1 **Structuring forces and β-diversity of benthic diatom metacommunities in soda**

2 **pans of the Carpathian Basin**

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Abstract

Small soda lakes represent one of the most vulnerable ecosystem types due to their high hydrological sensitivity to climate change and anthropogenic interventions. Since diatoms are excellent bioindicators, determining the β-diversity and the structuring dynamics of diatom metacommunities can provide valuable information for conservation planning of soda pans. In this study, two diatom metacommunities were surveyed monthly in a one-year period from distinct regions of the Carpathian basin: the Fertő-Hanság National Park (FH) between 2013 and 2014, and the Danube-Tisza Interfluve (DT) between 2014 and 2015. We explored whether β-diversity of diatom assemblages in the two regions is enhanced by species turnover or nestedness (related to richness differences) and investigated the role of deterministic and stochastic processes in shaping β-diversity patterns. Furthermore, we evaluated the contribution of environmental variables, geographic distance and temporal variation to community structure. High β-diversity (> 90%) was revealed for both metacommunities, and was maintained primarily by species turnover. Within the metacommunity of the DT where the natural hydrological cycle of soda pans is not disturbed, diatom communities assembled mainly by the selection force of environment at spatiotemporal scale. In the soda pans located in the habitat reconstruction area of the FH, besides species-sorting, significant temporal variation in community structure appeared due to the water management and periodic water supply. Our results point to the need for a conservation management strategy which maintains the natural hydrological regime of small saline lakes, and therefore their habitat heterogeneity which is of high conservation value.

41   **Key words:** deterministic mechanisms, diatom metacommunities, nestedness, spatial

42   and temporal variation, species-sorting, species turnover

43

Introduction

Inland saline lakes develop typically in endorheic basins (closed drainage basins that retain water) of arid or semi-arid areas, where the precipitation and evaporation are balanced (Williams, 2002). Limnological characteristics of small (< 50 ha), shallow (< 1 m) saline lakes are determined by the degree of precipitation and evaporation (Langbein, 1961), geomorphology (Dargám, 1995) and geochemistry (Simon *et al.*, 2011). Soda lakes (or soda pans) can be distinguished as a specific group of saline lakes with high alkalinity and the dominance of sodium, carbonate and hydrogen carbonate ions (Boros *et al.*, 2013). Soda pans respond sensitively even to relatively small fluctuations of weather and climate, which may result in irreversible changes in their natural properties (Hammer, 1990). Since they are hydrologically sensitive, soda lakes are especially vulnerable and there is an urgent need for conservation management, which focuses on the maintenance or restoration of their natural hydrological cycles (Boros *et al.*, 2013; Stenger-Kovács *et al.*, 2014; Lengyel *et al.*, 2016).

Diatoms have short generation times (Rott, 1991) and respond rapidly to environmental changes. In alkaline, saline lakes, diatoms have a competitive advantage against other algal groups as many diatom species can tolerate the extreme conditions due to e.g. their ability to osmoregulation, phenotypic plasticity, secondary photoprotective pigments (Bauld, 1981; Kirk, 1994; Krumbein *et al.*, 1977), hence they may become dominant. The strong relationship between the diatom assemblages and the main environmental variables supports the use of diatoms for tracking changes in the limnological features of soda pans (Stenger-Kovács *et al.*, 2014). Additionally, they are considered as early warning indicators of both anthropogenic pollution and habitat restoration management (Smol & Stoermer, 2010). To improve the ecological status

68   assessment and the efficiency of conservation management of these unique water

69   bodies, a continuous monitoring of diatoms and their application as bioindicators is

70   highly recommended (Stenger-Kovács *et al.*, 2014).

71   Studies of diatoms in soda pans of Central Europe have focused mostly on

72   revealing the relationship between the water chemistry and the community composition

73   (Stenger-Kovács *et al.*, 2014; Lengyel *et al.*, 2016; Stenger-Kovács *et al.*, 2016).

74   However, structuring forces of diatom assemblages in space and time have not been

75   investigated in such ecosystems so far, probably because this is a new and fast

76   developing area in ecology.

77   In general, local environmental conditions, species interactions, species dispersal

78   and stochastic processes influence community structure. The metacommunity

79   framework (Leibold *et al.*, 2004) provides an approach to investigate the dynamics of

80   local communities that are linked by species dispersal within a region forming a

81   metacommunity. The framework involves four different perspectives (Table 1, glossary

82   of terms) concerning the relative importance of local and regional processes that help to

83   understand mechanisms supporting β-diversity. β-diversity refers to the variation of

84   community composition among sampling units within a region due to the species

85   replacement and/or the richness differences along environmental, spatial or temporal

86   gradients.

87   Areas with high β-diversity might have high conservation value and their

88   preservation is essential even if the single sites have low species richness, since they can

89   host a variety of species assemblages and their high community variation is strongly

90   related to habitat heterogeneity (Manthey & Fridley, 2009). Thus, β-diversity studies

91   provide valuable information for developing conservation strategies (Whittaker, 1960)

92 and also contribute to preservation the high conservation value of heterogeneous

93 habitats.

94   In this study, the goals were (i) to assess the overall β-diversity of two spatially

95 separated benthic diatom metacommunities in soda pans located in different parts of the

96 Carpathian Basin (Fertő-Hanság region and Danube-Tisza Interfluve), and (ii) to

97 determine the driving forces of β-diversity in regions with distinct physical and

98 chemical features, and diatom assemblages at both spatial and temporal scales. More

99 specifically, we focused on whether dissimilarities are attributable mainly to species

100 turnover or to nestedness, and on the role of deterministic/stochastic processes in

101 establishment of β-diversity and its components (thus in establishment of communities,

102 as well). Furthermore, we discuss our results in context of conservation/restoration

103 management.

