BOREAL ENVIRONMENT RESEARCH 19: 195–208
ISSN 1239-6095 (print) ISSN 1797-2469 (online)

Helsinki 30 June 2014

Microclimatological consequences for plant and microbial composition in *Sphagnum*-dominated peatlands

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Received 22 Apr. 2013, final version received 21 Oct. 2013, accepted 12 Nov. 2013

Robroek, B. J. M., Wubs, E. R. J., Martí, M., Zając, K., Andersen, J. P., Andersson, A., Börjesson, G., Bragazza, L., Dise, N. B., Keuskamp, J. A., Larsson, M., Lindgren, P.-E., Mattiasson, P., Solomonsson, J., Sundberg, C., Svensson, B. H. & Verhoeven, J. T. A. 2014: Microclimatological consequences for plant and microbial composition in *Sphagnum*-dominated peatlands. *Boreal Env. Res.* 19: 195–208.

In three Scandinavian peatlands we studied to what extent plant and microbial community compositions are governed by local-scale microhabitat, with a special interest in the effect of aspect (i.e. exposition of slopes). Despite differences in solar irradiance between the south- and north-facing slopes, maximum temperature was elevated in the south-facing slopes at the most northern site only. Pore-water nutrient concentrations were not affected by aspect, yet dissolved organic carbon concentrations were higher in the south-facing microhabitats. This was likely caused by higher vascular plant biomass. Plant and microbial community compo-

Editor in charge of this article: Eeva-Stiina Tuittila

sition clearly differed among sites. In all three sites, microhabitat (i.e. prevailing water-table depth) affected the plant and microbial community compositions. Aspect, however, did not affect community composition, even though microclimate significantly differed between the south- and the north-facing aspects at the northernmost site. Our results highlight the complex link between plant community composition, microbial community and environmental conditions, which deserves much more attention than currently in order to fully understand the effects of climate change on peatland ecosystem function.

Introduction

In peatlands, plant species composition is directly controlled by prevailing hydrological conditions, i.e. water-table depth (Andrus *et al*. 1983, Rydin 1986). In addition, water availability can, directly or indirectly (Fisk *et al*. 2003, Kotiaho *et al*. 2013), control microbial community composition and functioning, thereby affecting nutrient and carbon cycling in the peat soil (Fisk *et al*. 2003, Jaatinen *et al*. 2007a, Peltoniemi *et al*. 2009). Moreover, spatial differences in the prevailing water-table depth are often associated with a characteristic pattern in the microtopography, ranging from wet depressions (hollows) via relatively dry, but regularly inundated lawns up to dry hummocks, all with a characteristic bryophyte and vascular plant species (Rydin 1986, Fisk *et al*. 2003, Mitchell *et al*. 2003).

Changes in the prevailing water-table depth, due to e.g., climate warming, may affect plant community structure in peatlands by altering competition between species of different functional plant types (Breeuwer *et al*. 2009, Kotiaho *et al*. 2013), but may also impact peatland microbial communities. Indeed, microbial community composition has been shown to respond directly to changes in the water table (Jaatinen *et al*. 2007b, Peltoniemi *et al*. 2009), or indirectly through water table-driven changes in the plant community composition (Straková *et al*. 2011, Peltoniemi *et al*. 2012, Andersen *et al*. 2013, Kotiaho *et al*. 2013). It has also been shown that the composition of microbial phospholipid fatty acids (PLFAs) differs among peatland types (Sundh *et al*. 1997). These differences in microbial composition among peatlands may be explained by site differences in temperature, moisture, nutrient levels, and water chemistry, highlighting the importance of the peatland physicochemical environment in structuring the microbial community (Jaatinen *et al*. 2007a, Andersen *et al*. 2010). It can therefore be expected that climate change will not only alter the environmental conditions in peatlands, it will presumably affect the community structure, and the abundance and diversity of plants and microbes (Wiedermann *et al*. 2007, Breeuwer *et al*. 2009, Jassey *et al*. 2011).

Although the hydrological controls over spatial distribution of plant species and microbial communities in peatlands are relatively well understood (e.g., Sottocornola *et al*. 2008, Andersen *et al*. 2011), much less is known about their small-scale spatial distribution (i.e. their spatial orientation relative to the hummock-hummock slope-lawn gradient). To date no published record exists on the effect of aspect (south-*versus* north-facing slope) on the distribution of peatland plants and microbial communities, and potential mechanisms that may cause apparent small-scale differences in peatland plant and microbial communities. Bragazza (2008) reported that an extreme drought, as caused by a summer heat wave in the Italian Alps, caused a die-off of peat mosses with irreversible desiccation effects most apparent on the southern-facing slopes of the hummocks. The observed difference in solar irradiance, 20% higher on south-than north-facing slopes, was hypothesized to cause differences in water content due to evapotranspiration (Shimoyama *et al*. 2004, Bragazza 2008). This close relationship between slope orientation and solar irradiance can therefore be expected to be important in regard to the water balance, as has been shown in arid ecosystems (Breshears *et al*. 1997, Zou *et al*. 2007). Additionally, a coupling between irradiance and soil temperature has been reported (Bridgham *et al*. 1999), which may ultimately affect nutrient availability, through temperature-dependent increases in decomposition rates (Updegraff *et al*. 1995).

Irradiance differences between north- and south-facing slopes in peat bogs may thus lead to different moisture, temperature and hydrochemical conditions, with cascading effects on plant and microbe community compositions.

