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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 α- and β_1-diversity, and environment related β_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 α-diversity was much lower and

25 β_1-diversity higher than predicted by null model and both measures varied substantially

26 among habitat types and along most individual environmental gradients. The β_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 β_2-diversity varied greatly among individual environmental

30 gradients. The difference between the expected and observed β_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

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 conservational 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; Árva 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

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   Árva 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; Árva 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 α-diversity (i.e. local taxon richness and Shannon diversity

89   index) and among sample β_1-diversity vary among *a priori* defined characteristic habitat types

90   of the lake; (2) how sample level α-diversity and among sample β_1-diversity change along the

91   gradient of individual environmental factors (e.g. water depth, substratum type); and (3) to

92   what extent β_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^2; 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^{-1} of Ca^{2+} and Mg^{2+}(HCO$_3$$^-$)$_2$) with a decreasing

102   trophic gradient (i.e. chlorophyll-a concentration from 26.6 to 9.7 µg l^{-1}, 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) 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 macrohytes 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^2), 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[®].

132   Identification was performed to species or the lowest possible taxonomic level (species group

133   to genus; for more details see Árva 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 ≤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 ≥ 80%; 2) both silt and mollusc shells > 20%; 3) both silt and sand > 20%;

156 4) both sand and mollusc shells > 20%; 5) sand ≥ 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 $^{\circ}$C for 72 hours) samples of the upper 2 cm sediment layer according

161 to the loss-on-ignition method at 550 $^{\circ}$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 (γ-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 α-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 $-\Sigma p_i (\ln p_i)$, where p_i is the proportional abundance of

193 taxon i. We tested differences of average α-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 α-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 α- and two β-diversity components to total chironomid

202 diversity (γ-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 γ is the

207 total number of taxa identified in the system (40 taxa in this case), α is the mean number of

208 taxa at individual sampling sites, β_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 β_2

210 corresponds to variation of taxon composition among habitat types and levels of individual
211 environmental gradients. Note that α is the same in the additive and multiplicative models,
212 whereas the value and unit of β-diversity differs between the two models (β is unitless in the
213 multiplicative model). While the Shannon diversity index naturally partitions into
214 independent and additive α and β components (Jost, 2007). Observed values of α- and β-
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 α- and particular β-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 (γ) chironomid diversity, individual environmental gradients were ranked according to
222 the difference ($\beta_{2\,observed} - \beta_{2\,expected}$) and ratio ($\beta_{2\,observed} * \beta_{2\,expected}^{-1}$) between the observed and
223 expected β_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 γ-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; γ-diversity of
232 taxon richness) of chironomids belonging to three subfamilies: Tanypodinae (7 taxa),
233 Orthocladiinae (4 taxa) and Chironominae (29 taxa). Total Shannon (γ-) diversity proved to be
234 2.66. Detailed list of captured taxa, their numbers of individuals and habitat uses are
235 presented in Árva 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, *Tanypus 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*

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 (β₁-diversity)

276

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 $\beta_{2observed} * \beta_{2expected}^{-1}$) 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

310   the captured total diversity is due to β-diversity components. Sample level α-diversity

311   accounted for only 20.5% of within lake diversity. This value is very similar to sample level

312   macroinvertebrate α-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 α and β-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 α and hierarchical β-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 α-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%; α-diversity) and among sampling unit variability (47.2%; β_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 α-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 β-diversity into two components, to β_2-diversity which is directly related to

335   various attributes of environmental heterogeneity and to β_1-diversity which represents

336   unexplained among site variability. Both β 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 β_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 α-

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 β-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. β_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 β-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 β-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 β_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 β 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 β-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) β_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 β_2-

424   diversity level) will be displayed as β_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 β-

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 β-diversity. Consequently, the independent effect of dispersal

434   limitation in site-to-site species turnover will also be included in β_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 (α-diversity) and

440   which dimensions of environmental heterogeneity support the highest species turnover (i.e. β-

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,

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.

