

Szabó, B; Lengyel, E; Padisák, J; Vass, M; Stenger-Kovács, C. Structuring forces and β -diversity of benthic diatom metacommunities in soda pans of the Carpathian Basin. EUROPEAN JOURNAL OF PHYCOLOGY 53: 2 pp. 219-229. (2018)

Structuring forces and β -diversity of benthic diatom metacommunities in soda pans of the Carpathian Basin

Beáta Szabó^{1,2*}, Edina Lengyel¹, Judit Padisák^{1,2}, Máté Vass³, Csilla Stenger-Kovács²

¹MTA-PE Limnoecology Research Group, Hungarian Academy of Sciences, Egyetem str. 10, H-8200 Veszprém, Hungary

²Department of Limnology, University of Pannonia, Egyetem str. 10, H-8200 Veszprém, Hungary

³Department of Ecology and Genetics/Limnology, Uppsala University, Norbyvägen 18D, 75236 Uppsala, Sweden

Short running title: β -diversity of diatom metacommunities in soda pans

*corresponding author: e-mail: szabobea@almos.uni-pannon.hu

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

assessment and the efficiency of conservation management of these unique water bodies, a continuous monitoring of diatoms and their application as bioindicators is highly recommended (Stenger-Kovács *et al.*, 2014).

Studies of diatoms in soda pans of Central Europe have focused mostly on revealing the relationship between the water chemistry and the community composition (Stenger-Kovács *et al.*, 2014; Lengyel *et al.*, 2016; Stenger-Kovács *et al.*, 2016). However, structuring forces of diatom assemblages in space and time have not been investigated in such ecosystems so far, probably because this is a new and fast developing area in ecology.

In general, local environmental conditions, species interactions, species dispersal and stochastic processes influence community structure. The metacommunity framework (Leibold *et al.*, 2004) provides an approach to investigate the dynamics of local communities that are linked by species dispersal within a region forming a metacommunity. The framework involves four different perspectives (Table 1, glossary of terms) concerning the relative importance of local and regional processes that help to understand mechanisms supporting β -diversity. β -diversity refers to the variation of community composition among sampling units within a region due to the species replacement and/or the richness differences along environmental, spatial or temporal gradients.

Areas with high β -diversity might have high conservation value and their preservation is essential even if the single sites have low species richness, since they can host a variety of species assemblages and their high community variation is strongly related to habitat heterogeneity (Manthey & Fridley, 2009). Thus, β -diversity studies provide valuable information for developing conservation strategies (Whittaker, 1960)

and also contribute to preservation the high conservation value of heterogeneous habitats.

In this study, the goals were (i) to assess the overall β -diversity of two spatially separated benthic diatom metacommunities in soda pans located in different parts of the Carpathian Basin (Fertő-Hanság region and Danube-Tisza Interfluve), and (ii) to determine the driving forces of β -diversity in regions with distinct physical and chemical features, and diatom assemblages at both spatial and temporal scales. More specifically, we focused on whether dissimilarities are attributable mainly to species turnover or to nestedness, and on the role of deterministic/stochastic processes in establishment of β -diversity and its components (thus in establishment of communities, as well). Furthermore, we discuss our results in context of conservation/restoration management.

Materials and methods

Study areas

There are two large regions in the Carpathian Basin where *ex lege* protected (Magyar Közlöny, 1996) soda pans can be found: one is in the Kiskunság National Park in the Danube-Tisza Interfluve and the other area is located around Lake Fertő/Neusiedlersee in the Fertő-Hanság National Park. These water bodies are endorheic, shallow waters with Secchi transparency of only a few centimeters (Horváth *et al.*, 2013), pH of 9-10 (Stenger-Kovács *et al.*, 2014), very high conductivity (may exceed 70,000 $\mu\text{S cm}^{-1}$, Boros *et al.*, 2014) and daily temperature fluctuation (nearly 20°C, Vörös & Boros, 2010). Despite these similarities, the two main hydrological basins (Danube-Tisza

Interfluve and Fertő-Hanság) differ substantially regarding some physical and chemical parameters and the biota of the pans (Stenger-Kovács *et al.*, 2014). Water supply of soda pans in the Danube-Tisza Interfluve is provided by saline water from deep-layer aquifers (Mádl-Szőnyi & Tóth, 2009) and precipitation, therefore their hydrological sensitivity is very high (Hammer, 1990). In the Danube-Tisza Interfluve, soda pans are either in natural or in degraded status. In this study we sampled only natural soda pans in this region. In contrast, all soda pans sampled in the Fertő-Hanság region (at the Hungarian side of Lake Fertő) are under habitat reconstruction (Boros *et al.*, 2013) aiming to ensure sufficient aquatic areas for migratory and nesting waterfowl. However, recent studies conducted on different organisms (Tóth *et al.*, 2014; Lengyel *et al.*, 2016) emphasized that the current condition of these reconstructed soda pans is far from the natural ones: they have worse ecological status compared to the reference pans which are located at the Austrian side of Lake Fertő.

Sampling and processing of samples

Benthic diatom samples were collected from soda pans in two different parts of the “Hungarian lowlands” ecoregion: Fertő-Hanság (FH) and Danube-Tisza Interfluve (DT) (Fig. 1). Sampling was conducted monthly in the Fertő-Hanság region from three pans between July 2013 and August 2014, and in the Danube-Tisza Interfluve from six pans between August 2014 and July 2015. Sampling sites, their GPS coordinates and the sample numbers are summarized in Table 2. Epipellic samples were collected from mud (King *et al.*, 2006) in the littoral region where the water depth varied between 5–10 cm. Samples were treated by hot hydrogen-peroxide method, then diatom valves were

embedded in Zrax[®] resin (CEN, 2003). To determine the relative abundance of species, at least 400 valves per slide were counted using Zeiss Axio Imager A1 with Planapochromat DIC lense at 1000× magnification under oil immersion (Zeiss, 518N). Small taxa were investigated with a Hitachi S-2600 N scanning electron microscope. Standard and specific taxonomic guides (Krammer & Lange-Bertalot, 1991, 1999a, 1999b, 2000; Witkowski *et al.*, 2000; Krammer, 2000, 2002, 2003; Lange-Bertalot, 2001; Taylor *et al.*, 2007; Levkov, 2009; Bey & Ector, 2010; Hofmann *et al.*, 2011; Lange-Bertalot *et al.*, 2011; Levkov *et al.*, 2013; Stenger-Kovács & Lengyel, 2015) were used to identify diatoms at species level.