104

105 **Materials and methods**

106

107 *Study areas*

108 There are two large regions in the Carpathian Basin where *ex lege* protected (Magyar

109 Közlöny, 1996) soda pans can be found: one is in the Kiskunság National Park in the

110 Danube-Tisza Interfluve and the other area is located around Lake Fertő/Neusiedlersee

111 in the Fertő-Hanság National Park. These water bodies are endorheic, shallow waters

112 with Secchi transparency of only a few centimeters (Horváth *et al.*, 2013), pH of 9-10

113 (Stenger-Kovács *et al.*, 2014), very high conductivity (may exceed 70,000 μS cm^{-1},

114 Boros *et al.*, 2014) and daily temperature fluctuation (nearly 20°C, Vörös & Boros,

115 2010). Despite these similarities, the two main hydrological basins (Danube-Tisza

116 Interfluve and Fertő-Hanság) differ substantially regarding some physical and chemical

117 parameters and the biota of the pans (Stenger-Kovács *et al.*, 2014). Water supply of

118 soda pans in the Danube-Tisza Interfluve is provided by saline water from deep-layer

119 aquifers (Mádl-Szőnyi & Tóth, 2009) and precipitation, therefore their hydrological

120 sensitivity is very high (Hammer, 1990). In the Danube-Tisza Interfluve, soda pans are

121 either in natural or in degraded status. In this study we sampled only natural soda pans

122 in this region. In contrast, all soda pans sampled in the Fertő-Hanság region (at the

123 Hungarian side of Lake Fertő) are under habitat reconstruction (Boros *et al.*, 2013)

124 aiming to ensure sufficient aquatic areas for migratory and nesting waterfowl. However,

125 recent studies conducted on different organisms (Tóth *et al.*, 2014; Lengyel *et al.*, 2016)

126 emphasized that the current condition of these reconstructed soda pans is far from the

127 natural ones: they have worse ecological status compared to the reference pans which

128 are located at the Austrian side of Lake Fertő.

129

130 ***Sampling and processing of samples***

131

132 Benthic diatom samples were collected from soda pans in two different parts of the

133 "Hungarian lowlands" ecoregion: Fertő-Hanság (FH) and Danube-Tisza Interfluve (DT)

134 (Fig. 1). Sampling was conducted monthly in the Fertő-Hanság region from three pans

135 between July 2013 and August 2014, and in the Danube-Tisza Interfluve from six pans

136 between August 2014 and July 2015. Sampling sites, their GPS coordinates and the

137 sample numbers are summarized in Table 2. Epipelic samples were collected from mud

138 (King *et al.*, 2006) in the littoral region where the water depth varied between 5–10 cm.

139 Samples were treated by hot hydrogen-peroxide method, then diatom valves were

140 embedded in Zrax$^{©}$ resin (CEN, 2003). To determine the relative abundance of species,

141 at least 400 valves per slide were counted using Zeiss Axio Imager A1 with

142 Planapochromat DIC lense at 1000× magnification under oil immersion (Zeiss, 518N).

143 Small taxa were investigated with a Hitachi S-2600 N scanning electron microscope.

144 Standard and specific taxonomic guides (Krammer & Lange-Bertalot, 1991, 1999a,

145 1999b, 2000; Witkowski *et al.*, 2000; Krammer, 2000, 2002, 2003; Lange-Bertalot,

146 2001; Taylor *et al.*, 2007; Levkov, 2009; Bey & Ector, 2010; Hofmann *et al.*, 2011;

147 Lange-Bertalot *et al.*, 2011; Levkov *et al.*, 2013; Stenger-Kovács & Lengyel, 2015)

148 were used to identify diatoms at species level.

149 During the sampling, conductivity, oxygen saturation (DO%), pH and water

150 temperature were measured *in situ* with an HQ40d Hach Lange multimeter. Irradiance

151 (LI) was measured by a LI 1400 (LI-COR) apparatus equipped with a 143 spherical (4π)

152 quantum micro sensor (US-SQS/L, Heinz Walz GmbH) directly above the epipelon in

153 the shoreline. Water samples for laboratory analyses were also collected. Concentration

154 of SRSi (Wetzel & Likens, 2000), nitrogen forms (NO_2^-, NO_3^-, NH_4^+), soluble reactive

155 (SRP) and total phosphorous (TP) were measured with spectrophotometry (APHA,

156 1998) using a Metertech UV/VIS Spectrophotometer, SP8001. CO_3^{2-}, HCO_3^-, Cl^-, SO_4^{2-}

157 and COD were measured with titrimetric methods (APHA, 1998). To assess the amount

158 of humic substances, intensity of the brown colour in platinum (Pt) units was

159 determined according to Cuthbert & del Giorgio (1992).

160

161 ***Statistical analyses***

162

163   Relative abundance data of diatom species were transformed into presence-absence

164   data, and then regional β-diversity was calculated for both regions separately using

165   multiple-site Sørensen dissimilarity index (β_{SOR}) (Baselga, 2010). β_{SOR} was partitioned

166   into two components: $\beta_{SOR} = \beta_{SIM} + \beta_{NES}$, where β_{SIM} (Simpson's dissimilarity) is the

167   dissimilarity originating from species turnover and β_{NES} (nestedness-driven

168   dissimilarity) is related to differences in species richness (Baselga *et al.*, 2007; Baselga,

169   2010). Calculation of the regional β-diversity and its components was conducted in the

170   betapart R package version 1.3 (Baselga *et al.*, 2013).

