

## Temporal and spatial dynamics of diatom (Bacillariophyceae) communities in a peatland area

Petra Thea MUTINOVÁ<sup>a,b\*</sup>, Jana KULICHOVÁ<sup>b</sup> & Karl Inne UGLAND<sup>c</sup>

<sup>a</sup>Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway

<sup>b</sup>Department of Botany, Faculty of Science, Charles University, Benátská 2, 128 01 Prague, Czech Republic

<sup>c</sup>Marine Biology Research Group, Department of Biology, University of Oslo, Pb 1066 Blindern, 0316 Oslo, Norway

**Abstract** – This study was conducted to simultaneously investigate the spatial and temporal dynamics of diatom communities inhabiting two microhabitat types (Sphagnum periphyton and epipelon) in a peatland area of the Czech Republic. The changes in diatom community structure and corresponding diversity indices at both large (*i.e.*, variation between sites) and small (*i.e.*, variation between two microhabitats) scales were assessed through time. The results indicated clear spatial patterns at large, but not at small scale, and only limited seasonal dynamics in the diatom community. At the large scale, significant differences in diatom communities among sites were associated with both geographic position and environmental conditions (pH and conductivity). A significant effect of microhabitat type was detectable within sampling sites; the relationship between other factors and species data was not important on a small scale. The results of this study showed that both diatom diversity and community structure are good indicators of ecological heterogeneity associated with relatively high spatial and/or environmental variability. However, subtle differences in environmental conditions are hardly detectable or hidden using traditional diatom species.

**Diatoms / microhabitat / peatland / spatial dynamics / temporal dynamics**

### INTRODUCTION

The temporal and spatial dynamics of communities are important components of biodiversity. The focus on these aspects of communities has increased in recent years, because knowledge of biodiversity aids understanding of ecosystem functions and improves monitoring and restoration programs (Legendre *et al.*, 2005). Peatlands are inhabited by specific protist communities, which play key roles in the nutrient and energy cycles of the habitat (Gilbert *et al.*, 1998a, 1998b; Mitchell *et al.*, 2003). The majority of existing research on this topic has considered testate amoebae (Arcellinida and Euglyphida; e.g. Lamentowicz & Mitchell, 2005; Mieczan, 2007, 2009) and desmids (Desmidiiales; e.g. Štěpánková *et al.*, 2008; Šťastný, 2010; Neustupa *et al.*, 2012; Svoboda *et al.*, 2014). These two characteristic protist groups are dominant in peatlands, and they are frequently used in paleoecological studies

\* Corresponding author: [petra.mutinova@niva.no](mailto:petra.mutinova@niva.no)

and peatland monitoring programs (Coesel, 2001, 2003; Mitchell *et al.*, 2008). Diatoms (Bacillariophyceae) are also potential model organisms for biomonitoring (Dixit *et al.*, 1992; Pouličková *et al.*, 2004; Charles *et al.*, 2006; Kelly *et al.*, 2012), and they are equally as important as testate amoebae and desmids in the peatland microbenthos. However, studies focusing on the community structure of diatoms in peatlands are relatively scarce and rather covered by those considering the entire microphytobenthos (Mataloni, 1999; Borics *et al.*, 2003; Nováková, 2007; Tropea *et al.*, 2007; Machová-Černá & Neustupa, 2009).

