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Spatio-temporal community structure of peat bog benthic desmids on a microscale

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Abstract Significant spatial variation in species composition of microphytobenthos often occurs at scales of decimetres. This microscale variation is typically more connected with dispersal-related events than to environmental factors. In this study, 4 microscale transects were delimited at 4 temperate lowland peat bog localities to investigate spatial and temporal microscale variations in benthic desmids (Desmidiales, Viridiplantae). Significant spatial autocorrelation was detected in most of the transects taken 3 times, in September and December 2010 and March 2011. The relative abundance of species data produced more pronounced spatial patterns than the presence–absence data. Spatial autocorrelation mostly decreased during the winter period, possibly due to meteorological disturbances, resulting in less spatially structured phytobenthic community in the March transects. In most cases, spatial distance accounted for a significant part of the variation in a community structure, even in analyses that controlled for the effects of environmental and temporal factors. This indicated that pure spatial factors should be considered important for structuring phytobenthic communities, even across a temporal time span of 6 months. The reduced data sets that included only 25 % of the most frequented species produced very similar patterns in spatial and temporal autocorrelation as the full data sets. Consequently, we concluded that microscale variation of benthic desmids may be sufficiently represented by dynamics of the common species.

Keywords Desmidiales · Microscale · Microphytobenthos · Peat bogs · Spatial structure

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Introduction

Microscale spatial variation has recently been recognised as one of the important properties of phytobenthic community structure both in marine and in freshwater habitats (Benedetti-Cecchi 2001; Coleman 2002; Machová-Černá and Neustupa 2009). Recruitment and local extinctions have been proposed as important drivers of spatial heterogeneity of benthic algae on scales of centimetres to metres (Saburova et al. 1995; Rindi and Cinelli 2000; Benedetti-Cecchi 2001; Coleman 2003; Rindi and Batelli 2005; Machová-Černá and Neustupa 2009). Environmental variability at this scale is usually less important and less correlated with community structure than at higher scales, such as mesoscale (tens of metres or greater) or

macroscale (kilometres or greater). Therefore, effects of purely spatial factors or variation random to environmental factors are typically more important on a microscale, whereas the meso- and macroscales may rather reflect habitat structure and other environmental factors (Méléder et al. 2007; Veselá 2009; Soininen et al. 2011; Astorga et al. 2012). Nevertheless, abiotic factors may still play a significant role even on a microscale level, for example, in habitats with high substrate heterogeneity (Machová-Černá and Neustupa 2009) or in habitats that are primarily structured by a single physical factor, such as the current velocity in streams (Passy 2001; Soininen 2003).

Significant spatial autocorrelation of phytobenthos on a microscale has repeatedly been detected in samples taken at least 10 cm apart along transects (Benedetti-Cecchi 2001; Coleman 2002; Azovsky et al. 2004). The purely spatial autocorrelation usually diminishes in samples taken several metres apart, where environmental factors typically account for most of the variation in the community structure (Méléder et al. 2007; Černá 2010). Long-term temporal consistency of the small-scale spatial structure of algal community species composition was illustrated by Coleman (2002). She suggested that seasonal changes (such as variation in recruitment levels) had a rather negligible effect on patterns of spatial variability of inter- and subtidal phytobenthic communities in subtropical Australia. Conversely, non-seasonal effects operating on small temporal scales may have been more important in these habitats. Azovsky et al. (2004) demonstrated that temporal variation, while still detectable, was much less important than spatial heterogeneity in describing community structure of microphytobenthos in boreal intertidal sandflats. Interestingly, there was about the same minor part of variation in community structure of diatoms described by spatial scale in decimetres and temporal range of 30 days, whereas larger spatial scales spanned most of the variation. However, temporal stability of microscale spatial structure was questioned by Machová-Černá and Neustupa (2009), who detected consistent changes in spatial autocorrelation of phytobenthic samples taken along microscale transects in a lowland peat bog 3 times during the year (12th May, 30th August, and 28th October). The microscale spatial autocorrelation generally decreased in most benthic microhabitats, which was explained by colonisation processes that continuously homogenised the phytobenthic community during the season. The authors hypothesised that the effects of winter disturbance, including temperature drops, freezing, and periods of snow cover, may have led to further decrease in the microscale spatial autocorrelation. In addition, diversity of the phytobenthic community is generally increased during the season, so that the relatively low spring levels may be result of local extinctions of less frequented species during the winter disturbance, followed by their subsequent recolonisation.

Heino and Soininen (2010) illustrated that the spatial and environmental factors on macroscale levels may be sufficiently represented by the dynamics of common species, that is, of 25 % of the most frequented species in samples. They concluded that macroscale studies could mostly concentrate on the common species, as the rare species have little effect on turnover description along spatial or environmental gradients in aquatic communities. Conversely, Benedetti-Cecchi et al. (2008) highlighted the role of rare species in fluctuating environments through density-dependent regulation. They illustrated that rare benthic species of algae and invertebrates may be important in driving the temporal changes, as they were highly susceptible to environmental fluctuations. However, on a microscale level, the role of rare species in relation to spatial, temporal, or environmental gradients was not investigated.

In this study, we specifically evaluated the effects of the winter period on microscale spatial structure of desmid epipelon at 4 different temperate lowland acidic localities. In addition, the relative effects of spatial, temporal, and 2 important environmental factors (pH, conductivity) were evaluated. The pH values have repeatedly been reported the single most important physico-chemical structuring factor of peatland microphytobenthos (Coesel 1982; 2001, Neustupa et al. 2009). In addition, conductivity, which approximates the concentration of solute ions, has also been considered highly correlated with community structure dynamics (Coesel 1982, Černá 2010). Specifically, we asked whether the spatial structure on a microscale remained more or less stable during the winter disturbance, that is, whether the purely spatial effects spanned a significant part of the total variation in species composition of samples taken along combined spatial and temporal gradients. To span the

extent of temporal climatic fluctuations in temperate Europe, transects were delimited in 2 European lowland regions with pronounced differences in annual temperature amplitudes. Two transects in northern Bohemia, Czech Republic, typically experience prolonged freezing during the winter period, whereas 2 transects sampled in Aquitaine, France, usually do not freeze as the mean temperatures in the winter months remain mostly in positive values. Finally, we also asked whether the common species adequately represented variation in the community structure along the investigated gradients, and whether the species frequencies data described patterns in community structure dynamics that were not perceived by the presence–absence-based matrices.

The microphytobenthos in this study was represented by a green algal group of desmids (Desmidiales) that typically form a dominant component of such assemblages in freshwater acidic wetlands (Brook 1981; Coesel and Meesters 2007). Desmids have frequently been used as a model group in freshwater ecology, especially in studies analysing the effects of abiotic factors (Spijkerman and Coesel 1998; Černá and Neustupa 2010; Stamenković and Hanelt 2011), as well as in biomonitoring and biodiversity studies of peatland habitats (Coesel 1982, 2001; Neustupa et al. 2009). The diversity optima of desmid communities in phytobenthos are in moderately acidic (pH, 5.5–7.0) and mesotrophic peatland habitats such as minerotrophic fens and bogs (Coesel 1982; Coesel and Meesters 2007). Numerous temperate desmid species have growth rate optima in relatively high temperatures (Brook 1981; Spijkerman and Coesel 1998), but desmid communities form an omnipresent part of acidic freshwater phytobenthos year-round (Brook 1981; Neustupa et al. 2011).