We studied small-scale spatial patterns of plant and microbial communities and how they are affected by aspect (i.e. either south- or north-facing in the lawn-hummock gradient) and the differences in environmental conditions (micro-scale), in three geographically dispersed Scandinavian peatlands. As south-facing microhabitats receive more solar irradiance, we predict that (1) soil temperatures in south-facing microhabitats are higher. This may lead to increased decomposition and mineralization rates in south-facing microhabitats, resulting in (2) higher contents of dissolved organic carbon (DOC) and nutrients. Ultimately, (3) difference in microclimate will cause south and north-facing microhabitats to differ in their plant and microbial communities composition. As the difference in solar irradiance will be larger at higher latitudes due to lower solar angle, we expect that (4) differences in all of these factors will be greater at higher latitudes.

Material and methods

Site selection

Three Scandinavian *Sphagnum*-dominated peatlands across a climatological gradient distributed over the nemoral, hemiboreal and boreal zone were selected: Tofte Mose, Lille Vildmose, Denmark; Store Mosse National Park, Sweden; and Degerö Stormyr, Sweden; respectively. At each of these sites, we measured heights and cross-sectional length of 50 hummocks. Mean hummock heights at these sites did not differ (ANOVA: $F_{2,147} = 0.91$, $p = 0.41$; Table 1). Among these 50 hummocks, five were randomly selected and lawn-hummock transects were established. Each transect was laid out in a south–north direction and comprised five plots (50 × 50 cm): south-facing lawn (Lawn S), south-facing hummock (Slope S), hummock top (Hummock), north-facing hummock (Slope N), and north-facing lawn (Lawn N). This resulted in 75 plots distributed across five transects and three peat bogs.

Measurements of abiotic factors

Daily solar irradiance (MJ m^{-2} day^{-1}) was calculated for each of the slopes on north and south sides of all 50 hummocks per site following Bragazza (2008). Calculations were performed using the PV-GIS web-based application developed by Šúri *et al*. (2005). The model assumes clear sky conditions, but accounts for geographical position, time of year and the inclination of the surface. Irradiance was calculated as a daily average value for July.

Each plot was equipped with a single channel temperature data logger (SL51T Signatrol, Tewkesbury, UK), which recorded temperature at 5 cm below the *Sphagnum* surface at 1.5-hour

Table 1. Site characteristics and dominant plant species in the bryophyte and vascular plant communities.

Site	Coord.	Hummock height (cm)*	Mean annual temp. (°C)	Dominant *Sphagnum* mosses**	Dominant vascular plants**
Lile Vildmose	56°50´N, 10°11´E	26.9 ± 1.0	7.6	H: *S. magellanicum*, *S. rubellum* L: *S. cuspidatum*	H: *Calluna vulgaris*, *Erica tetralix* L: *Rhynchospora alba*
Store Mosse	57°16´N, 13°55´E	25.7 ± 0.9	6.2	H: S. *magellanicum*, *S. rubellum* L: *S. cuspidatum*	H: *Calluna vulgaris*, *Andromeda polifolia* L: *Rhynchospora alba*, *Eriophorum vaginatum*
Degerö Stormyr	64°10´N, 19°33´E	27.5 ± 1.1	1.0	H: *S. fuscum* L: *S. balticum*	H: *Empetrum nigrum*, *Andromeda polifolia* L: *Eriophorum vaginatum*

* mean ± SEM, $n = 50$; ** H = hummock microhabitats, L = lawn microhabitats.

intervals, from 12 June to 7 September 2009. For each plot, these data were used to calculate the overall median soil temperature, mean daily maximum and minimum temperatures, daily amplitude and the number of degree days (i.e. sum of daily mean temperatures).

In July, we collected pore-water samples from all plots using Rhizon soil moisture samplers (type MOM, pore size 0.1 μm, Eijkelkamp, Giesbeek, NL), which extracted water from the 10-cm layer below the peat surface. After collection, all samples were kept cool and in darkness. The samples were analysed for dissolved organic carbon (DOC), nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}), within two weeks after collection, using a Skalar SAN^{PLUS} segmented flow analyser (Skalar analytical b.v., Breda, NL).

Vegetation survey

In early July, vascular plant and bryophyte species composition and abundance in all subplots were recorded using the point-intercept method (Jonasson 1988) with a 90-point frame (25 × 30 cm). At every point, a needle was lowered to the moss surface and all contacts with the vascular plant vegetation were noted, specifying species for each hit. For the moss layer, each grid point of the pin-point frame accounted for one individual of a certain bryophyte species (Breeuwer *et al*. 2010).

Plant tissue chemistry

In early July, total above-ground vascular plant biomass was collected from within a 10 × 10 cm frame just outside the plots. All vascular plants were clipped flush with the moss surface and sorted into plant functional types (PFT). Additionally, we collected all lichens and (*Sphagnum*) mosses (first 2 cm) from within the frame. Dry weights were determined for all PFTs after oven-drying for 48 h at 70 °C. Ericoid, graminoid and *Sphagnum* PFT, i.e. the dominant PFTs, samples were then separately ground after which their carbon (C) and nitrogen (N) tissue contents were determined using an EA 1110 CHNS-O analyser (CE instruments, Wigan, UK).

