organization of biotic diversity more completely, we suggest examining the distribution of  
426 diversity in alternative hierarchical sampling designs (i.e. spatial scale vs. various direct  
427 environmental gradients). Dispersal limitation is another potential mechanism influencing  $\beta$ -  
428 diversity especially at broader geographical scales (Palmer et al., 1996; Thrush et al., 2010;  
429 Logue et al., 2011). The relevance of dispersal limitation was also indicated in Lake Balaton  
430 using direct gradient analysis based on relative abundance data (Árva et al., 2015). However,  
431 regarding true diversity measures (i.e. species richness and Shannon index), to our  
432 knowledge, there is no appropriate statistical tool that could enable dissecting the effect of  
433 dispersal limitation from overall  $\beta$ -diversity. Consequently, the independent effect of dispersal  
434 limitation in site-to-site species turnover will also be included in  $\beta_1$ -diversity.

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

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

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

456

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458

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464

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- 654

655 **Figure captions**

656

657 **Fig. 1.** Distribution of sampling sites in Lake Balaton, Hungary. Examined habitats included  
658 offshore area, natural-like littoral habitat transects from the riparian edge of the reed grass  
659 stand towards the macrophyte-free inshore area (typically one to three sites within the reed  
660 grass stand, one in the edge of the reed grass stand and the open water, and at 50 and 200 m  
661 distances from the reed grass stand; examples of typical northern littoral and southern littoral  
662 transects are presented), small boat harbours situated within the reed grass stand, stands of the  
663 most characteristic submerged and floating leaved macrophytes, and modified littoral areas,  
664 large sailing-vessel and ship harbours, ripraps and nearby littoral areas. The small map of  
665 Hungary in the upper left corner indicates the location of Lake Balaton.