During the sampling, conductivity, oxygen saturation (DO%), pH and water temperature were measured *in situ* with an HQ40d Hach Lange multimeter. Irradiance (LI) was measured by a LI 1400 (LI-COR) apparatus equipped with a 143 spherical (4π) quantum micro sensor (US-SQS/L, Heinz Walz GmbH) directly above the epipelon in the shoreline. Water samples for laboratory analyses were also collected. Concentration of SRSi (Wetzel & Likens, 2000), nitrogen forms (NO_2^- , NO_3^- , NH_4^+), soluble reactive (SRP) and total phosphorous (TP) were measured with spectrophotometry (APHA, 1998) using a Metertech UV/VIS Spectrophotometer, SP8001. CO_3^{2-} , HCO_3^- , Cl^- , SO_4^{2-} and COD were measured with titrimetric methods (APHA, 1998). To assess the amount of humic substances, intensity of the brown colour in platinum (Pt) units was determined according to Cuthbert & del Giorgio (1992).

Statistical analyses

Relative abundance data of diatom species were transformed into presence-absence data, and then regional β -diversity was calculated for both regions separately using multiple-site Sørensen dissimilarity index (β_{SOR}) (Baselga, 2010). β_{SOR} was partitioned into two components: $\beta_{\text{SOR}} = \beta_{\text{SIM}} + \beta_{\text{NES}}$, where β_{SIM} (Simpson's dissimilarity) is the dissimilarity originating from species turnover and β_{NES} (nestedness-driven dissimilarity) is related to differences in species richness (Baselga *et al.*, 2007; Baselga, 2010). Calculation of the regional β -diversity and its components was conducted in the betapart R package version 1.3 (Baselga *et al.*, 2013).

Relationship of turnover and nestedness components to overall β -diversity values expected “under” and “beyond” random community assemblage given an Equiprobable-Fixed (EF) null model was investigated (Ulrich & Gotelli, 2007). At first, for the observed presence-absence data overall β -diversity was computed using pairwise Sørensen dissimilarity index (β_{SOR}), which was partitioned into β_{sim} and β_{nes} following Baselga's framework (Baselga, 2010) in both regions. Then, EF null models were implemented to randomize the observation data matrix to generate “null” communities (permutations = 1000) using the permatfull function in the vegan R package (Oksanen *et al.*, 2015). At the EF null models, observed species richness of sites were maintained (r0 algorithm) during the randomization and sample species from the regional species pool equiprobably. Then, pairwise Sørensen dissimilarity index was calculated for each of the 1000 null matrices and their mean was computed ($\beta_{\text{SOR-null}}$). The differences between the observed β -diversity (β_{SOR}) and β -diversity derived from null communities ($\beta_{\text{SOR-null}}$) were quantified ($\beta_{\text{SOR-diff}} = \beta_{\text{SOR}} - \beta_{\text{SOR-null}}$), thereby the β -diversities independent of and beyond random chance was determined ($\beta_{\text{SOR-diff}}$). To explore the relationship of the overall β -diversities (β_{SOR}), turnover (β_{sim}) and nestedness (β_{nes}) components to the

expected β -diversities under ($\beta_{\text{sor-null}}$) and beyond ($\beta_{\text{sor-diff}}$) null models, significances of the Pearson correlations were computed using Mantel permutation tests (permutations = 999). The results of this analysis can provide an insight into whether our observed diatom communities are assembled by deterministic or stochastic processes or by both, in time.

We quantified the effect of environmental variables, as well as the spatial and temporal variation on establishment of diatom communities for both regions. Estimates were carried out for Hellinger transformed relative abundance (Legendre & Gallagher, 2001; Borcard *et al.*, 2011) and presence-absence data. Prior to the final statistical analyses, a model selection procedure of redundancy analysis (RDA) (each term analysed sequentially from first to last) was conducted using analysis of variance (ANOVA) to determine which physical and chemical parameters affect significantly the variance of diatom communities. During the subsequent analyses, these factors were included in the group “environmental variables”. All other physical and chemical parameters were eliminated. Before conducting RDA, all environmental factors were standardized. To define the group “spatial distance”, a principal coordinate analysis (PCoA) of the geographical distance matrix among the soda pans within both regions was carried out to compute distance-based Moran’s eigenvector map (dbMEM) (Borcard & Legendre, 2002; Borcard *et al.*, 2004), then dbMEM eigenvectors were considered as explanatory variables. For “temporal variation”, the days elapsed between two samplings were used as explanatory variables. Variation partitioning was conducted to reveal the importance of pure and shared effects of the three explanatory variable groups (environmental, spatial, temporal) on the variance of diatom assemblages, resulting in a total of seven fractions and residuals indicating the unexplained variance

(Anderson & Gribble, 1998). Significance of adjusted R^2 values provided by variation partitioning for testable fractions (pure environmental, spatial and temporal effect) was determined with ANOVA (permutations = 999) of RDA models (Peres-Neto *et al.*, 2006). Variation partitioning was performed with the varpart function in the vegan R package (Oksanen *et al.*, 2015).

All statistical analyses were carried out separately for the two regions and were performed in R statistical and computing environment (R. 3.1.1; R Development Core Team, 2014).

Results

A total of 163 diatom species were identified in the Fertő-Hanság (FH) region ($n = 29$) and 117 in the Danube-Tisza (DT) Interfluvium ($n = 47$). Species richness per sample varied between 15 and 57 (average and standard deviation: 34 ± 11) in the FH region, and between 2 and 32 (average and standard deviation: 17 ± 7) in the DT region. Dissimilarity according to the multiple-site framework was fairly high in both regions ($\beta_{\text{SOR}} > 0.90$). Patterns of β -diversity in the epilimnion were mainly attributed to pure species turnover (β_{SIM}), and nestedness (β_{NES}) component was considerably lower in both cases (Table 3).

