

Spatial and temporal community structure of desmids on a small spatial scale

Pavel Svoboda · Jana Kulichová · Jan Št'astný

Received: 26 June 2013 / Revised: 25 September 2013 / Accepted: 5 October 2013 / Published online: 26 October 2013
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Abstract Besides spatial heterogeneity, another important component of the diversity of protist communities is the variation in species assemblages through time. Despite its importance, temporal turnover of benthic communities has been studied to a lesser extent than spatial heterogeneity has. In this study, we examine the desmid assemblages on small spatial scale in relation to the spatial, temporal, and environmental parameters. The samples were collected within two different types of peatland localities in the Czech Republic over 3 years. The differences in species composition between samples were mainly correlated with the geographic distance, while the effects of the environmental and temporal variables were much weaker. Since the spatial heterogeneity of the assemblages was not induced by the variation of the environmental factors or by the restricted dispersal ability at such a small spatial scale, we assume that both the temporal stability and strong spatial autocorrelation might have been the result of a priority effect,

with subsequent monopolization of resources. Stochasticity in colonization can introduce noise into the match between community composition and environmental conditions, which may result in stronger effect of the spatial parameters on the community structure.

Keywords Community structure · Desmids · Microphytobenthos · Monopolization · Temporal turnover · Spatial heterogeneity

Introduction

Natural communities are variable in space and time, and an understanding of these dynamics represents one of ecology's greatest challenges. In particular, knowledge of the spatio-temporal structure of assemblages underlies the understanding of such ecological processes as colonization, succession, niche differentiation, and competition (Ricklefs & Schluter, 1993). Moreover, identifying the spatio-temporal pattern of species composition in water ecosystems is crucial for the evaluation of their biodiversity, as well as the formulation of appropriate conservation strategies (Coleman, 2002). Therefore, spatial (and to a lesser extent also temporal) analyses have recently become a rapidly growing field in aquatic ecology (Steinbauer et al., 2012).

At various spatial scales, different factors appeared to reflect the heterogeneity of the phytobenthic communities (Soininen, 2007). On the small spatial

Handling editor: Judit Padišák

Electronic supplementary material The online version of this article (doi:10.1007/s10750-013-1713-4) contains supplementary material, which is available to authorized users.

P. Svoboda (✉) · J. Kulichová · J. Št'astný
Department of Botany, Faculty of Science, Charles
University in Prague, Benátská 2, Prague 128 01, Czech
Republic
e-mail: p.svoboda@natur.cuni.cz

scale (centimeters to meters), a stronger effect of the geographic distance, compared to the effects of environmental parameters, is usually attributed to the relatively homogeneous environmental factors between microsites (Černá, 2010). Community patchiness is often ascribed to the local biotic processes such as colonization, intensity of grazing, niche differentiation, and extinction (Saburova et al., 1995; Rindi & Cinelli, 2000; Benedetti-Cecchi, 2001; Coleman, 2003; Machová-Černá & Neustupa, 2009). On the large spatial scale (kilometers and greater), geographical distance as well as physicochemical factors often play a similar role in structuring benthic algal assemblages in freshwater ecosystems (Potapova & Charles, 2002; Soininen et al., 2004; Charles et al., 2006). Despite the fact that protists are generally considered as good passive dispersers (i.e., the well-known ubiquity model; Becking, 1934; Finlay & Clarke, 1999), several recent studies have demonstrated the limited dispersal ability of various protists groups at large distances (reviewed by Foissner, 2006). Therefore, the spatial autocorrelation in community composition may be associated with broad-scale historical or evolutionary factors and/or with a restricted dispersal ability (Telford et al., 2006; Soininen, 2007).

However, variation in the species community structure, in relation to the spatial scale, is only one aspect of diversity. The other important component is the temporal turnover (MacArthur & Wilson, 1963; Korhonen et al., 2010). A survey conducted for an extended period of time at one locality is not only very important for the detection of seasonal dynamics, but also for the pertinent detection of α -diversity of the microorganisms. Many microorganisms may only occur at certain times of year, and may therefore be easily overlooked during a one-time sampling; resulting in an underestimation of species diversity at that particular locality (Zalack et al., 2006). However, despite its importance, temporal variability of benthic communities is studied to a lesser extent in comparison with studies on plankton (Micheli et al., 1999; Vadeboncoeur et al., 2002). Some investigations focused on algal assemblages in various benthic freshwater biotopes described seasonal changes in primary production (O'Reilly, 2006; Kolayli & Sahin, 2009), diversity, and species composition (Ledger & Hildrew, 1998; Aberle & Wiltshire, 2006; Machová-Černá &

Neustupa, 2009; Špačková et al., 2009). These seasonal changes in community structure may be induced by the changes in water temperature (Špačková et al., 2009), fluctuations of nutrient content (Talling & Parker, 2002; Aberle & Wiltshire, 2006; Zalack et al., 2006), variations of light intensity (Keithan & Lowe, 1985; Ledger & Hildrew, 1998), and disturbances such as seasonal drying events (Gell et al., 2002; Lane et al., 2009) or freezing (Machová-Černá & Neustupa, 2009).