Microbial community composition

At the same time as above mentioned sampling, samples for microbial community composition (MCC) analysis were collected from five lawn-hummock transects, which were not used in the survey of plant community composition but were among the earlier-mentioned 50 hummocks. We did not sample the same plots as those used for vegetation and biogeochemical analyses because MCC sampling was destructive, and would hamper biogeochemical and soil sampling. Peat cores were taken from all plots using a Holmen auger (diameter ca. 10 cm). Two subsamples from each core were selected for the analysis: one from the peat surface, the other from the peat close to the water table (subsurface). For all plots, the surface peat sample was defined as the top 5 cm of the profile after removing the living surface biomass. The depth of the subsurface samples, representing the peat near the water table, differed among microhabitats, as the water table at the different microhabitats differed. All samples were stored at 4 °C until frozen at –20 °C within 20 hours after collection. The water content of the samples was determined gravimetrically after drying at 105 °C for 20 h. pH of all samples was measured from the pore water.

Phospholipid fatty acids (PFLAs) were extracted from the peat samples according to Bligh and Dyer (1959) with Börjesson *et al*.'s (1998) modification. In short, total lipids were extracted from 2.5 g of fresh peat for 2 hours in a solvent phase of 3.0 ml 50 mM phosphate buffer (pH 7.0), 3.8 ml chloroform ($CHCl_3$), 7.6 ml methanol (MeOH), and 4 ml Bligh and Dyer (1959) reagent ($CHCl_3$: MeOH: P-buffer; 1/2/0.8, v/v/v). PLFA 19:0 (Larodan Malmö, Sweden) was added as internal standard to the phospholipid fraction. PLFAs were derivated to fatty acid methyl esthers (FAMEs) using 1 ml 0.2 M methanolic-KOH (Sundh *et al*. 1997, Chowdhury and Dick 2012). PLFAs were analyzed using a gas chromatograph according to Steger *et al*. (2003).

Data handling and statistical analyses

PFLAs were expressed as nmol g^{-1} peat and

then used to represent relative abundance of the microbial biomass components. Fatty acids are designated in terms of the total number of C atoms: the number of double bonds, followed by the position of the first double bond from the aliphatic end of the molecule. For an estimation of microbial biomass (nmol g^{-1} peat) and fungal/bacterial ratios, PLFAs determined as being bacterial or fungal origin were used (Wilkinson 1988, Lindahl *et al*. 1997, Ehlers *et al*. 2008, Brockett *et al*. 2012).

For several variables (NO_3-N, NH_4-N, PO_4-P, pH, DOC, plant tissue N contents, bacterial and fungal biomass and the temperature variables) some values ($1 < n < 9$) were missing. These values were imputed by multiple imputation using bootstrap and predictive mean matching (999 bootstrap replicates) (*Hmisc* package ver. 3.10-1 for R). Degrees of freedom for statistical tests were manually adjusted to correct for the imputed values.

Irradiance, temperature, edaphic variables and microbial biomass were analysed using split-plot ANOVA, with site as the whole-plot factor and microhabitat as the split-plot factor. Planned contrasts in the split-plot design were performed using a simple paired *t*-test, as Tukey's HSD tests often lead to inflated Type I error rates in split-plot designs (Maxwell 1980). As we were interested in the differences between north- and south-facing sides of hummocks and lawns, and differences among microhabitats are pretty well described, we only tested the former. Where the split-plot ANOVA indicated a significant microhabitat × site interaction, we performed contrasts per site.

Redundancy analyses (RDA) were performed to examine the effects of site, microhabitat, sampling depth (microbial data) and aspect on the structure of the plant and microbial community composition. Both community data sets were Hellinger-transformed prior to analyses, and data from the hummock top microhabitats were omitted in order to enable specific test for the effects of microhabitat and aspect. Depth was an important factor determining the microbial community composition ($F_{1,96} = 19.6$, $p \leq 0.001$, $r^2 = 0.10$). Therefore we decided to analyse the effects of site, microhabitat and aspect on the microbial community composition for the two depths separately. As site was always a very important explanatory factor in RDA, we further tested for the effects of microhabitat and aspect by partialling out the effect of site. Significance tests were performed by 999 Monte Carlo permutations restricted within transects. Additionally, variation partitioning using (partial) RDA and adjusted r^2 were used to compare the respective effect of all factors and their interactions (Peres-Neto *et al*. 2006). (Partial) RDA analyses were performed using the *vegan* package for R. All statistical analyses were performed in R ver. 2.15.2 (R Core Team 2012).

Results

Irradiance & temperature

Calculated solar irradiance at the three sites was significantly higher on south-facing slopes as compared with that on north-facing slopes ($F_{1,147} = 2263.6$, $p \leq 0.001$; Table 2). However, this difference in irradiance was larger in Degerö Stormyr than in Store Mosse and Lille Vildmose (site × aspect interaction: $F_{2,147} = 47.9$, $p \leq 0.001$; Table 2). Although the three sites and the microhabitats differed in all temperature variables (Fig. 1 and Table 2), the aspect appeared to affect temperature in only Degerö Stormyr, where the mean daily temperature amplitude (Fig. 1) and the mean daily maximum temperature (Table 2) were highest in the south-facing hummocks.

Pore water and plant tissue nutrients

Pore water NH_4^+ and PO_4^{3-} concentrations differed among sites. The NH_4^+ concentration was highest in Store Mosse, while that of PO_4^{3-} was highest in Lille Vildmose (Table 2). In general, the NO_3^- and NH_4^+ concentrations were highest in the drier microhabitats (slopes and hummocks), except for Store Mosse. At this site, the NH_4^+ concentration was relatively high in the lawns. Pore-water nutrient concentrations were, however, not affected by aspect (Table 2). Similarly, the plant tissue N concentrations remained unaffected by aspect (Fig. 2), although

Table 2. Mean ± SD values for several variables per site and microhabitat/aspect. Split-plot ANOVA results with site as the whole-plot factor and microhabitat as the split-plot factor. Planned contrasts in the split-plot design were performed using a simple paired *t*-test testing differences between south- and north-facing slopes. Only results with $p \leq 0.1$ are shown.