Materials and methods

Localities and sampling

The transects were delimited in physiognomically homogenous shallow pools of the following peatland localities: Aquitaine 1 (A1), a pool within the Étang Hardy bog (43°43′09.98″N, 01°22′07.52″W, altitude 15 m a.s.l.), area 90 m^2, depth of the sampling site 20–25 cm; Aquitaine 2 (A2), a pool close to the Marais du Cla (44°31′11.16″N, 00°36′57.43″W, altitude 67 m a.s.l.), area 400 m^2, depth of the sampling site 25–40 cm; Bohemia 1 (B1), a pool at the U Klucku minerotrophic fen (50°34′41.32″N, 14°39′41.35″E, altitude 265 m a.s.l.), area 200 m^2, depth of the sampling site 20–30 cm; and Bohemia 2 (B2), northern part of the Swamp peat bog (50°35′42.08″N, 14°38′44.27″E, altitude 254 m a.s.l.), area 275 m^2, depth of the sampling site 15–20 cm. The actual geographic distance between A1 and A2 transects was 107.4 km, and it was 2.2 km between B1 and B2 pools. The samples were taken 3 times: 6–14 September 2010, 15–22 December 2010, and 12–19 March 2011. The sampling was performed on the same days both in Aquitaine and in Bohemian localities. The annual temperature amplitudes (i.e. the difference of mean minimum and maximum monthly values) of Aquitaine localities reached 12.3 °C (Biarritz station, 32 km from A1) and 14.8 °C (Mérignac station, 39 km from A2), respectively. The lowest mean winter temperatures are 8.2 °C (A1) and 5.6 °C (A2), respectively. The annual number of frosty days (with maximum temperature below 0 °C) typically varied from 0 to 2 at the Biarritz station and from 0 to 4 at the Mérignac station. The annual temperature amplitude of the Bohemian localities reached 20.7 °C, with the lowest mean winter temperatures at −2.8 °C (Prague Ruzyne station, 63 km from B1 and B2). There are 25–80 annual frost days at the Ruzyne station. The climatic data were acquired from public sources (http://www.worldclimate.com and http://www.tutiempo.net/en/).

All the investigated localities represent natural lowland minerotrophic peatlands with different acidity and conductivity. These values were measured in the fields using a combined pH/conductometer (WTW 340i; WTW GmbH, Weilheim, Germany). The probes were submerged, so that the values were always measured at about 2 cm above the bottom of the pools. At each locality, a linear 400-cm-long transect was delimited. In total, 10 samples were taken along each transect, separated by a distance of 40 cm from each other. We chose to sample the investigated localities along the linear transects as it is a good way to clearly visualise the changes in community structure taking place along the line. The samples along transects were taken using a precisely identical pattern at four investigated localities, and this also allowed a straightforward comparison of microscale structure of individual communities. An individual sample

consisted of 2 cm^2 of epipelon taken from the uppermost 5-mm layer by using a 100-ml plastic syringe. The samples were fixed with Lugol's solution in the field (3–4 % final concentration), and later examined under an Olympus BX 51 light microscope. In total, 200 desmid cells from each sample were identified in the course of the systematic inspection of the microscopic slides at 400 × magnification.

Species data analysis

The two-dimensional non-metric multidimensional scaling (NMDS) with a Bray–Curtis distance measure was used to illustrate patterns of species composition at individual localities. The coefficients of determination (R^2) were computed for each axis to determine the proportion of variance of the scaled data, which was accounted for by the NMDS procedure. Reliability of each NMDS ordination, that is, correspondence of original multivariate distances among samples to resulting distances in the NMDS diagram was reported by Kruskal's stress values (Borg and Groenen 2005). Significance of differences in species composition among individual sampling dates was tested by a non-parametric 2-group analysis of similarities (ANOSIM) based on Bray–Curtis distance measure (Clarke 1993). Bray–Curtis distance of 2 samples j and k is defined as

$$BC = \frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i (x_{ij} + x_{ik})}$$

where x_{ij} and x_{ik} are abundances of the i-th species in samples j and k, respectively (Hammer 2011). The spatial autocorrelation of species composition along individual transects was tested by 2- and 3-matrix (partial) Mantel tests (Fortin and Gurevitch 1993). The 2-matrix tests evaluated correlations between species composition and spatial distances among individual sampling points, with no regard to other factors. The 3-matrix tests evaluated these correlations, with the effects of environmental factors removed. The species data were represented by Bray–Curtis distance matrices based on their frequencies in samples. Alternatively, the Jaccard index matrices based on the presence–absence species data were also used. The spatial matrix was based on actual distances among individual sampling points. The environmental factors were depicted as matrices based on the Euclidean distances among standardised pH and conductivity values from individual sampling points. The ANOSIM and Mantel tests were carried out in PAST, ver. 2.08. (Hammer et al. 2001), with 9999 permutations used.

Partition of variance in community structure attributed to individual factors was performed using 2 parallel approaches. The redundancy analysis (RDA)-based variance partition (Borcard et al. 1992) was conducted using *varpart* function of the package *vegan* (Oksanen et al. 2011) in R, ver. 2.13.0. (R Development Core Team 2011). The adjusted R^2 values were used for the partitioning of variance (Peres-Neto et al. 2006). The function used the standardised spatial and temporal factors. Environmental factors were combined from the standardised pH and conductivity values. Standardisation involved subtracting mean values of the particular parameter from the actual values and their subsequent dividing by standard deviation of the data set. The permutational multivariate analysis of variance using distance matrices (permutational MANOVA) was conducted with both Bray–Curtis and binary Jaccard distance indices (Anderson 2001; Oksanen et al. 2011). The function *adonis* of the package *vegan* in R, ver. 2.13.0., was used. This distribution-free function partitions distance matrices (typically based on species-in-sites data) among different sources of variation and has been considered a robust alternative to parametric MANOVA, as well as to ordination methods (Legendre and Anderson 1999). The tests evaluating how variation was attributed to different factors are sequential, that is, individual terms are tested in the order as they are quoted in the *adonis* function formula. Therefore, the 'pure' effects of individual factors (such as spatial, temporal, or environmental factors) can be ascertained, their significance evaluated, when they appear as the last at the predictor part of the formula (Oksanen et al. 2011). Therefore, several *adonis* models were conducted, each with a different order of factors. The significant p values were assessed using permutation tests on pseudo-F ratios, with 9999 permutations used. The R^2 values corresponded to different factors or to their joint effects, as well as to the adjusted R^2 values of the RDA-based variance partition and were illustrated using Venn diagrams.

The 25 % most frequently occurring taxa were considered as common species (Heino and Soininen 2010), and only these were left in the reduced data sets. The NMDS ordination patterns of the original and

reduced data sets were compared using the function *protest* of the *vegan* package in R, ver. 2.13.0. In this method, the Procrustes superimposition is used to rotate the matrices of site ordination scores to maximum similarity by minimising the sum of their squared differences (Peres-Neto and Jackson 2001). Significance of the Procrustes statistics was assessed by permutation tests (9999 permutations) on the correlation statistics derived from the sum of squares of superimposed configurations (Oksanen et al. 2011). The Mantel tests and the permutational MANOVA- and RDA-based variance partitions were conducted with the reduced data sets in the same way as described above. Differences in Mantel *r* values between the original and reduced data sets, between analyses with species data matrices based on Bray–Curtis and Jaccard distances, and between full and partial Mantel *r* values were evaluated by linear correlation analyses.

Results

In total, there were 129 desmid species recovered in samples from the investigated transects (Supplementary Tables 1–4). There were also apparent differences in species richness among individual transects. The B1 transect, for which the highest pH values were recorded (Supplementary Table 5), had a total of 80 species, while there were 38 species recovered in the transect A1, 36 at A2, and 25 at B2. The pH and conductivity values were either largely stable across both the temporal and spatial gradients (such as the pH values in the B1 or conductivity in the A2 transects) or they apparently differed among sampling dates, but remained relatively stable in samples from individual transects (Supplementary Table 5). The NMDS ordination plots of samples taken along individual transects suggested some degree of temporal effects on species composition. The temporal separation was apparent in B1 and, to a lesser degree, also in A1 and A2 (Fig. 1). These patterns were largely confirmed by the ANOSIM tests that illustrated significant differences in community structure among all the temporal groups of samples along the A2 and B1 transects (Table 1). On the other hand, temporal variability of samples was seemingly lower in the A1 and B2 transects. However, the September and March samples from the A1 transect as well as the September and December samples from the B2 transect were still significantly different. The NMDS ordination patterns

