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## Global change and the functional diversity of cryptogams in northern biomes

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## Chapter 2

# Determinants of cryptogam composition and diversity in *Sphagnum*-dominated peatlands: the importance of temporal, spatial and functional scales

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### Summary

1. Changing temperature regimes and precipitation patterns in the Subarctic will impact on vegetation composition and diversity including those of bryophyte and lichen communities, which are major drivers of high-latitude carbon and nutrient cycling and hydrology.
2. We investigated the relative importance of such impacts at different temporal, spatial and plant functional scales in subarctic *Sphagnum fuscum*-dominated peatlands, comprising both an *in situ* warming experiment and natural climatic and topographic gradients in northern Sweden and Norway. We applied multivariate analyses to investigate the relationships among cryptogam and vascular plant species composition and abiotic (temperature, moisture) and biotic (*Sphagnum* growth) regimes at various scales.
3. At the short-term temporal scale (4-year warming experiment), increased temperature yielded no clear effect on cryptogam or vascular plant species composition. Spatially, direct effects of temperature were decisive for overall species composition across regions (macro-scale) rather than within one region (meso-scale). Moisture and *Sphagnum* growth were drivers of species composition at all spatial scales, and *Sphagnum* growth itself depended on its position on the microtopographic gradient and on temperature.
4. Grouping of bryophytes and lichens at increasing scales of functional aggregation from species, growth form to the major higher taxon level (*Sphagnum*, other mosses, liverworts, lichens) revealed mostly increasing correlation with climate regimes and *Sphagnum* growth. Excluding liverworts from the analysis tended to reduce the correlation.

5. Abundances of lichens, liverworts, non-*Sphagnum* mosses and (to a lesser degree) vascular plants were negatively related to *Sphagnum* abundance. Few cryptogam and vascular plant species showed a positive relationship with *Sphagnum* abundance. Correspondingly, cryptogam species richness and Shannon Index on peatlands strongly declined as *Sphagnum* abundance increased, whilst indices for vascular plants showed no significant relationship.

6. *Synthesis*. Scale, be it spatial or functional, strongly determined which environmental drivers showed the clearest relationships with vegetation composition and diversity. Our findings will help to optimize predictions about long-term effects of climate on peatland vegetation composition, and subsequently its feedbacks to carbon and water cycles, at the regional scale.

## **Introduction**

Climate change at high latitudes, both north and south, is predicted to be of greater impact and progressing more rapidly than in any other region on Earth. In wide regions in the Arctic, not only temperatures but also precipitation are expected to increase (ACIA 2005). In these northern, arctic ecosystems non-vascular cryptogams, i.e. lichens and bryophytes, contribute more to biodiversity than vascular plants (Matveyeva & Chernov 2000). Over extensive areas, cryptogams also exceed vascular plants in abundance and represent the main driver of ecosystem functions (Longton 1997; Cornelissen *et al.* 2007) such as regulation of hydrology (Beringer *et al.* 2001), carbon balance (Rydin & Jeglum 2006), nitrogen fixation (Solheim *et al.* 1996) and preservation of permafrost (Dyrness 1982; Yoshikawa *et al.* 2003). Increasing temperatures and precipitation might induce permafrost melting (Johansson *et al.* 2006; Cheng & Wu 2007), leading, amongst other effects, to a changed hydrology. The growth of cryptogams is highly sensitive to changes in moisture regimes and particularly *Sphagnum* growth is positively related to moisture in the majority of species, albeit in species-specific ways (Weltzin *et al.* 2001; Robroek *et al.* 2007). By building up peat the genus *Sphagnum* accounts for a carbon storage of 600 Gt in northern peatlands, an amount equivalent to all CO<sub>2</sub> stored in the atmosphere (Clymo 1998). Its peat-building ability and increased growth at high moisture regimes may have strong repercussions for the global carbon budget as *Sphagnum* growth may partly counteract the effect of greenhouse gases, thereby making it a potential buffer against climate change.