Variable	Microhabitat, Aspect					ANOVA	
	Lawn S	Slope S	Hum	Slope N	Lawn N	Effects	Contrasts S *vs.* N
Solar irradiance ($MJ\ m^{-2}\ d^{-1}$)							
Lille Vildmose		19.0 ± 0.1		16.9 ± 0.5		Site: $p \leq 0.001$	$t = -27.2$, $p \leq 0.001$
Store Mosse		18.3 ± 0.1		16.3 ± 0.5		Aspect: $p \leq 0.001$	$t = -25.4$, $p \leq 0.001$
Degerö Stormyr		19.1 ± 0.1		16.0 ± 0.6		Site × Aspect: $p \leq 0.001$	$t = -30.0$, $p \leq 0.001$
Temperature (median; °C)							
Lille Vildmose	16.7 ± 0.5	15.4 ± 0.2	15.4 ± 0.2	15.7 ± 0.8	16.8 ± 0.6	Site: $p \leq 0.001$	–
Store Mosse	16.2 ± 0.8	14.9 ± 0.2	14.9 ± 0.4	15.0 ± 0.5	16.0 ± 0.5	Microhabitat: $p \leq 0.001$	–
Degerö Stormyr	13.6 ± 0.2	13.5 ± 0.6	13.2 ± 0.4	13.1 ± 0.4	13.7 ± 0.8	Site × MH: $p \leq 0.05$	–
Temperature (mean daily max.; °C)							
Lille Vildmose	18.1 ± 0.3	18.4 ± 0.4	18.6 ± 1.0	18.0 ± 1.2	18.3 ± 1.0	Site: $p \leq 0.05$	–
Store Mosse	18.5 ± 0.1	16.0 ± 0.8	16.0 ± 0.6	16.2 ± 1.2	18.8 ± 0.6	Microhabitat: $p \leq 0.001$	–
Degerö Stormyr	16.4 ± 0.6	18.7 ± 1.8	16.7 ± 1.3	15.6 ± 0.5	16.2 ± 0.8	Site × MH: $p \leq 0.05$	Slope: $t = 4.1$, $p = 0.015$
Pore water NO_3-N ($mg\ l^{-1}$)							
Lille Vildmose	0.02 ± 0.01	0.03 ± 0.01	0.06 ± 0.03	0.03 ± 0.01	0.02 ± 0.01	Microhabitat: $p \leq 0.001$	–
Store Mosse	0.02 ± 0.00	0.02 ± 0.00	0.04 ± 0.01	0.02 ± 0.01	0.02 ± 0.00	Site × MH: $p = 0.07$	–
Degerö Stormyr	0.02 ± 0.00	0.04 ± 0.01	0.04 ± 0.02	0.03 ± 0.00	0.02 ± 0.00	–	–
Pore water NH_4-N ($mg\ l^{-1}$)							
Lille Vildmose	0.12 ± 0.16	0.12 ± 0.03	0.44 ± 0.59	0.13 ± 0.02	0.08 ± 0.06	Site: $p = 0.07$	–
Store Mosse	0.29 ± 0.12	0.31 ± 0.25	0.39 ± 0.24	0.24 ± 0.10	0.43 ± 0.17	Microhabitat: $p \leq 0.001$	–
Degerö Stormyr	0.11 ± 0.03	0.25 ± 0.08	0.70 ± 0.49	0.22 ± 0.15	0.10 ± 0.03	Site × MH: $p \leq 0.05$	–

Pore water PO_4-P ($mg \times 100\ l^{-1}$)							
Lille Vildmose	3.21 ± 0.24	3.63 ± 1.27	8.75 ± 12.1	5.06 ± 2.95	2.90 ± 0.47	MH: $p = 0.07$	–
Store Mosse	3.40 ± 0.72	2.76 ± 0.69	2.65 ± 0.42	3.26 ± 1.39	2.57 ± 0.47	–	–
Degerö Stormyr	2.37 ± 0.30	2.12 ± 0.41	5.67 ± 7.73	2.25 ± 5.66	2.28 ± 0.64	–	–
Dissolved organic carbon ($mg\ l^{-1}$)							
Lille Vildmose	61.6 ± 7.1	69.6 ± 6.5	65.5 ± 5.2	63.8 ± 4.3	63.9 ± 4.6	Site: $p \le 0.01$	$t = 2.04$, $p = 0.06$
Store Mosse	52.1 ± 6.9	61.3 ± 5.7	63.0 ± 4.7	58.0 ± 9.8	52.7 ± 4.9	Microhabitat: $p \le 0.001$	$t = 2.04$, $p = 0.06$
Degerö Stormyr	58.5 ± 9.5	66.9 ± 12.6	70.0 ± 5.5	59.1 ± 8.2	52.7 ± 2.6	Aspect: $p = 0.08$	$t = 2.04$, $p = 0.06$
Bacterial biomass (surface; $nmol\ g^{-1}$)							
Lille Vildmose	533 ± 318	454 ± 120	357 ± 85	362 ± 199	500 ± 110	–	–
Store Mosse	620 ± 335	354 ± 134	364 ± 72	547 ± 268	247 ± 176	–	–
Degerö Stormyr	383 ± 100	414 ± 68	338 ± 134	344 ± 102	400 ± 87	–	–
Fungal biomass (surface; $nmol\ g^{-1}$)							
Lille Vildmose	67 ± 93	63 ± 50	68 ± 50	47 ± 41	24 ± 5	Site $p \le 0.01$	–
Store Mosse	16 ± 14	27 ± 22	48 ± 27	16 ± 9	5 ± 8	–	–
Degerö Stormyr	72 ± 47	144 ± 44	65 ± 50	114 ± 55	65 ± 56	–	–
Fungal/Bacterial ratio (surface)							
Lille Vildmose	0.10 ± 0.07	0.13 ± 0.08	0.18 ± 0.11	0.12 ± 0.10	0.05 ± 0.01	Site $p \le 0.01$	–
Store Mosse	0.02 ± 0.02	0.09 ± 0.08	0.13 ± 0.07	0.03 ± 0.01	0.01 ± 0.02	–	–
Degerö Stormyr	0.17 ± 0.10	0.36 ± 0.15	0.23 ± 0.16	0.31 ± 0.09	0.16 ± 0.14	–	–