Generally, freshwater microalgae are affected in space and time by prevailing environmental conditions, particularly pH, conductivity, and nutrients (e.g. Mataloni, 1999; Potapova & Charles, 2002; Pouličková *et al.*, 2004; Soininen, 2004; Soininen *et al.*, 2004; Nováková, 2007; Štěpánková *et al.*, 2008; Fránková *et al.*, 2009; Machová-Černá & Neustupa, 2009; Neustupa *et al.*, 2013). The effects of random processes and biotic interactions, which are typically indirectly estimated, may also be important for community structure (Leibold *et al.*, 2004; Svoboda *et al.*, 2014). Seasonal dynamics have significant effects on the structure of planktonic communities, and this is commonly described by the PEG-model (Phytoplankton Ecology Group; Sommer *et al.*, 1986, 2012). However, the microphytobenthos is more likely to be spatially structured, and geographic distance significantly affects microphytobenthos species composition at a large scale (e.g. Potapova & Charles, 2002; Soininen, 2004; Soininen *et al.*, 2004; Pals *et al.*, 2006; Machová-Černá & Neustupa, 2009; Veselá, 2009; Heino *et al.*, 2010; Neustupa *et al.*, 2012, 2013; Svoboda *et al.*, 2014; Mutinová *et al.*, 2016). Noticeable within site differences have been detected at a small scale, and these differences might be enhanced if two distinct microhabitat types (e.g., soft versus hard substrates or biologically active versus biologically inert substrates) are considered (Lim *et al.*, 2001; Borics *et al.*, 2003; Pouličková *et al.*, 2004; Soininen & Eloranta, 2004; Potapova & Charles, 2005; Townsend & Gell, 2005; Veselá, 2009). Nevertheless, in most cases, the differences in the microphytobenthos at a large scale (i.e., between ecologically distinct sites) are usually more striking as compared to spatial variation within a single site (Soininen, 2004; Pals *et al.*, 2006; Mutinová *et al.*, 2016), and this could lead to the false assumption that the microhabitats have minor effects on the structure of their associated communities.

This study aimed to investigate the diversity of diatoms and to quantify the importance of temporal and spatial factors on the diatom community structure in a peatland area. Variation in the following response variables was statistically partitioned: *time* (seasonal and inter-annual environmental changes), *space* (distance between sampling sites and different types of microhabitats), and *environment* (pH, conductivity, and temperature). In previous studies (Nováková, 2007; Neustupa *et al.*, 2011), temporal dynamics have primarily been examined as seasonal changes in the community. We sampled for two successive years to study inter-annual or aperiodic fluctuations in diatom diversity and community structure that may be attributed to seasonal changes during a short-term investigation. The spatial dynamics of diatom communities were studied at two scales: among sampling sites (hereafter referred to as “large scale”) and within sites (*i.e.*, among microhabitats; hereafter referred to as “small scale”). We expected to find profound spatial dynamics and at least some detectable temporal changes in the diatom communities in peatland microhabitats. We hypothesized that dark shallow peatland pools undergo numerous, rapid changes in environmental factors, which would result in detectable temporal dynamics of microphytobenthic communities (as reported by Machová-Černá & Neustupa (2009) and Neustupa *et al.* (2012) in relation to winter disturbances).

## MATERIAL AND METHODS

### Sampling and sample processing

Samples were collected at six sites from two microhabitats in the peatland pools surrounding Mácha Lake (altitude 266 m a.s.l.) in the Czech Republic (Table 1). The samples were collected from May 2010 to March 2012, and collections were made during all four seasons (Supplementary Table 1, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.). During the winter months, an ice cover was carefully removed and replaced after sampling. This study design resulted in eight successive sampling events (Supplementary Table 1), so it was possible to detect both intra-annual (*i.e.*, seasonal) and inter-annual variability of the diatom communities.

Sites 1 and 2 were located in the lowland minerotrophic fen “U Klůčku”. The other four sites were set in the adjacent peatland pools of the Swamp Nature Reserve and in the northern part of Mácha Lake. All sites were classified as lowland minerotrophic transitional bogs characterized by acidic and oligo-mesotrophic conditions (Neustupa *et al.*, 2013). Environmental factors (pH and conductivity) were measured in the field using a combined pH/conductometer WTW 340i (WTW GmbH, Weilheim, Germany) in the immediate vicinity of sampled microhabitats. Mean temperatures for a period of 30 days prior to sampling were obtained from publicly available websites for the Prague Ruzyně Station that is located 63 km from the sampling area (<http://www.vurv.cz/meteo/default.asp>). A summary of the sampling sites and environmental conditions are shown in Table 1 and Supplementary Table 1 (see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.). The difference among sampling sites based on pH and conductivity values are illustrated in a scatter plot (Fig. 1).