Given these important roles of cryptogams, and the distinct contributions of different cryptogam species and types to ecosystem functions and climate feedback, predicting the responses of cryptogam diversity and abundance is a high research priority. However,

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compared to the great emphasis on vascular plant responses (Arft *et al.* 1999; Van Wijk *et al.* 2004; Walker *et al.* 2006), cryptogams often have been neglected in global change investigations, partly due to difficulties in identification and their small size. From the existing experimental climate manipulation studies we cannot draw conclusions about the general patterns of cryptogam composition or diversity in response to climate change. With few exceptions where cryptogams were identified (partly) to species level (Molau & Alatalo 1998; Press *et al.* 1998; Hollister *et al.* 2005) the existing studies mainly treated bryophytes or lichens as one group (Epstein *et al.* 2004; Wahren *et al.* 2005). Others concentrated on distribution and/or growth of a single species only (Potter *et al.* 1995; Callaghan *et al.* 1997). In contrast to these studies, bryophytes along environmental gradients in peatlands have been studied at species level, focusing on the biodiversity of these systems (e.g. Vitt *et al.* 1995; Gignac *et al.* 1998). Lichens, however, were not included in these studies. Thus, whilst all of the above investigations have addressed components of the large puzzle of peatland cryptogam composition and diversity responses to climatic variation, a more comprehensive and multi-scale study is still lacking.

Climate manipulation experiments and natural climatic gradient studies suggest that the observed responses depend strongly on the temporal, spatial or plant functional scale at which the study is conducted. Short-term experiments were poor predictors of the long-term responses of vascular plants to climate manipulation field experiments (Chapin *et al.* 1995; Shaver *et al.* 2001). This might hold true even more when considering the relatively slowly growing cryptogams. Spatial scales, from local to regional, as demonstrated by Hollingsworth *et al.* (2006), determined the differing environmental drivers of vascular and non-vascular species distribution in a boreal forest (see also Andrew *et al.* 2003). We expect that the magnitude of variation in climatic parameters increases with the coarseness of spatial scale, since microclimate, mesoclimate (as dependent for instance on altitude) and macroclimate (as dependent for instance on maritime influence) each hierarchically contribute their own set of climatic variation to that experienced by any given local community. Epstein *et al.* (2001) showed that by aggregating vascular plant species by species, functional type, life form or vegetation type, functional scale strongly influenced the outcome of the analysis (see also Wright *et al.* 2006). Similarly, Gordon *et al.* (2001) revealed that bryophytes respond to fertilization in different ways, and therefore should not be aggregated into one functional group. Thus, the scale at which a study is conducted, be it temporal, spatial or functional, may determine which environmental drivers are decisive for cryptogam composition and diversity, and to which degree.

## Northern peatland cryptogam composition and scale

The problems associated with scale issues (temporal, spatial or functional) can be overcome in various ways. One approach is to use multi-year experimental manipulations of environment and studies along natural gradients in different regions to explicitly compare responses among different functional grouping schemes. Most climate change studies have been carried out in either experimental setups (Walker *et al.* 2006) or along climatic or hydrological gradients (Gignac & Vitt 1990; Vitt 1990). The combination of approaches may reveal particularly robust insights (Callaghan *et al.* 1999; Cornelissen *et al.* 2001). Here, for the first time, we simultaneously test the importance of temporal, spatial and functional scales as determinants of cryptogam responses to climate. Specifically, we compare the climate responses of cryptogam composition and diversity in subarctic peatlands in an *in situ* warming experiment with natural variation along smaller and larger environmental gradients, and at different levels of species aggregation.

