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

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

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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.
Key words: deterministic mechanisms, diatom metacommunities, nestedness, spatial and temporal variation, species-sorting, species turnover
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 μS 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. Epipelic 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 (NO₂⁻, NO₃⁻, NH₄⁺), soluble reactive (SRP) and total phosphorous (TP) were measured with spectrophotometry (APHA, 1998) using a Metertech UV/VIS Spectrophotometer, SP8001. CO₃²⁻, HCO₃⁻, Cl⁻, SO₄²⁻ 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 ($\beta_{\text{SOR}}$) (Baselga, 2010). $\beta_{\text{SOR}}$ was partitioned into two components: $\beta_{\text{SOR}} = \beta_{\text{SIM}} + \beta_{\text{NES}}$, where $\beta_{\text{SIM}}$ (Simpson’s dissimilarity) is the dissimilarity originating from species turnover and $\beta_{\text{NES}}$ (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 ($\beta_{\text{sor}}$), which was partitioned into $\beta_{\text{sim}}$ and $\beta_{\text{nes}}$ 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 ($\beta_{\text{sor}}$) 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 ($\beta_{\text{sor}}$), turnover ($\beta_{\text{sim}}$) and nestedness ($\beta_{\text{nes}}$) 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) Interfluve ($n = 47$). Species richness per sample varied between 15 and 57 (average and standard deviation: $34 \pm 11$) in the FH region, and between 2 and 32 (average and standard deviation: $17 \pm 7$) in the DT region.

Dissimilarity according to the multiple-site framework was fairly high in both regions ($\beta_{SOR} > 0.90$). Patterns of $\beta$-diversity in the epipelon were mainly attributed to pure species turnover ($\beta_{SIM}$), and nestedness ($\beta_{NES}$) component was considerably lower in both cases (Table 3).

In the FH region, the overall $\beta$-diversity ($\beta_{sor}$) was not related to the $\beta$-diversity values expected under the null model ($\beta_{sor-null}$), but it was strongly positively correlated to that of deviations beyond null model expectations ($\beta_{sor-diff}$) (Figs 2A, 2B). The turnover component ($\beta_{sim}$) showed no correlation with $\beta_{sor-null}$, but it was positively related to $\beta_{sor-diff}$ (Figs 2C, 2D). The nestedness component ($\beta_{nes}$) displayed neither a
significant relationship with $\beta_{\text{sor-null}}$ nor with $\beta_{\text{sor-diff}}$ (Figs 2E, 2F). In the DT region, although $\beta_{\text{sor}}$ 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: $\beta_{\text{sim}}$ correlated strongly to $\beta_{\text{sor-diff}}$ and it displayed non-significant relationship with $\beta_{\text{sor-null}}$ (Figs 3C, 3D). The nestedness component ($\beta_{\text{nes}}$) 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$^-$ ($Df = 1, F = 3.2031, P < 0.05$) 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 $\beta$-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 $\alpha$-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 $\beta$-diversity

Soda pans located in Central Europe have a rather low $\alpha$-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 $\beta$-diversity to a great extent (Chase et al., 2011), which was supported by our results as high overall $\beta$-diversity (> 90%) of diatom communities was observed in both study areas. Partitioning of overall $\beta$-diversity revealed that dissimilarity of diatom communities originates mainly from the replacement of species in one community by different species in the other community.
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 epipelic 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 $\beta$-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 km²). 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-dülő 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 $\beta$-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 $\beta$-diversity studies) is suggested and they should be considered during the ecological status assessment and the development of a proper conservation management.

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References


Table 1. Glossary of terms.

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
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<tbody>
<tr>
<td>Neutral theory</td>
<td>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.</td>
</tr>
<tr>
<td>Mass-effect</td>
<td>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.</td>
</tr>
<tr>
<td>Patch-dynamic</td>
<td>Population dynamics in a number of identical patches are driven by colonization and extinction influenced by interactions between species.</td>
</tr>
<tr>
<td>Species-sorting</td>
<td>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.</td>
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Table 2. The investigated soda pans, their region, GPS coordinates and the number of samples.

<table>
<thead>
<tr>
<th>Soda pans</th>
<th>Regions</th>
<th>GPS coordinates</th>
<th>No. of samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Borsodi-dűlő</td>
<td>FH</td>
<td>N 47.6815</td>
<td>E 16.8400</td>
</tr>
<tr>
<td>2. Legény-tó</td>
<td>FH</td>
<td>N 47.6632</td>
<td>E 16.8134</td>
</tr>
<tr>
<td>3. Nyéki-szállás</td>
<td>FH</td>
<td>N 47.6770</td>
<td>E 16.8328</td>
</tr>
<tr>
<td>5. Bogárzó-szék</td>
<td>DT</td>
<td>N 46.8048</td>
<td>E 19.1408</td>
</tr>
<tr>
<td>8. Sósér</td>
<td>DT</td>
<td>N 46.7892</td>
<td>E 19.1470</td>
</tr>
<tr>
<td>9. Zab-szék</td>
<td>DT</td>
<td>N 46.8375</td>
<td>E 19.1698</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th></th>
<th>Fertő-Hanság (n = 29)</th>
<th>Danube-Tisza Interfluve (n = 47)</th>
</tr>
</thead>
<tbody>
<tr>
<td>βSOR</td>
<td>0.902</td>
<td>0.942</td>
</tr>
<tr>
<td>βSIM</td>
<td>0.857</td>
<td>0.909</td>
</tr>
<tr>
<td>βNES</td>
<td>0.046</td>
<td>0.033</td>
</tr>
</tbody>
</table>

βSOR = overall β-diversity; βSIM = turnover component; βNES = 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 $\beta$-diversity ($\beta_{\text{sor}}$), and its turnover ($\beta_{\text{sim}}$) and nestedness ($\beta_{\text{nes}}$) components with the overall $\beta$-diversity expected under ($\beta_{\text{sor-null}}$) and beyond null model ($\beta_{\text{sor-diff}}$) 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 ($\beta_{sor}$), and its turnover ($\beta_{sim}$) and nestedness ($\beta_{nes}$) components with the overall β-diversity expected under ($\beta_{sor-null}$) and beyond null model ($\beta_{sor-diff}$) in the Danube-Tisza Interfluve. Pearson correlation coefficients ($r$) are shown. $P$ values were computed using Mantel tests. Significance codes: ‘**’ 0.01 ‘*’ 0.05.
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.