666

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

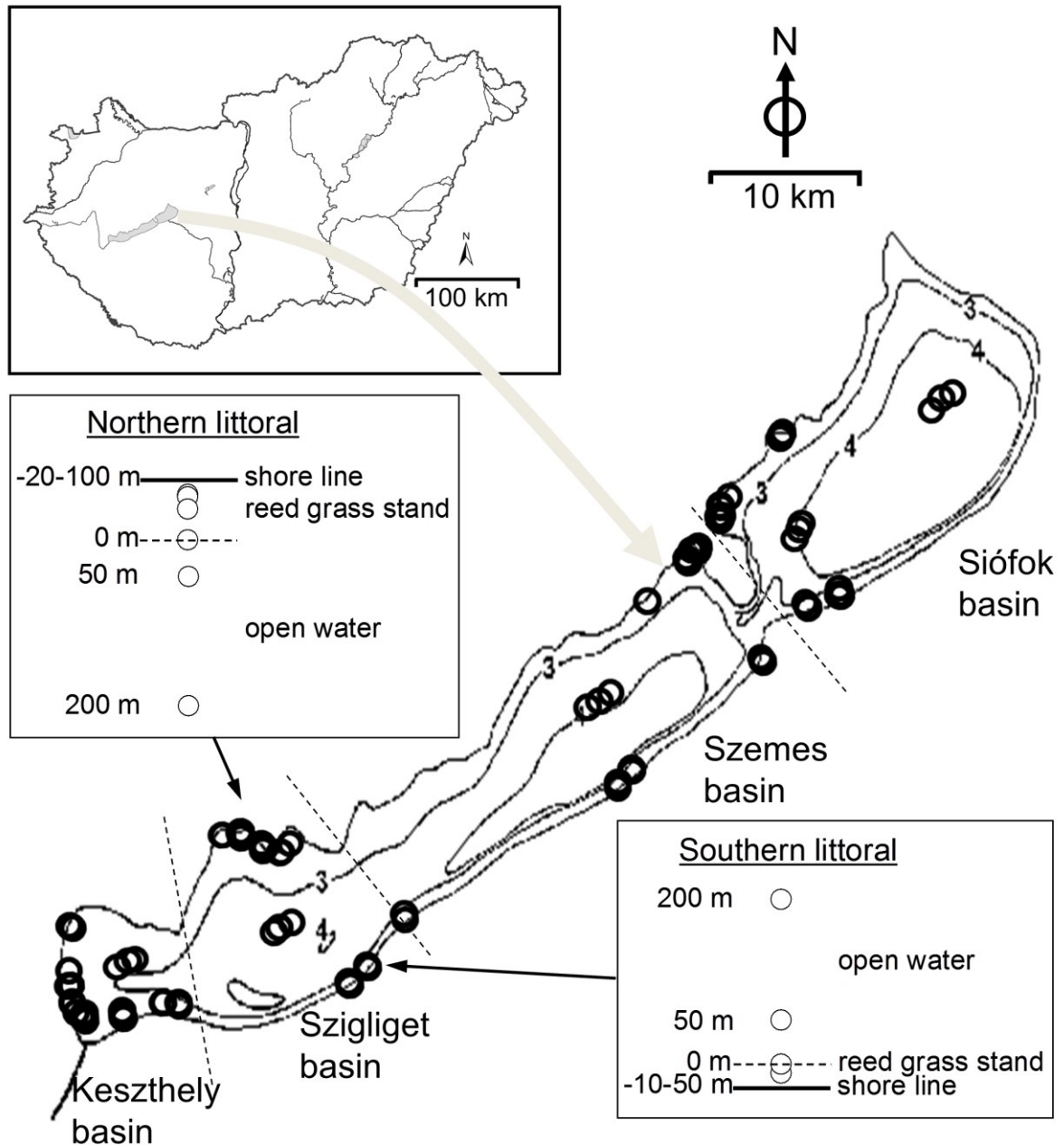
669

670 **Fig. 3.** Additive (a) and multiplicative (b) partitioning of taxon richness and additive  
671 partitioning of Shannon index (c) of sediment-dwelling chironomids by habitat type, indirect  
672 spatial (i.e. lake-scale geographical variables) and direct environmental gradients in Lake  
673 Balaton (Hungary) at two hierarchical sampling scales: sample ( $\alpha$  and  $\beta_1$ ) and environmental  
674 gradient ( $\beta_2$ ; habitat type, environmental gradients). The relative importance of each  
675 individual gradient in chironomid diversity was characterized by the difference and ratio  
676 between the observed and expected  $\beta_2$ -diversity in the additive and multiplicative approaches,  
677 respectively. Note that in the multiplicative model of taxon richness  $\beta$ -diversity components  
678 are unitless. Note also that since all habitat type and gradient based analyses were performed  
679 on the same 128 samples,  $\alpha$ - and  $\gamma$ -diversities are constant in both additive and multiplicative  
680 taxon richness models (8.2 and 40 taxa, respectively;  $\alpha$ -diversity is not plotted on Fig. 3b),  
681 and therefore, the product of multiplicative  $\beta_1$  and  $\beta_2$  is constant (4.9) as well. Abbreviations  
682 of spatial and environmental variables are explained in Appendix A.

