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

2   chironomid assemblages

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10

11   **Abstract**

12

13   Understanding the distribution of biotic diversity across various spatial scales and

14   environmental gradients is important from fundamental, practical and conservation biological

15   aspects. We applied a hierarchical diversity partitioning framework to quantify the variability

16   of sample level α- and β_1-diversity, and environment related β_2-diversity of benthic

17   chironomid assemblages within and among *a priori* defined habitat types, and along the

18   gradients of individual environmental factors in a large and shallow lake (Lake Balaton,

19   Hungary). Taxon richness (both additive and multiplicative) and Shannon index based

20   diversity approaches yielded highly concordant results. The α-diversity was much lower and

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

22   among habitat types and along most individual environmental gradients. The β_2-diversity

23   indicated a marked variability of taxon (identified at species to genus level) pool among

24   habitat types and higher than predicted taxon turnover along all examined environmental

25   gradients. Moreover, the observed β_2-diversity varied greatly among individual environmental

26   gradients. The difference between the expected and observed β_2-diversity values suggests that

27   taxon turnover was most influential (in decreasing order) along the algae coverage gradient,

28   the lake bed substratum gradient and the macrophyte coverage gradient among others. We

29   argue that within-lake environmental heterogeneity and its effect on the taxon richness should

30   receive more attention in biodiversity assessment and conservation. Management could

31   benefit from the identification of within lake gradients along which taxonomic turnover

32   maximizes.

33

34   *Keywords:* beta diversity, diversity partitioning, species accumulation, species richness,

35   species turnover, within lake environmental gradient.

36

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

71 diverse environmental optima and tolerances and relatively good dispersal ability in their

72 winged terrestrial adult phase (Armitage, 1995). Thus according to metacommunity theory

73 (Leibold et al., 2004; Cottenie, 2005; Beisner et al., 2006) environmental filtering (i.e. species

74 sorting) shapes their fine scale species distribution patterns, while the role of spatial processes

75 (i.e. dispersal limitation) become influential in their assemblage organization only at broad

76 geographical scales (Mykrä et al., 2007; Landeiro et al., 2012; Heino, 2013a, 2013b; but see

77 Árva et al., 2015). Accordingly, in lakes with high environmental heterogeneity a substantial

78 part in their species turnover could be related directly to habitat types and environmental

79 gradients due to inter-specific separation of species optima and tolerance ranges (Rae, 2004;

80 Puntí et al., 2009; Árva et al., 2015). Thus not just relative abundance patterns but also

81 species turnover rates can predictably differ among various within lake environmental

82 gradients. To our knowledge, however, there are no studies comparing the role of species

83 turnover along various within lake environmental gradients. Specific aims of the study are to

84 analyse: (1) how sample level α-diversity (i.e. local taxon richness and Shannon diversity

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

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

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

88 what extent β_2-diversity among the habitat types and along particular environmental gradients

89 contribute to total chironomid diversity of the lake.

90

91 **Materials and methods**

92

93 *Study area*

94

95 Balaton is the largest shallow lake (surface area: 596 km^2; mean depth: 3.2 m) in Central

96 Europe, situated at 46° 42' - 47° 04' N, 17° 15' - 18° 10' E and 104.8 m above sea level (Fig.

97 1). The lake is slightly alkaline (400 mg l^{-1} of Ca^{2+} and Mg^{2+}(HCO$_3^-$)$_2$) with a decreasing

98 trophic gradient (i.e. chlorophyll-a concentration from 26.6 to 9.7 µg l^{-1}, mean data of 2008-

99 2012; Ministry of Environmental Protection and Water Management of Hungary,

100 http://www.ktm.hu/balaton/lang_en/index.htm) from SW to NE along its longitudinal axis

101 (see also Istvánovics et al., 2007). Based on habitat characteristics, Lake Balaton can be

102 divided into a little variable open water area spreading to >85% of the lake with silt substrate,

103 largely homogeneous physico-chemical features and with no macrovegetation, and to a much

104 heterogeneous littoral zone exhibiting marked environmental gradients along the distance

105   from shore, water depth, macrophyte coverage, swash exposition (i.e. the northern littoral is

106   much less affected by wind induced waves than the southern littoral) and human impact

107   including the establishment of artificial habitat types as well (measured ranges of

108   environmental gradients are shown in Appendix A). Today only about 47% of the lake shore

109   is covered by emergent macrovegetation (dominant species is reed grass *Phragmites*

110   *australis*), whereas submerged macrohytes form loose and sporadic stands in the littoral zone.

111   Significant sections (>50%) of the shore have been protected with concrete or rocks (artificial

112   habitat covered by rocks hereafter referred to as riprap) which are generally covered by

113   filamentous algae (mainly *Cladophora* sp.) up to 0.5 m water depth. Several large, and many

114   small boat harbours were built along the lake for commercial and recreational purposes.

115

116   *Chironomid sampling and identification*

117

118   Benthic chironomid assemblages were sampled at 128 sites between 26 June and 13 July

119   2012 (Fig. 1). The sites were distributed across the whole lake and covered all ranges of

120   habitat and environmental gradients (see below). Three merged Ekman grab sediment samples

121   were taken per site (total sampled area per site: $0.036 \ m^2$), washed through a 0.25 mm mesh

122   sieve and transported to the laboratory in a cooling box. Riprap habitats were sampled by

123   cleaning and washing algal coating and sediment from a measured rock surface corresponding

124   to area of Ekman grab samples into plastic containers. Chironomids were separated from

125   sediment samples alive by sugar flotation method (Anderson, 1959), and euthanized and

126   preserved in 70% ethanol for later identification. Chironomids were digested in KOH

127   (potassium hydroxide) to eliminate non-chitinous tissues and slide-mounted in Euparal®.

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

129   to genus; for more details see Árva et al., 2015).