Table 1. Overview of the sampling sites, corresponding environmental factors (mean  $\pm$  standard deviation), and species richness based on 300 cell counts. Species richness is also given separately for epipelon (EPI) and *Sphagnum* spp. periphyton (PERI) microhabitats

Site	GPS	pH	Conductivity [ $\mu$ S/cm]	Species richness		
				EPI	PERI	Total
1	50°34'39.4"N, 14°39'46.0"E	6.7 $\pm$ 0.3	281 $\pm$ 113	27	30	35
2	50°34'36.7"N, 14°39'46.7"E	6.3 $\pm$ 0.2	383 $\pm$ 113	23	25	30
3	50°34'33.0"N, 14°40'15.5"E	5.0 $\pm$ 0.4	95 $\pm$ 43	32	26	40
4	50°35'40.7"N, 14°38'44.9"E	5.0 $\pm$ 0.6	70 $\pm$ 32	21	17	24
5	50°34'30.7"N, 14°40'06.1"E	4.5 $\pm$ 0.5	104 $\pm$ 37	24	12	26
6	50°35'43.1"N, 14°38'36.8"E	4.0 $\pm$ 0.2	92 $\pm$ 38	8	9	10

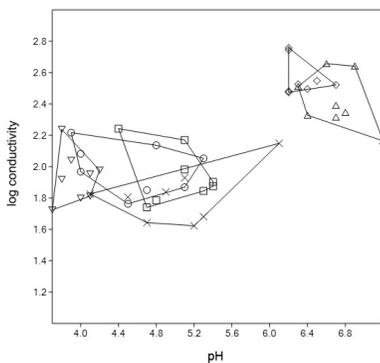


Fig. 1. Scatter plot illustrating the differences in environmental parameters among individual sites. Triangle = site 1, diamond = site 2, square = site 3, cross = site 4, circle = site 5, inverted triangle = site 6.

Two types of microhabitats, epipelon (EPI) and *Sphagnum* spp. periphyton (PERI) were chosen. Epipelon microhabitat samples were carefully collected from an area of approximately 0.25 m<sup>2</sup>, but only the top surface layer of sediment was sampled to prevent mixing with the underlying sediment layer. Samples from the periphyton microhabitat were obtained by squeezing the tops of *Sphagnum* clumps (approximately 25 g) until no water could be expressed from them by manual pressure. At each sampling event, samples were taken at almost exactly the same spots within each site to avoid small-scale differences in the diatom communities (as reported in e.g. Machová-Černá & Neustupa, 2009). Samples were immediately preserved in Lugol's solution in the field to prevent changes to the species ratio in each community, which could have been caused by sudden changes to the ambient conditions. In total, 84 samples were collected. Epipelon samples were collected during all eight sampling events (48 samples; eight sampling events at six sites). Periphyton samples were not collected during the first two samplings, so only 36 samples (six sampling events at six sites) were obtained (see also Supplementary Table 1, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.).

Community structure was based on the relative abundances of diatom species in the samples. Diatoms were counted using permanent slides, which were made according to the standard method of annealing over a gas burner flame (Battarbee *et al.*, 2001) and subsequent mounting into Naphrax medium (Brunel Microscopes Ltd. Wiltshire, UK). From each sample, 300 randomly encountered diatom cells were identified to the species level using an Olympus CX 31 light microscope at 1000× magnification and standard taxonomic monographs: Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b), Krammer (2000, 2002, 2003), Lange-Bertalot & Metzeltin (1996), Lange-Bertalot (2001), Lange-Bertalot *et al.* (2011). Up to 10 cells were counted for diatom colonies that occasionally occurred in the samples.