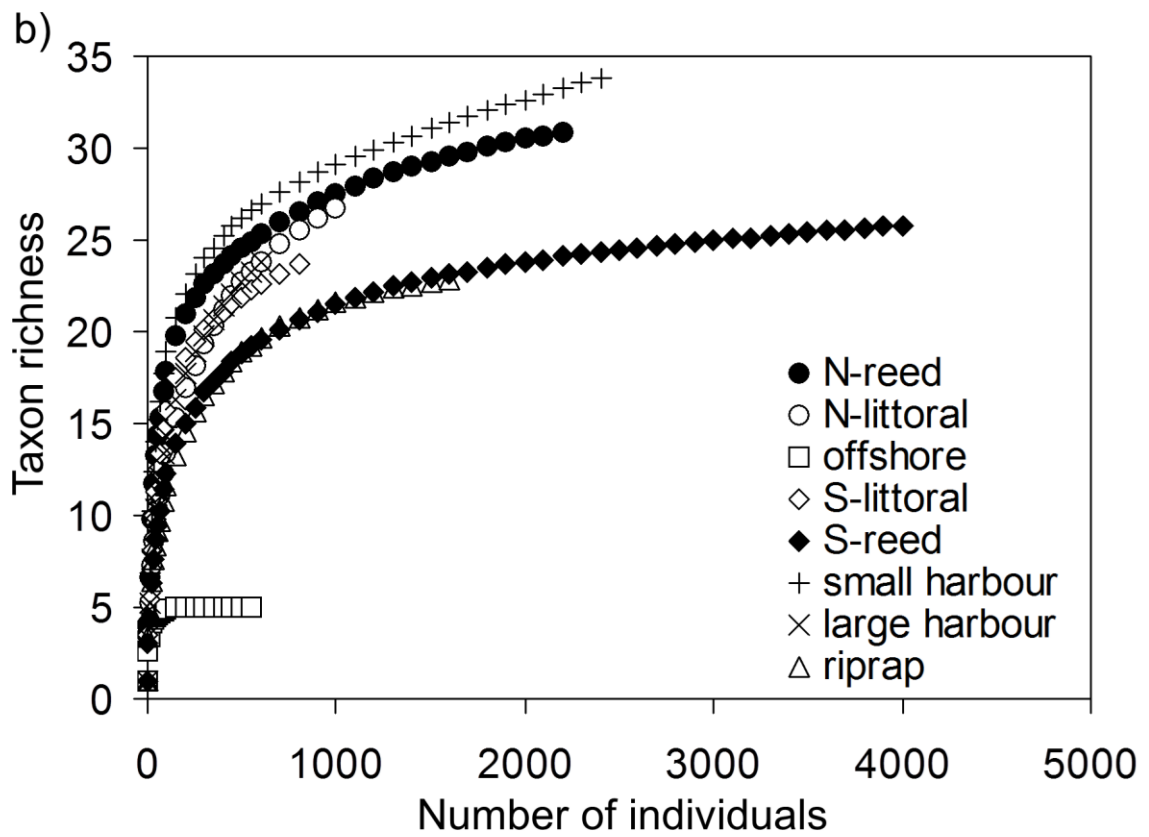
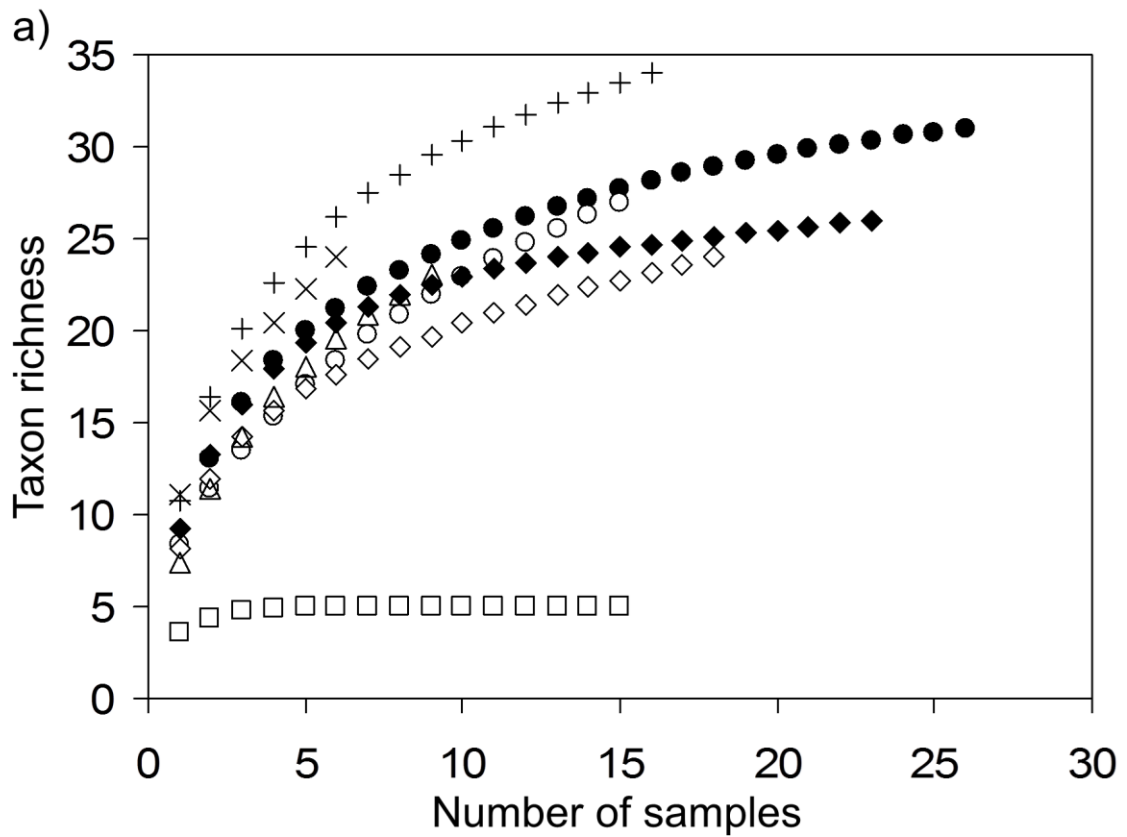
683