130

131   *Habitat assessment and environmental factors*

132

133   Parallel to chironomid sampling, we measured a series of environmental factors (Appendix

134   A) that have been found influential on the distribution of chironomids (e.g. Real et al., 2000;

135   Rae, 2004; Free et al., 2009; Puntí et al., 2009; Tóth et al., 2012). To cover all environmental

136   gradients in the lake, first, the position of each sampling site was characterized with six lake-

137   scale geographical variables including lake basin (i.e. Keszthely-, Szigliget-, Szemes- and

138   Siófok-basins), location along the north-to-south transect of the lake (i.e. northern littoral,

139   offshore and southern littoral) and distances from shore, emergent macrophyte, submerged

140   and floating leaved macrophytes and open water. Then, we recorded 16 local environmental

141   factors. We measured water depth, redox potential of the uppermost sediment layer, and

142   dissolved oxygen, pH and conductivity of the water close to the bottom. Visual estimates of

143   emergent (dominantly reed grass), submerged and floating leaved macrophytes and

144   filamentous algae (*Cladophora* sp.) coverage (%) were made within a circle of 3 m diameter

145   around the origin of chironomid samples and the area of the submerged and floating leaved

146   macrophyte stands were recorded by GPS and calculated by MapSource version 6.16.3.

147   software (Garmin Ltd., Olathe, US, www.garmin.com). The substratum of the lake bed was

148   inspected for percentage composition of clay (grain size ≤0.002 mm), silt (0.002-0.06 mm),

149   sand (0.06-2 mm), rock (>200 mm) and mollusc shell (5-25 mm; mainly *Dreissena*

150   *polymorpha* (Pallas, 1771) and *D. bugensis* (Andrusov, 1897), and then classified into six

151   categories: 1) silt ≥ 80%; 2) both silt and mollusc shells > 20%; 3) both silt and sand > 20%;

152   4) both sand and mollusc shells > 20%; 5) sand ≥ 80%; and 6) rock = 100% (i.e. ripraps). The

153   sediment was examined for occurrence of pure reed grass root (characteristic in some

154   degrading reed grass stands) and fine and coarse decomposing organic matter particles and

155   reed grass leaves and rated on a six category scale (0-5). Relative organic matter content was

156   assessed from dry (at 50 $^\circ$C for 72 hours) samples of the upper 2 cm sediment layer according

157   to the loss-on-ignition method at 550 $^\circ$C for 1 hour (LOI550; Heiri et al., 2001).

158

159   *Statistical analysis*

160

161   We ran two parallel analyses to explore the distribution of chironomid diversity in the lake.

162   In the first, we examined how biodiversity is distributed within and among eight *a priori*

163   distinguished habitat types. The habitat types were as follows: 1) northern reed grass stand; 2)

164   northern reed-free littoral area; 3) offshore area without macrophyte; 4) southern reed-free

165   littoral area; 5) southern reed grass stand; 6) small boat harbour rounded by reed grass; 7)

166   large commercial harbour sheltered by riprap; and 8) riprap (lake side, exposed to swash).

167   Then, samples were also classified according to their positions along the gradient of each

168   individual environmental factor. These environmental factors were either *ab ovo* recorded at

169   six category scales (except lake basin with four and location along the north-to-south transect

170   of the lake with three categories) or divided to six intervals later in the data analyses.

171   Environmental gradients measured on percentage scales were directly divided to six equal

172   intervals. The remaining continuous factors were logarithmic transformed first and divided to

173   six equal intervals afterwards. Rationale of the logarithmic transformation was to decrease the

174   weight of underrepresented extreme environmental ranges and to obtain a more balanced

175   distribution of samples across gradient levels.

176   Since observed number of taxa is a function of sampling effort, thus taxon richness cannot

177   be directly compared between samples differing in sampling effort in any respect (Gotelli and

178   Colwell, 2001). Therefore, we examined the relationship between the sampling effort and

179   observed taxon richness by sample- and individual based rarefaction analyses (10,000

180   permutations) performed with EcoSim 7.72 software (Gotelli and Entsminger 2011). Rarefied

181   taxon richness enables to assess the adequacy of sampling effort in term of taxa detection (i.e.

182   species accumulation curve reaches an asymptote when all taxa in the system are captured)

183   and comparing taxon richness (γ-diversity) between groups of samples (i.e. habitat types) with

184   unequal sample sizes (Gotelli and Colwell, 2001).

185   For the purpose of this study, we defined α-diversity as the taxon richness and Shannon

186   diversity of individual sampling sites (i.e. three merged Ekman grab samples per site).

187   Shannon diversity index (*H*) emphasises abundance ratios of taxa (dominant and rare taxa are

188   weighted equally) and was calculated as $-\Sigma p_i (\ln p_i)$, where p_i is the proportional abundance of

189   taxon *i*. We tested differences of average α-diversity among sample groups (i.e. habitat types

190   and levels of environmental gradients) by analysis of variance (ANOVA) supplemented with

191   Tukey HSD post hoc test in case of significant factor effect. We also investigated the pattern

192   of α-diversity along each continuous environmental factor by using series of regression tools

193   (results not shown for brevity), however, the only significant relationship we found was the

194   slight decreasing tendency of taxon richness with increasing water depth and related

195   environmental gradients (i.e. increasing distances from shore, from emergent macrophyte and

196   from submerged and floating leaved macrophytes).

197   Relative contribution of local α- and two β-diversity components to total chironomid

198   diversity (γ-diversity) was investigated based on hierarchical diversity partitioning

199   framework, comparing observed patterns with null model distributions (Crist et al., 2003;

200   Gering et al., 2003). We considered both additive and multiplicative approaches of taxon

201   richness organization (Lande, 1996; Veech et al., 2002) dividing total observed diversity into

202   the following components: $\gamma = \alpha + \beta_1 + \beta_2$ and $\gamma = \alpha \times \beta_1 \times \beta_2$, respectively, where γ is the

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

204   taxa at individual sampling sites, β_1 corresponds to the variation in taxon composition among

205   sampling sites of a particular habitat type and level of a given environmental gradient, and β_2

206 corresponds to variation of taxon composition among habitat types and levels of individual

207 environmental gradients. Note that α is the same in the additive and multiplicative models,

208 whereas the value and unit of β-diversity differs between the two models (β is unitless in the

209 multiplicative model). While the Shannon diversity index naturally partitions into

210 independent and additive α and β components (Jost, 2007). Observed values of α- and β-

211 diversity components were tested against null model distributions obtained from individual

212 based unrestricted randomizations (10,000 randomizations) in the software package

213 PARTITION 3 (Veech and Crist, 2009). Specifically, it was tested whether the observed

214 values of α- and particular β-diversity components significantly differed from chance. A more

215 detailed description of the null model generation and the randomization procedure is provided

216 by Crist et al. (2003). To evaluate the relative importance of different environmental gradients

217 in total (γ) chironomid diversity, individual environmental gradients were ranked according to

218 the difference ($\beta_{2\ observed}$-$\beta_{2\ expected}$) and ratio ($\beta_{2\ observed} * \beta_{2\ expected}^{-1}$) between the observed and

219 expected β_2 values in additive (i.e. species richness and Shannon index) and multiplicative

220 (i.e. species richness) diversity partitioning approaches, respectively.