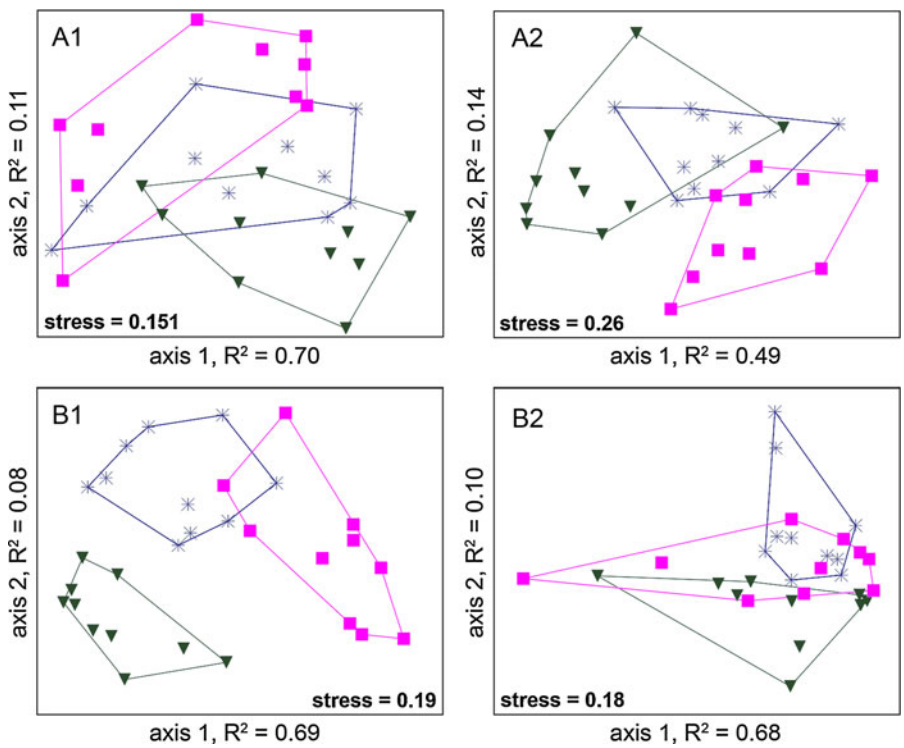

Fig. 1 The NMDS ordination plot of samples from 4 transects based on their species composition. The *squares* correspond to the September, the *stars* to the December, and the *triangles* to the March samples. The R^2 values determine the proportion of variance accounted for by the ordination procedure. The stress values evaluate the total fits of original multivariate distances among samples to the scaled distances depicted in the ordination plots

Table 1 The results of two-group ANOSIM tests on differentiation among transect samples taken in different seasons. The *R* values are indicated in the upper triangle, the permutation *p* values in the lower triangle of the table. The *R* and *p* values of the full and reduced data sets are separated by slashes

	Sep	Dec	Mar
Sep		A1: 0.11/0.11	A1: 0.37/0.36
		A2: 0.50/0.19	A2: 0.67/0.46
		B1: 0.64/0.49	B1: 0.87/0.81
		B2: 0.20/0.16	B2: 0.08/0.05
Dec	A1: n.s./n.s.		A1: 0.09/0.10
	A2: ***/*		A2: 0.25/0.22
	B1: ***/***		B1: 0.63/0.55
	B2: **/*		B2: 0.09/0.07
Mar	A1: **/**	A1: n.s./n.s.	
	A2: ***/***	A2: **/**	
	B1: ***/***	B1: ***/***	
	B2: n.s./n.s.	B2: n.s./n.s.	

*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$; n.s., $p > 0.05$

based on the reduced data sets (i.e. including the common species only) were similar with high to moderate correlations of Procrustes rotations between and reduced configurations (A1, $r = 0.99$; A2, $r = 0.88$; B1, $r = 0.92$; B2, $r = 0.76$). All these correlations were significant at the 0.01 % level. In addition, the ANOSIM tests on reduced data sets illustrated very similar patterns of temporal differentiation between samples (Table 1). Whereas the *R*-statistic values were generally lower with the reduced data sets than with the original data tables (i.e. including the rare species), the significance values illustrated identical pattern, with strong differentiation of the A2 and B1 transects and weak temporal differences among samples from the A1 and B2 transects.

Spatial autocorrelation along individual transects, with species data evaluated by the quantitative Bray–Curtis distance measure, generally decreased with time (Table 2; Fig. 2a and c). The partial Mantel tests of species data distances versus spatial distances, with the environmental factors controlled, illustrated very similar pattern of time-related general decrease in Mantel *r* values (linear correlation analysis, Bray–Curtis distance matrices: Pearson's $r = 0.98, p < 0.001$; Jaccard distance matrices: Pearson's $r = 0.98$, $p < 0.001$). However, the presence–absence species data evaluated by Jaccard distance index illustrated rather different trends in Mantel *r* values among temporal transects (Table 2; Fig. 2b and d). Indeed, the linear correlation analysis illustrated a non-significant relation of the Mantel *r* values acquired using species data coded by Bray–Curtis and by Jaccard distance matrices (linear correlation analysis of the 2-matrix Mantel *r* values: Pearson's $r = 0.29, p > 0.05$; 3-matrix Mantel *r* values: Pearson's $r = 0.41$, $p > 0.05$). The Mantel tests based on the presence–absence species data illustrated generally less significant spatial autocorrelation than the Mantel tests based on relative abundances. The reduced species data sets coded by Bray–Curtis distance matrices produced very similar spatial autocorrelation patterns as the full data sets (2-matrix Mantel *r* values: Pearson's $r = 0.93$, $p < 0.001$; 3-matrix Mantel *r* values: Pearson's $r = 0.92$, $p < 0.001$). Conversely, the correlation between the Mantel *r* values of the full and reduced species data sets evaluated by the presence–absence Jaccard distance matrices was non-significant (2-matrix Mantel *r* values: Pearson's $r = 0.34$, $p > 0.05$; 3-matrix Mantel *r* values: Pearson's $r = 0.32$, $p > 0.05$). The *r* values of the Mantel tests based on frequency data of common species generally decreased with time, but this pattern was not evident from analyses based on the presence–absence species data matrices (Table 2).

The RDA- and permutational MANOVA-based variance partitions resulted in very similar patterns at individual transects (Fig. 3; Supplementary Table 6). The permutational MANOVA models generally reported low proportions of unexplained variance. The purely spatial effects were dominant along the A1 and B2 transects, whereas they were moderately (A2) or weakly important (B1) in other transects. These purely spatial effects related neither to environmental nor to temporal factors and were significant in 3 out of the 4 transects. On the other hand, purely temporal factors, that is, the effects of temporal change in species composition, were only significant in samples from the most species-rich B1 transect. Environmental factors (pH and conductivity) explained rather modest variance proportions, but their pure effects on community structure were significant in 2 transects (A2 and B1). Relatively high temporal variation of environmental factors was reflected by substantial proportion of community structure explained by correlated temporal and environmental variation along the transects A1, A2, and B1. However, high proportions of

Table 2 The results of Mantel tests evaluating spatial autocorrelation of individual transects

Two-matrix (full) tests	Mantel *r*	Three-matrix (partial) tests	Mantel *r*
A1			
Bray–Curtis distance versus spatial distance	0.74***/0.55**/0.56** 0.72***/0.57**/0.56***	Bray–Curtis distance versus spatial distance, controlled for environmental factors	0.71***/0.53**/0.57** 0.70***/0.54**/0.57**
Jaccard distance versus spatial distance	$0.26^{n.s.}$/$0.12^{n.s.}$/0.30* $0.18^{n.s.}$/$0.17^{n.s.}$/$0.12^{n.s.}$	Jaccard distance versus spatial distance, controlled for environmental factors	$0.23^{n.s.}$/$0.09^{n.s.}$/$0.28^{n.s.}$ $0.17^{n.s.}$/$0.19^{n.s.}$/$0.12^{n.s.}$
A2			
Bray–Curtis distance versus spatial distance	0.40*/0.37*/$0.16^{n.s.}$ 0.49**/$0.26^{n.s.}$/$0.22^{n.s.}$	Bray–Curtis distance versus spatial distance, controlled for environmental factors	0.40*/0.40*/$0.22^{n.s.}$ 0.51**/0.29*/0.29*
Jaccard distance versus spatial distance	$0.01^{n.s.}$/0.31*/$0.12^{n.s.}$ $-0.04^{n.s.}$/$0.29^{n.s.}$/$-0.04^{n.s.}$	Jaccard distance versus spatial distance, controlled for environmental factors	$-0.02^{n.s.}$/0.33*/$0.05^{n.s.}$ $-0.04^{n.s.}$/0.37*/$-0.01^{n.s.}$
B1			
Bray–Curtis distance versus spatial distance	0.44**/0.34*/0.29* 0.33*/$0.18^{n.s.}$/$0.25^{n.s.}$	Bray–Curtis distance versus spatial distance, controlled for environmental factors	0.55***/0.34*/$0.26^{n.s.}$ 0.45**/$0.18^{n.s.}$/$0.22^{n.s.}$
Jaccard distance versus spatial distance	0.53***/0.31*/$0.13^{n.s.}$ $0.14^{n.s.}$/$-0.06^{n.s.}$/$0.14^{n.s.}$	Jaccard distance versus spatial distance, controlled for environmental factors	0.60***/0.31*/$0.18^{n.s.}$ $0.16^{n.s.}$/$-0.07^{n.s.}$/$0.18^{n.s.}$
B2			
Bray–Curtis distance versus spatial distance	0.28*/0.42*/$0.04^{n.s.}$ $0.16^{n.s.}$/0.38*/$0.00^{n.s.}$	Bray–Curtis distance versus spatial distance, controlled for environmental factors	0.30*/0.44*/$0.05^{n.s.}$ $0.19^{n.s.}$/0.40*/$0.04^{n.s.}$
Jaccard distance versus spatial distance	0.44*/$0.09^{n.s.}$/$0.00^{n.s.}$ $-0.07^{n.s.}$/$0.10^{n.s.}$/$-0.26^{n.s.}$	Jaccard distance versus spatial distance, controlled for environmental factors	0.43*/$0.09^{n.s.}$/$0.02^{n.s.}$ $-0.05^{n.s.}$/$0.09^{n.s.}$/$-0.07^{n.s.}$