## Statistical analyses

The original species data were initially tested for the influence of rare and less common species. The first dataset included a complete set of all 300 identified cells from each sample (hereafter referred to as the complete dataset). In the second dataset, all rare diatom species, that did not reach greater than 1% abundance in any of the samples, were excluded. The third dataset was comprised of the top 25% of the most common species in the complete dataset. As suggested by Heino & Soininen (2010) and subsequently supported by Neustupa *et al.* (2012), this approach should be sufficient to reveal ecological patterns in aquatic communities. The degree of dataset concordance was estimated with the Procrustes statistics (PROTEST; Peres-Neto & Jackson (2001), for an explanation see also Neustupa *et al.* (2012) and Mutinová *et al.* (2016)) using 9999 permutations. The compared distance matrices were based on the two-dimensional non-metric multidimensional scaling (NMDS; Kruskal, 1964) using the Bray-Curtis index (Bray & Curtis, 1957). Pair-wise comparisons revealed that there were no significant differences between datasets, so the first complete dataset was used for subsequent statistical analyses. Statistical analyses were conducted using PAST version 3 software (Hammer *et al.*, 2001) and the *vegan* package (Oksanen *et al.*, 2012) in R version 2.15.1 software (R Development Core Team, 2012).

Regarding large-scale processes, factors were separated into three groups. Time-series and seasons were merged into the *time* factor group. Geographical

distances (hereafter referred to as GPS; included sampling site information) and microhabitat type were merged into the *space* factor group. The geographic distances were obtained from GPS coordinates by creating a similarity matrix that was used for principle coordinates analyses (PCoA) using PAST. The scores from the first 12 PCoA axes were used as a space variable. The pH, conductivity, and mean temperature factors were standardized and then merged into the *environment* factor group.

The complete species dataset was Hellinger-transformed (Legendre & Gallagher, 2001). The quantification of joint and pure effects of factor groups on the diatom community structure was performed in R (R Development Core Team, 2012) with a permutational multivariate analysis of variance using the Bray-Curtis similarity index and 9999 permutations (permutational MANOVA; Anderson, 2001). Factor effects were sequentially estimated in the model. For example, when *environment*, *space*, and *time* were on the first, second, and third rows, respectively, the first row quantified the pure effect of *environment* plus the joint effects of *environment* with other two factors. The second row included the pure effect of *space* plus the joint effects of *space* and *time*, minus the effect of *environment*. The last row estimated the pure effect of *time* after the effects of the other two factors were subtracted.

To investigate variation in the diatom community in detail at a large scale, similar models of permutational MANOVA analyses were conducted using individual variables (only those variables that were found to have significant effects in the preceding analysis were considered, Table 2). The same approach was used to investigate small-scale processes within single sites. The complete dataset was divided into six sub-datasets corresponding to the individual sampling sites, and only the microhabitat type was included in the analysis as a spatial factor. It is important to note that the resulting  $R^2$  values are highly dependent on the number of samples in the dataset and the degrees of freedom associated with each factor. Therefore,  $R^2$  values are not comparable between different permutational MANOVA models. Thus, we also provided adjusted  $R^2$  values, which are comparable with each other in all cases, and we refer always to adjusted  $R^2$  values below.

Table 2. Partitioning of variation in the diatom community structure at the large scale (*i.e.*, within sites) by permutational MANOVA tests using the Bray-Curtis similarity index and 9999 permutations. The analysis considered (A) *time*, *space*, and *environment* factor groups and (B) individual GPS, microhabitat, pH, conductivity, and temperature factors. In each case, only the pure effect is shown. Complete results of individual permutational MANOVA tests are listed in Supplementary Tables 4 and 5. \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ , n.s.  $P > 0.05$

		<i>df</i>	<i>Sums of squares</i>	<i>F ratio</i>	$R^2$	<i>Adjusted R<sup>2</sup></i>	<i>P value</i>
A	time	6	1.083	1.237	0.040	0	n.s.
	space	13	10.019	5.284	0.371	0.254	***
	environment	2	0.825	2.829	0.031	0.007	**
	residuals	61	8.897	–	0.330	–	–
B	GPS	12	9.813	5.490	0.363	0.256	***
	microhabitat	1	0.321	2.156	0.012	0.000	n.s.
	temperature	1	0.065	0.436	0.002	0	n.s.
	conductivity	1	0.585	3.924	0.022	0.010	**
	pH	1	0.147	0.985	0.005	0	n.s.
	residuals	67	9.979	–	0.370	–	–