In the FH region, the overall β -diversity (β_{SOR}) was not related to the β -diversity values expected under the null model ($\beta_{\text{SOR-null}}$), but it was strongly positively correlated to that of deviations beyond null model expectations ($\beta_{\text{SOR-diff}}$) (Figs 2A, 2B). The turnover component (β_{SIM}) showed no correlation with $\beta_{\text{SOR-null}}$, but it was positively related to $\beta_{\text{SOR-diff}}$ (Figs 2C, 2D). The nestedness component (β_{NES}) displayed neither a

significant relationship with $\beta_{\text{sor-null}}$ nor with $\beta_{\text{sor-diff}}$ (Figs 2E, 2F). In the DT region, although β_{sor} values were significantly correlated to the predictions of the null model ($\beta_{\text{sor-null}}$), it showed a considerably stronger relationship with its residuals ($\beta_{\text{sor-diff}}$) (Figs 3A, 3B). Regarding the turnover component, we found similar results as in the FH region: β_{sim} correlated strongly to $\beta_{\text{sor-diff}}$ and it displayed non-significant relationship with $\beta_{\text{sor-null}}$ (Figs 3C, 3D). The nestedness component (β_{nes}) was related significantly both to $\beta_{\text{sor-null}}$ and $\beta_{\text{sor-diff}}$, but the positive correlation was stronger with the null expectations ($\beta_{\text{sor-null}}$) (Figs 3E, 3F).

The model selection procedure displayed a significant impact of SRP ($Df = 1$, $F = 1.836$, $P < 0.05$) and SRSi ($Df = 1$, $F = 1.724$, $P < 0.05$) in the FH region and that of COD ($Df = 1$, $F = 2.7401$, $P < 0.01$), NO_3^- ($Df = 1$, $F = 3.2104$, $P < 0.01$), CO_3^{2-} ($Df = 1$, $F = 3.2473$, $P < 0.01$) and Cl^- ($Df = 1$, $F = 2.6031$, $P < 0.05$) in the DT region. Variation partitioning for both regions revealed that establishment of community structure using either abundance or presence-absence data was related mainly to the pure environmental effect, which was significant in each case but explained a higher proportion of the variations in diatom communities in the DT (16% and 7.1%) than in the FH region (5.6% and 2.3%). In the FH region, the pure temporal variation also had a significant impact on the community structures, however, the explained variation was lower (3.9% and 2.2%). All the other fractions (pure and shared) of explanatory data sets were negligible in terms of variance explanation. In all models presented, variation in community structure was not fully explained, leaving considerable portion of residuals unexplored. Furthermore, the amount of unexplained variation was higher using presence-absence data in both regions (Fig. 4).

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 Interfluvium 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

(namely, as a result of high species turnover). Algarte *et al.* (2016) reported 50% mean β -diversity for periphytic diatoms in lakes connected to the Paraná River, however the authors calculated pair-wise dissimilarity instead of multiple-site dissimilarity because they focused on β -diversity between each pair of lakes among the sampling years. Despite the difference of the applied dissimilarity measures, their findings also supported pure species turnover (Algarte *et al.*, 2016), similar to our observations. Moreover, they found that damming on the studied area resulted in new environmental conditions compelling replacement processes between species with time, but each lake contributed equally to the regional species-pool as there was no significant richness difference. Maloufi *et al.* (2016) published extremely high β -diversity (> 96%) using multiple-site framework for phytoplankton from lakes in the Paris area, which was also driven by high species turnover, whereas the results were mainly explained by distinct local environmental conditions at regional scale due to different anthropogenic impacts and landscape.

Our observations provide a new insight into community ecology with applying null models in order to determine the role of deterministic and stochastic processes in diatom community variation. Both in the Fertő-Hanság region and Danube-Tisza Interfluve, overall β -diversity and turnover component values matched much less to random expectations than to deviations beyond null model expectations indicating that epipelagic diatom communities are assembled predominantly by deterministic processes (e.g. species-sorting by environmental filters) similarly to periphytic diatoms (Algarte *et al.*, 2016) or to phytoplankton communities (Maloufi *et al.*, 2016) in other studies. In contrast, nestedness component showed a different relationship to the expectations with and beyond null models in the two areas: no correlation was observed in the FH region,

but it showed a strong relation to the expectation with null model indicating a signal of stochastic processes (a multitude of random processes) in the DT region. However, this component was quite low in both areas regarding the overall β -diversity.

Key components of deterministic mechanisms

The modern metacommunity concept, which helps ecologists to understand responses to environmental changes, is based on four widely used paradigms proposed by Leibold *et al.* (2004): neutral, mass-effect, patch-dynamic and species-sorting models (Table 1, glossary of terms). According to the model selection procedure applied in this study, pure environmental processes affected diatom assemblages but the significant environmental parameters were different for the two sampled areas (SRSi and SRP in the Fertő-Hanság region, and COD, NO_3^- , CO_3^{2-} and Cl^- in the Danube-Tisza Interfluve). Furthermore, it was reported that physical and chemical features of the soda pans differ not only between the two regions but also among the soda pans within a region (Stenger-Kovács *et al.*, 2014; Lengyel *et al.*, 2016). In the DT region, variation of community structures was associated merely to the pure environmental effects due to the unique environmental characteristics of the pans, thus species-sorting can be regarded as perfect. Our findings might originate from the natural status of these soda pans. As their water supply is provided solely by precipitation and groundwater (no man-made freshwater ingress), their natural saline features (the decisive physical and chemical parameters) can serve as environmental filters for diatom species.

Different observations are presented in the literature regarding the key drivers of 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 ($< 500 \text{ km}^2$). 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 overcome 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

explanation offered previously by other authors (Beisner *et al.*, 2006; Heino *et al.*, 2010).

Although, physical and chemical factors played a key role in the reconstructed soda pans of the FH region as well, pure temporal variation also influenced the community structure. We assume that this result may be related to the restoration management applied for the soda pans in this area aiming the re-establish migrating and nesting waterfowl population density. Legény-tó has a permanent linkage to one of the numerous drainage canals in the region, which results in a more or less constant water level and low conductivity. Lengyel *et al.* (2016) reported that lack of the natural hydrological regime resulted in high diversity and dominance of freshwater diatoms in Legény-tó. Water level and surface area of Borsodi-dűlő and Nyéki-szállás are regulated by sluices built on the Hanság Main Canal and they receive a periodical water supply from Lake Fertő and the surrounding area. In addition, due to the proximity, their occasional water supply can be also provided by strong winds from Lake Fertő when its water level is relatively high. Lengyel *et al.* (2016) stated that repeated shifts or reversions in the succession process can appear due to the water management and the occasional water supply originated from Lake Fertő that could provide a reasonable explanation for our findings, as well. Algarte *et al.* (2016) also reported that water management (namely damming) resulted in significant compositional changes in diatom communities due to variation of environmental characteristics in freshwater lakes connected to the Paraná River over a ten-year period. Thus, along environmental changes, temporal variation was the most important in terms of assembly, similarly to our observed mechanisms in the FH region.