Acknowledgements

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654

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.
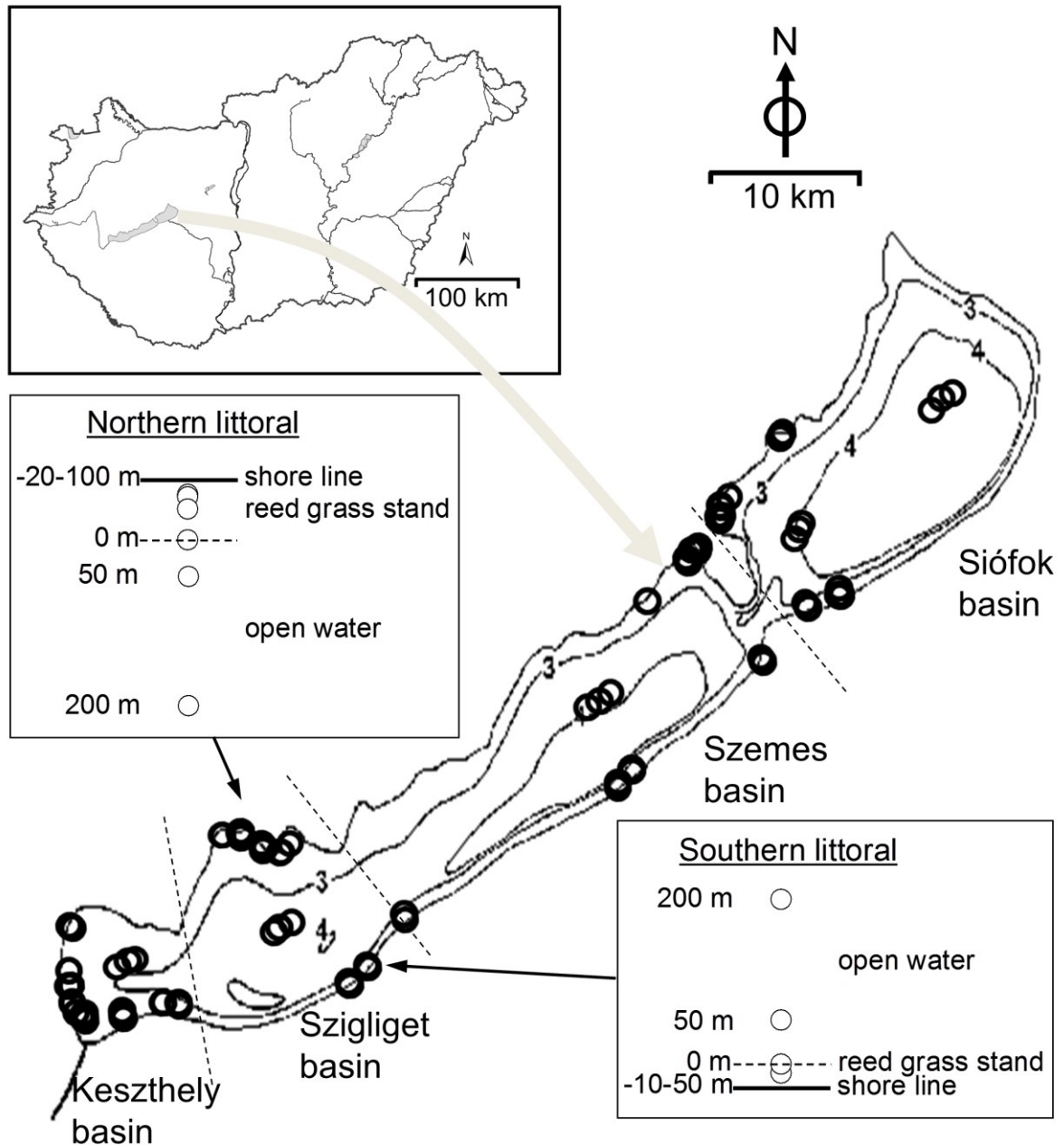
Fig. 3. Additive (a) and multiplicative (b) partitioning of taxon richness and additive