684 **Fig. 4.** Additive (a) and multiplicative (b) partitioning of taxon richness and additive  
685 partitioning of Shannon index (c) of sediment-dwelling chironomids by habitat types in Lake  
686 Balaton (Hungary) at the sample scale ( $\alpha$  and  $\beta_1$ ). The relative importance of among sample  
687  $\beta_1$ -diversity in each individual habitat type was characterized by the difference and ratio

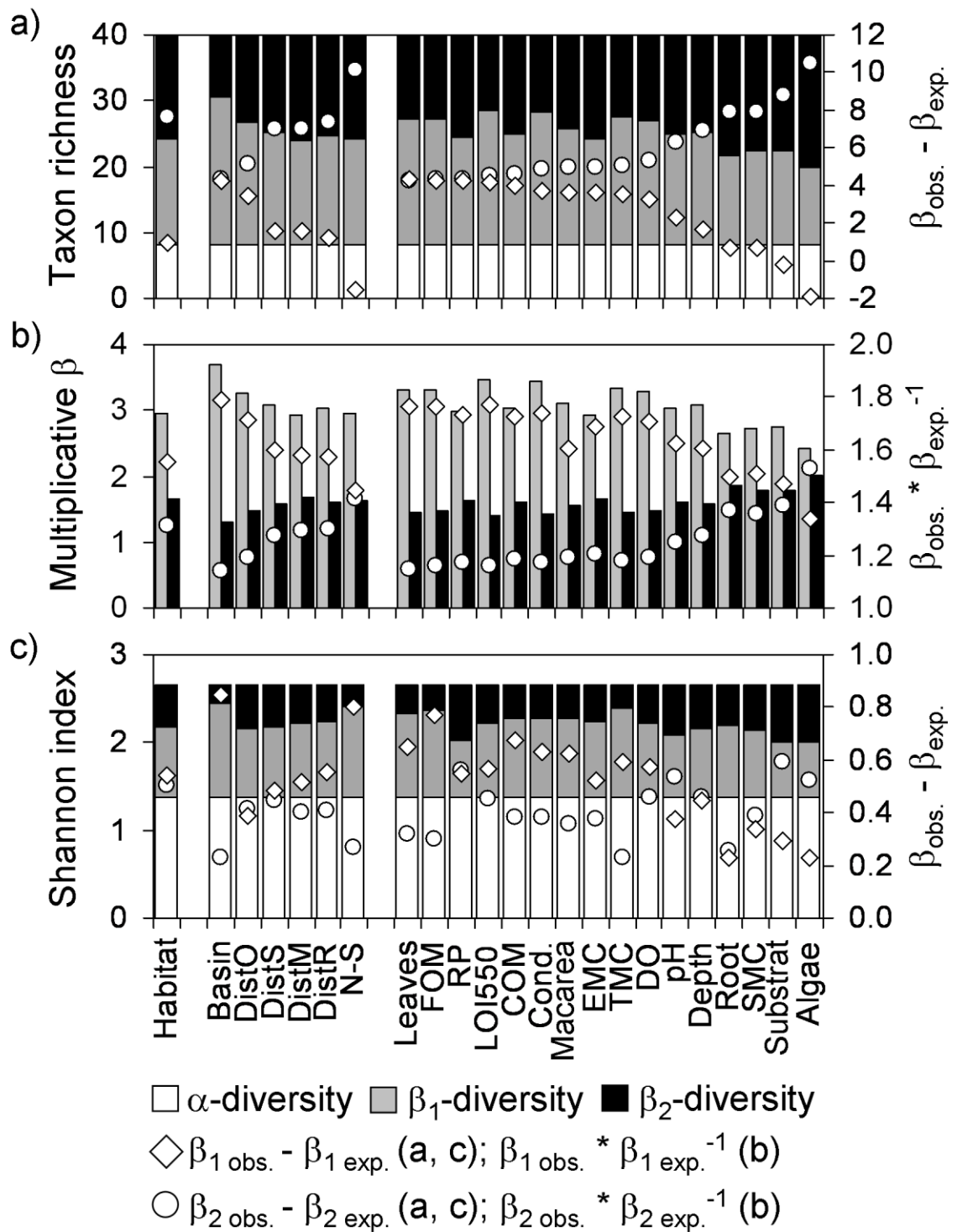
688 between the observed and expected  $\beta_1$ -diversities in the additive and multiplicative  
 689 approaches, respectively. Note that  $\alpha$  has the same value in additive and multiplicative taxon  
 690 richness models, and thus, it is not plotted on Fig. 4b. Note also that in the multiplicative  
 691 model of taxon richness  $\beta$ -diversity components are unitless. The  $\alpha$ -diversity varied  
 692 significantly among habitat types (ANOVA,  $df=7,12$ ,  $P<0.001$ ) and statistically homogenous  
 693 groups (Tukey HSD post hoc test,  $P<0.05$ ) are indicated by lettering on Fig. 4a and 4c.