In conclusion, diatoms in extremely stressed ecosystems (high conductivity, pH, turbidity and daily temperature fluctuation) such as soda pans, are assembled predominantly by deterministic processes. High β -diversity of diatom metacommunities due to the continuous species turnover along environmental gradients reflects that soda pans within two regions (DT and FH) provide a variety of niches for different diatom assemblages. Since single soda pans host a low number of diatom species, these habitats have high conservation value due to their vulnerability. Climate change and anthropogenic interventions (e.g. water drainage, dredging, pumping of groundwater) induce irreversible changes in their natural hydrological cycle, thus threatening their good ecological status and even their existence (Williams, 2002; Stenger-Kovács *et al.*, 2014). As diatom assemblages showed in the FH region, restoration activities applying permanent or periodical water supply tend to cause significant temporal changes in diatom communities. Since diatoms proved to be suitable for indicating the changes in limnological characteristics of soda pans, continuous monitoring of diatoms (including β -diversity studies) is suggested and they should be considered during the ecological status assessment and the development of a proper conservation management.

Acknowledgements

We thank Attila Pellinger, Dr András Ambrus, Gábor Takács, Péter Kugler (Fertő-Hanság National Park), Tamás Sápi, Dr Csaba Pigniczki, Sándor Kovács (Kiskunság National Park) for their help in field sampling. We acknowledge the contribution of colleagues and students of Department of Limnology, University of Pannonia for their technical assistance in laboratory analyses. Dr Krisztina Buczkó (Hungarian Natural

History Museum) helped in the electron microscopic analysis. This study was financially supported by the National Scientific Research Foundation (OTKA K81599), the National Research Development and Innovation Office (NKFIH K120595), the European Regional Development Fund (GINOP-2.3.2-15-2016-00019) and the Széchenyi 2020 under the EFOP-3.6.1-16-2016-00015.

References

- Algarte, V.M., Dunck, B. & Rodrigues, L. (2016). Periphytic diatom ecological guilds in floodplain: Ten years after dam. *Ecological Indicators*, **69**: 407–414.
- Anderson, M.J. & Gribble, N.A. (1998). Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Australian Journal of Ecology*, **23**: 158–167.
- APHA (American Public Health Association) (1998). *Standard methods for the examination of water and wastewater*. United Book Press, Baltimore (MD).
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity: partitioning beta diversity. *Global Ecology and Biogeography*, **19**: 134–143.
- Baselga, A., Jimenez-Valverde, A. & Niccolini, G. (2007). A multiple-site similarity measure independent of richness. *Biology Letters*, **3**: 642–645.
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J. & Leprieur, F. (2013). Betapart: Partitioning Beta Diversity Into Turnover and Nestedness Components. R Package version 1.3.

426 Bauld, J. (1981). Occurrence of benthic microbial mats in saline lakes. In *Salt Lakes.*
427 *Developments in Hydrobiology*, Vol. 5. (Williams, W.D., editor), 87–111.
428 Springer Netherlands, Dordrecht.

429 Beisner, B.E., Peres-Neto, P.R., Lindström, E.S., Barnett, A. & Longhi, M.L. (2006).
430 The role of environmental and spatial processes in structuring lake communities
431 from bacteria to fish. *Ecology*, **87**: 2985–2991.

432 Bey, M.-Y. & Ector, L. (2010). *Atlas des diatomées des cours d'eau de la région*
433 *Rhône-Alpes*, Tome 1-6. Direction régionale de l'Environnement, de
434 l'Aménagement et du Logement Rhône-Alpes, Lyon.

435 Borcard, D. & Legendre, P. (2002). All-scale spatial analysis of ecological data by
436 means of principal coordinates of neighbour matrices. *Ecological Modelling*,
437 **153**: 51–68.

438 Borcard, D., Gillet, F. & Legendre, P. (2011). *Numerical Ecology With R*. Springer,
439 New York.

440 Borcard, D., Legendre, P., Avois-Jacquet, C. & Tuomisto, H. (2004). Dissecting the
441 spatial structure of ecological data at multiple spatial scales. *Ecology*, **85**: 1826–
442 1832.

443 Boros, E., Ecsedi, Z. & Oláh, J. (2013). Ecology and management of soda pans in the
444 Carpathian Basin. Hortobágy Environmental Association, Balmazújváros.

445 Boros, E., Horváth, Z., Wolfram, G. & Vörös, L. (2014). Salinity and ionic composition
446 of the shallow astatic soda pans in the Carpathian Basin. *Annales de Limnologie*
447 – *International Journal of Limnology*, **50**: 59–69.

448 CEN (Comité Européen de Normalisation) (2003). *Water Quality Guidance Standard*
449 *for the Routine Sampling and Pretreatment of Benthic Diatoms from Rivers*. EN
450 13946:2003, Geneva.

451 Chase, J.M., Kraft, N.J.B., Smith, K.G., Vellend, M. & Inouye, B.D. (2011). Using null
452 models to disentangle variation in community dissimilarity from variation in α -
453 diversity. *Ecosphere*, **2**: 1–11.

454 Cuthbert, I.D. & del Giorgio, P. (1992). Toward a standard method of measuring colour
455 in freshwater. *Limnology and Oceanography*, **37**: 1319–1326.

456 Dargám, R.M. (1995). Geochemsitry of waters and brines from the Salinas Grandes
457 basin, Córdoba, Argentina. I. Geomorphology and hydrochemical
458 characteristics. *International Journal of Salt Lake Research*, **3**: 137–158.

459 Dong, X., Li, B., He, F., Gu, Y., Sun, M., Zhang, H., Tan, L., Xiao, W., Liu, S. & Cai,
460 Q. (2016). Flow directionality, mountain barriers and functional traits determine
461 diatom metacommunity structuring of high mountain streams. *Scientific Reports*,
462 **6**: 24711.

463 Hammer, U.T. (1990). The effects of climate change on the salinity, water levels and
464 biota of Canadian prairie saline lakes. *Internationale Vereinigung für*
465 *Theoretische und Angewandte Limnologie*, **24**: 321–326.

466 Heino, J., Bini, L.M., Karjalainen, S.M., Mykrä, H., Soininen, J., Vieira, L.C.G. &
467 Diniz-Filho, J.A.F. (2010). Geographical patterns of micro-organismal
468 community structure: are diatoms ubiquitously distributed across boreal
469 streams? *Oikos*, **119**: 129–137.