Desmids (Zygnematophyceae, Streptophyta) belong to the most common and often dominant phytobenthic groups, particularly in oligotrophic and slightly acidic freshwater habitats (Coesel & Meesters, 2007), where they might play an important role in substrate stabilization, and serve as an important nutritional source for heterotrophs (Domozych & Domozych, 2008). Due to the fact that they are frequently used as bioindicators for the environmental monitoring of freshwater wetlands (Coesel, 2001; Krasznai et al., 2008), knowledge of the spatial and temporal changes in their community structure is essential for developing a reliable algal-based bioassessment methodology. Moreover, the detection of their diversity is also crucial for formulation of appropriate conservation strategies; for example, the method for assessing the nature conservation value (NCV), developed by Coesel (2001). However, there are still only a few papers which have investigated the significance of both the spatio-temporal variability in desmid assemblages and the factors affecting their diversity (Machová-Černá & Neustupa, 2009; Neustupa et al., 2012).

The purpose of this study was to describe and examine the patterns of distribution and diversity within desmid assemblages in relation to the spatial, temporal, and environmental parameters from two different peatland types (a minerotrophic lowland fen and an ombrotrophic raised bog). Since desmids respond with sensitivity to the main physicochemical factors (Coesel, 1975, 2001; Štátný, 2010), we hypothesized that the desmid assemblages would be structured by the environmental variables and also by the spatial distance, as a result of small-scale biotic processes. Second, we assumed a lower species diversity accompanied by changes in species composition in the winter, as a result of disturbances by freezing; followed by its increase through the season, owing to the colonization processes.

Materials and methods

Two different types of peatland localities were chosen within the Czech Republic for collecting the algal materials: The Swamp Nature Reserve (50°34′33.271″N, 14°40′15.248″E), an oligo-mesotrophic transitional lowland fen; and the Na Čihadle Nature Reserve (50°49′58.304″N, 15°13′52.171″E), an oligotrophic raised bog. The algal material was collected seasonally from autumn 2009 to winter 2012 (Table 1) from nine sampling sites at each locality (three sites within three pools which were from meters to hundreds of meters apart; Supplementary Table 1). Unfortunately, two winter samples were not taken at the raised bog due to conditions unfavorable for sampling (for details, see Table 1). Samples were collected from an area of 0.25 m² by sucking up the algae from the upper layer of the epipelon with a plastic syringe. The samples of algae were fixed with formaldehyde (2% final concentration) within 6 h from sampling. At the time of the sampling, pH and conductivity were measured at the sampling sites using a combined pH/conductivity meter WTW 340i (WTW, Germany). The total nitrogen (TN) and total phosphorus (TP) concentrations were measured in the laboratory by a Hach colorimeter DR/890 (Hach total nitrogen kit, method no. 10071; Hach total phosphorus kit, method no. 8190). The temperature was computed as the mean value of the 30 days preceding the sampling date; temperature data were acquired from a publicly available source from the Prague Ruzyně station (<http://www.vurv.cz/meteo/default.asp>).

Table 1 The seasons and dates of individual sampling events

Season	Date	
	Lowland fen	Raised bog
Autumn	October, 2009	November, 2009
Spring	March, 2010	April, 2010
Summer	July, 2010	July, 2010
Autumn	November, 2010	November, 2010
Winter	February, 2011	February, 2011 ^a
Spring	May, 2011	May, 2011
Summer	July, 2011	July, 2010
Autumn	October, 2011	October, 2011
Winter	February, 2012	April, 2012

^a Sampling when we were not able to collect two samples from the raised bog

The fixed algal samples were examined under an Olympus BX 31 light microscope. In total, 200 single-celled desmids from each sample were identified according to Růžicka (1977, 1981), Lenzenweger (1996, 1997, 1999, 2003), and Coesel & Meesters (2007). The missing species data for the winter samples (which we were not able to take at the raised bog) were obtained by calculating the mean abundances from corresponding sampling sites for each species from the other seasons (following the recommendations of Legendre & Legendre, 1998). All species found were used for computing species richness and Shannon diversity index (Shannon & Weaver, 1949). Differences between diversity metrics (e.g., between sampling sites, pools, or seasons) were evaluated using non-parametric Kruskal–Wallis tests with post hoc Mann–Whitney pairwise comparisons (Mann & Whitney, 1947; Kruskal, 1964) in PAST software, ver. 2.17b (Hammer et al., 2001). In order to reduce the influence of rare and dominant species in the multivariate analyses, we adjusted the raw species data. Only species occurring with greater than a 1% relative abundance, or present in three or more samples, were included (Weilhoefer & Pan, 2006). The resulting data set was subsequently square root transformed (McCune & Grace, 2002). All environmental variables (pH, conductivity, TN, TP, and mean temperature) and site coordinates were standardized by subtracting the mean and dividing by the standard deviation (Legendre & Legendre, 1998).