The Mantel *R* values and their significance evaluated by permutation tests are indicated. The *R* values of the September, December, and March transects are separated by slashes. The full data sets are depicted in upper and the reduced data sets in the lower parts of cells

*** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$; n.s., $p > 0.05$

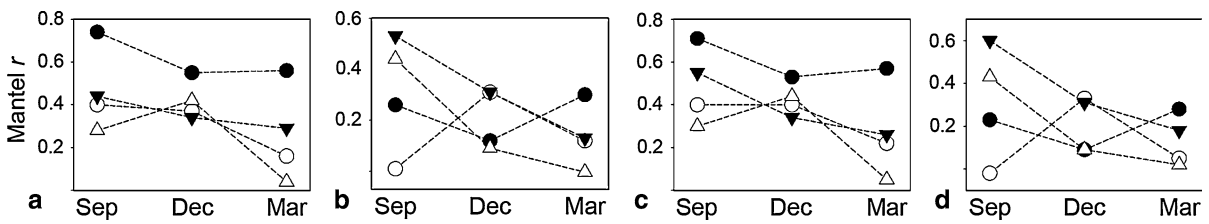

Fig. 2 Spatial autocorrelation indicated by the Mantel *r* values of individual transects in September, December, and March samples with species data matrices based on **a** the full data sets and Bray–Curtis distances, **b** the full data sets and Jaccard distances, **c** the reduced data sets and Bray–Curtis distances, and **d** the reduced data sets and Jaccard distances. The *filled circles* correspond to the A1, the *hollow circles* to the A2, the *filled triangles* to the B1, and the *hollow triangles* to the B2 transects

unexplained variance indicated that there still were substantial parts of variation in species data not perceived by any of the analysed factors. The Jaccard index–based variance partitions did not substantially differ from the quantitative Bray–Curtis distance-based matrices. The relative proportions among individual factors remained largely unchanged, but the proportions of unexplained variance slightly increased in all transects (data not shown). Variance partitions of the reduced data sets produced very similar results to the full data sets analyses. The differences among all the individual proportions in all transects (including proportions of the unexplained variation) did not differ by more than 3 percentage points, so that their overall proportions remained almost identical as in the original full data sets, including the rare species. At the same

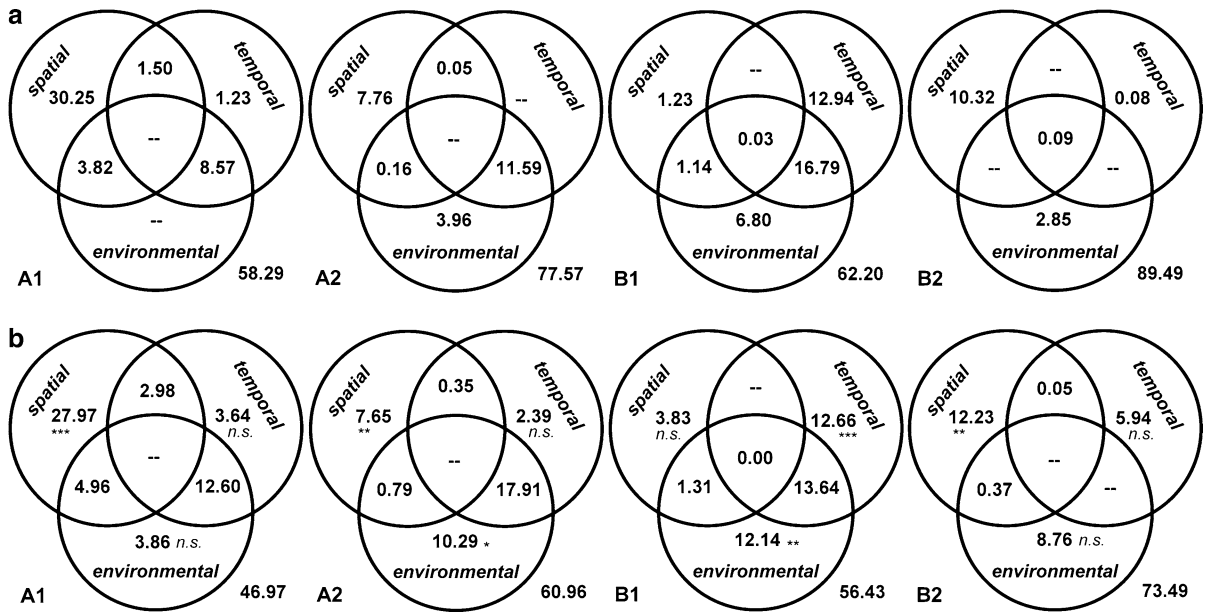

Fig. 3 The Venn diagrams illustrating partition of variance spanned by individual factors using **a** the redundancy analysis and **b** permutational MANOVA. The values outside the diagrams represent unexplained variation. The significance values in the permutational MANOVA plots are represented as *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, *n.s.* $p > 0.05$

time, the results of permutation tests that evaluated effects of individual pure factors in the *adonis* procedure using reduced species data sets were generally identical to the full data sets (data not shown).

Discussion

Significant spatial autocorrelation was detected at 10 out of the total 12 investigated transects. These results generally confirmed previous studies from various habitats that reported significant spatial effects in community structure in scales of decimetres (Benedetti-Cecchi 2001; Coleman 2002; Rindi and Batelli 2005; Machová-Černá and Neustupa 2009). Interestingly, spatial autocorrelation decreased with time, both in the Aquitaine and in the Bohemian transects. This indicates that the effects of winter disturbance (possibly related to drop in temperatures and enhanced mixing probability due to high wind intensity and precipitation) acted in both regions with climatic conditions that spanned gradient from oceanic to continental climate. Interestingly, meteorological differences between both regions did not result in any clear-cut differences in spatial structure effects clearly distinguishing localities in Aquitaine and Bohemia. During the 2010/2011 winter season, there were 4 frosty days at the Mérignac station and 2 frosty days at the Biarritz station, respectively. Conversely, there were 73 frosty days at the Ruzyně station in the Czech Republic, resulting in a prolonged freezing period at the investigated Bohemian localities (B1 and B2) in December 2010 and January 2011. While the B1 transect was the only one with significant pure temporal effects on community structure, the pattern of spatio-temporal dynamics of the B2 transect was largely similar to those of Aquitainian transects. Machová-Černá and Neustupa (2009) identified similar trends of decreasing microscale spatial autocorrelation of peat bog phytobenthos in a study that illustrated temporal changes in autocorrelation during the vegetation season. Our present data indicated that this trend of decreasing spatial autocorrelation continued over the winter period. Consequently, we suggest that the microscale spatial structure of peat bog phytobenthos recovers in spring and in early summer months, when higher water temperatures lead to increased growth rates of species from differently sized overwintering populations, resulting in strong spatially autocorrelated communities. Sommer (2000) illustrated that herbivory may increase the small-scale spatial autocorrelation of microphytobenthos, and

such factors cannot be excluded as drivers of spring structuring of peat bog benthic communities. However, colonising events during late summer, especially the autumnal and winter disturbances, seem to continually decrease spatial autocorrelation, resulting in communities with low autocorrelation at the scales of decimetres, as illustrated in this study. This pattern of spring recovery of microscale spatial structure should be tested in the future, in studies specifically designed for the identification of spring changes in spatial structure of microphytobenthic communities.