171   Relationship of turnover and nestedness components to overall β-diversity

172   values expected "under" and "beyond" random community assemblage given an

173   Equiprobable-Fixed (EF) null model was investigated (Ulrich & Gotelli, 2007). At first,

174   for the observed presence-absence data overall β-diversity was computed using pairwise

175   Sørensen dissimilarity index (β_{sor}), which was partitioned into β_{sim} and β_{nes} following

176   Baselga's framework (Baselga, 2010) in both regions. Then, EF null models were

177   implemented to randomize the observation data matrix to generate "null" communities

178   (permutations = 1000) using the permatfull function in the vegan R package (Oksanen

179   *et al.*, 2015). At the EF null models, observed species richness of sites were maintained

180   (r0 algorithm) during the randomization and sample species from the regional species

181   pool equiprobably. Then, pairwise Sørensen dissimilarity index was calculated for each

182   of the 1000 null matrices and their mean was computed ($\beta_{sor-null}$). The differences

183   between the observed β-diversity (β_{sor}) and β-diversity derived from null communities

184   ($\beta_{sor-null}$) were quantified ($\beta_{sor-diff} = \beta_{sor} - \beta_{sor-null}$), thereby the β-diversities independent of

185   and beyond random chance was determined ($\beta_{sor-diff}$). To explore the relationship of the

186   overall β-diversities (β_{sor}), turnover (β_{sim}) and nestedness (β_{nes}) components to the

187 expected β-diversities under ($β_{sor-null}$) and beyond ($β_{sor-diff}$) null models, significances of

188 the Pearson correlations were computed using Mantel permutation tests (permutations =

189 999). The results of this analysis can provide an insight into whether our observed

190 diatom communities are assembled by deterministic or stochastic processes or by both,

191 in time.

192　　　We quantified the effect of environmental variables, as well as the spatial and

193 temporal variation on establishment of diatom communities for both regions. Estimates

194 were carried out for Hellinger transformed relative abundance (Legendre & Gallagher,

195 2001; Borcard *et al.*, 2011) and presence-absence data. Prior to the final statistical

196 analyses, a model selection procedure of redundancy analysis (RDA) (each term

197 analysed sequentially from first to last) was conducted using analysis of variance

198 (ANOVA) to determine which physical and chemical parameters affect significantly the

199 variance of diatom communities. During the subsequent analyses, these factors were

200 included in the group "environmental variables". All other physical and chemical

201 parameters were eliminated. Before conducting RDA, all environmental factors were

202 standardized. To define the group "spatial distance", a principal coordinate analysis

203 (PCoA) of the geographical distance matrix among the soda pans within both regions

204 was carried out to compute distance-based Moran's eigenvector map (dbMEM)

205 (Borcard & Legendre, 2002; Borcard *et al.*, 2004), then dbMEM eigenvectors were

206 considered as explanatory variables. For "temporal variation", the days elapsed between

207 two samplings were used as explanatory variables. Variation partitioning was conducted

208 to reveal the importance of pure and shared effects of the three explanatory variable

209 groups (environmental, spatial, temporal) on the variance of diatom assemblages,

210 resulting in a total of seven fractions and residuals indicating the unexplained variance

211 (Anderson & Gribble, 1998). Significance of adjusted R^2 values provided by variation

212 partitioning for testable fractions (pure environmental, spatial and temporal effect) was

213 determined with ANOVA (permutations = 999) of RDA models (Peres-Neto *et al.*,

214 2006). Variation partitioning was performed with the varpart function in the vegan R

215 package (Oksanen *et al.*, 2015).

216   All statistical analyses were carried out separately for the two regions and were

217 performed in R statistical and computing environment (R. 3.1.1; R Development Core

218 Team, 2014).

219

220 **Results**

221

222 A total of 163 diatom species were identified in the Fertő-Hanság (FH) region (n = 29)

223 and 117 in the Danube-Tisza (DT) Interfluve (n = 47). Species richness per sample

224 varied between 15 and 57 (average and standard deviation: 34 ± 11) in the FH region,

225 and between 2 and 32 (average and standard deviation: 17 ± 7) in the DT region.

226 Dissimilarity according to the multiple-site framework was fairly high in both regions

227 ($\beta_{SOR} > 0.90$). Patterns of β-diversity in the epipelon were mainly attributed to pure

228 species turnover (β_{SIM}), and nestedness (β_{NES}) component was considerably lower in

229 both cases (Table 3).

230   In the FH region, the overall β-diversity (β_{sor}) was not related to the β-diversity

231 values expected under the null model ($\beta_{sor-null}$), but it was strongly positively correlated

232 to that of deviations beyond null model expectations ($\beta_{sor-diff}$) (Figs 2A, 2B). The

233 turnover component (β_{sim}) showed no correlation with $\beta_{sor-null}$, but it was positively

234 related to $\beta_{sor-diff}$ (Figs 2C, 2D). The nestedness component (β_{nes}) displayed neither a

235   significant relationship with $\beta_{sor-null}$ nor with $\beta_{sor-diff}$ (Figs 2E, 2F). In the DT region,

236   although β_{sor} values were significantly correlated to the predictions of the null model

237   ($\beta_{sor-null}$), it showed a considerably stronger relationship with its residuals ($\beta_{sor-diff}$) (Figs

238   3A, 3B). Regarding the turnover component, we found similar results as in the FH

239   region: β_{sim} correlated strongly to $\beta_{sor-diff}$ and it displayed non-significant relationship

240   with $\beta_{sor-null}$ (Figs 3C, 3D). The nestedness component (β_{nes}) was related significantly

241   both to $\beta_{sor-null}$ and $\beta_{sor-diff}$, but the positive correlation was stronger with the null

242   expectations ($\beta_{sor-null}$) (Figs 3E, 3F).