Two-dimensional NMDS diagrams (Kruskal, 1964; Clarke, 1993), allowed for visualization of the effects of season, site, or microhabitat on diatom communities, were constructed in PAST using the Bray-Curtis similarity index. We also examined diversity indices, particularly species richness, and the Shannon diversity index. These indices were calculated for every sample using the complete dataset (Supplementary Table 2, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.), and were subsequently divided into the following groups of variables: time-series, season, site, and microhabitat. The Mann-Whitney test (Mann & Whitney, 1947) was used to compare the two microhabitat types. In all other cases, the Kruskal-Wallis test (Kruskal, 1964), with post-hoc Mann-Whitney pair-wise comparisons using the Bonferroni correction, was performed. Boxplots were created to illustrate differences in the diversity indices of individual groups. Lastly, the relationships between diversity indices and particular environmental factors (pH and conductivity) were tested using ordinary least square regression and were illustrated with biplots.

## RESULTS

In total, 73 diatom species, belonging to 31 genera, were identified in 84 samples (Supplementary Table 3, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.). The species richness per sample ranged from 2 to 26, and mean species richness was 11.3 with a standard deviation of 5.0. Species richness values that were recorded during individual seasons and at individual sites are given in Table 1 and Supplementary Table 1 (see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.). The top 25% of the most abundant species are as follows in descending order: *Frustulia saxonica* Rabenhorst, *Eunotia bilunaris* (Ehrenberg) Schaarschmidt, *Brachysira serians* (Brébisson) Round & D.G. Mann, *Eunotia paludosa* Grunow, *Encyonopsis* cf. *delicatissima* (Hustedt) Krammer, *Eunotia* cf. *arcubus* Nörpel & Lange-Bertalot, *Achnantheidium minutissimum* (Kützing) Czarnecki, *Brachysira neoexilis* Lange-Bertalot, *Brachysira* cf. *neoexilis* Lange-Bertalot, *Eunotia exigua* (Brébisson ex Kützing) Rabenhorst, *Pinnularia rhombarea* Krammer, *Pinnularia pseudogibba* Krammer, *Cymbella falaisensis* (Grunow) Krammer & Lange-Bertalot, *Kobayasiella* sp., *Eunotia glacialis* Meister, *Pinnularia macilenta* Ehrenberg, *Tabellaria flocculosa* (Roth) Kützing, *Fragilaria construens* (Ehrenberg) Grunow, *Nitzschia* sp. 1.

Variation partitioning of pure and joint factor effectors by permutational MANOVA, showed strong spatial structuring of diatom communities at both scales (Tables 2, 3). At the large scale (i.e., differences among all six sites), the pure effect of *space* accounted for 25% ( $P < 0.001$ ) of the total variation in the diatom community structure (Table 2). The fraction of variance explained by the *environment* decreased from 22.7% ( $P < 0.001$ ) to 0.7% ( $P < 0.01$ ) after *space* and *time* were included in the model (Supplementary Table 4). Both the NMDS ordination plot (similarity among diatom communities, Fig. 2) and scatter plot (pH versus conductivity values, Fig. 1) revealed clear differences among localities. Temporal changes within sites were not significant at the large scale (Table 2 and Supplementary Table 4 (doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.)). Moreover, high covariation of geographic position with environmental factors was observed at the large scale (Supplementary Tables 4, 5), and covariation of temporal changes with environmental factors was seen at the small scale (Table 3). For example, sites 1 and 2 were characterized by relatively high pH and conductivity, whereas site 6 had the lowest

Table 3. Partitioning of variation in the diatom community structure at the small scale (*i.e.*, within sites) by permutational MANOVA tests using the Bray-Curtis similarity index and 9999 permutations. In each case, only the pure effect is shown. The analyses accounting for microhabitat, *time*, and *environment* factors were conducted for all six sites. The pure effect of the *environment* was imperceptible, so it was excluded from the table. For site 1, tests considering the individual variables microhabitat, time-series, and season were conducted. \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ , n.s.  $P > 0.05$