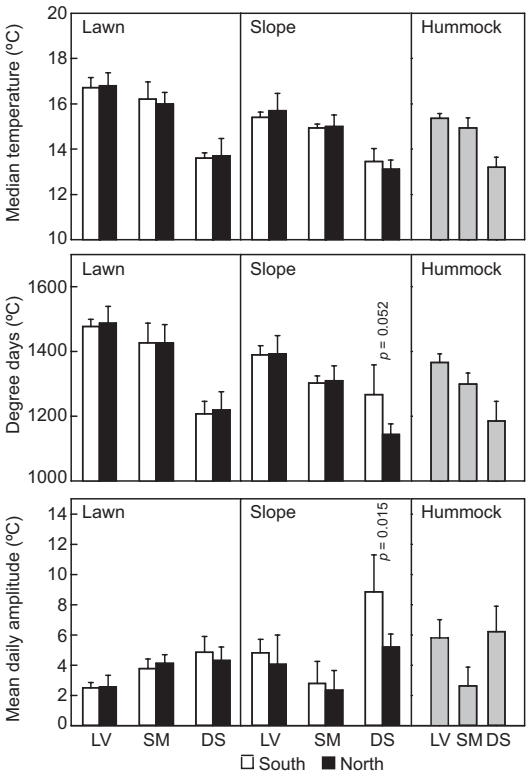

Fig. 1. Temperature variables (mean + SD) measured in three peatlands along a microtopographic gradient (LV = Lille Vildmose, SM = Store Mosse, DS = Degerö Stormyr). Significant planned contrasts are shown.

the graminoid and ericoid tissue N concentrations in Degerö Stormyr were slightly higher in the south-facing lawns as compared with those in the north-facing lawns (graminoids: $t = 2.6$, $p = 0.06$; ericoids: $t = 3.14$, $p = 0.035$). At all sites, the dissolved organic carbon (DOC) concentrations were higher in south-facing hummock slopes as compared with those north-facing hummock slopes (Table 2). The pore-water DOC concentrations were positively related to above-ground vascular plant biomass ($r^2 = 0.63$, $p < 0.05$).

Vegetation composition

In general, plant species richness and diversity were highest in the northernmost site, Degerö Stormyr (richness: $F_{2,60} = 30.4$, $p \leq 0.01$; diversity: $F_{2,60} = 12.3$, $p \leq 0.05$). Additionally, at all three sites, richness and diversity were higher on the slopes and hummocks than in the lawns (richness: $F_{2,60} = 34.4$, $p \leq 0.001$; diversity: $F_{2,60} = 33.6$, $p \leq 0.001$). Species richness was lower on the south-facing slopes in Store Mosse ($t = -2.9$, $p = 0.045$), while the opposite was found for Lille Vildmose ($t = 6.0$, $p = 0.004$). Plant diversity remained unaffected by aspect.

The redundancy analysis (RDA) showed that variation in the plant community composition was largely, and significantly, explained by site and microhabitat. Together these factors explained 44% of the variation, while about 75% of the variation was explained by the full model (Table 3, model 1). Hence opposite to our *a priori* expectations, aspect did not contribute to explaining any variance in the plant community composition. Partial RDA (pRDA) showed that, independently from the factor site, the plant community composition was significantly different between lawns and hummock slopes (Table 3 and Fig. 3). Interestingly, the lawn and hummock plant community composition at Degerö Stormyr was separated from their counterparts at Lille Vildmose and Store Mosse (Table 3 and Fig. 3). Even though we found differences in irradiance and temperature between south- and north-facing slopes at Degerö Stormyr (Table 2), plant community composition did not differ between south- and north-facing microhabitats at any site (Table 3 and Fig. 3).

Microbial composition (PLFAs)

Extraction of PLFAs from the peat samples resulted in 31 different PLFAs. Only one PLFA (18:2) could be used as a marker for fungi, while 24 PLFAs were identified to be of bacterial origin. Microbial communities distinctly differed between the two depths ($F_{1,16} = 19.1$, $p \leq 0.001$), indicating a large role for substrate quality and redox conditions in structuring peat microbial communities. At both depths, surface and subsurface, RDA showed that most of the variation in the microbial PLFA community composition could be attributed to the factor site (Table 3). Partialling out the effect of site, microhabitat accounted for 5% of the variation in the surface microbial PLFA community composition (Table 3 and Fig. 4A), but did not contribute to explain-