470 Hofmann, G., Werum, M. & Lange-Bertalot, H. (2011). *Diatomeen im Süßwasser-*
471 *Benthos von Mitteleuropa*. Koeltz Scientific Books, Königstein.

- 472 Horváth, Z., Vad, C.F., Vörös, L. & Boros, E. (2013). The keystone role of anostracans
473 and copepods in European soda pans during the spring migration of waterbirds.
474 *Freshwater Biology*, **58**: 430–440.
- 475 King, L., Clarke, G., Bennion, H., Kelly, M. & Yallop, M. (2006). Recommendation for
476 sampling littoral diatoms in lakes for ecological status assessment. *Journal of*
477 *Applied Phycology*, **18**: 15–25.
- 478 Kirk, J.T.O. (1994). *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge
479 University Press, Cambridge.
- 480 Krammer, K. (2000). *Diatoms of Europe: Diatoms of the European Inland Waters and*
481 *Comparable Habitats* (Vol. 1. The Genus *Pinnularia*). A.R.G. Gantner Verlag
482 K.G., Ruggel.
- 483 Krammer, K. (2002). *Diatoms of Europe: Diatoms of the European Inland Waters and*
484 *Comparable Habitats* (Vol. 3. *Cymbella*). A.R.G. Gantner Verlag K.G., Ruggel.
- 485 Krammer, K. (2003). *Diatoms of Europe: Diatoms of the European Inland Waters and*
486 *Comparable Habitats* (Vol. 4. *Cymbopleura, Delicata, Navicymbula,*
487 *Gomphocymbellopsis, Afrocymbella*). A.R.G. Gantner Verlag K.G., Ruggel.
- 488 Krammer, K. & Lange-Bertalot, H. (1991). *Bacillariophyceae 4. Teil: Achnanthaceae.*
489 *Kritische Ergänzungen zu Navicula (Lineolatae) und Gomphonema*. In
490 Süßwasserflora von Mitteleuropa, Band 2/4 (Ettl, H., Gerloff, J., Heynig, H. &
491 Mollenhauer, D., editors), Spektrum Akademischer Verlag, Heidelberg.
- 492 Krammer, K. & Lange-Bertalot, H. (1999a). *Bacillariophyceae 1. Teil: Naviculaceae.*
493 In Süßwasserflora von Mitteleuropa, Band 2/1 (Ettl, H., Gerloff, J., Heynig, H.
494 & Mollenhauer, D., editors), Spektrum Akademischer Verlag, Heidelberg.

- 495 Krammer, K. & Lange-Bertalot, H. (1999b). *Bacillariophyceae 2. Teil: Bacillariaceae,*
 496 *Epithemiaceae, Surirellaceae.* In Süßwasserflora von Mitteleuropa, Band 2/2
 497 (Ettl, H., Gerloff, J., Heynig, H. & Mollenhauer, D., editors), Spektrum
 498 Akademischer Verlag, Heidelberg.
- 499 Krammer, K. & Lange-Bertalot, H. (2000). *Bacillariophyceae 3. Teil: Centrales,*
 500 *Fragilariaceae, Eunotiaceae.* In Süßwasserflora von Mitteleuropa, Band 2/3
 501 (Ettl, H., Gerloff, J., Heynig, H. & Mollenhauer, D., editors), Spektrum
 502 Akademischer Verlag, Heidelberg.
- 503 Krumbein, W.E., Cohen, Y. & Shilo, M. (1977). Solar lake (Sinai). 4. Stromatolitic
 504 cyanobacterial mats. *Limnology and Oceanography*, **22**: 635–655.
- 505 Langbein, W.B. (1961). *Salinity and hydrology of closed lakes.* Geological Survey
 506 Professional Paper 412. United States Government Printing Office, Washington
 507 (DC), USA.
- 508 Lange-Bertalot, H. (2001). *Diatoms of Europe Diatoms of the European Inland Waters*
 509 *and Comparable Habitats* (Vol. 2. Navicula sensu stricto. 10 genera separated
 510 from Navicula sensu lato. *Frustulia*). A.R.G. Gantner Verlag K.G., Ruggel.
- 511 Lange-Bertalot, H., Malgorzata, M. & Witkowski, A. (2011). *Diatoms of Europe*
 512 *Diatoms of the European Inland Waters and Comparable Habitats* (Vol. 6.
 513 *Eunotia* and some related genera). A.R.G. Gantner Verlag K.G., Ruggel.
- 514 Legendre, P. & Gallagher, E. (2001). Ecologically meaningful transformations for
 515 ordination of species data. *Oecologia*, 129: 271–280.
- 516 Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes,
 517 M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzales, A.

518 (2004). The metacommunity concept: a framework for multi-scale community
 519 ecology. *Ecology Letters*, **7**: 601–613.

520 Lengyel, E., Padisák, J., Hajnal, É., Szabó, B., Pellingner, A. & Stenger-Kovács, C.
 521 (2016). Application of benthic diatoms to assess efficiency of conservation
 522 management: a case study on the example of three reconstructed soda pans,
 523 Hungary. *Hydrobiologia*, **777**: 95–110.

524 Levkov, Z. (2009). *Diatoms of Europe: Diatoms of the European Inland Waters and*
 525 *Comparable Habitats* (Vol. 5. Amphora sensu lato). A.R.G. Gantner Verlag
 526 K.G., Ruggel.

527 Levkov, Z., Metzeltin, D. & Pavlov, A. (2013). *Diatoms of Europe: Diatoms of the*
 528 *European Inland Waters and Comparable Habitats* (Vol. 7. Luticola and
 529 *Luticolopsis*). Koeltz Scientific Books, Königstein.

530 Mádl-Szőnyi, J. & Tóth, J. (2009). A hydrogeological type section for the Duna-Tisza
 531 Interfluve, Hungary. *Hydrogeology Journal*, **17**: 961–980.

532 Magyar Közlöny (1996). 1996. évi LIII. törvény a természet védelméről. **53**: 3305–
 533 3325.

534 Maloufi, S., Catherine, A., Mouillot, D., Louvard, C., Couté, A., Bernard, C. &
 535 Troussellier, M. (2016). Environmental heterogeneity among lakes promotes
 536 hyper β -diversity across phytoplankton communities. *Freshwater Biology*, **61**:
 537 633–645.