		<i>df</i>	<i>Sums of squares</i>	<i>F ratio</i>	$R^2$	<i>Adjusted R<sup>2</sup></i>	<i>P value</i>
site 1	time	4	0.195	2.261	0.361	0.077	**
	microhabitat	1	0.124	5.740	0.049	0	***
	residuals	5	0.108	–	0.200	–	–
site 2	time	4	0.181	1.022	0.126	0	n.s.
	microhabitat	1	0.780	17.577	0.541	0.503	***
	residuals	5	0.222	–	0.154	–	–
site 3	time	4	0.154	1.140	0.164	0	n.s.
	microhabitat	1	0.491	14.551	0.522	0.483	***
	residuals	5	0.169	–	0.179	–	–
site 4	time	4	0.117	1.080	0.182	0	n.s.
	microhabitat	1	0.145	5.364	0.225	0.161	**
	residuals	5	0.135	–	0.210	–	–
site 5	time	4	0.225	1.242	0.285	0	n.s.
	microhabitat	1	0.105	2.324	0.133	0.061	n.s.
	residuals	5	0.227	–	0.286	–	–
site 6	time	4	0.050	1.201	0.278	0	n.s.
	microhabitat	1	0.049	4.726	0.273	0.213	*
	residuals	5	0.052	–	0.289	–	–

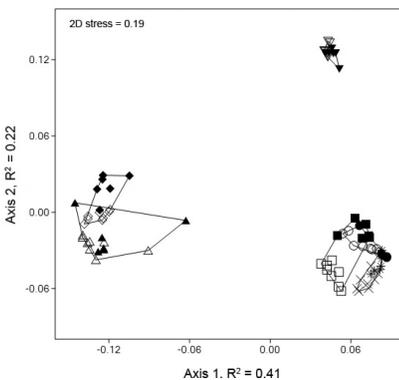


Fig. 2. NMDS ordination plot based on the diatom composition of samples collected at individual sites and individual microhabitats. Triangle = site 1, diamond = site 2, square = site 3, cross = site 4, circle = site 5, inverted triangle = site 6. Empty symbol = epipelton, filled symbol and star = *Sphagnum* spp. periphyton.

pH of all sites (Table 1, Fig. 1). A similar separation of sites based on the diatom community is clear in the NMDS graph as well (Fig. 2), even though in this case the separation of site 6 seems more profound than in the illustration based on environmental factors (Fig. 1).

We also focused on the effects of individual spatial and environmental variables between sites (Table 2 part B, complete models are given in Supplementary

Table 5 (doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.)) in subsequent analyses. The detailed inspection of pure and joint effects of individual variables at the large scale indicated that the spatial variability of diatom communities was affected by the geographic positions of sites (represented by GPS coordinates) but not differences between microhabitats (Supplementary Table 5, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.; also shown in Fig. 2). Regarding environmental factors, only conductivity was found to have a significant effect on diatom community structure after the effects of other variables were removed from the model.

A significant effect of the pure effect of microhabitat was revealed in the analysis of variation at a small scale (*i.e.*, within sites; Table 3). Microhabitat type played a significant role in shaping diatom communities at five of the six sites, whereas the effect of time was mostly insignificant (Table 3). As expected, the pure effects of both *environment* and *time* were imperceptible at the small scale. Temporal changes were not important at the large scale, and environmental variability mainly represented temperature values. In the case of site 1 only, there was as much as 7.7% of variation in the diatom community structure that was significantly explained by *time* ( $P < 0.01$ ). Regarding all models that considered both the small and large scale, the fraction of unexplained variability, ranged from 15.4% to 37% ( $R^2$  values of residuals; Tables 2 and 3).

Comparisons of diversity indices (species richness and Shannon diversity index) revealed that there were no detectable differences associated with temporal changes (including both time-series and season), but the effect of space on species diversity was clear at both the large (Fig. 3) and small scales (Kruskal-Wallis tests,  $P < 0.001$  at both scales). Post-hoc Mann-Whitney pair-wise comparisons using Bonferroni corrections indicated that sites could be generally divided into three groups with more or less similar species richness and Shannon diversity index values (also shown in Fig. 3):

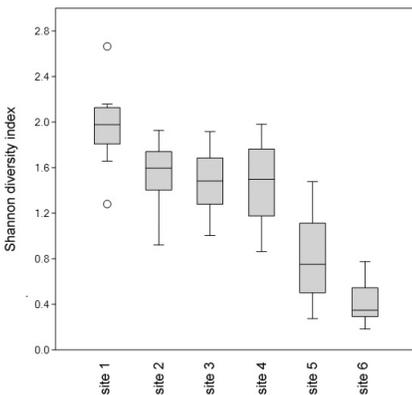


Fig. 3. Box plots illustrating differences in Shannon diversity indices of diatom communities among individual sites.