243   The model selection procedure displayed a significant impact of SRP ($Df = 1$, F

244    $= 1.836$, $P < 0.05$) and SRSi ($Df = 1$, $F = 1.724$, $P < 0.05$) in the FH region and that of

245   COD ($Df = 1$, $F = 2.7401$, $P < 0.01$), NO_3^- ($Df = 1$, $F = 3.2104$, $P < 0.01$), CO_3^{2-} ($Df = 1$,

246    $F = 3.2473$, $P < 0.01$) and Cl^- ($Df = 1$, $F = 2.6031$, $P < 0.05$) in the DT region. Variation

247   partitioning for both regions revealed that establishment of community structure using

248   either abundance or presence-absence data was related mainly to the pure environmental

249   effect, which was significant in each case but explained a higher proportion of the

250   variations in diatom communities in the DT (16% and 7.1%) than in the FH region

251   (5.6% and 2.3%). In the FH region, the pure temporal variation also had a significant

252   impact on the community structures, however, the explained variation was lower (3.9%

253   and 2.2%). All the other fractions (pure and shared) of explanatory data sets were

254   negligible in terms of variance explanation. In all models presented, variation in

255   community structure was not fully explained, leaving considerable portion of residuals

256   unexplored. Furthermore, the amount of unexplained variation was higher using

257   presence-absence data in both regions (Fig. 4).

258

Discussion

This study revealed that high β-diversity of diatom assemblages was enhanced mainly by species turnover due to deterministic processes such as species-sorting. However, structuring forces partly differed in the two investigated regions. Across natural soda pans in the Danube-Tisza Interfluve species replacements were driven chiefly by environmental characteristics of the water and resulted in low α-diversity assemblages. In contrast, in the Fertő-Hanság region, restoration management induced temporal variations in community structure by obstruction of the natural hydrological cycle of the pans acted most through environmental filtering effect. Our results might help to understand which dynamics maintain diatom diversity at regional scale in such extreme environments as soda pans and to assess how to preserve biodiversity by applying an appropriate management strategy in the future.

Main forces in β-diversity

Soda pans located in Central Europe have a rather low α-diversity (species richness and Shannon diversity; Stenger-Kovács *et al.*, 2016) in comparison to other lakes in the region with "average" environmental characteristics (e.g. Stenger-Kovács *et al.*, 2007). The low species richness could promote the importance of β-diversity to a great extent (Chase *et al.*, 2011), which was supported by our results as high overall β-diversity (> 90%) of diatom communities was observed in both study areas. Partitioning of overall β-diversity revealed that dissimilarity of diatom communities originates mainly from the replacement of species in one community by different species in the other community

283 (namely, as a result of high species turnover). Algarte *et al.* (2016) reported 50% mean

284 β-diversity for periphytic diatoms in lakes connected to the Paraná River, however the

285 authors calculated pair-wise dissimilarity instead of multiple-site dissimilarity because

286 they focused on β-diversity between each pair of lakes among the sampling years.

287 Despite the difference of the applied dissimilarity measures, their findings also

288 supported pure species turnover (Algarte *et al.*, 2016), similar to our observations.

289 Moreover, they found that damming on the studied area resulted in new environmental

290 conditions compelling replacement processes between species with time, but each lake

291 contributed equally to the regional species-pool as there was no significant richness

292 difference. Maloufi *et al.* (2016) published extremely high β-diversity (> 96%) using

293 multiple-site framework for phytoplankton from lakes in the Paris area, which was also

294 driven by high species turnover, whereas the results were mainly explained by distinct

295 local environmental conditions at regional scale due to different anthropogenic impacts

296 and landscape.

297 Our observations provide a new insight into community ecology with applying

298 null models in order to determine the role of deterministic and stochastic processes in

299 diatom community variation. Both in the Fertő-Hanság region and Danube-Tisza

300 Interfluve, overall β-diversity and turnover component values matched much less to

301 random expectations than to deviations beyond null model expectations indicating that

302 epipelic diatom communities are assembled predominantly by deterministic processes

303 (e.g. species-sorting by environmental filters) similarly to periphytic diatoms (Algarte *et*

304 *al.*, 2016) or to phytoplankton communities (Maloufi *et al.*, 2016) in other studies. In

305 contrast, nestedness component showed a different relationship to the expectations with

306 and beyond null models in the two areas: no correlation was observed in the FH region,

307 but it showed a strong relation to the expectation with null model indicating a signal of

308 stochastic processes (a multitude of random processes) in the DT region. However, this

309 component was quite low in both areas regarding the overall β-diversity.