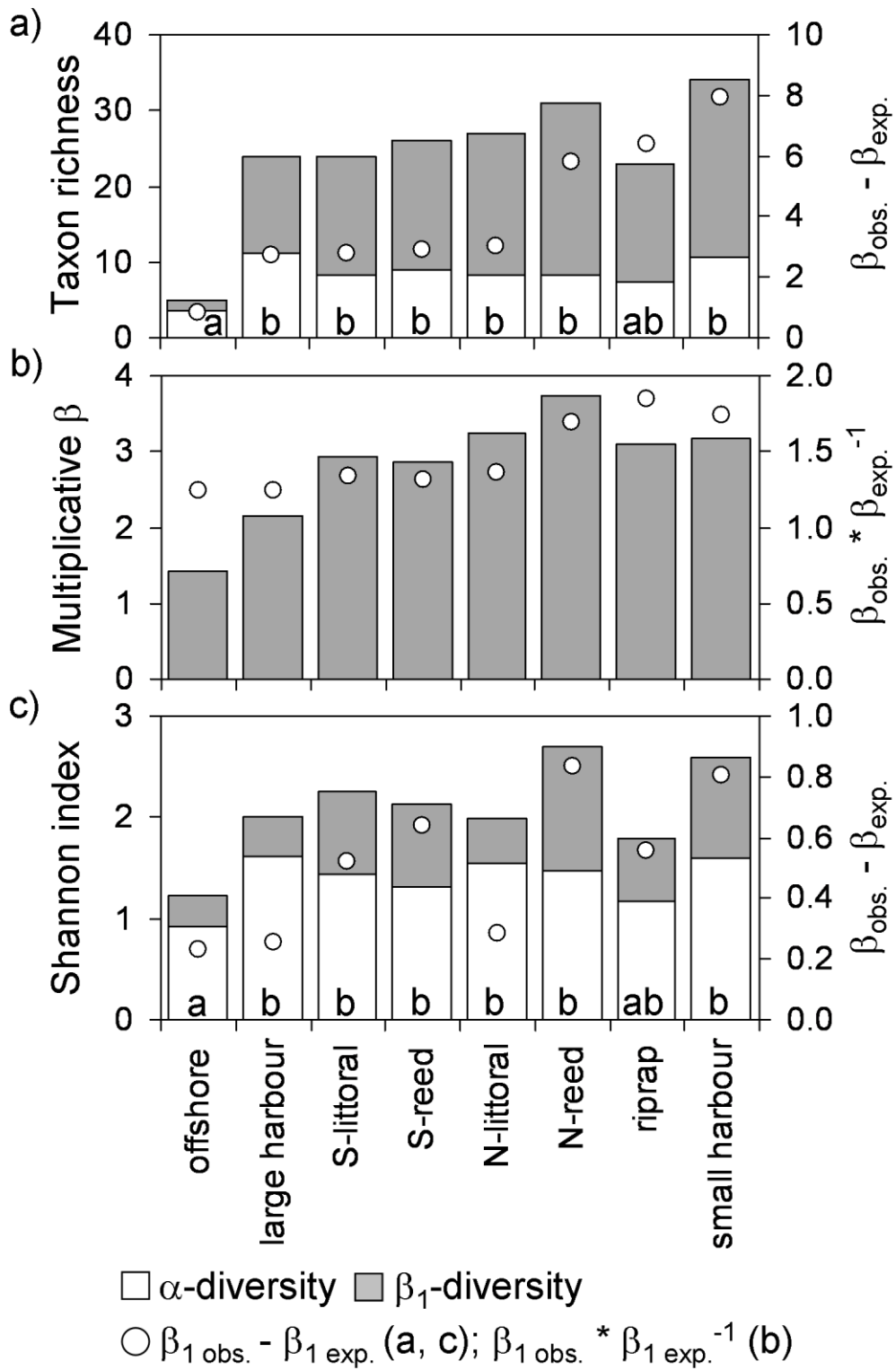


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**Table 1**

Results of the ANOVA statistics comparing mean sample level species richness ( $\alpha$ -diversity) of sediment-dwelling chironomids among ranges (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 environmental gradients in Lake Balaton, Hungary. In case of significant main effect, mean sample level species richness of classes were compared with Tukey HSD *post-hoc* test and statistically homogenous groups (at  $P < 0.05$ ) are indicated by lettering. Abbreviations of spatial and environmental variables are explained in Appendix A.

Environmental gradient	ANOVA									
	F	df <sub>numerator</sub>	df <sub>denominator</sub>	P	Class 1 mean $\pm$ SD	Class 2 mean $\pm$ SD	Class 3 mean $\pm$ SD	Class 4 mean $\pm$ SD	Class 5 mean $\pm$ SD	Class 6 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 <sup>b</sup>	3.5 $\pm$ 0.5 <sup>a</sup>	8.9 $\pm$ 3.2 <sup>b</sup>				
DistR	7.0	5,122	<0.001	8.9 $\pm$ 3.8 <sup>b</sup>	9.9 $\pm$ 3.5 <sup>b</sup>	9.6 $\pm$ 3.6 <sup>b</sup>	7.6 $\pm$ 3.9 <sup>b</sup>	9.0 $\pm$ 3.1 <sup>b</sup>	3.5 $\pm$ 0.5 <sup>a</sup>	