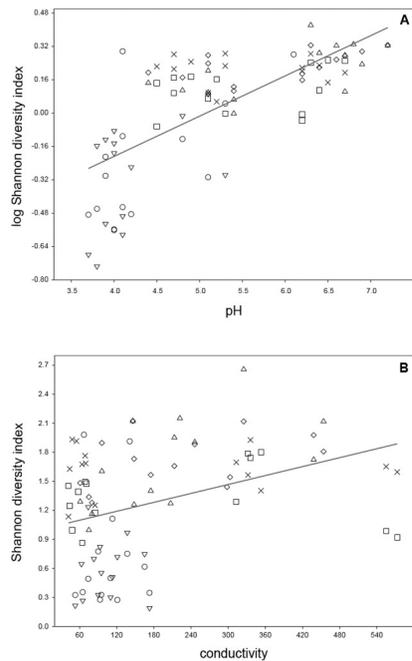


Fig. 4. Illustration of ordinary least square regression of Shannon diversity index depending on (A) pH and (B) conductivity. The individual sites are shown using the same symbols as in the ordinations. Triangle = site 1, diamond = site 2, square = site 3, cross = site 4, circle = site 5, inverted triangle = site 6.

(1) site 1 which was characterized by high diversity index values; (2) sites 2, 3, and 4 with intermediate values; and (3) sites 5 and 6 with low values. Differences in diversity between sites were associated with variability of the measured environmental factors. Species richness and the Shannon diversity index (Fig. 4) were positively correlated with both pH ( $r = 0.7/0.7$ ,  $R^2 = 0.49/0.5$ ,  $P < 0.001$ ) and conductivity ( $r = 0.38/0.4$ ,  $R^2 = 0.15/0.1$ ,  $P < 0.001$ ). Microhabitat type seemed to be an unimportant factor for diatom diversity at the large scale, but significant differences were revealed within the three sampling sites. In particular, species richness differed remarkably between sites 4 and 5, and the Shannon diversity indices differed at sites 3 and 4 (Mann-Whitney tests,  $P < 0.05$  at all sites).

## DISCUSSION

Distinct temporal dynamics of diatoms in peatland microhabitats were not found in this study. While this result is in agreement with the studies of Nováková (2007) and Svoboda *et al.* (2014), it does not support the findings of Machová-Černá & Neustupa (2009) and Neustupa *et al.* (2012), which detected noticeable changes in peatland microphytobenthos that were likely caused by freezing during the winter. The *time* factor group (both time-series and season) was essentially reflected in the temporal changes of environmental factors (as has been documented by Tahvanainen *et al.*, 2003). In our study, seasonal changes were detectable by the temperature. Two other investigated environmental factors, pH and conductivity, were not radically altered at a single site over time. We assumed that the lack of significant temporal dynamics in diatom communities detected at site 1 were due to the location of the site, which was very close to Mácha Lake. The temporal changes in the diatom communities and environmental conditions of Mácha Lake (Neustupa *et al.*, 2011) might affect both the species pool and environmental conditions at adjacent sites.