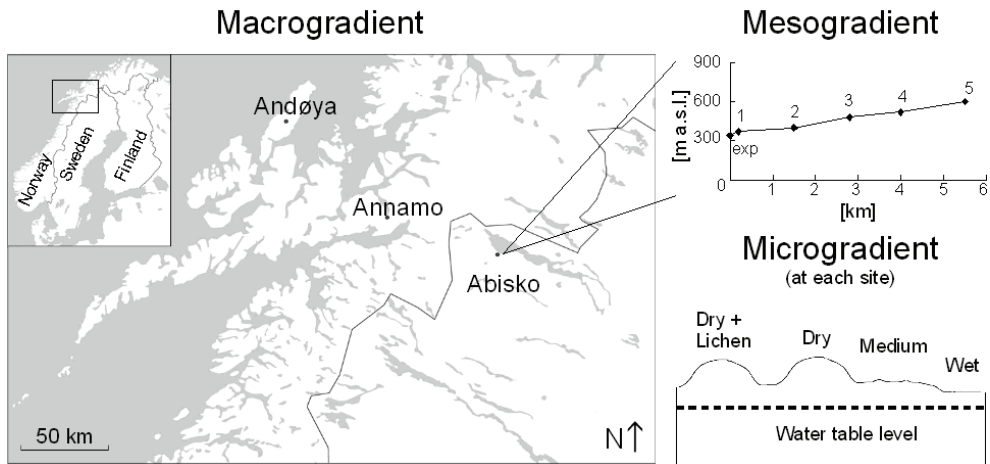
*Sphagnum fuscum*, of worldwide distribution and one of the most common and abundant bryophytes in boreal-subarctic peatlands (Isoviita 1966), constitutes the dominant peatland cryptogam of both the long-term warming experiment and gradient here. *Sphagnum* growth is known to be strongly influenced by the two direct effects of climate change, increased temperature (Dorrepaal *et al.* 2004) and increased precipitation (Rydin & McDonald 1985) or both (Gunnarsson 2005). The negative and positive interactions of *Sphagnum* with vascular plants have been studied in greater detail (Heijmans *et al.* 2002; Malmer *et al.* 2003) than for cryptogams (Vasander 1981; Hugonnot *et al.* 2003). However, existing studies indicate interactions and dependence of cryptogams on the performance of *Sphagnum* as the underlying growing substrate. Therefore, in the present study we introduced gradients at different scales covering not only the abiotic factors temperature and precipitation, but also the biotic factor *Sphagnum* growth as determinants of species distribution.

We hypothesize that (i) hydrology and temperature, mediated by *Sphagnum* competition, are the main drivers of cryptogam species distribution in *Sphagnum fuscum*-dominated peatlands, (ii) the relative importance of these drivers differs at different spatial, temporal and functional scales and (iii) the cryptogam species composition and diversity of these peatlands strongly depend on the development of *Sphagnum* as the underlying living substrate.

## Methods

Central to our study was a climate manipulation experiment on a sloping bog dominated by the peat moss *Sphagnum fuscum*, located in the vicinity of the Abisko Scientific

Research Station, North Sweden and a corresponding climatic natural gradient covering sites from Abisko, North Sweden to Annamo and Andøya, Norway (Fig. 1).



**Fig. 1.** Location of macrogradient in northern Scandinavia (Andøya, Annamo, Abisko), mesogradient (Abisko: sites one to five), warming experiment and location of plots along the microgradient across macro- and mesogradient.

## THE TEMPORAL SCALE STUDY

The experiment at the south shore of Lake Torne (Torneträsk) (68°21'N, 18°49'E, 340 m a.s.l.) was established in June 2000 using open-top chambers (OTC) for passive warming in different seasons and for snow accumulation (details in Aerts *et al.* 2004; Dorrepaal *et al.* 2004). Summer warming was annually from 1 June until the end of September, followed by the winter treatment from the end of September until late April and the spring treatment from late April to 1 June. The winter treatment featured mostly substantial passive snow accumulation, especially in the period January – April, with concomitant buffering of air and soil temperatures (climate details in Aerts *et al.* 2004; Dorrepaal *et al.* 2004). From a larger experimental design, we selected the four combinations of summer, winter and spring treatments which we considered the most relevant for future climate change scenarios: plots with warming all year round, warming in summer and winter, warming in summer only, and the control plots were sampled in 2004 and 2005 ( $N = 5$ , Table 1). Vapour pressure deficit did not differ significantly (Dorrepaal *et al.* 2004) in the OTCs vs. the control plots.