Non-metric multidimensional scaling analyses (NMDS; Kruskal, 1964) were performed to display similarities between sampling sites on the basis of species composition data using PAST software. The Kruskal stress value was used as the measure of goodness of fit in the representation of actual multivariate distances between localities in the resulting NMDS ordination diagram (Kruskal, 1964). The community structure between different groups of samples (sampling sites, pools, and sampling dates) was compared by two-way ANOSIM tests (sites and dates were tested with the pool as a covariate; pools with dates as a covariate). The procedures were carried out in PRIMER 6[®] software (Anderson et al., 2008) with 9,999 permutations. In both statistical methods, we used the Bray–Curtis similarity index (Bray & Curtis, 1957). The Mantel tests (Mantel, 1967; Smouse et al., 1986) were performed for testing the correlations between two distance matrices using *zt*

software, ver. 1.0 (Bonnet & Van der Peer, 2002). Species composition at the sampling sites (Bray–Curtis similarity index) was tested against: (i) the environmental distances (Euclidean distances of standardized environmental parameters), (ii) the geographic distances (in meters), and (iii) the temporal distances between individual sampling events (in days). We used both the full (two matrices) and the partial (two matrices without the influence of the third matrix) Mantel tests with 10,000 permutations. The correlations were illustrated by the linear regression models performed in R, ver. 2.14.2 (R Development Core Team, 2012). Distance-based linear models (DistLM; Legendre & Anderson, 1999) were used to assess the relative importance of spatial, environmental, and temporal factors on desmid communities (Anderson & Gribble, 1998). The matrix of two-dimensional geographic coordinates has been expanded by adding all terms of the third polynomial, which allows extracting more complex features (e.g., patches or gaps) than just the linear gradient pattern (Borcard et al., 1992). The spatial and environmental factors were first submitted to the DistLM procedure with forward selection of explanatory variables. Adjusted R^2 selection criterion, used in DistLM, allows the selection of variables by sequential testing, and helps to reduce the increase of explained variation, by mere chance, by the retention of redundant parameters in the model (Borcard et al., 1992). The variation partitioning was carried out in PRIMER 6[®] software with adjusted R^2 selection criterion and 9,999 permutations. The percentage of explained variation in species data (Bray–Curtis index) and covariance between spatial (distances in meters), environmental (standardized Euclidean distances), and temporal (a number of days since first sampling) variables were illustrated by Venn diagrams obtained by using R, ver. 2.14.2 and a *Vennneuler* package (Wilkinson, 2012).

The relationship between local population persistence and local abundance (according to Soininen & Heino, 2005) was assessed by the linear correlation analysis in R, ver. 2.14.2. Local population persistence was calculated for each species as the number of seasons with the presence of a particular species at the locality (averaged over the sampling sites); therefore, population persistence expresses the average number of seasons with the species present in the population. All the analyses were performed using both the maximum and mean local abundance of each species

at the locality. Mean abundances were calculated as the sum of abundances from all seasons divided by the number of sites with an occurrence of the species, and then were log-transformed to down-weight dominant taxa (Soininen & Heino, 2005).

Results

In total, 95 species of desmids were determined from 160 samples from both localities and all seasons (Supplementary Table 2); 85 species from the minerotrophic lowland fen, and 25 species from the ombrotrophic raised bog. The difference in the species richness and diversity (Shannon index) clearly reflected the different environmental conditions of both localities, particularly the pH and conductivity values (Table 2). Both the species richness and diversity (mean values from all seasons) were distinctly higher at the lowland fen (species richness = 49.3; diversity = 2.8) than at the raised bog (species richness = 15; diversity = 2.1). The NMDS ordination plots showed noticeable differences in species composition between both the individual pools (Fig. 1) and sampling sites (graph not shown) within the peatlands. The statistical significance of the differences in species composition between all pools and between the majority of individual sampling sites was confirmed by the non-parametric two-way ANOSIM tests (Table 3). Apart from that, all pools at the lowland fen, most of the pools at the raised bog, and most of the individual sampling sites at both localities had significantly different values of species richness and diversity (all Kruskal–Wallis tests: $P < 0.001$; results of pairwise comparisons not shown). These differences were associated with spatial, rather than environmental, distances according to DistLM analyses and Mantel tests. A strong correlation between spatial distance and similarity in species composition among samples was detected at both localities (Fig. 2). The significance of spatial autocorrelation was also confirmed by the partial Mantel tests (Table 4), with the effect of measured environmental variables controlled for. The similarity in species composition was only correlated with environmental parameters at the lowland fen (Fig. 3), but this effect was much smaller than the effect of geographical distance (Table 4).

Although ANOSIM analysis showed a significant temporal difference in the community structure within

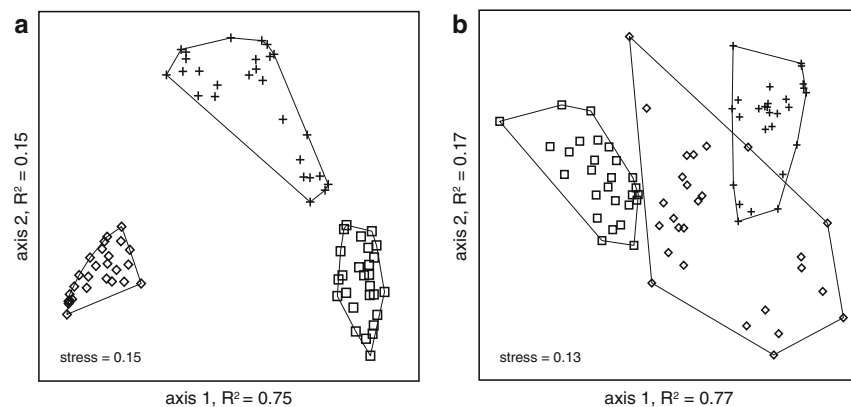
Table 2 Environmental characteristics of the investigated sampling sites through the sampling period