partitioning of Shannon index (c) of sediment-dwelling chironomids by habitat type, indirect spatial (i.e. lake-scale geographical variables) and direct environmental gradients in Lake Balaton (Hungary) at two hierarchical 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.
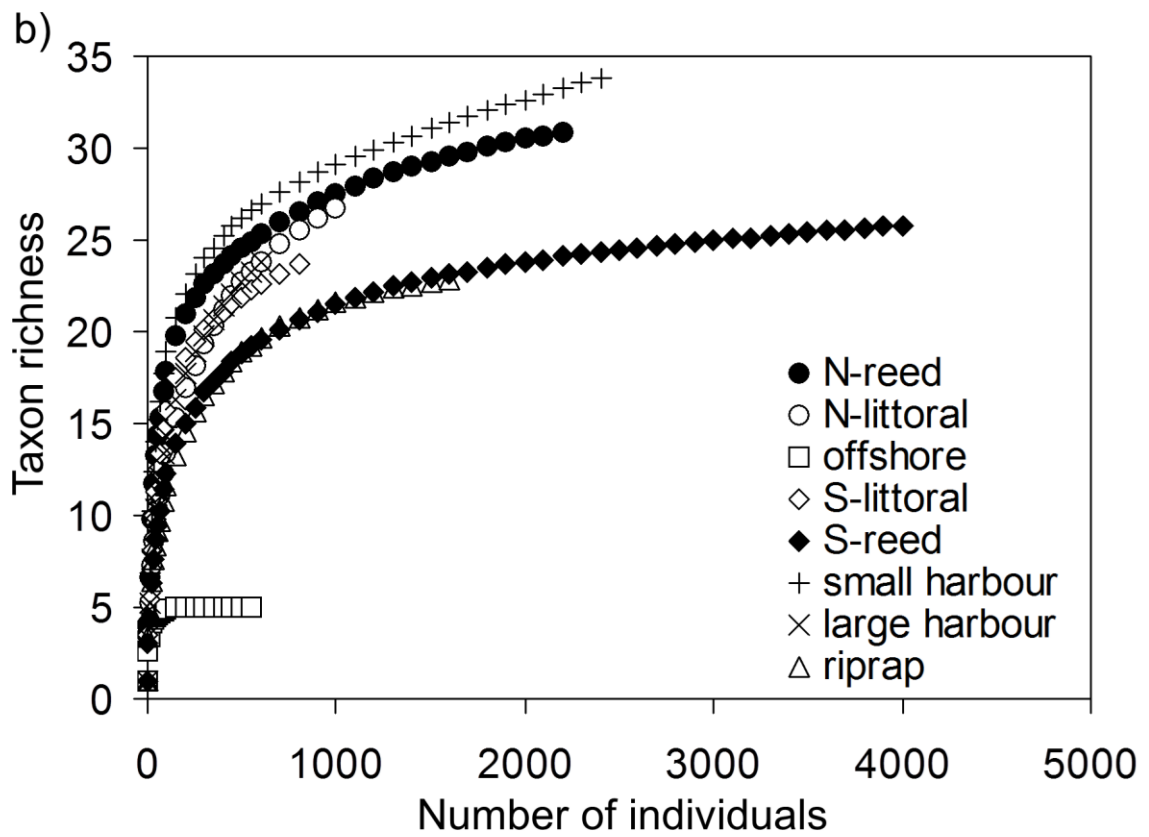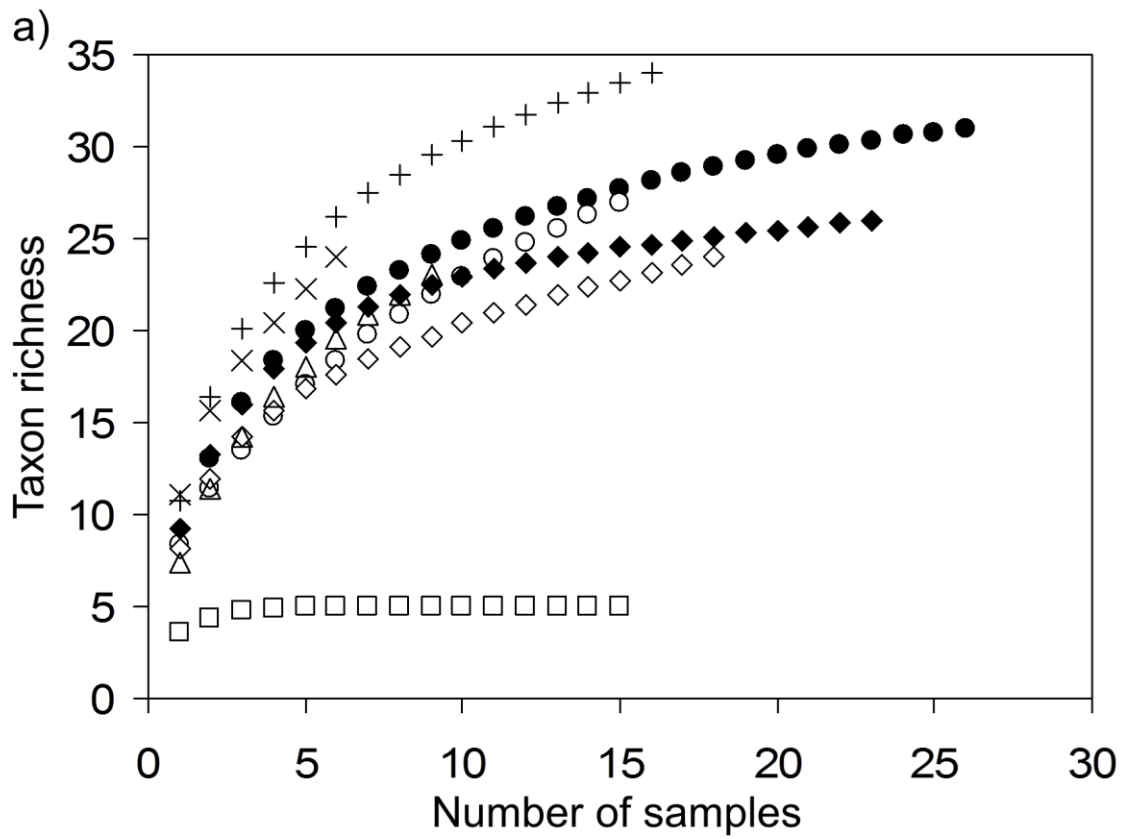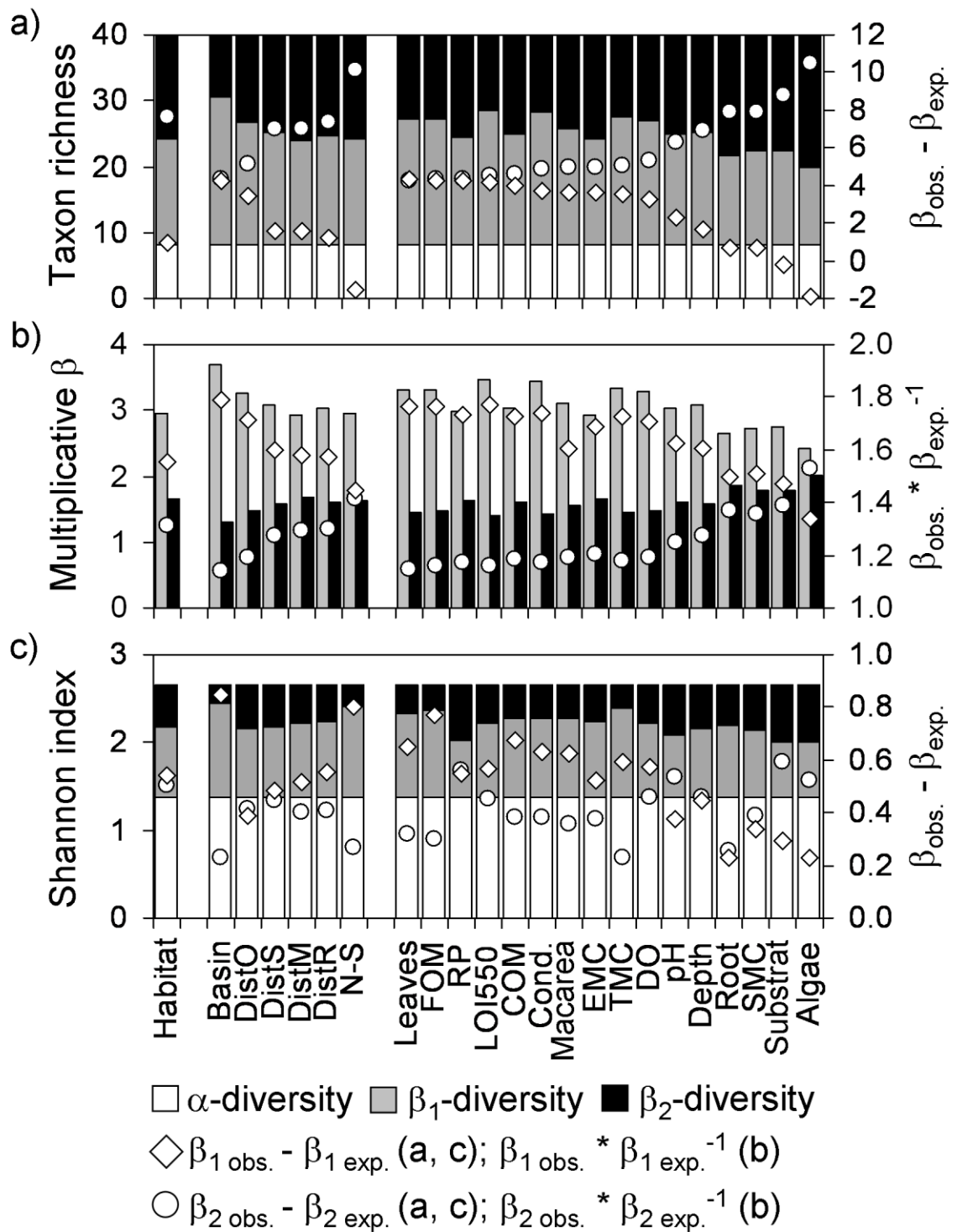
Fig. 4. Additive (a) and multiplicative (b) partitioning of taxon richness and additive partitioning of Shannon index (c) of sediment-dwelling chironomids by habitat types in Lake Balaton (Hungary) at the sample scale (α and β_1). The relative importance of among sample β_1-diversity in each individual habitat type was characterized by the difference and ratio