538 Manthey, M. & Fridley, J.D. (2009). Beta diversity metrics and the estimation of niche
 539 width via species co-occurrence data: reply to Zeleny. *Journal of Ecology*, **97**:
 540 18–22.

541 Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B.,
 542 Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015). Vegan:
 543 Community Ecology Package. R Package version 2.2-1.
 544 Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006). Variation partitioning of
 545 species data matrices: estimation and comparison of fractions. *Ecology*, **87**:
 546 2614–2625.
 547 R Development Core Team (2014). R: A Language and Environment for Statistical
 548 Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-
 549 900051-07-0. <http://www.R-project.org>
 550 Rott, E. (1991). Methodological aspects and perspectives in the use of periphyton for
 551 monitoring and protecting rivers. In *Use of Algae for Monitoring Rivers*
 552 (Whitton, B.A., Rott, E. & Friedrich, G., editors), 9–16. Institut für Botanik,
 553 Universität Innsbruck, Innsbruck, Austria.
 554 Simon, S., Mádl-Szőnyi, J., Müller, I. & Pogácsás, G. (2011). Conceptual model for
 555 surface salinization in an overpressured and a superimposed gravity flow field,
 556 Lake Kelemen-szék area, Hungary. *Hydrogeology Journal*, **19**: 707–711.
 557 Smol, J.P. & Stoermer, E.F. (2010) *The Diatoms: Applications for the Environmental*
 558 *and Earth Sciences*, 2nd edition. University Press, Cambridge.
 559 Stenger-Kovács, C. & Lengyel, E. (2015). Taxonomical and distribution guide of
 560 diatoms in soda pans of Central Europe. *Studia Botanica Hungarica*, **46**(Suppl):
 561 3–203.
 562 Stenger-Kovács, C., Buczkó, K., Hajnal, É. & Padisák, J. (2007). Epiphytic, littoral
 563 diatoms as bioindicators of shallow lake trophic status: Trophic Diatom Index
 564 for Lakes (TDIL) developed in Hungary. *Hydrobiologia*, **589**: 141–154.

565 Stenger-Kovács, C., Lengyel, E., Buczkó, K., Tóth, M.F., Crossetti, O.L., Pellingier, A.,
 566 Zámboné Doma, Z. & Padisák, J. (2014). Vanishing world: alkaline, saline lakes
 567 in Central Europe and their diatom assemblages. *Inland Waters*, **4**: 383–396.
 568 Stenger-Kovács, C., Hajnal, É., Lengyel, E., Buczkó, K. & Padisák, J. (2016). A test of
 569 traditional diversity measures and taxonomic distinctness indices on benthic
 570 diatoms of soda pans in the Carpathian Basin. *Ecological Indicators*, **64**: 1–8.
 571 Taylor, J.C., Archibald, C.G.M. & Harding, W.R. (2007). *An illustrated guide to some*
 572 *common diatom species from South Africa*. Water Research Commission,
 573 Pretoria.
 574 Tóth, A., Horváth, Z., Vad, C.F., Zsuga, K., Nagy, S.A. & Boros, E. (2014).
 575 Zooplankton of the European soda pans: fauna and conservation of a unique
 576 habitat type. *International Review of Hydrobiology*, **99**: 255–276.
 577 Ulrich, W. & Gotelli, N.J. (2007). Null model analysis of species nestedness patterns.
 578 *Ecology*, **88**: 1824–1831.
 579 Vilmi, A., Karjalainen, S.M., Hellsten, S. & Heino, J. (2016). Bioassessment in a
 580 metacommunity context: are diatom communities structured solely by species
 581 sorting? *Ecological Indicators*, **62**: 86–94.
 582 Vörös, L. & Boros, E. (2010). *Nodularia willei* Gardn. tömegprodukció: a planktonikus
 583 és bentonikus elsődleges termelés peremfeltételei egy kiskunsági szikes tóban
 584 (Kelemen-szék). *Acta Biologica Debrecina – Supplementum Oecologica*
 585 *Hungarica*, **22**: 139–152.
 586 Wetzel, R.G. & Likens, G.E. (2000). *Limnological Analyses*. Springer-Verlag, New
 587 York.

588 Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California.
589 *Ecological Monographs*, **30**: 279–338.

590 Williams, W.D. (2002). Environmental threats to salt lakes and the likely status of
591 inland saline ecosystems in 2025. *Environmental Conservation*, **29**: 154–167.

592 Witkowski, A., Lange-Bertalot, H. & Metzeltin, D. (2000). *Diatom flora of marine*
593 *coasts I*. In Iconographia Diatomologica Vol. 7. Annoted diatom micrographs
594 (Lange-Bertalot, H., editor), A.R.G. Gantner Verlag K.G., Ruggell.

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

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

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

Table 3. β -diversity and its components of benthic diatom communities in the Fertő-Hanság region and in the Danube-Tisza Interfluve.