310

311 *Key components of deterministic mechanisms*

312

313 The modern metacommunity concept, which helps ecologists to understand responses to

314 environmental changes, is based on four widely used paradigms proposed by Leibold *et*

315 *al.* (2004): neutral, mass-effect, patch-dynamic and species-sorting models (Table 1,

316 glossary of terms). According to the model selection procedure applied in this study,

317 pure environmental processes affected diatom assemblages but the significant

318 environmental parameters were different for the two sampled areas (SRSi and SRP in

319 the Fertő-Hanság region, and COD, NO_3^-, CO_3^{2-} and Cl^- in the Danube-Tisza

320 Interfluve). Furthermore, it was reported that physical and chemical features of the soda

321 pans differ not only between the two regions but also among the soda pans within a

322 region (Stenger-Kovács *et al.*, 2014; Lengyel *et al.*, 2016). In the DT region, variation

323 of community structures was associated merely to the pure environmental effects due to

324 the unique environmental characteristics of the pans, thus species-sorting can be

325 regarded as perfect. Our findings might originate from the natural status of these soda

326 pans. As their water supply is provided solely by precipitation and groundwater (no

327 man-made freshwater ingress), their natural saline features (the decisive physical and

328 chemical parameters) can serve as environmental filters for diatom species.

329   Different observations are presented in the literature regarding the key drivers of

330 diatom metacommunities in freshwater ecosystems. Vilmi *et al.* (2016) found that

diatom community structures in a large, well-connected lake system were determined by

shared effects of both spatial and local environmental factors instead of pure

environmental effects. They showed that the pure spatial effects interfered with

environmental variables due to dispersal processes. Nevertheless, since communities are

structured spatially mainly due to dispersal limitation at large scales (e.g. within a

continent, a region or a watershed), they drew attention to study spatial effects with

caution in relatively smaller geographical scales (Vilmi *et al.*, 2016). Dong *et al.* (2016)

showed that in high-mountain streams with intense environmental gradients related to

steep elevation affect the assembly of diatom metacommunities but spatial factors are

also important, since mountains prevent stream corridors to facilitate species dispersion

at a small spatial extent (< 500 km^2). In both of our study areas, soda pans (within each

region) are located relatively close to each other (≤ 10 kilometers). Hence there is no

dispersal limitation of passive dispersion of diatom species, i.e. geographic distance did

not play a key role. In such highly and multiply stressed ecosystems where

environmental parameters tend to reach extreme values (Stenger-Kovács *et al.*, 2014;

Lengyel *et al.*, 2016), spatial distance did not affect the variation of community

composition (i.e. the difference in community structure was not greater in more distant

lakes than in those close to each other): its effect was overcame by the chemical

properties of the water supporting species-sorting mechanism.

These patterns emerged more prominently when weighted species occurrences

were used during the analyses than in the analyses of merely presence-absence data.

Thus, the abundance dataset magnified the response of abundant taxa to changes along

environmental gradients to a greater extent in both metacommunities. This

interpretation of higher explained variance for abundance data is in line with

355   explanation offered previously by other authors (Beisner *et al.*, 2006; Heino *et al.*,

356   2010).

357   Although, physical and chemical factors played a key role in the reconstructed

358   soda pans of the FH region as well, pure temporal variation also influenced the

359   community structure. We assume that this result may be related to the restoration

360   management applied for the soda pans in this area aiming the re-establish migrating and

361   nesting waterfowl population density. Legény-tó has a permanent linkage to one of the

362   numerous drainage canals in the region, which results in a more or less constant water

363   level and low conductivity. Lengyel *et al.* (2016) reported that lack of the natural

364   hydrological regime resulted in high diversity and dominance of freshwater diatoms in

365   Legény-tó. Water level and surface area of Borsodi-dűlő and Nyéki-szállás are regulated

366   by sluices built on the Hanság Main Canal and they receive a periodical water supply

367   from Lake Fertő and the surrounding area. In addition, due to the proximity, their

368   occasional water supply can be also provided by strong winds from Lake Fertő when its

369   water level is relatively high. Lengyel *et al.* (2016) stated that repeated shifts or

370   reversions in the succession process can appear due to the water management and the

371   occasional water supply originated from Lake Fertő that could provide a reasonable

372   explanation for our findings, as well. Algarte *et al.* (2016) also reported that water

373   management (namely damming) resulted in significant compositional changes in diatom

374   communities due to variation of environmental characteristics in freshwater lakes

375   connected to the Paraná River over a ten-year period. Thus, along environmental

376   changes, temporal variation was the most important in terms of assembly, similarly to

377   our observed mechanisms in the FH region.

378

379   In conclusion, diatoms in extremely stressed ecosystems (high conductivity, pH,

380   turbidity and daily temperature fluctuation) such as soda pans, are assembled

381   predominantly by deterministic processes. High β-diversity of diatom metacommunities

382   due to the continuous species turnover along environmental gradients reflects that soda

383   pans within two regions (DT and FH) provide a variety of niches for different diatom

384   assemblages. Since single soda pans host a low number of diatom species, these habitats

385   have high conservation value due to their vulnerability. Climate change and

386   anthropogenic interventions (e.g. water drainage, dredging, pumping of groundwater)

387   induce irreversible changes in their natural hydrological cycle, thus threatening their

388   good ecological status and even their existence (Williams, 2002; Stenger-Kovács *et al.*,

389   2014). As diatom assemblages showed in the FH region, restoration activities applying

390   permanent or periodical water supply tend to cause significant temporal changes in

391   diatom communities. Since diatoms proved to be suitable for indicating the changes in

392   limnological characteristics of soda pans, continuous monitoring of diatoms (including

393   β-diversity studies) is suggested and they should be considered during the ecological

394   status assessment and the development of a proper conservation management.

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595

596   **Table 1.** Glossary of terms.