Spatial factors proved to be important determinants of species composition along our microscale transects. At 2 transects, pure spatial distance among samples was even the single most important factor describing their species structure across the time span of 6 months. At such localities, a distance of no more than 4 m in a single pool constantly produced more different species composition than samples taken after 6 months at the same place. This small-scale spatial heterogeneity was often overlooked in species inventories of microphytobenthos, but always has been intuitively perceived by practised experts on Desmidiales, who often pointed out that certain species may consistently occur at spatially limited spots (Heimans 1969) or that species composition of closely related, seemingly identical localities may be profoundly different (Messikommer 1942). Moreover, similar patterns of stable spatial heterogeneity at small scales were also reported for *Sphagnum*-inhabiting testate amoebae (Mitchell et al. 2000) for intertidal microbenthos (Azovsky et al. 2004) or for turfing algae (Coleman 2002, 2003). Fraschetti et al. (2005) stated that small-scale variability has to be perceived as an inherent property of benthic assemblages in marine coastal habitats. This study illustrated that this should also apply to freshwater peatland phytobenthos. Temporal variability was mostly much less conspicuous, even if purely temporal variation was still significant at the B1 transect. However, the temporal gradient was generally more correlated with the environmental data (pH and conductivity) than the spatial distances, and most of the temporal variation could not be distinguished from the environmental variation. Conversely, the effects of spatial distances on community structure were uncorrelated with the effects of environmental factors. This indicated that they were related to dispersal-related events, such as recruitment, colonisation, or extinction, rather than to small-scale environmental heterogeneity.

Heino and Soininen (2010) illustrated that macroscale spatial and environmental turnover of community structure may be represented by a dynamics of the 25 % most frequented species. Our results generally confirmed this pattern on a microscale level. The data sets reduced for rare species exhibited very similar patterns of spatial autocorrelation, the differences in species composition among groups, as well as of the relative proportions of spatial, environmental, and temporal factors. Similarly to Heino and Soininen (2010), we may conclude that microscale variation of desmid phytobenthos can be adequately described using common species, which may certainly be of much use to future studies on spatial structure of these communities. At the present, longer temporal or spatial extent of these studies is often limited by laborious and time-consuming microscopic species identification, often requiring substantial taxonomic expertise—see e.g. Coesel and Meesters (2007) or Šťastný (2010). However, our data suggested that less detailed enumerating and counting of rare species may not reduce ecological interpretability of results, possibly enabling a substantially more ambitious experimental design of studies based on a less number of cells counted in each sample. Heino and Soininen (2010) based their rarity measure on presence–absence data sets only. However, our results suggested that relative abundances of individual species carried an important piece of information on their microscale spatial turnover. Whereas the presence–absence data sets did not much differ in variance partition analyses, there were important differences in spatial autocorrelation patterns. Most of the spatial signal was lost in the presence–absence species data, and this pattern was even more apparent in the reduced data sets. We can, therefore, agree with Archambault and Bourget (1996), who reported that microscale community structure is especially shaped by abundances of individual taxa and cannot be adequately represented solely by presence–absence data.

In conclusion, we ascertained that purely spatial factors typically play a significant role in the microphytobenthic community variation on microscale gradients. However, the spatial autocorrelation has an important temporal dynamics, involving effects of the winter period, and possibly, the strong spatial structuring in the first half of the vegetation period. These effects were detected all across the climatic gradient of temperate European lowland peatlands and

should, therefore, not be specifically linked to relatively high weather amplitudes typical for continental localities. Our results were consistent, both with full and with reduced data sets, which indicated that relative abundances of common species may adequately represent the microphytobenthic community structure turnover on a microscale level.

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Supplementary table 1 Species data of samples taken from the transect A1.

A1	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
Actinotaenium cucurbita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Bambusina brebissonii	0	0	0	0	0	0	0	0	0	0	1	14	10	29	0	10	0	0	0	0	0	0	0	11	0	9	0	0	14	0
Closterium acutum	42	32	12	20	13	25	18	13	14	3	5	5	2	5	4	5	0	1	1	5	1	0	1	3	0	0	4	1	4	1
Closterium baylianum var. *alpinum*	19	10	18	44	61	37	49	34	28	28	26	6	9	25	56	55	75	53	38	53	7	11	15	24	26	89	103	97	68	48
Closterium calosporum	2	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Closterium costatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium dianae	4	1	1	0	0	0	0	0	0	0	0	2	0	5	1	4	2	0	1	0	0	0	0	0	0	0	1	0	0	0
Closterium intermedium	7	1	3	0	0	3	1	3	4	2	19	2	4	11	8	8	6	0	34	6	7	1	1	3	8	3	17	15	12	26
Closterium juncidum	5	3	2	7	4	7	9	3	7	16	10	5	3	15	12	8	9	9	38	6	6	1	3	0	4	0	14	11	17	14
Closterium kützingii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium lineatum	0	0	0	0	0	0	0	0	0	0	2	0	1	3	3	1	0	1	0	0	0	0	0	0	0	1	2	0	0	3
Closterium lunula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0
Closterium. ralfsii var. *hybridum*	1	0	0	0	0	2	0	0	0	1	0	1	0	0	0	3	0	0	1	0	0	0	0	0	0	0	1	1	0	1
Closterium setaceum	11	1	1	5	7	21	30	75	18	5	10	5	4	8	12	26	27	17	7	21	0	0	0	1	2	2	0	0	4	0
Cosmarium cymatonothophorum	0	0	0	2	0	2	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium quadratum	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Cosmarium prominulum var. *subundulatum*	0	1	0	1	0	2	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium pyramidatum	10	10	5	5	9	7	10	11	20	54	9	3	4	2	6	7	8	20	8	16	6	0	3	4	16	17	4	8	13	10
Desmidium grevillei	25	55	79	47	29	7	0	10	0	0	52	106	109	19	59	7	16	19	0	0	78	84	113	126	4	15	5	0	0	0
Docidium baculum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Haplotaenium minutum	6	18	11	21	17	48	38	26	44	46	3	2	1	2	9	11	21	37	14	49	1	0	2	6	7	16	1	13	6	11
Haplotaenium rectum	1	3	0	0	1	1	1	0	1	5	1	0	0	0	0	2	4	2	0	1	1	0	0	0	2	2	0	0	0	0
Hyalotheca dissiliens	0	0	0	0	0	0	0	0	8	0	0	0	30	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	7
Euastrum ansatum	1	0	2	0	4	2	2	1	4	0	1	0	0	2	0	2	0	1	5	1	4	1	0	1	8	3	3	1	5	0
Euastrum crassum var. *microcephalum*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Euastrum humerosum	0	0	0	4	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Euastrum luetkemuelleri var. *carniolicum*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Euastrum oblongum	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euastrum pectinatum	0	0	1	1	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
Micrasterias fimbriata	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micrasterias thomasiana	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Micrasterias truncata	2	0	0	0	1	0	0	0	0	3	2	1	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1
Pleurotaenium ehrenbergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	1	2	3	1	1	0	0
Pleurotaenium archeri	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staurastrum inflexum	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Staurastrum teliferum	27	7	7	9	9	11	13	15	28	13	6	3	0	7	6	5	8	16	18	15	2	0	1	1	6	5	2	3	11	2
Tetmemorus brebissonii	2	1	1	1	1	0	0	0	0	0	2	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0	0	1
Tetmemorus granulatus	33	56	56	31	43	24	22	8	21	24	47	42	23	64	19	44	20	20	33	26	83	101	57	8	110	34	41	49	46	73

Supplementary table 2 Species data of samples taken from the transect A2.