Sampling site (pool—site within pool)	pH	Conductivity ($\mu\text{S cm}^{-1}$)	TN (mg l^{-1})	TP (mg l^{-1})
Swamp Nature Reserve (lowland fen)				
Whole locality	5.0 (± 0.1)	100.1 (± 4.2)	3.4 (± 0.6)	0.14 (± 0.02)
1-1	4.6 (± 0.1)	91.6 (± 14.2)	2.3 (± 1.0)	0.17 (± 0.05)
1-2	5.5 (± 0.1)	95.4 (± 9.9)	2.3 (± 1.0)	0.17 (± 0.05)
1-3	5.3 (± 0.1)	90.6 (± 10.0)	2.3 (± 1.0)	0.17 (± 0.05)
2-1	5.7 (± 0.1)	96.7 (± 10.9)	3.0 (± 1.5)	0.18 (± 0.06)
2-2	5.8 (± 0.1)	89.3 (± 9.5)	3.0 (± 1.5)	0.18 (± 0.06)
2-3	5.3 (± 0.2)	92.8 (± 10.5)	3.0 (± 1.5)	0.18 (± 0.06)
3-1	4.3 (± 0.1)	116.7 (± 15.6)	5.0 (± 2.6)	0.07 (± 0.03)
3-2	4.4 (± 0.1)	115.4 (± 15.7)	5.0 (± 2.6)	0.07 (± 0.03)
3-3	4.4 (± 0.1)	112.4 (± 15.4)	5.0 (± 2.6)	0.07 (± 0.03)
Na Čihadle Nature Reserve (raised bog)				
Whole locality	4.4 (± 0.0)	15.3 (± 0.5)	7.0 (± 0.7)	0.12 (± 0.01)
1-1	4.6 (± 0.1)	15.0 (± 1.9)	9.1 (± 2.7)	0.10 (± 0.03)
1-2	4.6 (± 0.1)	11.8 (± 1.2)	8.9 (± 3.0)	0.10 (± 0.03)
1-3	4.5 (± 0.1)	16.1 (± 1.6)	9.1 (± 2.7)	0.10 (± 0.03)
2-1	4.3 (± 0.0)	15.6 (± 1.8)	7.5 (± 1.8)	0.10 (± 0.02)
2-2	4.3 (± 0.0)	18.8 (± 1.7)	7.5 (± 1.8)	0.10 (± 0.02)
2-3	4.3 (± 0.1)	17.8 (± 1.5)	7.5 (± 1.8)	0.10 (± 0.02)
3-1	4.4 (± 0.0)	16.0 (± 2.0)	4.5 (± 1.1)	0.16 (± 0.05)
3-2	4.5 (± 0.1)	13.1 (± 0.7)	4.5 (± 1.1)	0.16 (± 0.05)
3-3	4.4 (± 0.1)	13.5 (± 0.9)	4.7 (± 1.2)	0.16 (± 0.05)

Data are expressed as mean values calculated from all samplings (\pm standard error)

TN total nitrogen, TP total phosphorus

Fig. 1 The NMDS ordination plot of samples from individual pools within the lowland fen (**a**) and the raised bog (**b**), based on their species composition. The crosses correspond to pool 1, the squares to pool 2, and the diamonds to pool 3. The R^2 values determine the proportion of variance accounted for by the ordination procedure



samples from the raised bog ($R = 0.12$, $P < 0.05$), the overall significance was mostly caused by the differences of samples from autumn 2011 and winter 2012, including some samples from previous seasons (Table 5). In addition, seasonal changes in species

composition were not apparent in the NMDS ordination plot (Fig. 4) and the diversity of the desmid assemblages (Shannon diversity index) did not significantly differ between individual seasons (Fig. 5). Moreover, the Mantel tests (Table 4) showed that the

Table 3 Comparisons of species composition structure between pools and individual sampling sites within pools, calculated through the use of two-way ANOSIM tests

	Lowland fen	Raised bog
Pools		
Global test	0.93***	0.71***
1 × 2	0.75***	1.00***
1 × 3	0.96***	0.44***
2 × 3	1.00***	0.54***
Sampling sites		
Global test	0.58***	0.40***
1-1 × 1-2	1.00***	0.11 ^{n.s.}
1-1 × 1-3	1.00***	0.51***
1-2 × 1-3	0.99***	0.51***
2-1 × 2-2	0.18*	0.12 ^{n.s.}
2-1 × 2-3	0.85***	0.18*
2-2 × 2-3	0.59***	0.11 ^{n.s.}
3-1 × 3-2	0.03 ^{n.s.}	0.96***
3-1 × 3-3	0.26**	0.96***
3-2 × 3-3	0.38***	0.28***

Values of R statistics and P values are represented

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ^{n.s.} $P > 0.05$

correlation between similarity in species composition and temporal distance was insignificant. Local population persistence of epipellic desmids during the sampling period showed a significant positive relationship with both the maximum abundances (the lowland fen: $r = 0.747$; the raised bog: $r = 0.835$; $P < 0.001$; Fig. 6) and the mean abundances (the

lowland fen: $r = 0.682$; the raised bog: $r = 0.734$; $P < 0.001$; graph not shown) at both localities.