221

222 **Results**

223

224 *Chironomid assemblages and γ-diversity*

225

226   Sampling of diverse array of microhabitats in Lake Balaton yielded a total of 13,804

227 individuals and 40 taxa (identified at species, species group and genus levels; γ-diversity of

228 taxon richness) of chironomids belonging to three subfamilies: Tanypodinae (7 taxa),

229 Orthocladiinae (4 taxa) and Chironominae (29 taxa). Total Shannon (γ-) diversity proved to be

230 2.66. Detailed list of captured taxa, their numbers of individuals and habitat uses are

231 presented in Árva et al. (2015). Briefly, the chironomid fauna of Lake Balaton is comprised of

232 widely distributed taxa being characteristic for shallow, medium to high productivity,

233 temperate standing waters. Assemblage composition varied markedly among habitat types

234 and across environmental gradients and could be classified into four major type groups: (1)

235 *Cladopelma virescens* (Meigen, 1818), *Chironomus balatonicus* Dévai, Wüelker & Scholl,

236 1983, *Tanypus kraatzi* (Kieffer, 1918), *Chironomus dorsalis* Meigen, 1818 and

237 *Paratanytarsus* sp. were indicator taxa for the northern littoral sites and both small and large

238 boat harbours with macrovegetation; (2) *Cricotopus reversus* Hirvenoja, 1973, *Cricotopus*

239 *sylvestris* gr. and *Orthocladius oblidens* (Walker, 1856) were characteristic at ripraps; (3)

240 *Procladius choreus* (Meigen, 1804), *Microchironomus tener* (Kieffer, 1918) and *Tanypus*

241 *punctipennis* Meigen, 1818 dominated in the offshore macrophyte-free areas; and (4)

242 *Cladotanytarsus mancus* gr., *Cryptochironomus defectus* (Kieffer, 1913) and

243 *Stictochironomus* sp. occurred mainly in the southern, sandy littoral.

244   The four singleton (*Monopelopia tenuicalcar* (Kieffer, 1918), *Endochironomus tendens*

245 (Fabricius, 1775), *Parachironomus vitiosus* (Goetghebuer, 1921) and *Polypedilum sordens*

246 (van der Wulp, 1875) and one doubleton taxa (*Zavreliella marmorata* (van der Wulp, 1859))

247 indicated the importance of rare species in the total species pool. In addition, rarefaction

248 curves did not reach evident asymptotes, indicating that further sampling would probably

249 yield more taxa (Fig. 2).

250   Sample based rarefaction curves revealed that taxon richness varied among habitat types.

251 Taxon richness was the lowest in the offshore area with five taxa and highest in small boat

252 harbours situated in reed grass stands with 34 taxa (Fig. 2a). The rarefaction curves of other

253 habitat types did not separate markedly (i.e. their 95% CI ranges overlapped; note that for

254 clarity CIs are not shown on Fig. 2) from each other. Individual based rarefaction curves

255 supported the separation of the species poor offshore area, while the outstanding diversity of

256 small boat harbours was not justified (Fig. 2b).

257

258 *Local (α-) diversity*

259

260   At the lake level, observed α-diversity of taxon richness (mean: 8.2 taxa; Fig. 3) was less

261 than half of the predicted value (16.8 taxa) suggesting that there is a substantial non-random

262 pattern in the distribution of chironomid taxa across sampling sites. The mean number of taxa

263 per sampling site was significantly lower in the offshore area (3.5±0.5; mean±SD) than in

264 other habitat types, which showed similar values (7.4-11.0; means; Fig 4a). Mean taxon

265 richness of sites also varied significantly among gradient levels in 13 of the 22 investigated

266 environmental factors (Table 1), but no general trends were found.

267   Shannon α-diversity (mean: 1.38; Fig. 3) was also significantly less than the predicted

268 value (2.34), and its patterns showed good agreement with patterns of taxon richness across

269 habitat types (Fig. 4) and levels of environmental gradients.

270

271 *Among sites variability (β₁-diversity)*

272

273   Both additive and multiplicative diversity partitioning models revealed that among sample

274 β_1-diversity of taxa richness was larger than expected by chance alone across habitat types

275 and along most individual environmental gradients (Fig. 3). In addition, β_1-diversity was also

276 larger than expected within each habitat type (Fig. 4). Although β_1-diversity using the

277 Shannon index also proved to be higher than expected by chance, the result suggested a bit

278 different picture on the relative importance of β_1-diversity for some habitat types and

279 particular environmental gradients than that found for taxon richness.

280

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

282

283   Based on the additive taxon richness partitioning model, β_2-diversity was about 7.6 taxa

284 larger than predicted across habitats indicating a marked difference in species pools among

285 habitat types (Fig. 3a). Similarly, significant taxon turnover was revealed along all examined

286 environmental gradients with β_2-diversity values 4.2 to 10.5 taxa larger than expected.

287 Difference between the expected and observed β_2-diversity values indicated that taxon

288 turnover was most influential (in decreasing order) along algae coverage, lake bed substratum,

289 submerged and floating leaved macrophytes coverage, presence of reed grass root, distances

290 from emergent macrophyte, from submerged and floating leaved macrophytes and from

291 shore, water depth and pH gradients. Multiplicative taxon richness partitioning fully

292 supported the above results, however, the rank of individual gradients was slightly different in

293 term of divergence (expressed as $\beta_{2observed} * \beta_{2expected}^{-1}$) of observed from the expected β_2-

294 diversity (Fig. 3b). Although β_2-diversity using the Shannon index also proved to be higher

295 than expected by chance the result differed somewhat from the above picture (Fig. 3c). In

296 general, taxon richness based approach related larger part of the total diversity to β levels,

297 while diversity captured by the Shannon index was more concentrated at α level and with

298 relatively low amount of variability related to β_2 level.

299

300 **Discussion**

301

302   The present study is the first to compare distribution of within lake chironomid diversity

303 across *a priori* defined habitat types and along various individual environmental gradients.