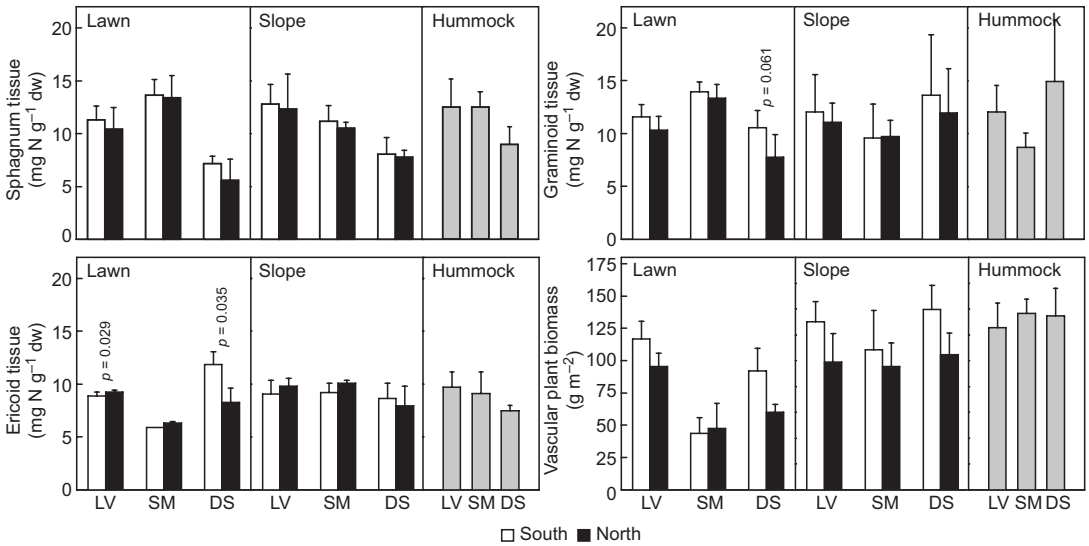

Fig. 2. Plant tissue nutrient content (mean + SD) in *Sphagnum* mosses, graminoids, ericoids and total vascular-plant aboveground biomass in June 2009 in three peatlands along a microtopographic gradient (LV = Lille Vildmose, SM = Store Mosse, DS = Degerö Stormyr). Significant planned contrasts are shown.

ing subsurface community variation (Table 3 and Fig. 4B). The subsurface PLFA communities were only significantly affected by microhabitat in Degerö Stormyr ($F_{1,16} = 4.2$, $p \leq 0.01$). Similarly to the plant community composition, microbial communities did not differ between south- and north-facing microhabitats (Table 3 and Fig. 4).

Bacterial biomass (surface samples) did not differ among sites, nor could we detect differences in bacterial biomass between microhabitats or aspects (Table 2). The fungal biomass, on the other hand, was lower in Store Mosse as compared with that at the other sites, resulting in a lower fungal/bacterial ratio in Store Mosse (Table 2). Additionally, the fungal/bacterial ratio was somewhat higher in the drier hummock and slope habitats than in the lawn microhabitats. Similar to bacterial biomass, fungal biomass was not affected by microhabitat or by aspect (Table 2).

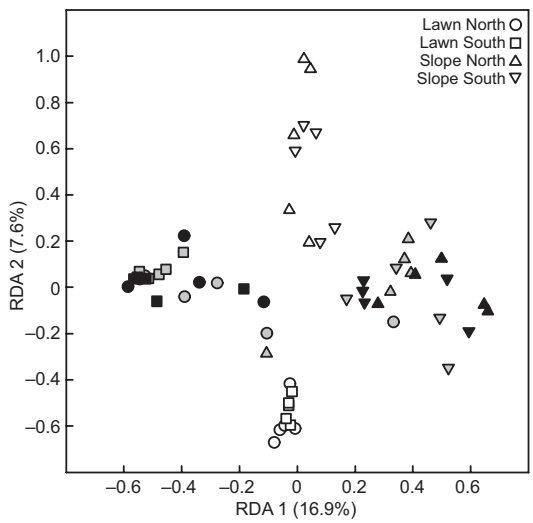

Fig. 3. Ordination biplot (partial redundancy analysis, pRDA) illustrating the effects of microhabitat and aspect on peatland plant community. pRDA was performed on the Hellinger-transformed plant community matrix, partialling out the effects of site. Biplot axis 1 and 2 (both significant; $p \leq 0.001$), and 'site scores' (types 2 scaling) are shown. Empty symbols = Degerö Stormyr; gray symbols = Store Mosse; filled symbols = Lille Vildmose.

Discussion

Site and microhabitat effects on plant and microbial community composition

The three peatlands clearly differed in the plant community composition. Degerö Stormyr, the northernmost site, significantly differed from the two other sites, due to differences in climatologi-

Table 3. Results from the redundancy analyses (RDA) testing the influence of site, microhabitat and aspect on the composition of the plant community (model 1), the surface microbial PLFA community (model 2), and the subsurface microbial community (model 3). Partial RDA was performed to 'partial out' the effect of site in further analyses (models 4–6). *F* and *p* were obtained form Monte Carlo permutations (n = 999). Variation partitioning using RDA and adjusted r^2 were applied to compare the respective effect of each individual factor and their interactions.