Congruent with previous analyses, the largest proportion of variability in species composition was explained by the positions of the sampling sites within the peatlands (Fig. 7); 47.5% ($P < 0.001$) of variance at the lowland fen, and 58.4% ($P < 0.001$) at the raised bog. Covariance of the spatial and environmental factors was relatively strong (the lowland fen: 34.9%; the raised bog: 11.0%), which corresponds with the results of partial Mantel tests (Table 4). The pure effect of environmental parameters was only associated with 0.3% ($P^{\text{n.s.}}$) of the variability in species composition at the lowland fen, and 1.8% ($P < 0.001$) at the raised bog. According to the DistLM procedures, the best environmental predictor, associated with species similarity at both localities, was pH (the lowland fen: $R^2 = 0.35$; the raised bog: $R^2 = 0.15$; $P < 0.001$). With the exception of TP at the lowland fen ($R^2 = 0.02$, $P < 0.01$), the addition of other environmental variables to the DistLM model did not increase the predicting power of the model significantly. Temporal aspects, themselves, explained an additional 0.7% ($P < 0.001$) and 2.3% ($P < 0.001$) variability at the lowland fen and the raised bog, respectively. Covariance of temporal parameters with environmental and/or spatial parameters was negligible (Fig. 7). The proportion of the unexplained variability in the species composition, which could not be accounted for by measured spatial, environmental, and temporal parameters was

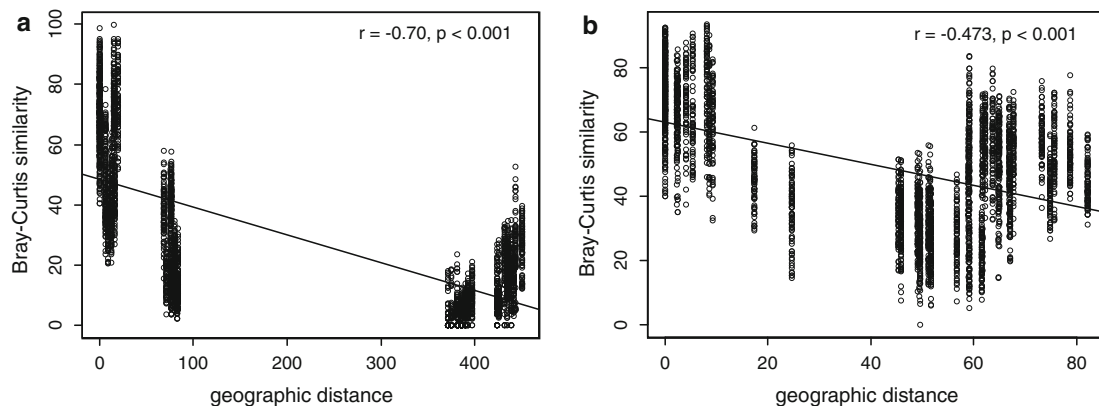
**Fig. 2** The relationship between species composition similarity of the individual sampling sites within the lowland fen (**a**) and the raised bog (**b**), and their geographic distance (in meters). The linear correlation r and the P values are indicated in the graphs

Table 4 The results of full and partial Mantel tests evaluating correlation between similarity in species composition, spatial distance, Euclidean distance of environmental parameters, and temporal distance

	Lowland fen	Raised bog
Similarity \times spatial distance	−0.70***	−0.49***
Similarity \times spatial distance (environmental parameters)	−0.69***	−0.48***
Similarity \times environmental parameters	−0.21***	−0.05 ^{n.s.}
Similarity \times environmental parameters (spatial distance)	−0.08 ^{n.s.}	−0.02 ^{n.s.}
Similarity \times temporal distance	−0.01 ^{n.s.}	−0.04 ^{n.s.}
Spatial distance \times environmental parameters	0.23***	0.08**
Temporal distance \times environmental parameters	0.10*	0.13**

Covariates used in partial Mantel tests are given in brackets. The linear correlation r and P values are represented

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ^{n.s.} $P > 0.05$

relatively small at both localities; 16.5% at the lowland fen, and 24.7% at the raised bog.

Discussion

This study illustrated the dominant effect of spatial distance on species composition of the epipellic desmids on a small spatial scale (i.e., within a single peatland). These results are comparable with previous studies that had reported a significant effect of spatial distance on community structure within various

freshwater peatlands (Machová-Černá & Neustupa, 2009; Černá, 2010; Neustupa et al., 2012). In this study, most of the sampling sites within and between the individual pools had a different species community structure, despite their very similar environmental parameters. Although we measured abiotic parameters (pH, conductivity, TP, TN, and temperature) which are generally considered as significant in shaping desmid assemblages (e.g., Coesel, 1982; Nováková, 2003; Neustupa et al., 2009), their effects were relatively unimportant. It is possible that some other abiotic factors, which influenced the desmid community structure in other studies, might be important; for example: alkalinity (Negro et al., 2003), humic acids content (Černá, 2010), and concentration of Pb or Mg^{2+} (Štěpánková et al., 2012). However, it is unlikely that the variability of these parameters would be more pronounced along such a small spatial scale. On the other hand, microorganisms may perceive physicochemical factors at a much finer resolution than we are able to measure at the sampling site (Azovsky, 2002). Nevertheless, even diurnal fluctuations of physicochemical parameters of water are often relatively large (e.g., due to photosynthetic/respiration activity; Talling, 1976; Kaplan & Bott, 1982); therefore, a more accurate measurement would probably not lead to a higher proportion of variability in the species composition explained by environmental factors.