304 Based on an extensive sampling representing the environmental heterogeneity of Lake

305 Balaton, we found low local taxon richness (sample level α-diversity) indicating that most of

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

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

308   macroinvertebrate α-diversity of 23% observed across the littorals of three Finnish lakes

309   (Suurkuukka et al., 2012), but it is much higher compared to 5–8% values obtained by

310   Stendera and Johnson (2005) for littoral macroinvertebrates across 677 Swedish lakes.

311   However, both latter studies were based on kick-samples which cover larger effective

312   sampling area and are with different selectivity than our Ekman grab samples. It is well

313   known that patterns of α and β-diversities are scale dependent and therefore the definition of

314   "local" diversity affects diversity partitioning (Matias et al., 2010; Beck et al., 2012) and the

315   relative importance of α and hierarchical β-diversity components (Schmera and Erős, 2008).

316   Nevertheless, lake sediment surface covered by Ekman grab can be considered as a standard

317   sampling unit in benthic macroinvertebrate studies, and thus, generally serves as the basis for

318   biodiversity assessment (sample level α-diversity; e.g. Free et al., 2009; Jyväsjärvi et al.,

319   2012; Molozzi et al., 2013). By using a sampling methodology comparable to ours, Molozzi

320   et al. (2013) found that most of macroinvertebrate diversity was related to sampling unit

321   (43.7%; α-diversity) and among sampling unit variability (47.2%; $β_1$-diversity), while only

322   little taxon turnover occurred among regions and reservoirs in Brazil. Surprisingly, we did not

323   find any characteristic trend in sample level α-diversity along within lake environmental

324   gradients, except that considerably less taxa occurred in the offshore samples than in littoral

325   sites. This result may indicate that at the lake scale different structuring processes are likely to

326   dominate than at broad geographical scales where much longer environmental gradients act

327   including climatic gradients (e.g. Nyman et al., 2005; Kraft et al., 2011). Compared with the

328   results of species richness, Shannon index provided a slightly different picture and revealed

329   the role of taxa relative abundances with giving more weight to sample level diversity.

330   We divided β-diversity into two components, to $β_2$-diversity which is directly related to

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

332   unexplained among site variability. Both β components were generally larger than expected

333   by chance alone based on either taxon richness or Shannon index. As we expected species

334   richness varied considerably across habitat types and high $β_2$-diversity indicated a significant

335   taxon turnover along this scale. Although largest part of Lake Balaton (ca. 85% of the total

336   lake area) is a macrophyte free offshore (open water) area, only 12.5% of the total identified

337   chironomid taxa inhabited this habitat, and as supported by the results of the rarefaction

338   analyses, no further taxa are likely to occur there. In addition, the relatively high ratio of α-

339   diversity (70.6%) within the total species richness indicated that taxa distribute much more

340 homogeneously within this habitat type than in others. Based on the low representation of

341 species in the offshore habitat, we suggest the better consideration of littoral habitats in

342 monitoring and bioassessment. The outstanding role of the littoral habitat heterogeneity in the

343 biotic diversity is also strongly supported by other macroinvertebrate groups (Muskó, 1992;

344 Muskó et al., 2007; 2010) and fish (Specziár et al., 2013) in Lake Balaton.

345   Unexpectedly, we observed the highest taxon richness in small boat harbours, a modified

346 habitat type with very small spatial extent relative to total lake area. Most of the taxa

347 identified in the lake were present here and rarefaction analyses suggested that further taxa are

348 likely to present. These findings seem to contradict with general knowledge on the

349 deteriorating effect of human induced habitat alteration on biological diversity (Ehrlich, 1988;

350 Moyle and Leidy, 1992; Dudgeon et al., 2006). The high species richness of this habitat type

351 may be explained by its high environmental heterogeneity (i.e. diverse submerged

352 macrophyte flora) and food richness (i.e. decomposing plant material and attached bacterial

353 flora). It is likely that small scale habitat alterations can actually increase overall

354 environmental heterogeneity in unstructured large lakes by establishing new habitat types. For

355 instance, boat harbours are sheltered from swash and have high submerged vegetation

356 coverage with very heterogeneous structure and high organic matter concentration, while

357 ripraps provide extremely well oxygenated algae meadows with high swash disturbance.

358 Similar microhabitats were very scarce or absent in pristine Lake Balaton. Artificial habitats

359 (i.e. ripraps and concrete and timber constructions of boat harbours) are also important

360 substrates for several crustacean and mollusc taxa, and thus, had a significant influence on the

361 macroinvertebrate community of Lake Balaton (Muskó et al., 2010). Although species

362 richness is a function of habitat area and structural complexity (Drakare et al., 2006; Thrush et

363 al., 2010; Triantis and Sfenthourakis, 2012; Hamerlík et al., 2014) our results reflect that

364 habitat heterogeneity is a much more influential factor in the within lake diversity of

365 chironomid assemblages than the area of habitat types.

366   Substantial proportion of the observed β-diversity was related to specific attributes (i.e.

367 local environmental factors) of among sites environmental heterogeneity in Lake Balaton.

368 This finding is congruent with our previous results (Árva et al., 2015), which showed that

369 optima and tolerances of chironomid species separate along some individual environmental

370 gradients, like lake bottom algae coverage, substratum physical attributes (i.e. percentage of

371 silt) and submerged macrophyte coverage. Moreover, Árva et al. (2015) have shown that

372 assemblage composition is related to some environmental gradients, and assemblage structure

373 and environmental conditions suggested substantially different habitat groups for Lake

374 Balaton. Present results also proved that the observed taxon turnover (i.e. β_2-diversity)

375 markedly varied among environmental gradients. By scaling our sampling sites along several

376 alternative dimensions (i.e. individual factors) of environmental heterogeneity, we identified

377 few individual environmental gradients (i.e. algae coverage, lake bed substratum, submerged

378 and floating leaved macrophyte coverage and presence of reed grass root on the sediment

379 surface), which explained higher proportion of overall β-diversity than did the *a priori*

380 defined habitat types. This result suggests that the application of gradient based approaches

381 can be useful at fine spatial scales as well, and they may yield more direct information on

382 diversity patterns and the underlying processes than conventional diversity partitioning

383 approaches based on hierarchical spatial units (i.e. lake area) or subjective habitat types.