## Northern peatland cryptogam composition and scale

**Table 1.** Experimental design and treatment codes used in the climate manipulation experiment (W, warming (with OTC); A, ambient; S, snow accumulation (with OTC); +: treatment applied)

Treatment	Summer	Winter	Spring	Code
1	+	+	+	WSW
2	+	+	-	WSA
3	+	-	-	WAA
4	-	-	-	AAA

### THE SPATIAL SCALE STUDY

We studied the effect of spatial scale on cryptogam diversity and abundance at various spatial scales, ranging from macroscale via mesoscale to microscale. The macrogradient consisted of (i) sites from Abisko, Sweden, at altitudes between 370 and 600 m, with a relatively continental climate (annual mean:  $-0.9$  °C, 301.2 mm, long-term average 1961-1990, continentality index expressed here as eastward distance from ocean: 208 km); (ii) warmer sites in Norway located close to Annamo at about 150 m a.s.l. ( $68^{\circ}32'N$ ,  $17^{\circ}13'E$ , no long-term climate data available, continentality index: 107 km); and (iii) sites on the island Andøya with a typically oceanic climate (annual mean:  $4.1$  °C, 870 mm, long-term average 1961-1990, [www.met.no](http://www.met.no), continentality index: 6 km) at about 40 m a.s.l. ( $69^{\circ}07'N$ ,  $15^{\circ}52'E$ ). The sites at Abisko, Annamo and on Andøya (Fig. 1) were chosen to aim for the highest similarity in geology and associated abiotic factors such as ion composition of the peat water and soil pH. The mesogradient comprised an altitudinal temperature gradient (370 – 600 m a.s.l.) on the Abisko side of the macrogradient with five sites, chosen at sequentially higher altitudes and thus hypothetically colder than the experiment (which was at the lowest altitude locally, see Appendix S1.1 in Supporting Information). The five sites at 370, 400, 480, 520 and 600 m a.s.l. corresponded to 1973.7, 2085.5, 2060.8, 1806.5 and 1902.3 degree days (measurement see abiotic factors: temperature). The site at the lowest altitude (370 m a.s.l.) displayed degree days which were lower compared to the site at 30 m higher elevation, a phenomenon which is due to the influence of the large water body of Lake Torne (Torneträsk) (T.V. Callaghan, pers. comm.). Also note that the site at the highest altitude was higher in degree days than the site 80 m lower, indicating that local geomorphological and climatic factors, for instance the trapping of cold air in depressions, interfered with the influence of the altitudinal gradient. To study the influence of varying soil moisture on *Sphagnum* and associated cryptogam communities at the microscale, a soil moisture microgradient was established at all sites along the macro- and mesogradients covering the mosaic of plots from (i) very wet hollows (Wet), (ii) medium wet, plane *Sphagnum* surfaces (Medium) to (iii) dry hummocks (Dry) and (iv) dry hummocks in the stage of stagnation in peat production

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where *Sphagnum fuscum* is partly dead and lichens start to overgrow the peat mosses (Dry + lichen); for temperature and moisture data see Appendix S1.2.