A2	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
Actinotaenium cucurbita	11	9	4	3	9	8	38	16	7	12	6	26	15	16	6	14	14	39	7	59	23	24	18	22	13	16	34	26	29	16
Actinotaenijm cucurbitinum	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bambusina brebissonii	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium acutum	0	1	4	0	0	3	3	2	0	0	0	0	0	0	0	0	2	0	0	0	1	0	2	0	1	2	0	13	0	0
Closterium baylianum var. *baylianum*	0	11	8	10	9	8	5	12	0	7	0	0	0	0	0	0	2	8	4	8	2	0	0	1	3	9	8	2	2	0
Closterium baylianum var. *alpinum*	2	17	4	14	9	15	5	4	5	10	0	0	0	0	0	3	0	1	0	0	3	4	0	11	5	7	2	0	0	0
Closterium calosporum	11	11	8	10	11	8	5	13	2	14	0	1	5	0	6	6	6	9	7	0	0	0	2	0	16	0	1	2	0	0
Closterium dianae var. *pseudodianae*	0	6	0	0	11	8	3	2	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium dianae var. *dianae*	69	59	71	67	45	37	29	37	31	48	71	35	46	62	39	70	42	43	33	31	53	45	41	60	48	56	32	57	25	48
Closterium gracile	4	3	4	7	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	6	4	13	0	0	2	0	0
Closterium juncidum	4	14	14	17	10	26	5	10	12	7	18	13	0	4	12	9	18	9	19	0	0	0	0	0	0	2	2	4	0	0
Closterium ralfsii var. *hybridum*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium rostratum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	0	9	0	0	0	1
Closterium setaceum	11	12	8	7	37	13	3	8	5	7	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium striolatum	11	6	4	7	0	0	0	4	2	2	0	3	15	8	6	3	8	5	0	0	8	0	6	11	11	7	8	2	7	0
Closterium turgidum	0	6	4	0	0	0	0	11	2	5	0	0	0	0	3	0	0	0	0	0	0	0	0	0	8	2	0	0	0	0
Cosmarium canaliculatum	4	9	13	14	9	10	18	6	45	21	6	31	22	12	22	9	10	5	15	19	13	13	20	7	3	9	20	16	49	30
Cosmarium pseudoconnatum	0	0	0	0	0	0	1	0	0	0	0	3	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium pseudopyramidatum	4	6	13	3	6	0	13	1	2	0	0	9	15	16	6	6	10	5	11	4	11	18	8	4	5	2	8	9	31	23
Cosmarium margaritiferum	1	0	0	0	6	0	5	1	0	2	1	0	5	0	0	0	2	0	7	12	3	9	2	4	0	4	3	4	5	12
Cosmarium sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Euastrum ampullaceum	20	3	4	0	9	13	16	8	7	12	13	22	37	20	39	26	27	27	26	27	23	31	30	27	11	18	11	14	17	18
Euastrum ansatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0
Euastrum crassum	9	0	0	7	0	8	5	2	5	0	9	6	15	4	3	3	4	4	7	0	5	2	6	4	3	0	3	1	5	15
Haplotaenium indentatum	4	0	0	0	0	0	0	2	0	0	12	3	0	4	0	6	2	4	4	0	2	4	2	0	3	0	5	0	0	0
Haplotaenium minutum	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haplotaenium rectum	18	23	25	17	18	28	15	23	23	7	34	23	10	30	15	14	25	9	37	8	27	36	28	7	9	11	7	9	16	11
Micrasterias thomasiana	4	0	0	7	1	3	5	6	13	2	0	0	0	4	0	0	0	0	0	0	3	0	2	4	0	4	0	2	0	0
Micrasterias truncata var. *quadrata*	1	3	0	0	1	1	0	6	2	9	0	3	5	4	3	3	2	0	0	4	3	0	4	0	0	7	2	5	1	0
Penium spirostriolatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	5	2	10	12	2	4
Staurastrum margaritaceum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0
Staurastrum teliferum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Tetmemorus brebissonii	0	0	0	0	3	3	5	0	2	2	3	0	0	0	0	3	4	5	4	4	1	1	2	4	3	0	2	0	2	4
Tetmemorus granulatus	0	0	4	3	0	0	0	4	0	2	6	0	0	4	6	11	4	4	15	4	8	2	12	15	27	24	37	13	5	2
Tetmemorus laevis	0	0	0	0	0	0	0	4	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Xanthidium armatum	12	0	8	7	6	8	13	15	33	27	21	22	10	12	30	11	14	21	4	20	11	11	2	11	11	7	5	6	4	15

Supplementary table 3 Species data of samples taken from the transect B1.

B1	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
Actinotaenium diplosporum	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0
Actinotaenium inconspicuum	1	0	0	0	0	0	1	0	2	0	0	0	3	1	1	0	1	1	1	1	0	0	0	1	0	0	1	1	0	0
Actinotaenium perminutum	3	1	0	4	6	6	2	1	5	1	1	2	4	2	3	0	1	4	6	3	0	2	1	0	4	1	0	0	0	2
Actinotaenium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Actinotaenium turgidum	5	4	5	2	4	1	2	1	1	0	0	2	8	1	2	2	4	0	3	4	3	4	2	3	1	2	3	3	0	1
Closterium acutum	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Closterium calosporum var. *brasiliense*	34	15	9	7	5	13	9	12	4	8	24	19	13	38	21	27	29	22	15	30	45	16	28	35	52	45	54	44	39	38
Closterium closterioides var. intermedium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium dianae	23	23	33	19	24	22	29	45	34	42	14	6	14	18	7	17	25	24	11	20	57	25	18	24	38	38	33	47	44	33
Closterium gracile	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium intermedium	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1	1	0	0	0
Closterium kützingii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Closterium cf. *macilentum*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium parvulum	1	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium angulosum	1	1	1	2	2	2	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Cosmarium bioculatum var. *depressum*	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium botrytis var. *botrytis*	0	1	1	0	0	0	2	1	0	0	5	3	3	3	4	1	2	0	3	0	3	2	0	0	0	2	1	3	2	2
Cosmarium botrytis var. *tumidum*	1	1	5	4	0	0	5	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium connatum	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Cosmarium contractum	5	16	10	9	17	3	17	11	19	15	7	9	16	5	12	12	13	20	9	15	10	13	14	10	8	9	7	4	7	7
Cosmarium depressum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Cosmarium difficile	1	0	4	4	2	1	2	2	0	1	0	0	2	1	6	0	0	1	4	0	1	1	3	3	0	2	2	3	3	0
Cosmarium goniodes	0	0	0	0	0	0	0	0	0	0	2	2	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium granatum	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Cosmarium humile	1	2	1	2	4	0	2	2	2	1	2	2	2	2	3	8	2	0	3	4	2	5	2	2	0	1	0	0	1	0
Cosmarium margaritatum	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cosmarium margaritiferum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	2	1	1	0	1	1	2	0	1	2	3	0
Cosmarium moniliforme var. *panduriforme*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	3	0	0	3	0	1	0	0
Cosmarium monochondrum var. *fallax*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium obtusatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Cosmarium ovale	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Cosmarium paragranatoides	0	0	0	0	0	0	0	0	0	0	4	2	5	0	5	1	0	0	0	0	2	1	4	4	1	3	2	2	1	5
Cosmarium perforatum	0	0	0	0	0	0	0	0	0	2	2	2	0	0	1	0	0	0	0	0	1	0	0	0	0	1	2	0	0	0
Cosmarium phaseolus var. *elevatum*	1	1	3	5	1	7	5	7	2	1	3	4	7	3	7	1	5	5	5	4	2	4	1	6	1	4	2	3	1	1
Cosmarium polygonum var. *depressum*	0	0	0	0	0	0	0	0	0	0	1	0	4	0	1	0	2	3	2	3	4	1	0	0	0	0	0	0	0	0
Cosmarium pseudoornatum	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Cosmarium pseudoretusum	28	20	44	45	35	34	36	28	37	35	28	42	38	22	36	34	26	30	37	22	12	18	34	35	18	16	18	19	23	23