DistM	6.9	5,122	<0.001	9.2 $\pm$ 4.0 <sup>b</sup>	8.7 $\pm$ 3.5 <sup>b</sup>	8.6 $\pm$ 4.6 <sup>b</sup>	8.6 $\pm$ 2.8 <sup>b</sup>	5.3 $\pm$ 3.5 <sup>ab</sup>	3.5 $\pm$ 0.5 <sup>a</sup>	
DistO	3.0	5,122	0.015	7.7 $\pm$ 3.8 <sup>ab</sup>	4.0 $\pm$ 2.0 <sup>a</sup>	9.2 $\pm$ 3.4 <sup>ab</sup>	10.5 $\pm$ 2.3 <sup>b</sup>	9.7 $\pm$ 4.7 <sup>b</sup>	9.2 $\pm$ 3.2 <sup>ab</sup>	
DistS	6.4	5,122	<0.001	8.9 $\pm$ 4.8 <sup>b</sup>	8.5 $\pm$ 3.7 <sup>b</sup>	9.6 $\pm$ 3.7 <sup>b</sup>	8.4 $\pm$ 3.6 <sup>b</sup>	8.3 $\pm$ 2.7 <sup>ab</sup>	3.5 $\pm$ 0.5 <sup>a</sup>	
Local environmental variables										
Depth	5.8	5,122	<0.001	7.6 $\pm$ 3.5 <sup>b</sup>	9.5 $\pm$ 3.7 <sup>b</sup>	9.5 $\pm$ 4.7 <sup>b</sup>	8.9 $\pm$ 3.4 <sup>b</sup>	7.4 $\pm$ 4.1 <sup>ab</sup>	3.6 $\pm$ 0.5 <sup>a</sup>	
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 <sup>ab</sup>	8.0 $\pm$ 3.1 <sup>ab</sup>	10.7 $\pm$ 5.1 <sup>b</sup>	10.5 $\pm$ 4.1 <sup>b</sup>	7.2 $\pm$ 3.5 <sup>a</sup>	7.6 $\pm$ 2.9 <sup>a</sup>	
RP	3.5	5,122	0.005	4.0 $\pm$ 0.0 <sup>ab</sup>	9.3 $\pm$ 2.5 <sup>ab</sup>	9.6 $\pm$ 2.5 <sup>b</sup>	9.6 $\pm$ 3.9 <sup>b</sup>	7.4 $\pm$ 4.2 <sup>ab</sup>	5.9 $\pm$ 3.5 <sup>a</sup>	