Term	Definition
Neutral theory	A system where species do not differ in their abilities (dispersion, competition and fitness) and local communities can be formed by immigration, emigration, speciation and extinction but all these processes are considered as random.
Mass-effect	Local population densities strongly depend on the spatial dynamics as follows: immigration prevents species with low competitive abilities from competitive exclusion, and emigration contributes to loss rates of population.
Patch-dynamic	Population dynamics in a number of identical patches are driven by colonization and extinction influenced by interactions between species.
Species-sorting	Patches are considered as heterogeneous, change in the community along environmental gradients are affected by local conditions. However, dispersal can facilitate changes in the composition to keep up with the environmental changes.

597

598

599 **Table 2.** The investigated soda pans, their region, GPS coordinates and the number of

600 samples.

Soda pans	Regions	GPS coordinates		No. of samples
1. Borsodi-dűlő	FH	N 47.6815	E 16.8400	10
2. Legény-tó	FH	N 47.6632	E 16.8134	12
3. Nyéki-szállás	FH	N 47.6770	E 16.8328	7
4. Bába-szék	DT	N 46.7405	E 19.1503	8
5. Bogárzó-szék	DT	N 46.8048	E 19.1408	7
6. Böddi-szék	DT	N 46.7608	E 19.1437	9
7. Kelemen-szék	DT	N 46.7974	E 19.1831	9
8. Sósér	DT	N 46.7892	E 19.1470	7
9. Zab-szék	DT	N 46.8375	E 19.1698	7

601 FH = Fertő-Hanság, DT = Danube-Tisza Interfluve.

602

603 **Table 3.** β-diversity and its components of benthic diatom communities in the Fertő-

604 Hanság region and in the Danube-Tisza Interfluve.

		Fertő-Hanság (n = 29)	Danube-Tisza Interfluve (n = 47)
	β_{SOR}	0.902	0.942
β-diversity	β_{SIM}	0.857	0.909
	β_{NES}	0.046	0.033

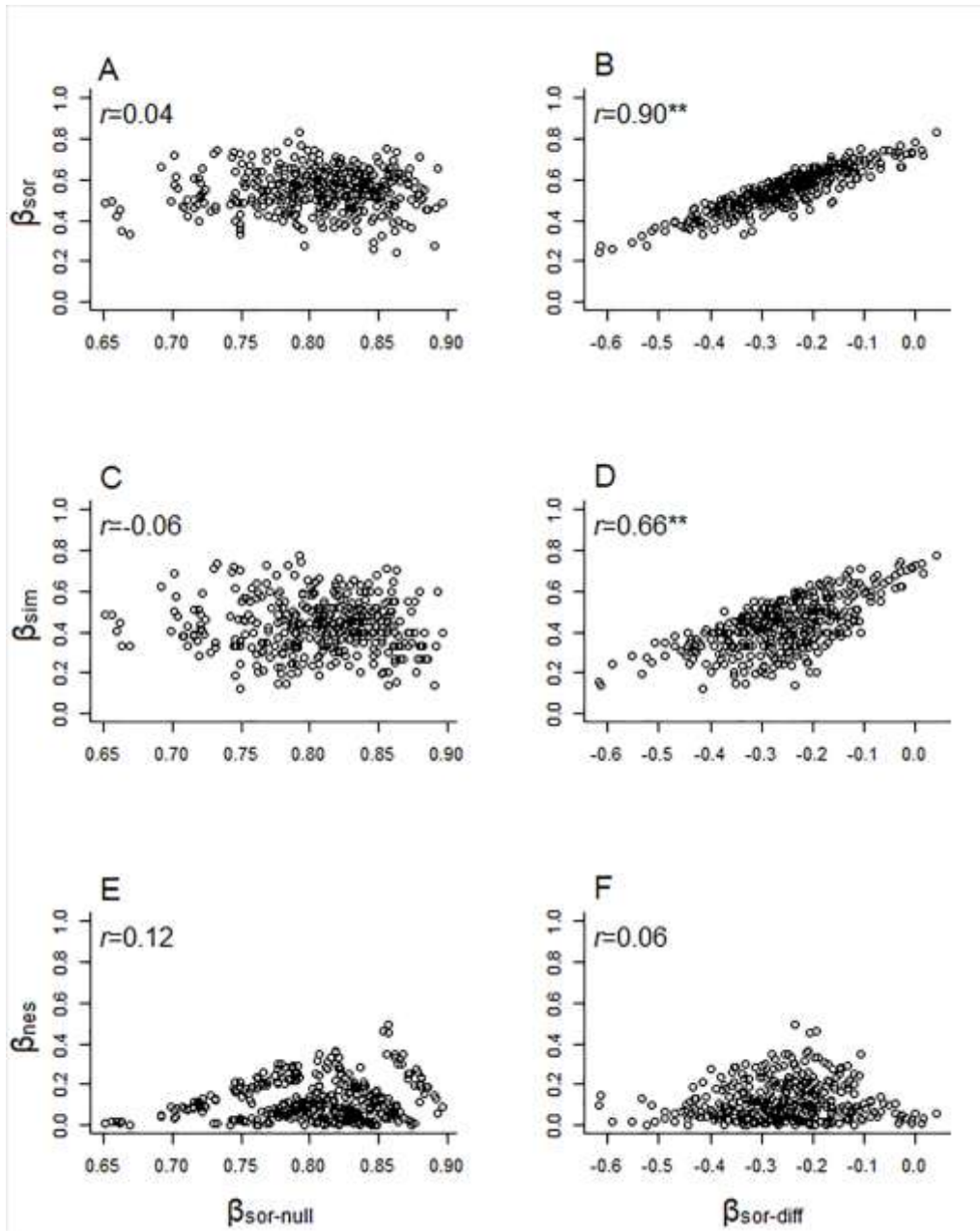605 β_{SOR} = overall β-diversity; β_{SIM} = turnover component; β_{NES} = nestedness component.