384   The highest rates of taxon turnover were found along the algae coverage gradient, the lake

385 bed substratum gradient and the submerged and floating leaved macrophyte coverage

386 gradient. Coverage of algae increases towards decreasing water depth, more compact

387 substratum (i.e. sand and rock) and less decomposed organic matter, and also coincides with

388 higher oxygen concentration in Lake Balaton. The role of algae coverage is well known in the

389 distribution of chironomids (Čerba et al., 2010; Tóth et al., 2013). Increasing algae coverage

390 causes a characteristic shift in assemblage structure towards the dominance of *C. sylvestris* gr.

391 and *C. reversus* in Lake Balaton (Árva et al., 2015). Substratum heterogeneity is an important

392 driver of macroinvertebrate β-diversity (Stoffels et al., 2005; Ligeiro et al., 2010; Hepp et al.,

393 2012; Suurkuukka et al., 2012), and it is well known that benthic chironomid taxa have

394 different substratum preferences (Wolfram 1996; Fesl 2002; Rae 2004; Árva et al., 2015). In

395 Lake Balaton, most chironomid taxa prefer soft, silty substratum and their abundances

396 strongly decrease or they even disappear towards harder substratum such as sand and rock.

397 Sites with sandy bottom clearly separated from other sites by their assemblages dominated by

398 *C. mancus* gr.; *C. defectus* and *Stictochironomus* sp. While, riprap habitats with rock

399 substratum also have individual assemblages characterised by *C. sylvestris* gr., *C. reversus*

400 and *O. oblidens* (Árva et al., 2015). It is known that macrophytes have diverse effect on

401 chironomid assemblages as they influence habitat structure and heterogeneity, physico-

402 chemical properties of the water and the sediment and food conditions (e.g. Ali et al., 2007;

403 Bogut et al., 2007). Submerged and floating leaved macrophyte coverage was most preferred

404 by *Parachironomus varus* (Goetghebuer, 1921) and *Parachironomus* sp., while avoided by

405 e.g. all Tanypodinae species, *C. reversus* and *O. oblidens* (Árva et al., 2015).

406   Significant proportion of the total diversity was unexplained β_1-diversity indicating an

407 aggregated species distribution, which is independent on the structuring effect of the habitat

408 or environmental gradients captured by particular higher β levels. Unlike in relative

409 abundance based approaches (Cushman and McGarigal, 2002; Peres-Neto et al., 2006), we do

410 not have an appropriate statistical tool that enables decomposing overall β-diversity in means

411 of taxonomic richness or Shannon index into multiple parallel components related to series of

412 environmental stressors (only the effect of hierarchical factors can be tested). This is a

413 problem because environmental gradients generally are not independent from each other, and

414 therefore, their effects can overlap. For example, we found that algae coverage tended to

415 increase towards harder lake bed substratum (i.e. sand and rock) and to decrease with

416 increasing water depth. Consequently, (1) β_2-diversity related to a specific environmental

417 gradient will include both the pure and shared effects of the concerning environmental factor

418 and these two effects are not separable, (2) independent effects of all concurrent

419 environmental factors that are not included in the analysis (i.e. as the factor that specifies β_2-

420 diversity level) will be displayed as β_1-diversity. Therefore, in order to understand

421 organization of biotic diversity more completely, we suggest examining the distribution of

422 diversity in alternative hierarchical sampling designs (i.e. spatial scale vs. various direct

423 environmental gradients). Dispersal limitation is another potential mechanism influencing β-

424 diversity especially at broader geographical scales (Palmer et al., 1996; Thrush et al., 2010;

425 Logue et al., 2011). The relevance of dispersal limitation was also indicated in Lake Balaton

426 using direct gradient analysis based on relative abundance data (Árva et al., 2015). However,

427 regarding true diversity measures (i.e. species richness and Shannon index), to our

428 knowledge, there is no appropriate statistical tool that could enable dissecting the effect of

429 dispersal limitation from overall β-diversity. Consequently, the independent effect of dispersal

430 limitation in site-to-site species turnover will also be included in β_1-diversity.

431   From a conservation biological point of view, direct gradient based diversity partitioning

432 could be beneficial and supplement the traditional approach based on pure spatial hierarchy of

433 samples (e.g. sample, lake-area, lake, geographical region; Gering et al., 2003; Stendera and

434 Johnson, 2005) especially at finer spatial scales like for example within a lake. Assemblage

435 level conservation needs assessing which habitats support most species (α-diversity) and

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

437 diversity). While at broad geographical scales taxon turnover is much dependent on habitat

438 connectivity and dispersal processes, at finer spatial scale the role of environmental filtering

439 becomes more dominant. Our results suggest that for maintaining diverse macroinvertebrate

440 assemblages care should be taken to maintain a diversity of natural environmental gradients,

441 besides protecting the most natural habitat types, because environmental gradients play a

442 critical role in shaping taxon turnover.

443   In conclusion, our analyses prove the high importance of non-random β-diversity

444 components which are related to various within lake environmental gradients in shaping the

445 total taxon richness and Shannon diversity of chironomids. We argue that within-lake

446 heterogeneity and its effect on true diversity measures should receive more attention in

447 biodiversity assessment even in studies analysing diversity patterns and underlying

448 mechanisms at broad spatial scales (e.g. ecoregion and biographical region). The

449 comprehensive information on how biotic diversity is structured across multiple scales and

450 how taxon turnover rate varies among different within-lake environmental gradients could be

451 used to identify the appropriate area for conservation.

452

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454

460

461 **References**

462

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650

651 **Figure captions**

652

653 **Fig. 1.** Distribution of sampling sites in Lake Balaton, Hungary. Examined habitats included

654 offshore area, natural-like littoral habitat transects from the riparian edge of the reed grass

655 stand towards the macrophyte-free inshore area (typically one to three sites within the reed

656 grass stand, one in the edge of the reed grass stand and the open water, and at 50 and 200 m

657 distances from the reed grass stand; examples of typical northern littoral and southern littoral

658 transects are presented), small boat harbours situated within the reed grass stand, stands of the

659 most characteristic submerged and floating leaved macrophytes, and modified littoral areas,

660 large sailing-vessel and ship harbours, ripraps and nearby littoral areas. The small map of

661 Hungary in the upper left corner indicates the location of Lake Balaton.

662

663 **Fig. 2.** Rarefied number of taxa of sediment-dwelling chironomids as a function of number of