Cosmarium quadratum	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	1	1	0	1
Cosmarium regnellii	4	2	6	3	1	1	2	0	1	1	2	4	1	2	4	0	2	2	5	0	0	2	0	0	0	0	0	2	1	0
Cosmarium reniforme	1	1	1	1	0	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cosmarium sp. 1	0	0	0	0	0	0	0	0	0	1	2	0	3	6	7	5	6	4	5	4	1	2	2	3	6	7	3	1	3	2
Cosmarium sp. 2	1	4	2	4	5	4	4	1	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cosmarium subgranatum	8	8	18	17	12	15	16	15	10	14	7	17	7	8	14	13	12	10	12	11	8	6	8	8	5	9	7	4	7	5
Cosmarium varsoviense	1	0	0	1	1	0	1	3	4	4	2	1	1	0	1	2	0	3	1	0	0	4	2	0	1	1	0	2	3	0
Desmidium aptogonum	1	13	2	3	4	23	3	15	2	2	0	4	3	4	3	1	0	0	6	6	0	1	7	5	0	0	3	0	0	2
Desmidium baileyi var. *coelatum*	0	0	0	0	0	0	0	0	0	0	4	4	0	0	4	1	0	0	0	0	8	0	6	0	0	0	0	5	10	9
Desmidium swartzii	0	2	2	0	0	1	0	1	10	1	3	0	1	0	3	1	4	1	9	1	1	12	3	1	1	0	12	0	0	0
Euastrum ansatum var. *ansatum*	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0
Euastrum ansatum var. *rhomboidale*	2	0	1	3	11	7	5	2	5	2	3	4	2	4	0	3	2	3	1	4	2	3	3	5	3	6	3	2	4	2
Euastrum oblongum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Euastrum pectinatum	0	0	0	0	2	0	1	1	2	1	1	1	1	0	0	0	2	0	2	0	1	2	0	1	3	1	2	0	0	2
Euastrum verrucosum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	1
Gonatozygon aculeatum	0	0	1	1	1	0	0	0	0	0	7	1	0	0	0	1	3	1	2	7	2	0	0	0	0	1	0	0	1	0
Gonatozygon brebissonii	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	2	1	0	0	1	0	1	0	1
Haplotaenium rectum	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	0	3	0	1	0	0	0	1	0	0	0	0
Hyalotheca dissiliens	24	4	0	0	0	0	0	0	0	0	9	2	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Mirasterias crux-melitensis	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Micrasterias pinnatifida	3	2	6	4	3	3	4	3	5	3	2	2	7	1	3	6	1	2	2	3	1	2	2	5	0	2	1	3	2	2
Micrasterias truncata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Pleurotaenium archeri	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleurotaenium crenulatum	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleurotaenium trabecula	0	0	1	1	0	3	1	1	1	1	1	1	2	0	2	1	3	2	1	1	1	2	2	0	0	1	0	1	1	0
Sphaerozosma filiforme	8	25	2	10	13	7	0	0	0	3	15	19	2	28	4	6	3	9	2	1	0	23	21	18	20	11	0	4	0	24
Staurastrum alternans	3	7	2	4	6	2	2	0	4	8	6	6	8	4	4	9	5	7	3	5	4	4	2	5	5	6	7	5	12	7
Staurastrum bieneanum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staurastrum eurycerum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staurastrum furcigerum	0	0	0	1	0	0	3	0	1	0	0	2	1	0	2	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1
Staurastrum crassangulatum	4	4	3	2	6	3	7	4	2	6	2	6	0	0	1	2	3	3	0	0	4	3	1	1	2	2	3	7	8	7
Staurastrum lapponicum	0	0	0	0	0	0	0	0	0	0	2	4	1	5	4	3	5	3	4	6	1	0	2	0	0	0	3	1	0	0
Staurastrum manfeldtii	1	1	3	3	1	1	0	0	3	0	2	1	3	2	1	2	1	4	2	2	0	0	1	0	1	1	1	0	0	2
Staurastrum muticum	0	0	0	0	2	2	0	1	1	0	1	1	0	0	0	1	1	0	1	0	0	2	1	4	1	1	5	0	2	4
Staurastrum polytrichum	1	5	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Staurastrum pseudotetracerum	25	27	22	29	18	26	34	26	27	32	14	15	21	18	19	19	15	23	30	24	10	10	15	9	15	11	8	16	6	5
Staurastrum sebaldi var. *gracile*	1	1	5	5	5	4	0	2	5	5	5	4	4	4	5	2	1	2	3	5	1	3	2	1	2	3	2	0	3	2
Staurastrum teliferum	0	1	1	2	1	2	1	4	1	0	3	1	0	1	1	1	1	1	1	2	3	5	3	1	0	2	2	0	2	2
Staurastrum tetracerum	1	2	1	2	1	2	0	2	0	1	1	1	4	5	3	4	5	2	0	1	0	4	3	3	5	2	1	6	0	1
Staurastrum vestitum	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0
Staurodesmus dejectus var. *apiculatus*	0	3	1	0	2	1	1	1	1	1	2	2	3	5	1	3	1	3	2	1	0	0	0	4	0	1	3	2	4	6
Teilingia granulata	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	5	0	0	3	2	1	1	0	0	0	0	0	0	0
Tetmemorus granulatus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table 4 Species data of samples taken from the transect B2.

B2	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
Actinotaenium cucurbita	2	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bambusina brebissonii	12	7	0	0	35	14	18	10	3	20	4	5	2	12	8	12	8	5	0	18	0	0	0	0	14	0	0	0	0	0
Closterium baylianum var. *alpinum*	7	3	6	4	0	3	0	1	0	0	3	12	1	3	9	2	8	7	12	8	5	6	3	0	8	10	0	1	3	2
Closterium calosporum	4	1	4	3	0	2	0	0	4	5	0	0	3	1	2	5	0	0	0	1	1	2	0	0	0	1	0	1	0	1
Closterium cynthia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Closterium gracile	17	17	119	61	52	54	14	18	25	29	3	4	42	16	55	43	2	42	15	5	12	22	102	171	18	29	43	20	11	6
Closterium juncidum	6	2	7	20	31	32	35	30	20	48	33	31	14	20	21	16	23	25	32	26	11	10	13	3	22	5	57	53	60	43
Closterium lunula	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	3	0	0	0	1	0	0	1	0
Closterium navicula	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0
Closterium ralfsii var. *hybridum*	30	1	12	4	2	7	1	0	0	2	2	12	1	2	3	0	1	1	0	0	7	16	13	3	5	3	7	5	0	1
Closterium striolatum	27	77	21	30	24	47	10	14	13	25	39	38	17	21	7	10	14	32	20	25	20	32	10	13	26	17	35	32	13	15
Cosmarium pyramidatum	0	0	0	0	0	0	0	0	0	0	0	1	2	0	5	6	15	1	15	16	0	0	0	0	4	4	0	8	2	5
Desmidium swartzii	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euastrum ansatum	2	2	0	2	1	2	2	2	1	2	72	49	37	14	20	33	26	1	12	13	20	29	8	0	13	24	3	5	2	20
Euastrum humerosum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	5	0	2	3	1	0	0	0	3	1	0	0	2	3
Micrasterias jenneri	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Micrasterias rotata	0	0	0	0	0	0	0	0	0	0	0	5	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Micrasterias truncata	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1	2	0	0	1	0	0	0	0	0	1	0	0	0	0
Penium cylindrus	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Penium spirostriolatum	4	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	10	0	0	0	0	0	0	0	0
Staurastrum hirsutum	0	10	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Staurastrum punctulatum	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staurastrum simonyi	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetmemorus laevis	11	8	6	6	0	1	1	2	10	0	11	1	0	3	4	1	2	3	7	7	2	0	2	0	0	1	0	2	2	5
Tetmemorus granulatus	70	67	20	65	54	38	119	123	117	69	32	39	78	107	65	67	89	81	85	77	115	70	48	10	87	102	55	73	104	97