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

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

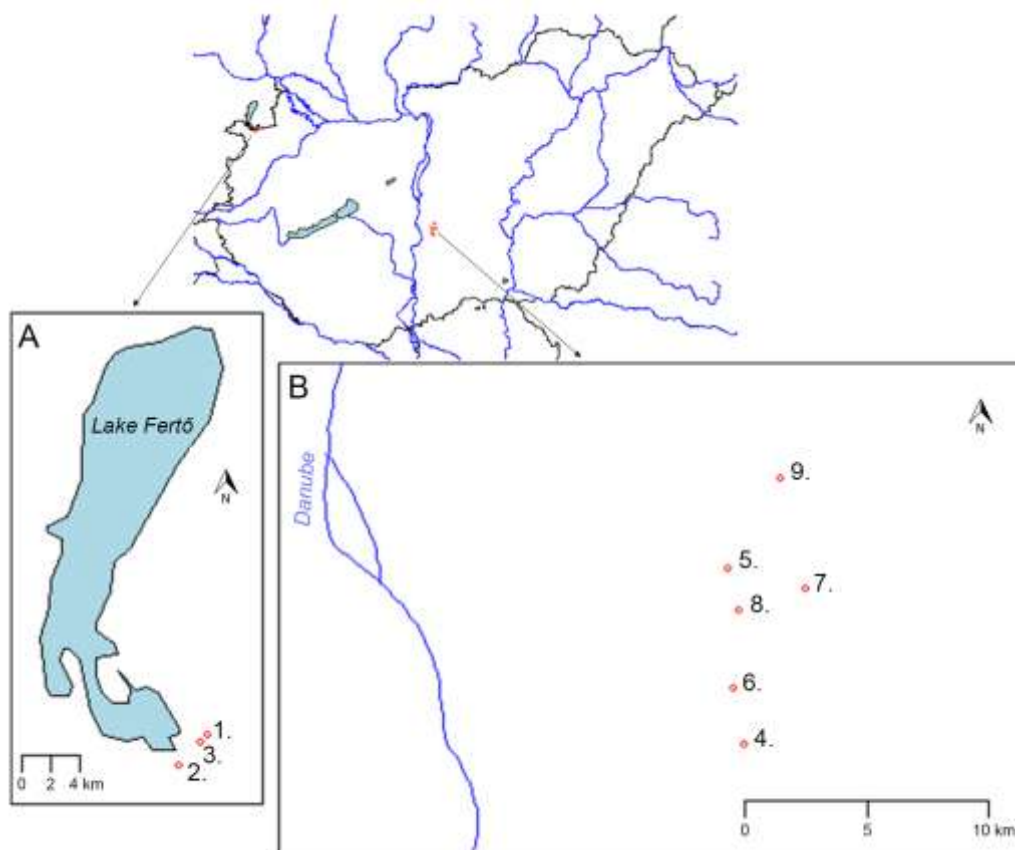


Fig. 1. Sampling sites in the Fertő-Hanság region (A) and in the Danube-Tisza Interfluve (B). Soda pan numbers are listed in Table 2.

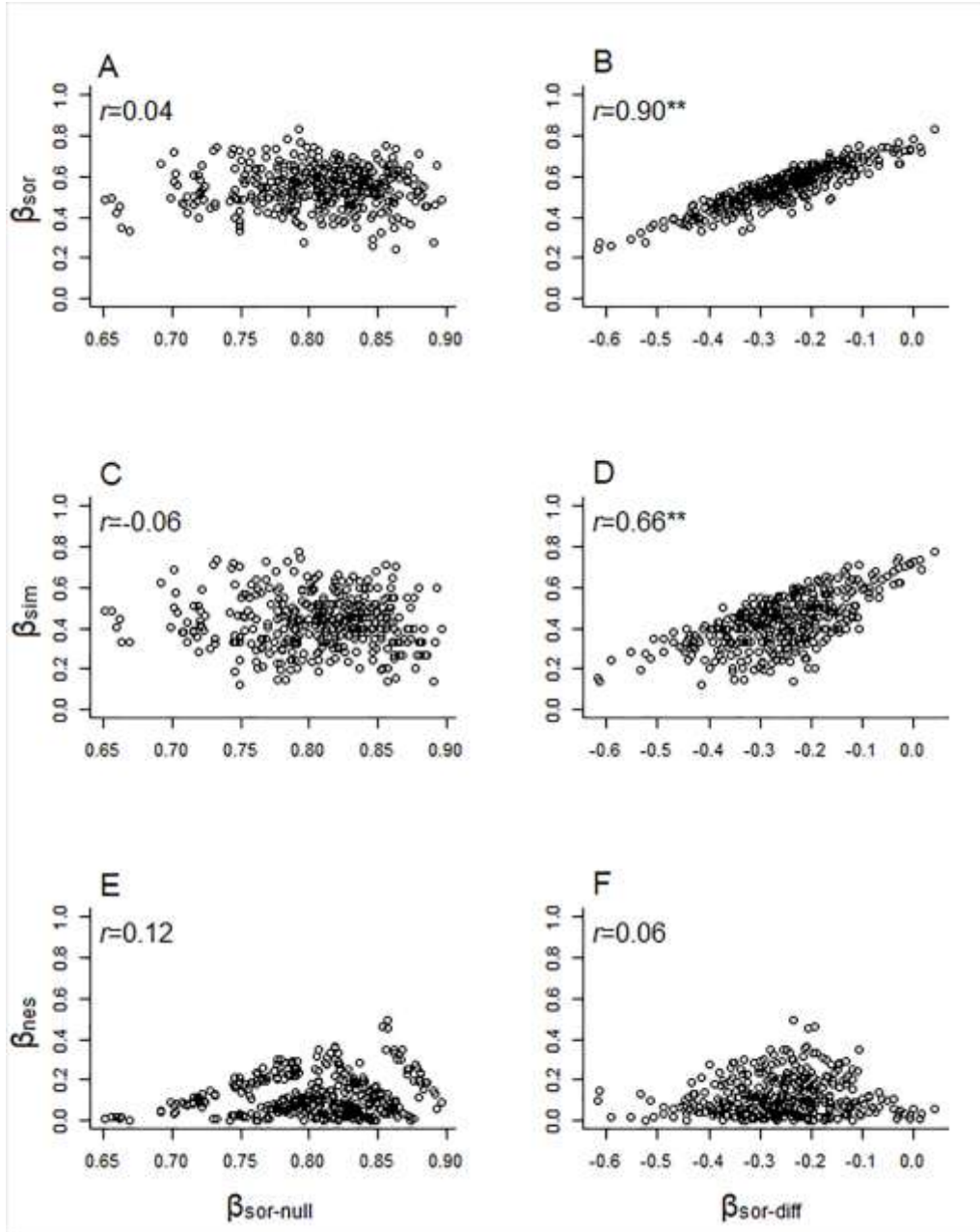


Fig. 2. The relationship of overall β -diversity (β_{sor}), and its turnover (β_{sim}) and nestedness (β_{nes}) components with the overall β -diversity expected under ($\beta_{sor-null}$) and beyond null model ($\beta_{sor-diff}$) in the Fertő-Hanság region. Pearson correlation coefficients (r) are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