664 samples (a) and number of individuals (b) by habitat types in Lake Balaton, Hungary.
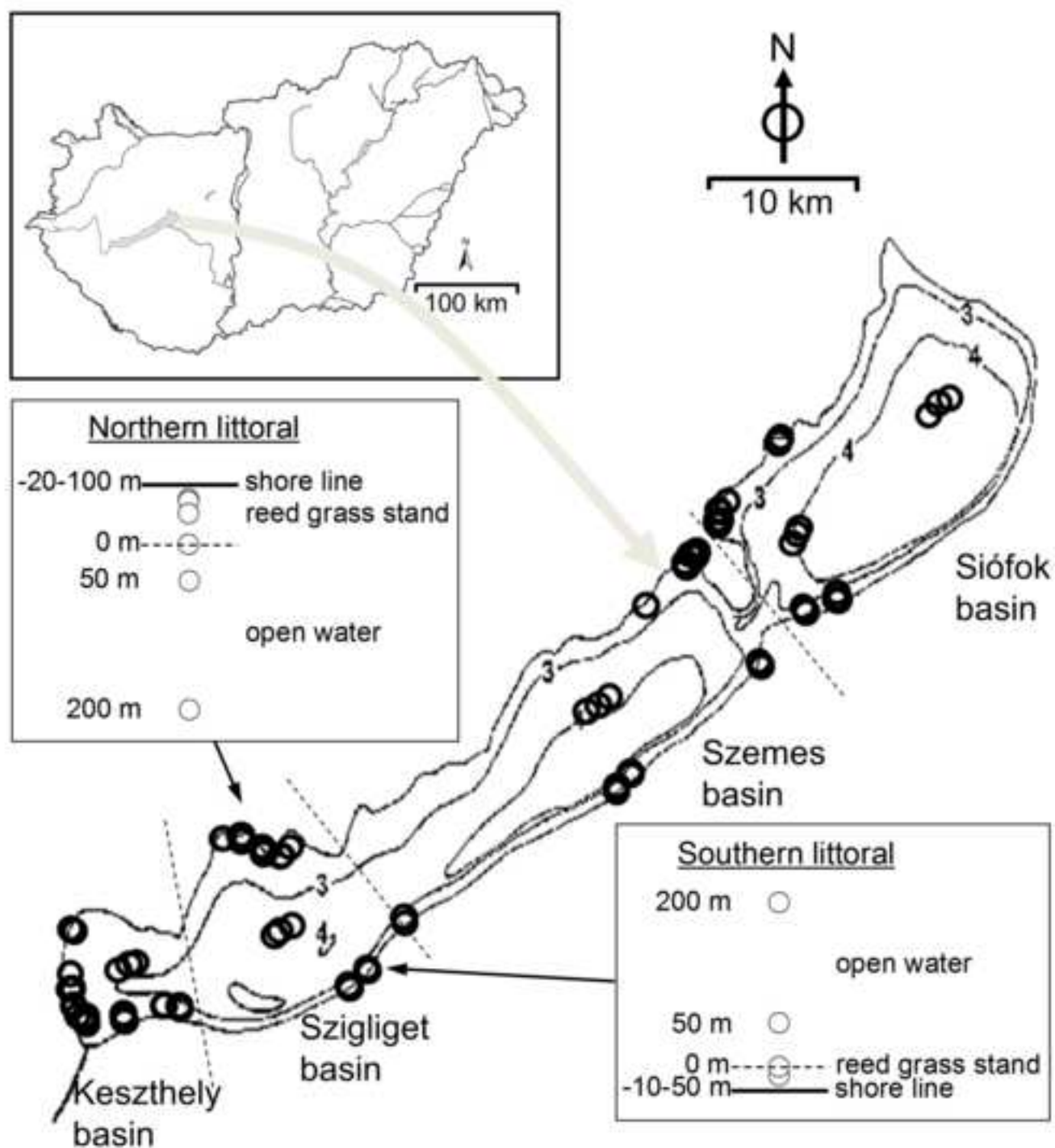
665

666 **Fig. 3.** Additive (a) and multiplicative (b) partitioning of taxon richness and additive

667 partitioning of Shannon index (c) of sediment-dwelling chironomids by habitat type, indirect

668 spatial (i.e. lake-scale geographical variables) and direct environmental gradients in Lake

669 Balaton (Hungary) at two hierarchical sampling scales: sample (α and β_1) and environmental

670 gradient (β_2; habitat type, environmental gradients). The relative importance of each

671 individual gradient in chironomid diversity was characterized by the difference and ratio

672 between the observed and expected β_2-diversity in the additive and multiplicative approaches,

673 respectively. Note that in the multiplicative model of taxon richness β-diversity components

674 are unitless. Note also that since all habitat type and gradient based analyses were performed

675 on the same 128 samples, α- and γ-diversities are constant in both additive and multiplicative

676 taxon richness models (8.2 and 40 taxa, respectively; α-diversity is not plotted on Fig. 3b),

677 and therefore, the product of multiplicative β_1 and β_2 is constant (4.9) as well. Abbreviations

678 of spatial and environmental variables are explained in Appendix A.