	df	*F*	*p*	r^2
Plant community				
Model 1 (full model)				0.59
Site	2	24.6	≤ 0.001	0.32
Microhabitat	1	19.9	≤ 0.001	0.12
Aspect	1	1.6	0.11	–0.01
Site × Microhabitat	2	10.7	≤ 0.001	0.59
Site × Aspect	2	1.3	0.21	0.31
Microhabitat × Aspect	1	0.6	0.74	0.11
Site × Microhabitat × Aspect	2	0.7	0.82	0.59
Residual	48			
Model 4 (Site effect partialled out)				0.21
Microhabitat	1	19.9	≤ 0.001	0.12
Aspect	1	1.6	0.13	–0.01
Site × Microhabitat	2	10.7	≤ 0.001	0.59
Site × Aspect	2	1.3	0.22	0.31
Microhabitat × Aspect	1	0.6	0.72	0.11
Site × Microhabitat × Aspect	2	0.7	0.83	0.59
Residual	48			
Microbial (PLFA) community; surface				
Model 2 (full model)				0.28
Site	2	9.8	≤ 0.001	0.21
Microhabitat	1	5.7	≤ 0.01	0.05
Aspect	1	1.6	0.15	0
Site × Microhabitat	2	1.6	0.12	0.28
Site × Aspect	2	0.7	0.75	0.21
Microhabitat × Aspect	1	0.7	0.59	0.05
Site × Microhabitat × Aspect	2	1.1	0.3	0.28
Residual	48			
Model 5 (Site effect partialled out)				0.05
Microhabitat	1	5.7	≤ 0.01	0.05
Aspect	1	1.6	0.13	0
Site × Microhabitat	2	1.6	0.12	0.28
Site × Aspect	2	0.7	0.74	0.21
MH × Aspect	1	0.7	0.56	0.05
Site × Microhabitat × Aspect	2	1.1	0.29	0.28
Residual	48			
Microbial (PLFA) community; subsurface				
Model 3 (full model)				0.20
Site	2	8.5	≤ 0.001	0.20
Microhabitat	1	0.8	0.52	–0.01
Aspect	1	0.6	0.8	–0.01
Site × Microhabitat	2	1.7	≤ 0.05	0.22
Site × Aspect	2	0.4	1	0.10
Microhabitat × Aspect	1	1.1	0.3	–0.02
Site × Microhabitat × Aspect	2	0.8	0.62	0.2
Residual	48			
Model 6 (site effect partialled out)				–0.05
Microhabitat	1	0.8	0.53	–0.01
Aspect	1	0.6	0.8	–0.01
Site × Microhabitat	2	1.7	≤ 0.05	0.22
Site × Aspect	2	0.4	1	0.18
Microhabitat × Aspect	1	1.1	0.32	–0.02
Site × Microhabitat × Aspect	2	0.8	0.65	0.20
Residual	48			

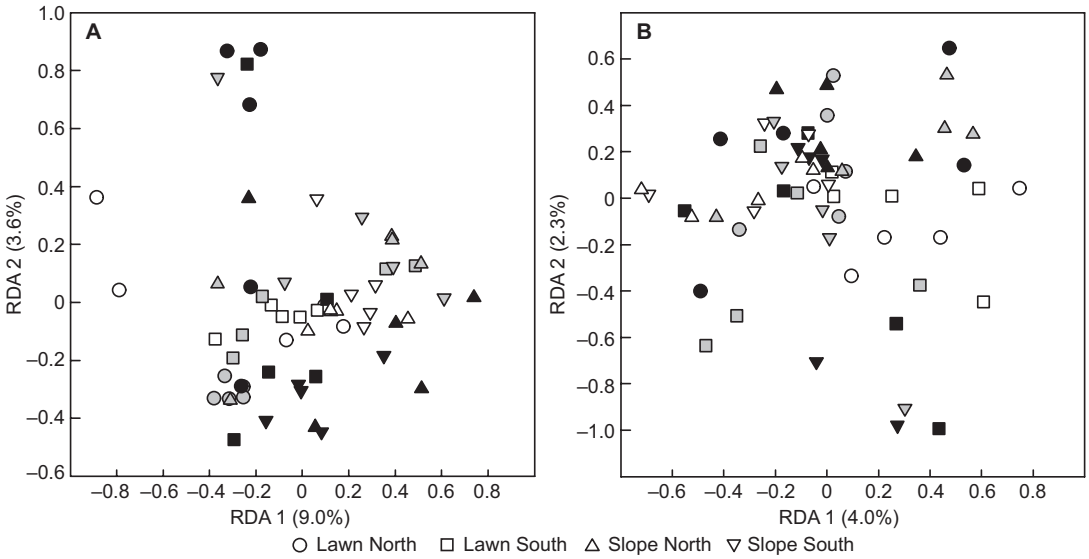

Fig. 4. Ordination biplot (partial redundancy analysis, pRDA) illustrating the effects of microhabitat and aspect on peatland microbial PLFA community from (**A**) surface and (**B**) subsurface samples. pRDA was performed on the Hellinger-transformed PLFA matrices, partialling out the effects of site. RDA axis 1 (**A**: $F_{1,48} = 7.4$, $p \leq 0.01$; **B**: $F_{1,48} = 3.0$, $p \leq 0.01$) and RDA axis 2 (**A**: $F_{1,48} = 2.9$, $p \leq 0.01$; **B**: $F_{1,48} = 1.7$, $p = 0.07$), and 'site scores' (types 2 scaling) are shown. Empty symbols = Degerö Stormyr; gray symbols = Store Mosse; filled symbols = Lille Vildmose.

cal conditions (Sundh *et al*. 1997). Post-glacial colonization rates might also have played a role in the differences in the plant community composition among the three peatlands (Svenning *et al*. 2008). Similarly, microbial community composition was strongly affected by site, yet communities also differed with depth along the peat profile. Jaatinen *et al*. (2007a) demonstrated that the composition of microbial communities in boreal peatlands strongly depends on peatland type, and is not only related to water-table depth but also to plant community composition. Prevailing water-table depth (WTD) and plant species composition are, however, themselves related (Straková *et al*. 2011, Peltoniemi *et al*. 2012). Hence, changes in WTD may affect plant communities with knock-on effects on microbial community composition.