688 between the observed and expected β_1-diversities in the additive and multiplicative

689 approaches, respectively. Note that α 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 β-diversity components are unitless. The α-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.

694

a)

b)

695

a)

b)

c)

Taxon richness
Multiplicative β
Shannon index

$\beta_{obs.} - \beta_{exp.}$
$\beta_{obs.} * \beta_{exp.}^{-1}$
$\beta_{obs.} - \beta_{exp.}$

Habitat | Basin | DistO | DistS | DistM | DistR | N-S | Leaves | FOM | RP | LOI550 | COM | Cond. | Macarea | EMC | TMC | DO | pH | Depth | Root | SMC | Substrat | Algae

□ α-diversity   ▨ β₁-diversity   ■ β₂-diversity

◇ β₁ obs. − β₁ exp. (a, c); β₁ obs. * β₁ exp.⁻¹ (b)

○ β₂ obs. − β₂ exp. (a, c); β₂ obs. * β₂ exp.⁻¹ (b)

696

a)

b)

c)

offshore
large harbour
S-littoral
S-reed
N-littoral
N-reed
riprap
small harbour

□ α-diversity ■ β₁-diversity

○ $\beta_{1\,obs.} - \beta_{1\,exp.}$ (a, c); $\beta_{1\,obs.} * \beta_{1\,exp.}^{-1}$ (b)
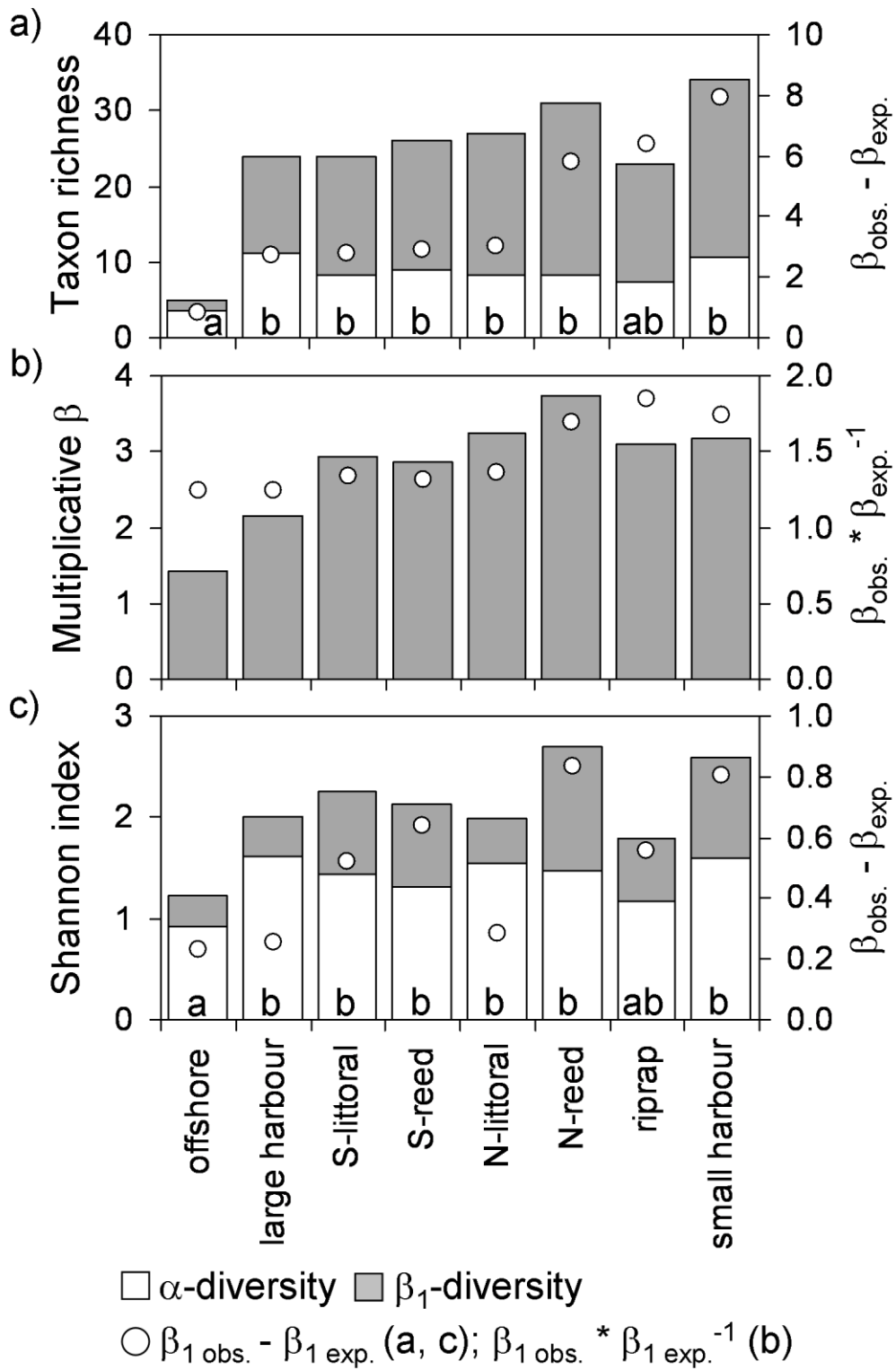
697

Table 1

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