Supplementary table 5 Abiotic data (pH and conductivity) of individual samples

	pH	conductivity		pH	conductivity		pH	conductivity		pH	conductivity
A1_Sep_01	5.1	150	A2_Sep_01	5.2	135	B1_Sep_01	7.3	194	B2_Sep_01	6.1	55
A1_Sep_02	4.8	150	A2_Sep_02	5.2	134	B1_Sep_02	7.3	193	B2_Sep_02	6.0	55
A1_Sep_03	4.9	152	A2_Sep_03	5.1	137	B1_Sep_03	7.2	192	B2_Sep_03	5.9	55
A1_Sep_04	4.9	145	A2_Sep_04	5.3	135	B1_Sep_04	7.3	196	B2_Sep_04	5.9	58
A1_Sep_05	4.8	145	A2_Sep_05	5.2	134	B1_Sep_05	7.4	195	B2_Sep_05	5.7	52
A1_Sep_06	4.9	146	A2_Sep_06	5.1	138	B1_Sep_06	7.4	195	B2_Sep_06	5.8	56
A1_Sep_07	4.7	145	A2_Sep_07	5.1	132	B1_Sep_07	7.4	194	B2_Sep_07	5.8	57
A1_Sep_08	4.9	150	A2_Sep_08	5.4	133	B1_Sep_08	7.4	195	B2_Sep_08	5.6	52
A1_Sep_09	4.8	142	A2_Sep_09	5.1	137	B1_Sep_09	7.4	197	B2_Sep_09	5.8	54
A1_Sep_10	4.9	140	A2_Sep_10	5.1	132	B1_Sep_10	7.4	198	B2_Sep_10	5.9	54
A1_Dec_01	5.1	68	A2_Dec_01	6.8	122	B1_Dec_01	7.2	233	B2_Dec_01	6.1	44
A1_Dec_02	5.3	66	A2_Dec_02	6.8	122	B1_Dec_02	7.1	235	B2_Dec_02	6.0	40
A1_Dec_03	5.1	69	A2_Dec_03	6.7	123	B1_Dec_03	7.1	234	B2_Dec_03	5.9	41
A1_Dec_04	5.0	72	A2_Dec_04	6.8	123	B1_Dec_04	7.1	232	B2_Dec_04	5.3	48
A1_Dec_05	5.1	73	A2_Dec_05	6.8	124	B1_Dec_05	7.3	230	B2_Dec_05	5.9	45
A1_Dec_06	4.9	72	A2_Dec_06	6.7	125	B1_Dec_06	7.1	229	B2_Dec_06	5.9	55
A1_Dec_07	5.1	75	A2_Dec_07	6.8	126	B1_Dec_07	7.2	231	B2_Dec_07	6.1	41
A1_Dec_08	5.1	69	A2_Dec_08	6.6	123	B1_Dec_08	7.2	234	B2_Dec_08	5.4	37
A1_Dec_09	5.0	72	A2_Dec_09	6.7	122	B1_Dec_09	7.3	232	B2_Dec_09	5.9	58
A1_Dec_10	4.7	72	A2_Dec_10	6.6	123	B1_Dec_10	7.2	230	B2_Dec_10	6.2	56
A1_Mar_01	4.6	57	A2_Mar_01	5.7	124	B1_Mar_01	7.1	247	B2_Mar_01	5.6	75
A1_Mar_02	5.0	58	A2_Mar_02	5.9	124	B1_Mar_02	7.1	248	B2_Mar_02	5.6	96
A1_Mar_03	4.8	60	A2_Mar_03	5.6	125	B1_Mar_03	7.1	246	B2_Mar_03	5.9	91
A1_Mar_04	4.9	52	A2_Mar_04	5.8	123	B1_Mar_04	7.2	247	B2_Mar_04	5.8	74
A1_Mar_05	5.0	64	A2_Mar_05	5.8	126	B1_Mar_05	7.2	247	B2_Mar_05	5.9	77
A1_Mar_06	4.7	60	A2_Mar_06	5.7	124	B1_Mar_06	7.2	247	B2_Mar_06	6.0	61
A1_Mar_07	4.7	60	A2_Mar_07	5.4	126	B1_Mar_07	7.2	246	B2_Mar_07	6.1	62
A1_Mar_08	4.7	53	A2_Mar_08	5.8	123	B1_Mar_08	7.2	247	B2_Mar_08	6.2	69
A1_Mar_09	5.0	62	A2_Mar_09	5.8	124	B1_Mar_09	7.2	248	B2_Mar_09	6.3	67
A1_Mar_10	4.8	61	A2_Mar_10	5.7	125	B1_Mar_10	7.1	248	B2_Mar_10	6.3	72

Supplementary table 6 The results of individual *adonis* tests partitioning variation in species composition evaluated by Bray-Curtis distance matrices. The effects of individual factors were evaluated sequentially so that pure effects of a particular factor could be ascertained after the two other were subtracted. env, environmental factors; spat, spatial factors; temp, temporal factors

A1

Factor	Df	Sums of Squares	F	R^2	*p*-value
env	2	0.70	4.91	0.18	***
spat	1	1.18	16.48	0.31	***
temp	1	0.14	1.94	0.04	n.s.
residuals	25	1.79	-	0.47	

Factor	Df	Sums of Squares	F	R^2	*p*-value
env	2	0.70	4.91	0.18	***
temp	1	0.25	3.52	0.07	*
spat	1	1.07	14.89	0.28	***
residuals	25	1.79	-	0.47	

Factor	Df	Sums of Squares	F	R^2	*p*-value
temp	1	0.62	8.64	0.16	***
spat	1	1.25	17.53	0.33	***
env	2	0.15	1.03	0.04	n.s.
residuals	25	1.79	-	0.47	

Factor	Df	Sums of Squares	F	R^2	*p*-value
spat	1	1.25	17.53	0.33	***
temp	1	0.62	8.64	0.16	***
env	2	0.15	1.03	0.04	n.s.
residuals	25	1.79	-	0.47	

A2

Factor	Df	Sums of Squares	F	R^2	*p*-value
env	2	0.66	5.87	0.29	***
spat	1	0.18	3.28	0.08	**
temp	1	0.05	0.98	0.02	n.s.

residuals	25	1.40	-	0.61	

Factor	Df	Sums of Squares	F	R^2	*p*-value
env	2	0.66	5.87	0.29	***
temp	1	0.06	1.12	0.03	n.s.
spat	1	0.18	3.14	0.08	**
residuals	25	1.40	-	0.61	

Factor	Df	Sums of Squares	F	R^2	*p*-value
temp	1	0.47	8.33	0.20	***
spat	1	0.19	3.47	0.08	**
env	2	0.12	2.11	0.10	*
residuals	25	1.40	-	0.61	

Factor	Df	Sums of Squares	F	R^2	*p*-value
spat	1	0.19	3.47	0.08	**
temp	1	0.47	8.33	0.20	***
env	2	0.12	2.11	0.10	*
residuals	25	1.40	-	0.61	

B1

Factor	Df	Sums of Squares	F	R^2	*p*-value
env	2	0.56	6.10	0.28	***
spat	1	0.07	1.50	0.03	n.s.
temp	1	0.26	5.61	0.13	***
residuals	25	1.14	-	0.56	

Factor	Df	Sums of Squares	F	R^2	*p*-value
env	2	0.56	6.10	0.28	***
temp	1	0.25	5.41	0.12	***
spat	1	0.08	1.70	0.04	n.s.
residuals	25	1.14	-	0.56	

Factor	Df	Sums of Squares	F	R^2	*p*-value
temp	1	0.53	11.65	0.26	***
spat	1	0.10	2.28	0.05	*

env	2	0.25	2.69	0.12	**
residuals	25	1.14	-	0.56	

Factor	Df	Sums of Squares	F	R^2	*p*-value
spat	1	0.10	2.28	0.05	*
temp	1	0.53	11.65	0.26	***
env	2	0.25	2.69	0.12	**
residuals	25	1.14	-	0.56	

B2

Factor	Df	Sums of Squares	F	R^2	*p*-value
env	2	0.21	1.41	0.08	n.s.
spat	1	0.31	4.18	0.12	**
temp	1	0.15	2.02	0.06	n.s.
residuals	25	1.85	-	0.73	

Factor	Df	Sums of Squares	F	R^2	*p*-value
env	2	0.21	1.41	0.08	n.s.
temp	1	0.15	2.04	0.06	n.s.
spat	1	0.31	4.16	0.12	**
residuals	25	1.85	-	0.73	

Factor	Df	Sums of Squares	F	R^2	*p*-value
temp	1	0.13	1.75	0.05	n.s.
spat	1	0.32	4.29	0.13	**
env	2	0.22	1.49	0.09	n.s.
residuals	25	1.85	-	0.73	

Factor	Df	Sums of Squares	F	R^2	*p*-value
spat	1	0.32	4.29	0.13	**
temp	1	0.13	1.75	0.05	n.s.
env	2	0.22	1.49	0.09	n.s.
residuals	25	1.85	-	0.73	

***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; n.s., $p > 0.05$