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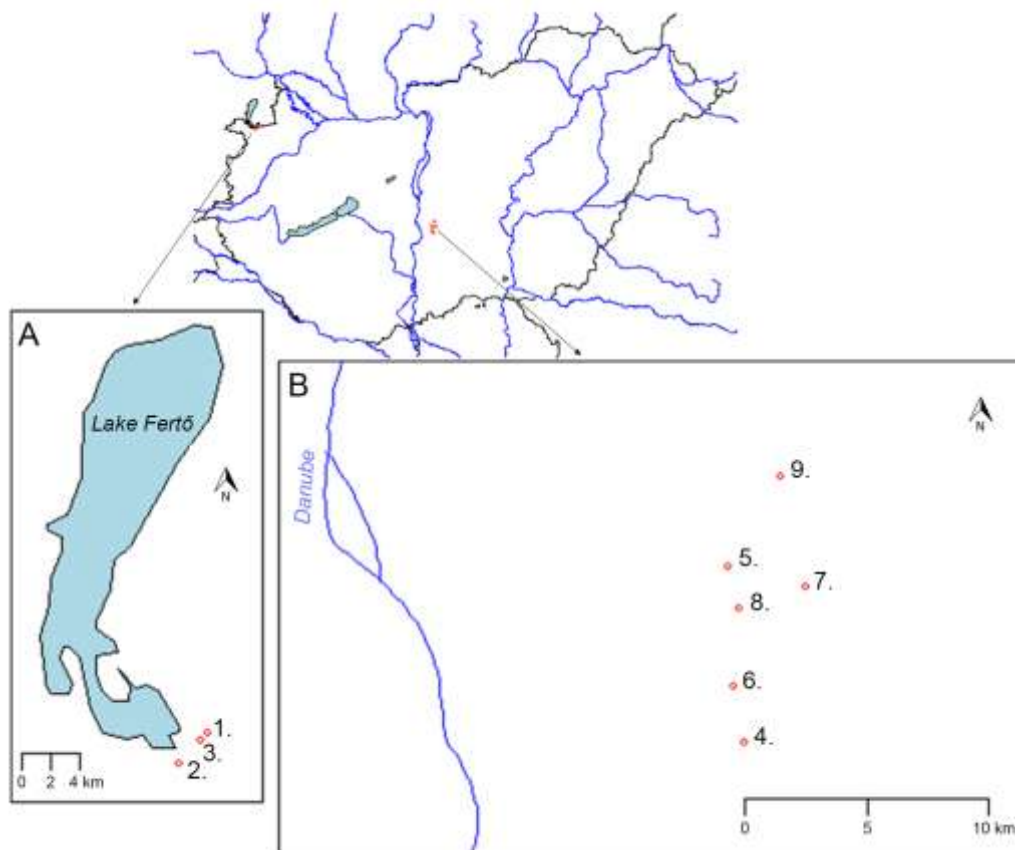
Fig. 1. Sampling sites in the Fertő-Hanság region (A) and in the Danube-Tisza Interfluve (B). Soda pan numbers are listed in Table 2.