In line with Kotiaho *et al*. (2013), plant communities differed between microhabitats, so that the hummock communities were different from the lawn and hollow communities. In our study, when partialling out site effects, the microbial community composition did follow this microtographical pattern, but only in the surface peat samples. Nevertheless, the plant communities from both microhabitats at Degerö Stormyr differed in composition from those at Store Mosse and Lille Vilmose, while the microbial communities did not show such divergence. These results indicate that the link between plant community composition and microbial community composition is rather complex and deserves much more attention then currently.

Microclimatological consequences of aspect on plant and microbial community composition

Our hypothesis that plant and microbial communities would be affected by aspect was based on the expectation that higher solar irradiance on south-facing slopes would elevate soil temperatures. Despite substantial differences in solar irradiance (2.0–3.1 MJ m^{-2} day^{-1}), the mean temperatures were significantly higher in the south-facing slopes at the northernmost site (Degerö Stormyr) only. Experimentally increasing irradiance using infra-red lamps has been reported to cause changes in soil temperatures in bog mesocosms (Bridgham *et al*. 1999, Noormets *et*

al. 2004), with cascading effects on plant species composition and productivity (Weltzin *et al*. 2000, 2003). Bragazza (2008) also reported the effects of an exceptionally warm and dry summer in the Italian Alps, with long-lasting detrimental effects on the plant community on southern exposed hummocks. Under drier conditions, ground heat flux and evaporative cooling may be hampered, and the differences in solar irradiance could lead to temperature differences between 5 °C and 7 °C between north- and south-facing slopes. Clearly this was not the case at any of our sites, as they were all continuously moist. We argue that evaporative cooling of the south-facing (higher irradiance) slopes may have alleviated potential warming. Indeed, only a small fraction (< 10%) of the net radiation reaches the peat soil below the vegetation, and most energy (ca. 80%) is lost through evapotranspiration (Bridgham *et al*. 1999, Heijmans *et al*. 2001, Noormets *et al*. 2004). Additionally, vascular plant biomass was somewhat higher in south-facing lawns and on hummock slopes, by which irradiance-induced heat at these microhabitats may have been mitigated by biomass-induced shading. Nevertheless, both the maximum soil temperatures and the temperature amplitude were generally higher in the south-facing hummock slopes, and this effect was strongest and significant in the northernmost site (Degerö Stormyr). The apparent changes in the microclimatological conditions between north- and south-facing microhabitats did however not result in changes in the plant community composition, nor in the microbial community composition. Even at Degerö Stormyr, where we hypothesized any effects to be larger, no effect of aspect was found for the plant community composition (RDA: $F_{1,16} = 1.1$, $p = 0.28$, $r^2 = -0.02$) and the microbial community composition (RDA: $F_{1,16} = 0.8$, $p = 0.48$, $r^2 = -0.01$).

In agreement with our hypothesis, dissolved organic carbon (DOC) concentrations in pore water were higher at south-facing microsites (Table 2), indicating increased decomposition rates or plant rhizodeposition. Recently it has been shown that increased vascular plant abundance enhances dissolved organic carbon concentrations in peatlands (Bragazza *et al*. 2013). Therefore, we argue that apart from a temperature-induced (i.e. decomposition) increase in DOC concentrations, the higher standing vascular plant biomass in the southern exposed microhabitats (Fig. 2) might have induced exudation of labile C. The slightly higher DOC concentration in the south-facing slopes, which is probably related to these biomass differences, did not lead to detectable differences in microbial biomass and microbial community composition. The absence of differences in the pore-water nitrate, ammonium, and phosphorus concentrations between south- and north-facing microhabitats may be explained by plant uptake. Both the higher vascular plant biomass and higher N concentration in ericoid tissue in south-facing *versus* north-facing lawns at Degerö Stormyr show that plant N uptake is clearly greater at the southern-exposed microsites. Interestingly, the Degerö Stormyr lawn habitats had a relatively high cover of the ericoid *Andromeda polifolia*, especially in the south-facing microhabitats. The increased leaf tissue N concentrations in the south-facing lawns of this site may be indicative of a strong mycorrhizal association with *A. polifolia* (Jacquemart 1998).

Conclusions

At the site scale, plants as well as microbial community composition are governed by microhabitat, i.e. microtopographical gradients associated with prevailing water-table depth. At the microhabitat scale, however, aspect does not seem to affect community composition, even though microclimate significantly differed between the south- and the north-facing aspect at the northernmost site. Any environmental change altering the hydrological condition at the microhabitat scale can then impact on the aboveground-belowground interactions with cascade consequences on C and nutrient cycling.

Acknowledgements: We thank the Aage V. Jensen Naturfond, Länsstyrelsen i Jönköpings län, and the Swedish University of Agricultural Sciences (SLU, Umeå), in particular Mats Nilsson, for access to the study sites. We are grateful to Marja Verhoeven, Mieke de Wit, Sebastian Schmidt, Christian Blodau, and Yuanqiao Wu for assistance during field sampling. Vincent Jassey was invaluable in giving his statistical advice. This study is part of the BiodivERsA-PEATBOG project, which is funded as an ERA-net project

within the European Union's 6th Framework Programme for Research through NWO-ALW (grant 832.09.003), and was partly supported by the Swiss National Science Foundation (grant 205321-129981 to LB). We are also indebted to the Dutch Foundation for the Conservation of Irish Bogs for financial support to BJMR.

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