679

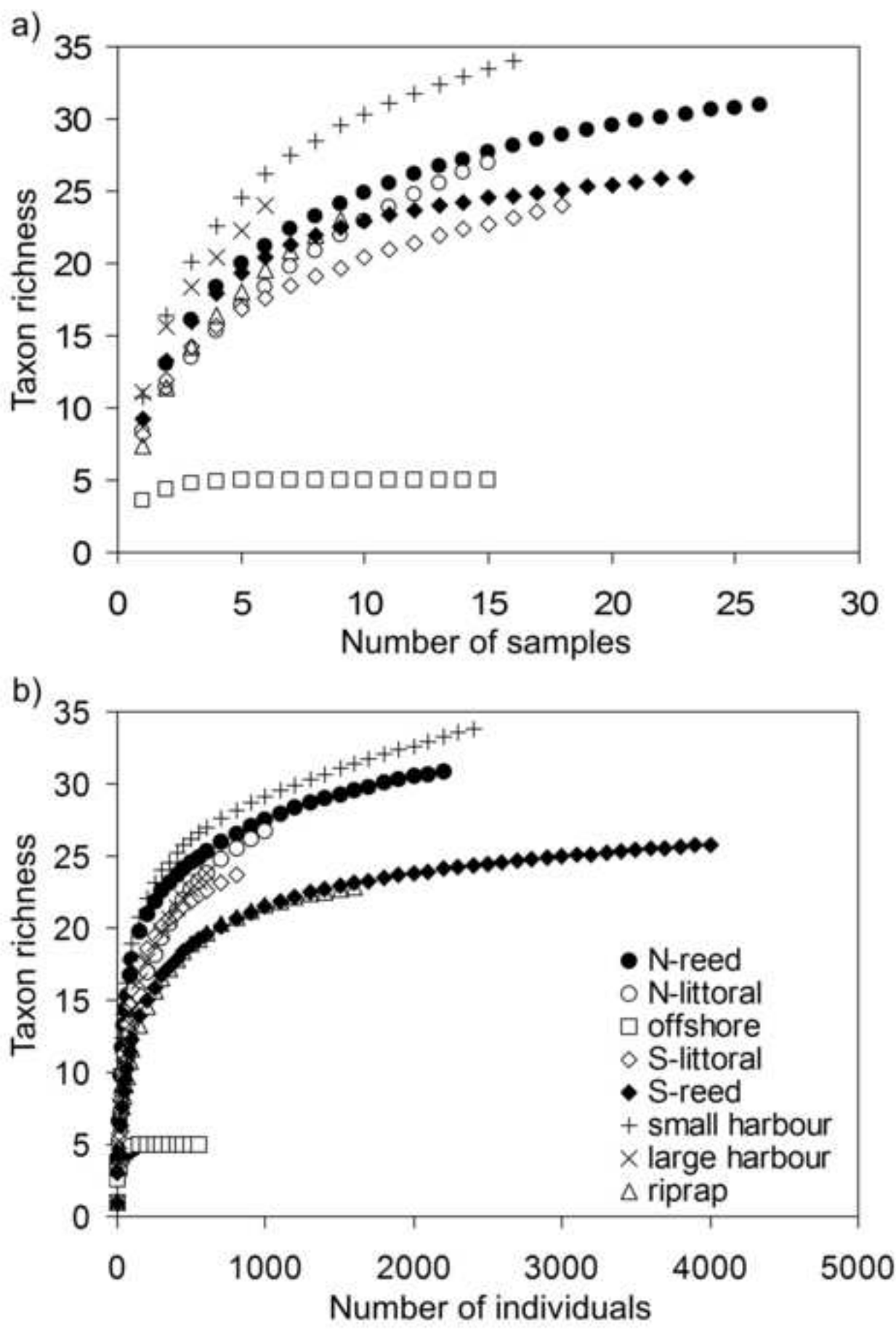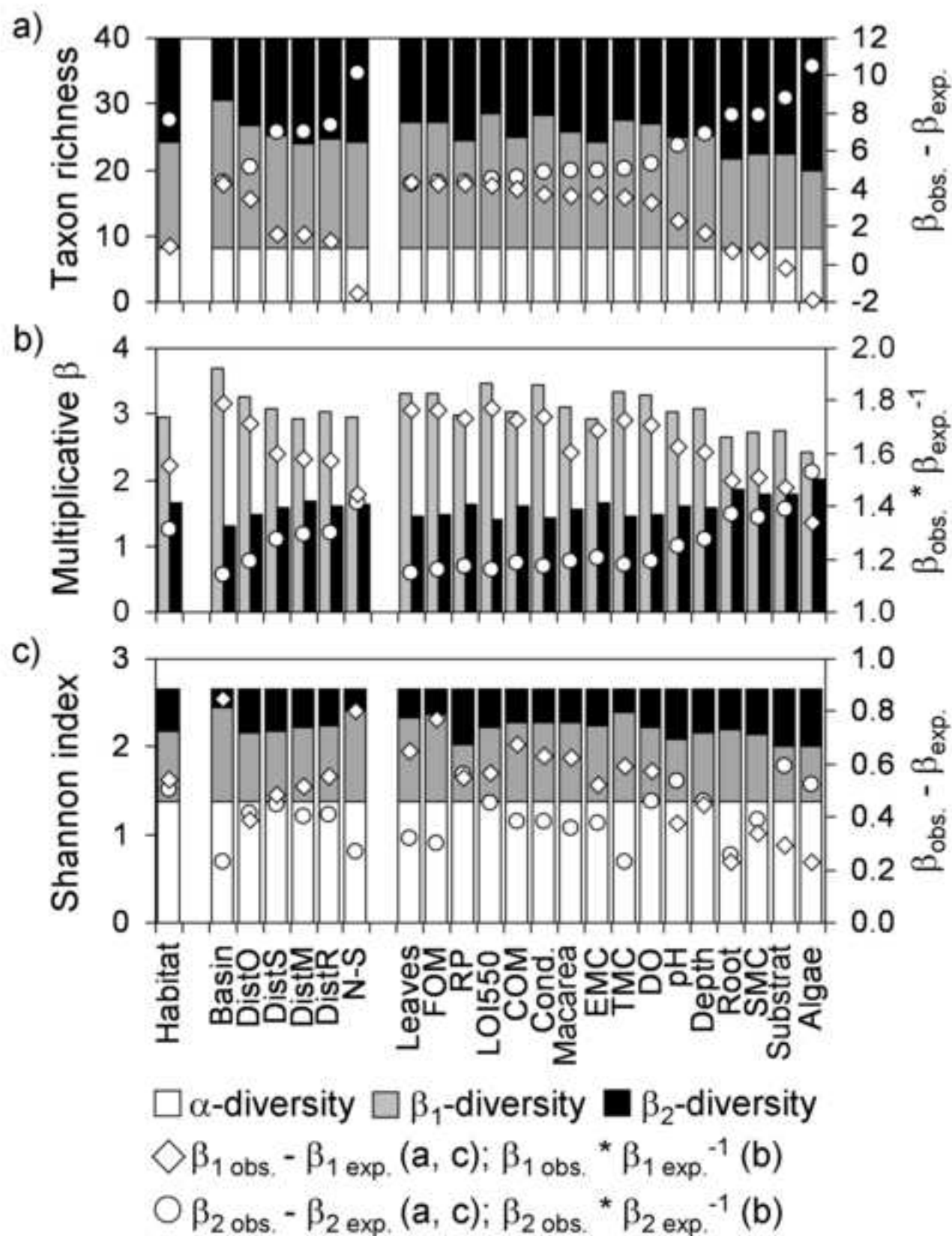680 **Fig. 4.** Additive (a) and multiplicative (b) partitioning of taxon richness and additive

681 partitioning of Shannon index (c) of sediment-dwelling chironomids by habitat types in Lake

682 Balaton (Hungary) at the sample scale (α and β_1). The relative importance of among sample

683 β_1-diversity in each individual habitat type was characterized by the difference and ratio

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

685   approaches, respectively. Note that α has the same value in additive and multiplicative taxon

686   richness models, and thus, it is not plotted on Fig. 4b. Note also that in the multiplicative

687   model of taxon richness β-diversity components are unitless. The α-diversity varied

688   significantly among habitat types (ANOVA, df=7,12, P<0.001) and statistically homogenous

689   groups (Tukey HSD post hoc test, P<0.05) are indicated by lettering on Fig. 4a and 4c.