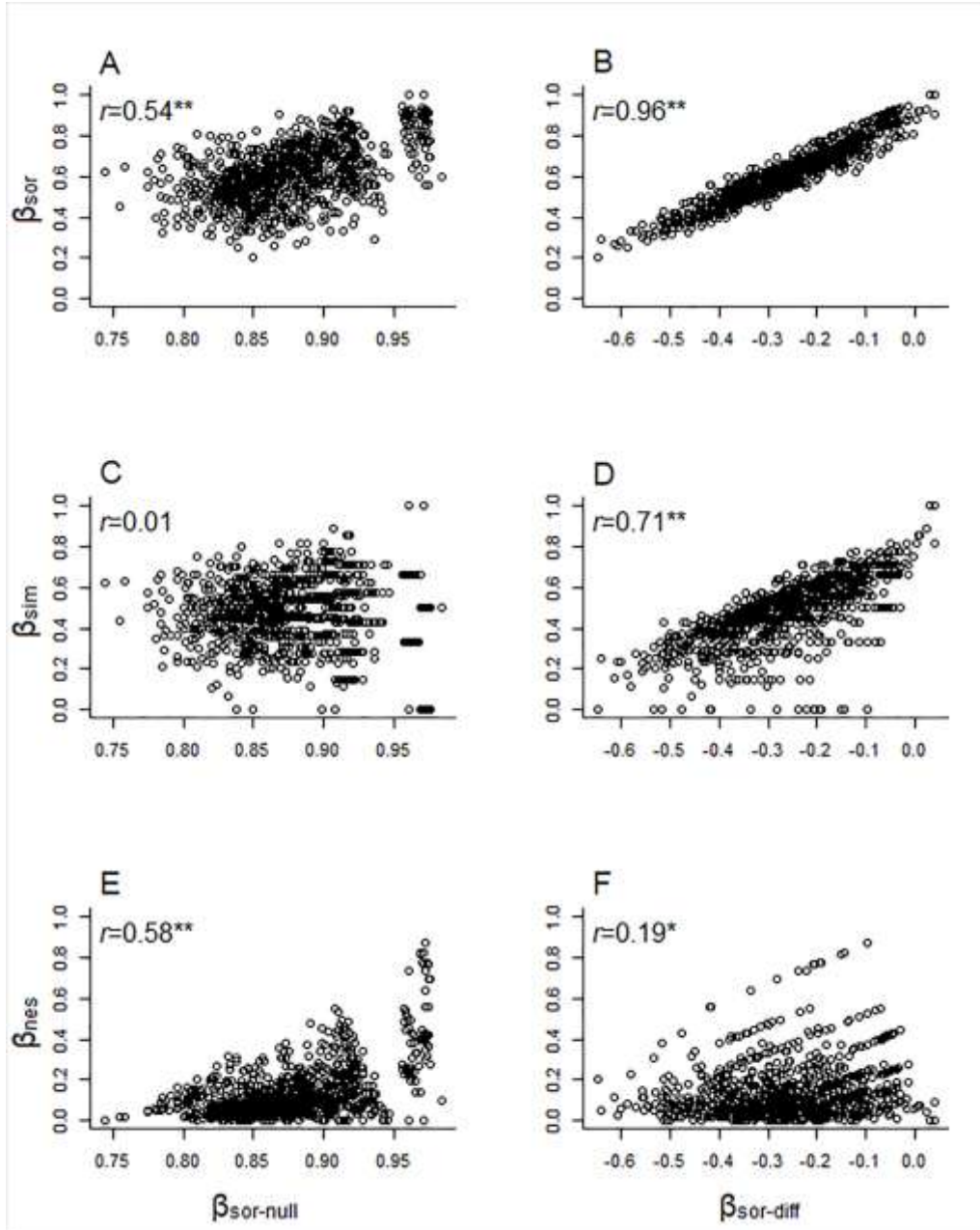
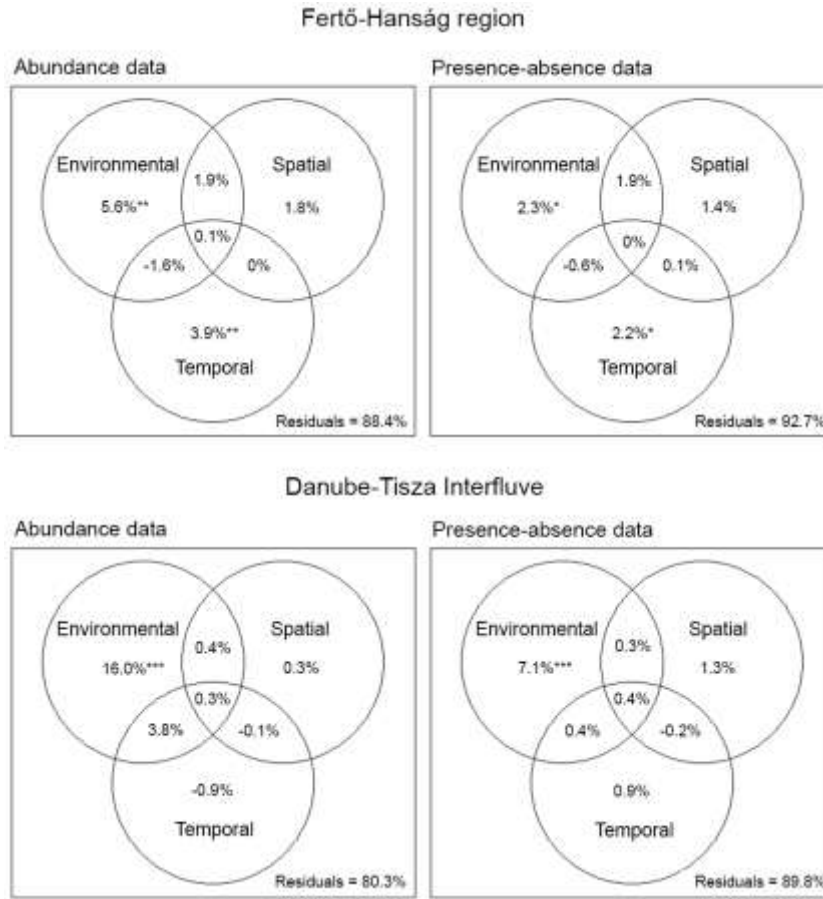


Fig. 3. The relationship of overall β -diversity (β_{sor}), and its turnover (β_{sim}) and nestedness (β_{nes}) components with the overall β -diversity expected under ($\beta_{\text{sor-null}}$) and beyond null model ($\beta_{\text{sor-diff}}$) in the Danube-Tisza Interfluvium. Pearson correlation coefficients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



624

625 **Fig. 4.** Results of variation partitioning for Hellinger transformed relative abundance
626 and presence-absence data in the Fertő-Hanság region and in the Danube-Tisza
627 Interfluve. Fractions are shown as percentages of total variation based on adjusted R^2
628 values (Environmental = environmental variables, Spatial = spatial distance, Temporal
629 = temporal variation). P values for testable fractions were computed using ANOVA of
630 RDA models. Residuals indicate the unexplained variances. Significance codes: ‘***’
631 0.001 ‘**’ 0.01 ‘*’ 0.05.