Consistent with our results, recent studies have demonstrated a significant effect of spatial distance on the structure of freshwater microphytobenthic communities (Potapova & Charles, 2002; Pouličková *et al.*, 2004; Soininen, 2004; Pals *et al.*, 2006; Machová-Černá & Neustupa, 2009; Veselá, 2009; Heino *et al.*, 2010; Neustupa *et al.*, 2012, 2013; Svoboda *et al.*, 2014; Mutinová *et al.*, 2016). In our study, spatial variation was associated with the variability of measured environmental factors (pH and conductivity), microhabitat type (periphyton or epipelon), and undetermined site-specific factors. The unknown spatial factors might incorporate the history of the site as well as any unmeasured abiotic factors (e.g., nitrogen, phosphorus and silicate, as well as light intensity) and biotic interactions (e.g., predation, competition and mutualism) with a spatial distribution (Borcard *et al.*, 1992; Anderson & Gribble, 1998). The spatial heterogeneity of diatoms is evident at the large scale, and it may conceal the effects of factors with small-scale distributions (as shown in Soininen, 2004; Pals *et al.*, 2006; Mutinová *et al.*, 2016). Therefore, the significance of the effect of individual environmental and spatial factors might depend on the spatial scale that is being investigated. Our study showed that the community structure of diatoms within localities differed between *Sphagnum* periphyton and epipelon microhabitats but were not significantly different at the large scale. Total species richness and Shannon diversity indices were similar between the two microhabitats. We suggest that although the characteristics of those microhabitats differ (e.g., living vs. inert substrates), both *Sphagnum* periphyton and

epipelon have similar potential to support rich diatom communities. Lim *et al.* (2001) and Soininen & Eloranta (2004) claimed that diatom communities in sediments should exhibit high species diversity because the sediment usually contains sets of diatoms from adjacent microhabitats and empty frustules. *Sphagnum* periphyton is a complex and biologically active habitat, so it supports a highly diverse community of microorganisms (Soininen & Eloranta, 2004; Taniguchi & Tokeshi, 2004; Townsend & Gell, 2005). However, our study did not focus on specific microhabitat details, so it is not possible to assess whether small-scale differences between diatom communities represent the effect of specific substrates or the spatial heterogeneity of ecologically neutral substrates.

Future diatom ecology research could be improved by progressively increasing the sensitivity of measurements of environmental variability in space and time (as in Tahvanainen *et al.*, 2003). We propose that studies based on traditional diatom morphospecies are relevant to our understanding of the ecology and community dynamics of freshwater microphytobenthos within a particular geographic area (e.g. Dixit *et al.*, 1992; Coesel, 2001, 2003; Pouličková *et al.*, 2004; Charles *et al.*, 2006) because the large factor gradients (e.g., differences among sites) are detectable using traditionally defined species (Mitchell *et al.*, 2014). However, small-scale and temporal community dynamics should be addressed using manipulated in situ experiments (Shurin, 2000) and/or by advanced morphological or molecular approaches (e.g., Lara *et al.*, 2011, Lew *et al.*, 2015) that provide higher taxonomic resolution to achieve more accurate diversity assessments (Heger *et al.*, 2009, Mitchell *et al.*, 2014). It was recently shown that some traditional diatom morphospecies represent different genetic and morphological entities that differ in their ecological preferences (Creach *et al.* 2006; Potapova & Hamilton 2007; Vanelslander *et al.* 2009; Veselá *et al.* 2012; Kulichová & Fialová 2016). In our study, several species complexes, which have been examined using a polyphasic approach, often occurred in high abundances: *Achnantheidium minutissimum* (Kützing) Czarnecki (Potapova & Hamilton, 2007; Pinseel *et al.*, 2017), *Eunotia bilunaris* (Ehrenberg) Schaarschmidt (Vanormelingen *et al.*, 2007), *Frustulia crassinervia-saxonica* (Veselá *et al.*, 2012; Kulichová & Fialová, 2016), *Gomphonema parvulum* (Kützing) Kützing (Kermarrec *et al.*, 2013), *Nitzschia palea* (Kützing) W.Smith (Trobajo *et al.*, 2009), and *Sellaphora* spp. (Mann *et al.*, 2004; Pouličková *et al.*, 2008). It is probable that if hidden diversity within traditional diatom species had been taken into account, the differences between microhabitats and/or seasons would have become clearer. Diatom species complexes have the potential to be used as reliable indicators for small-scale and temporal patterns. However, it is questionable whether variability in species complexes will exhibit a general trend or whether particular species complexes will respond specifically to environmental conditions.

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