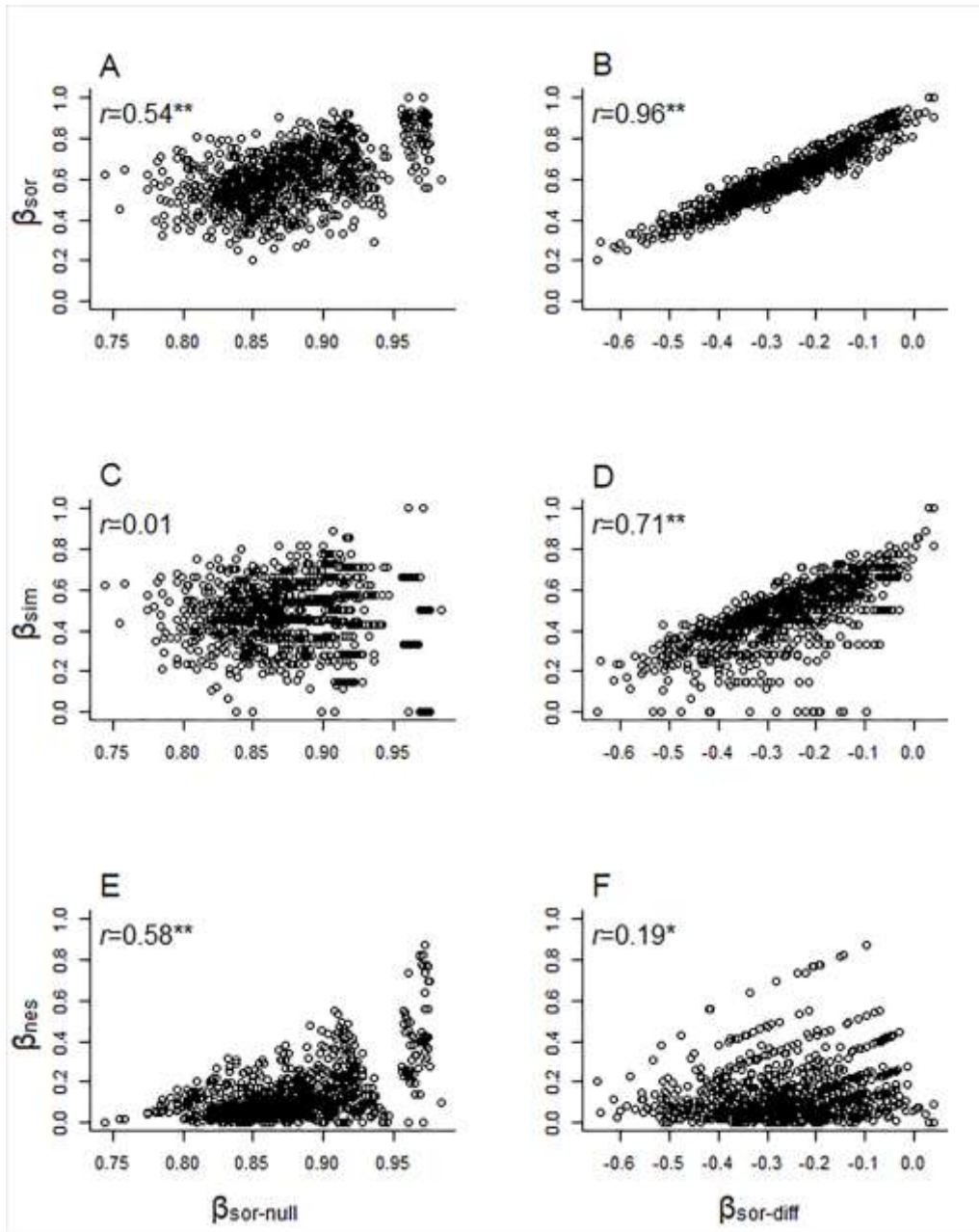610

611

Fig. 2. The relationship of overall β-diversity (β_{sor}), and its turnover (β_{sim}) and nestedness (β_{nes}) components with the overall β-diversity expected under ($\beta_{sor-null}$) and beyond null model ($\beta_{sor-diff}$) in the Fertő-Hanság region. Pearson correlation coefficients (*r*) are shown. *P* values were computed using Mantel tests. Significance codes: '**' 0.01 '*' 0.05.

617

Fig. 3. The relationship of overall β-diversity (β$_{sor}$), and its turnover (β$_{sim}$) and nestedness (β$_{nes}$) components with the overall β-diversity expected under (β$_{sor-null}$) and beyond null model (β$_{sor-diff}$) in the Danube-Tisza Interfluve. Pearson correlation coefficients (*r*) are shown. *P* values were computed using Mantel tests. Significance codes: '**' 0.01 '*' 0.05.

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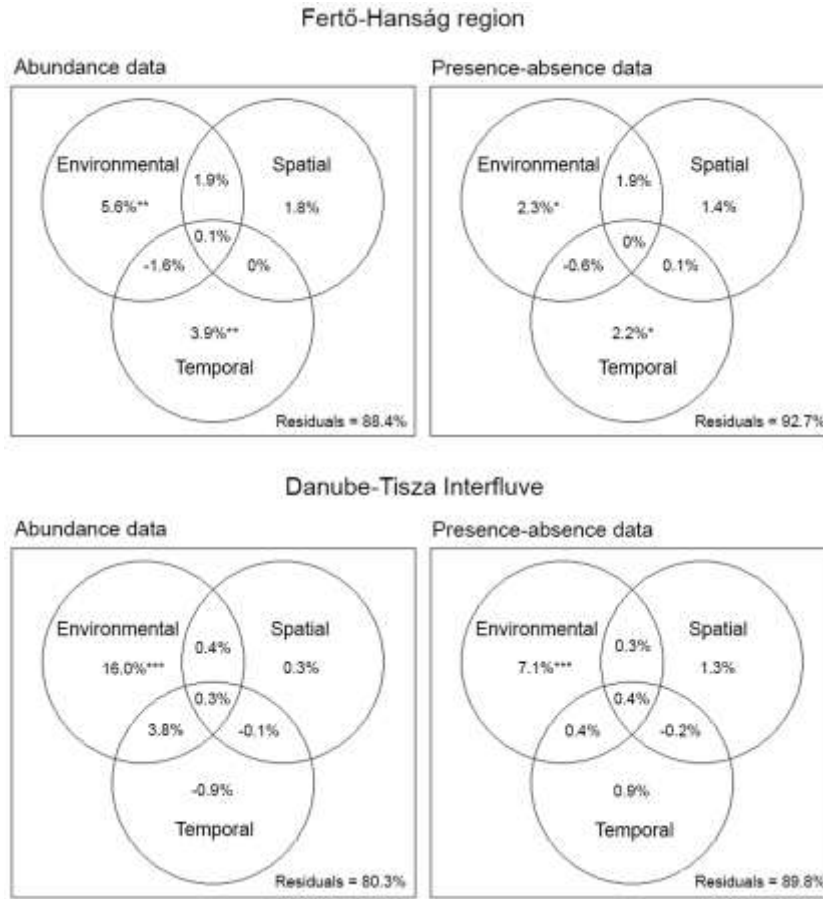
Fig. 4. Results of variation partitioning for Hellinger transformed relative abundance and presence-absence data in the Fertő-Hanság region and in the Danube-Tisza Interfluve. Fractions are shown as percentages of total variation based on adjusted R^2 values (Environmental = environmental variables, Spatial = spatial distance, Temporal = temporal variation). *P* values for testable fractions were computed using ANOVA of RDA models. Residuals indicate the unexplained variances. Significance codes: '***' 0.001 '**' 0.01 '*' 0.05.