Contrary to the strong effect of spatial distance on the desmid community structure, temporal changes were weak. Some studies of algal assemblages from various types of freshwater biotopes often describe

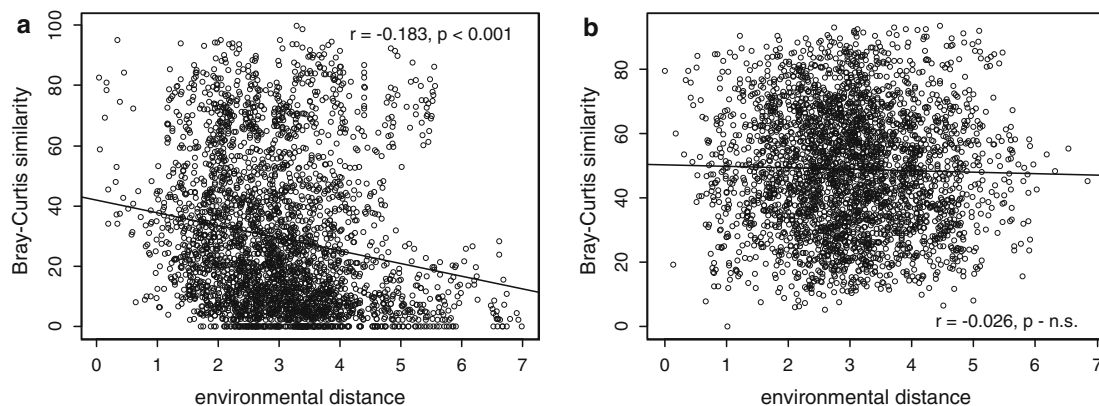
**Fig. 3** The relationship between species similarity of the individual sampling sites within the lowland fen (a) and the raised bog (b), and their environmental distances. The linear correlation r and the P values are indicated in the graphs

Table 5 Pairwise comparisons of species composition structure between individual sampling events calculated through the use of two-way ANOSIM tests

	Autumn (2009)	Spring (2010)	Summer (2010)	Autumn (2010)	Winter (2011)	Spring (2011)	Summer (2011)	Autumn (2011)	Winter (2012)
Autumn (2009)		−0.21 ^{n.s.}	0.14 ^{n.s.}	0.06 ^{n.s.}	0.16 ^{n.s.}	0.31 ^{n.s.}	0.33*	0.27 ^{n.s.}	0.38*
Spring (2010)	0.11 ^{n.s.}		0.11 ^{n.s.}	0.15 ^{n.s.}	0.19 ^{n.s.}	0.21 ^{n.s.}	0.27 ^{n.s.}	0.31 ^{n.s.}	0.35*
Summer (2010)	0.12 ^{n.s.}	0.24 ^{n.s.}		−0.22 ^{n.s.}	0.10 ^{n.s.}	0.30 ^{n.s.}	−0.07 ^{n.s.}	0.04 ^{n.s.}	0.06 ^{n.s.}
Autumn (2010)	−0.05 ^{n.s.}	0.05 ^{n.s.}	0.26 ^{n.s.}		0.06 ^{n.s.}	0.06 ^{n.s.}	−0.15 ^{n.s.}	−0.06 ^{n.s.}	−0.06 ^{n.s.}
Winter (2011)	0.15 ^{n.s.}	−0.05 ^{n.s.}	0.14 ^{n.s.}	−0.05 ^{n.s.}		0.07 ^{n.s.}	−0.14 ^{n.s.}	0.09 ^{n.s.}	0.09 ^{n.s.}
Spring (2011)	0.28*	0.17 ^{n.s.}	−0.04 ^{n.s.}	0.12 ^{n.s.}	0.12 ^{n.s.}		−0.12 ^{n.s.}	−0.06 ^{n.s.}	−0.04 ^{n.s.}
Summer (2011)	0.26 ^{n.s.}	0.22 ^{n.s.}	0.07 ^{n.s.}	0.14 ^{n.s.}	0.01 ^{n.s.}	−0.19 ^{n.s.}		−0.30 ^{n.s.}	−0.07 ^{n.s.}
Autumn (2011)	0.42*	0.31*	0.30*	0.36*	0.22 ^{n.s.}	0.01 ^{n.s.}	−0.16 ^{n.s.}		−0.15 ^{n.s.}
Winter (2012)	0.51**	0.33*	0.19 ^{n.s.}	0.43*	0.28 ^{n.s.}	−0.05 ^{n.s.}	−0.15 ^{n.s.}	−0.17 ^{n.s.}	

Values of R statistics and P values are represented. The values in the upper triangle represent samplings from the lowland fen, and the values in the lower triangle represent samplings from the raised bog