690

a)

b)

● N-reed
○ N-littoral
□ offshore
◇ S-littoral
◆ S-reed
+ small harbour
× large harbour
△ riprap
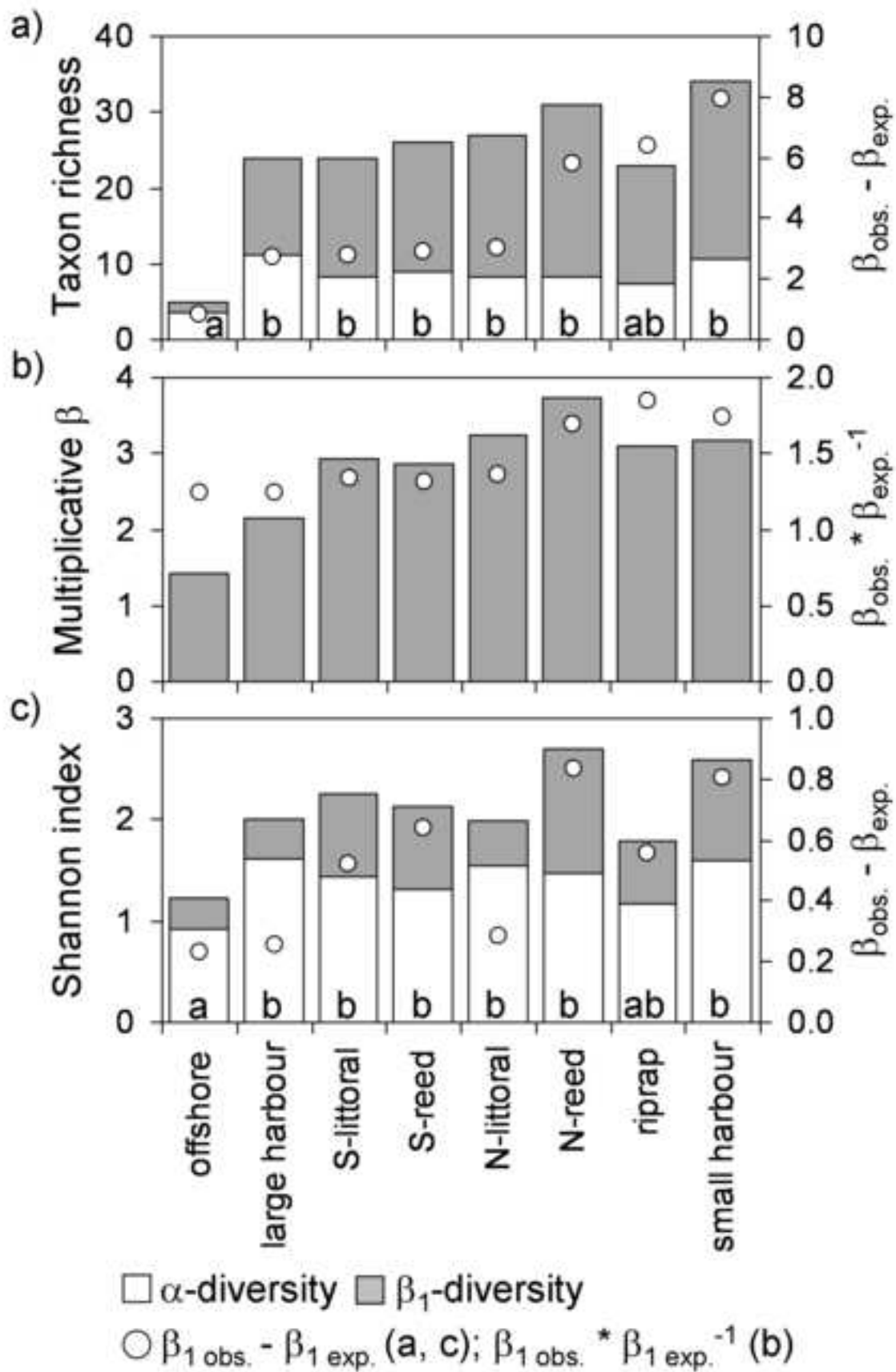
1 **Table 1**

2 Results of the ANOVA statistics comparing mean sample level species richness (α-diversity) of sediment-dwelling chironomids among ranges

3 (classes 1 to 6, except lake basin and north to south transect which had 4 and 3 classes, respectively) of lake-scale geographical and direct

4 environmental gradients in Lake Balaton, Hungary. In case of significant main effect, mean sample level species richness of classes were

5 compared with Tukey HSD *post-hoc* test and statistically homogenous groups (at P<0.05) are indicated by lettering. Abbreviations of spatial and

6 environmental variables are explained in Appendix A.

Environmental gradient	ANOVA 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]

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

7

1 **Appendix A**

2 Within lake environmental gradients considered in this study, their abbreviations and units, and true ranges by resource classes of continuous

3 variables in Lake Balaton, Hungary.

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

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

4 [1] Habitat type classes: 1) northern reed grass stands; 2) northern reed-free littoral zone; 3) offshore area without macrophyte; 4) southern reed-

5 free littoral zone; 5) southern reed grass stands; 6) small boat harbours rounded by reed grass; 7) large commercial harbours sheltered by ripraps;

6 and 8) ripraps.

7 [2] Lake basin classes correspond to the four basins of Lake Balaton from the major inflow River Zala to the only outflow Sió Canal (see also Fig.

8 1).

9 [3] Samples were classified into six subjective categories ranging between zero and the highest observed resource level.