** $P < 0.01$, * $P < 0.05$, ^{n.s.} $P > 0.05$

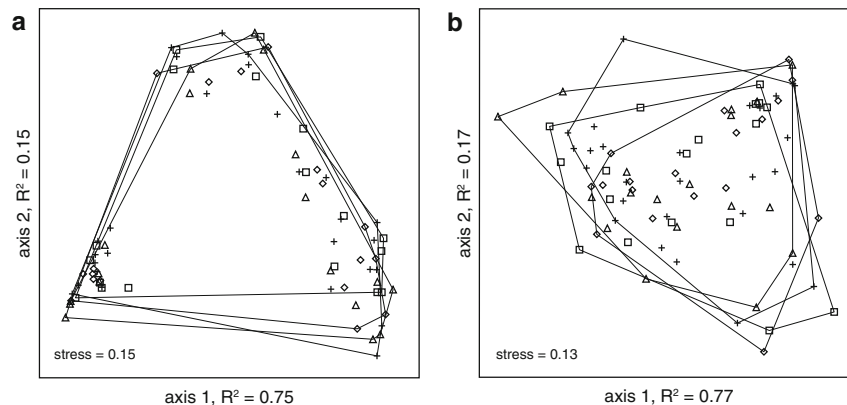


Fig. 4 The NMDS ordination plot of samples from individual seasons within the lowland fen (**a**) and the raised bog (**b**), based on their species composition. The *squares* correspond to those samples from spring, the *diamonds* to those from summer, the

crosses to the autumnal, and the *triangles* to the winter. The R^2 values determine the proportion of variance accounted for by the ordination procedure

seasonal changes in primary production (O'Reilly, 2006; Kolayli & Sahin, 2009), diversity and species composition (Ledger & Hildrew, 1998; Aberle & Wiltshire, 2006; Machová-Černá & Neustupa, 2009; Špačková et al., 2009), mainly in relationship to the

temporal variability of temperature, nutrient content, and light intensity. However, in our study, both localities had relatively stable and temporarily consistent community structures. These results were quite unexpected, since both localities were under relatively

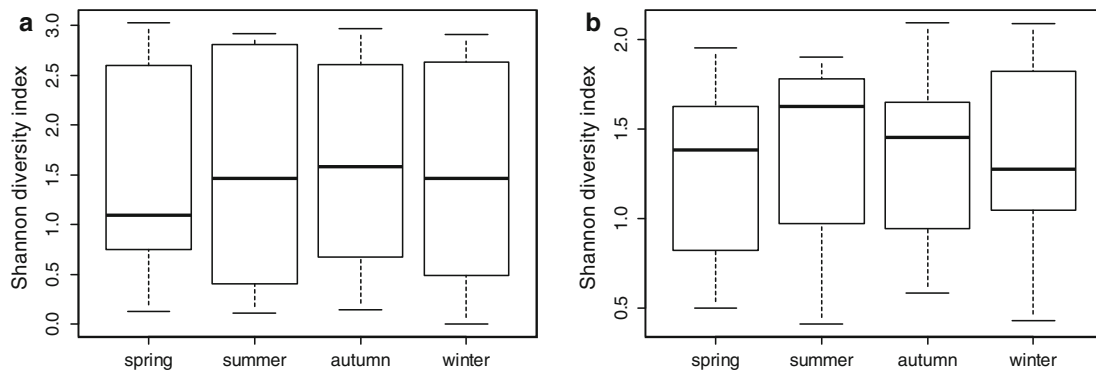


Fig. 5 The Shannon diversity indices of samples from individual seasons within the lowland fen (**a**) and the raised bog (**b**)

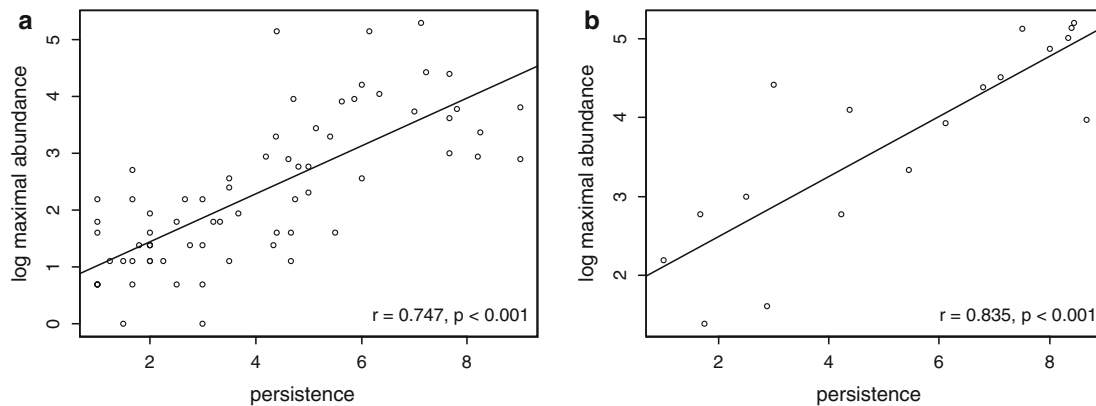
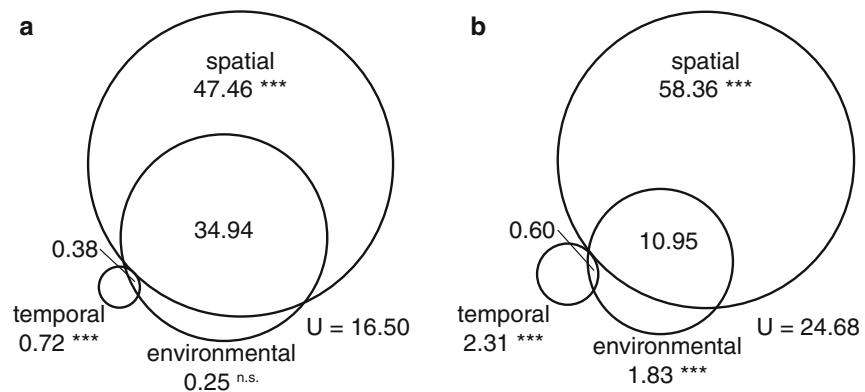


Fig. 6 The relationship between maximum abundance and population persistence of desmid species within the lowland fen (**a**) and the raised bog (**b**). The linear correlation r and the P values are indicated in the graphs

Fig. 7 The Venn diagrams illustrating partition of variance spanned by individual factors within the lowland fen (**a**) and the raised bog (**b**). U unexplained variation. The significance values in the plots are represented as *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$



thick snow cover and frozen to the bottom during winter seasons. However, it is worth mentioning that Heimans (1969) repeatedly observed the same desmid species in the same pools over time in the north

temperate peatlands. In addition, Duthie (1964) reported the fact that desmid cells can withstand freezing for a considerable period without drastic reductions in their populations; and Burkholder &

Sheath (1984) observed a relatively large proportion of reproducing taxa during all seasons, even in the winter. The significant positive relationship between local population persistence and the local abundance of desmid species through the sampling period also supports this assumption, which suggests that a high local abundance may prevent local extinctions, which can primarily be achieved via efficient cell division at a site (Soininen & Heino, 2005).

The most plausible theoretical explanation of the strong spatial effect on the desmid communities, and their striking temporal consistency, is the monopolization hypothesis (De Meester et al., 2002; Urban & De Meester, 2009), in which the main forces driving community structure are local biotic processes, such as colonization and competition. Species composition of assemblages may be strongly influenced by a priority effect, whereby early colonization provides a species an advantage in its interactions with future colonists (Shulman et al., 1983). The priority effect often emerges because a species arrives early enough to increase in numbers, monopolize the available resources, and thereby gain a competitive advantage over late-arriving colonists (Shulman et al., 1983). Apart from that, assuming that some species may penetrate into the community, their local abundance at the starting point would be low, and thus the local extinction probability higher than for resident species with higher local abundances (MacArthur & Wilson, 1967). For example, Shurin (2000) found that almost all (>91%) artificially introduced zooplankton species became extinct after a short time when introduced into ponds with already established resident communities. These introduced species remained rare thorough the whole experiment, which indicated a minor role of the immigrants input on the community structure. The proportion of introduced species that successfully colonized pools was also negatively correlated with native species diversity, which pointed to the importance of interspecies interactions in the process of potential colonization (Shurin, 2000). Similar results were obtained by Lenzenweger (2003) when he tried unsuccessfully to artificially introduce various desmid species (e.g., *Euastrum crassum* Ralfs) into a different peatland, but with very similar environmental conditions. We think that the remarkable temporal stability of the desmid communities in our systems might also have been a result of species interactions, since already adapted resident species have potentially better ability

to reject new immigrants. Furthermore, stochasticity in colonization can introduce noise into the match between community composition and environmental conditions, generating patterns that are superficially similar to those occurring through neutral dynamics (Urban & De Meester, 2009). This may result in a stronger effect of spatial parameters on the community structure at the expense of environmental conditions. The strong spatial autocorrelation in our data strongly supports this assumption, because it is very unlikely that desmids would be limited by their dispersal ability at such a small spatial scale as a single peatland.

The priority effect might also be enhanced when adaptation increases a resident population's performance in the local habitat (Urban & De Meester, 2009). Morphological plasticity increasing the fitness of organisms may represent such adaptation. For example, changes in cell morphology of desmids under various physicochemical conditions were observed in experimental studies (Neustupa et al., 2008; Černá & Neustupa, 2010), as well as in natural biotopes (Kouwets, 1988; Štěpánková et al., 2012). Moreover, Coesel & Krienitz (2008) stressed the assumption that desmids are effectively haploid organisms, thus potential mutation may be directly expressed in the phenotype; further, owing to the predominance of clonal reproduction, consequently also fixed in the population. Therefore, it is possible that such adaptations increasing fitness may help desmids to adapt to the local conditions and thus provide them a better competitive ability over the later colonizers.

In conclusion, we think that the monopolization hypothesis best describes the strong spatial autocorrelation and striking temporal consistency of benthic desmids, which we observed on a small spatial scale. The pattern was more or less similar at both localities, despite differences in their characteristics. This fact implies that this might be a general pattern, at least within well-established temperate peatlands. However, to the best of our knowledge, the priority effect and resource monopolization have not been considered in the case of microalgae so far. Therefore, future studies should use an appropriate experimental design to test the success of immigration, as well as the role of interactions between resident species and potential invaders, in order to examine the applicability of the monopolization hypothesis to the spatio-temporal community structure of the microphytobenthos.

Acknowledgments Financial support for this study was provided by a grant from the Charles University Science Foundation (B Bio 432311/2011). We thank the two anonymous reviewers for their useful comments that led us to the improvement of the manuscript.

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