### VEGETATION RECORDING AND PLANT FUNCTIONAL SCALE CLASSIFICATION

Vegetation was recorded in 2004 at the species level by means of the point intercept method (Jonasson 1988). At each microgradient site and each experimental plot, one frame was recorded. The portable aluminium frame covered an area of 50 by 50 cm with nine rows of thirty points each. A bubble level ensured that the frame was horizontal. Two experimental plots were recorded to decide how many points needed to be recorded for an adequate representation of species richness. We chose 270 points for lichens and bryophytes based on species saturation at 270 points per plot in species-rich plots (data not shown). For vascular plants, species saturation occurred at 60 to 150 points (data not shown). The number of hits per plot for vascular plants could thus be reduced to 150. At each point, all hits of vascular plants, lichens and bryophytes were recorded until the pointed tip ( $\varnothing < 0.5\text{mm}$ ) of the needle touched the ground. Bryophytes, lichens and litter were recorded as first hit only. *Dicranum fuscescens* and *D. elongatum* could not be safely distinguished in the field and were therefore recorded as one species. Tiny liverworts were not further distinguished in the field. *Anastrophyllum minutum*, *Calypogeia sphagnicola*, *Cephalozia bicuspidata*, *Cephalozia leucantha*, *Cephalozia loitlesbergeri*, *Cephalozia lunulifolia*, *Cladopodiella fluitans* and *Kurzia pauciflora* (or *K. trichocladus*, sterile plants cannot be distinguished) were part of this group. For vascular plants each foliated branch of *Empetrum hermaphroditum* or *Calluna vulgaris* was considered to be one hit since counting every hit leaf would lead to overestimation of abundance. For each vascular plant species the hits per plot were multiplied by 1.8 (270/150 points) to be comparable to the cryptogam data.

Nomenclature followed Hill *et al.* (2006) for all mosses except *Sphagnum*; Daniels & Eddy (1985) for *Sphagna*; Damsholt (2002) for liverworts; Santesson *et al.* (2004) for lichens; and Mossberg & Stenberg (2003) for vascular plants.

The functional scale classification for cryptogams was performed at various levels from species, growth form, major plant taxa to the classification used by Chapin III *et al.* (1996) which is based on vascular plant functional groups and the cryptogam groups *Sphagna*, non-*Sphagnum* mosses and lichens. Species were grouped in growth forms based on their presumed strategy to cope with the growth of *Sphagnum* as the underlying and continuously growing living substrate (species list and classification see Appendix



S2). Liverwort species adapted to active *Sphagnum* growth (erect liverworts) will exhibit vertical growth, which may enable them to keep pace with the growing *Sphagnum* turf, at the same time taking advantage of the micro-habitat created by *Sphagnum*. Albinsson (1997) introduced the term ‘compromise strategy’ for this adaptation. The ‘avoidance strategy’, in contrast, is followed by small, prostrate liverwort species that creep over dead *Sphagna* and tend to be typical for peat building stagnation. However, some prostrate liverworts cannot be confined to this avoidance strategy as they occur on living *Sphagna* and exhibit growth rates adapted to the growing *Sphagna* which in turn may be able to uplift them (Albinsson 1997). We classified the liverwort groups with avoidance strategy and those which cannot be confined to the avoidance strategy as prostrate liverworts since their growth form was similar and information on their strategy was not available for all species. We expected erect vs. prostrate habit to be relevant for performance in *Sphagnum* turf also for other cryptogams. Thus, cryptogams in our study were grouped into erect and prostrate mosses, liverworts and lichens. We also distinguished crust-forming lichens, which appear indicative of peat building stagnation. Crust-forming lichens also included *Cladonia* cup lichens which, in contrast to other reindeer lichens like *C. arbuscula* that are able to grow upwards as *Sphagnum* advances, are able to build crusts on the peat surface. The moss *Straminergon stramineum* was classified as prostrate, although it exhibits vertical growth inside deeper peat layers. However, attributing this moss to the erect growing mosses such as *Polytrichum* and *Dicranum* seemed unsatisfactory. Vascular plants were grouped into the functional groups of evergreen shrubs, deciduous shrubs, grasses, sedges, forbs and vascular cryptogams (Chapin III *et al.* 1996; Qusted *et al.* 2003). Further grouping comprised the major taxa of cryptogams which were defined as *Sphagnum*, mosses, liverworts, lichens and the vascular plant groups used above. The coarsest-scale grouping corresponded to Chapin III *et al.* (1996) with *Sphagnum*, non-*Sphagnum* mosses and lichens as cryptogam groups and the above defined vascular plant functional groups.

#### THE BIOTIC FACTOR *SPHAGNUM* GROWTH

*Sphagnum* growth measurements were conducted using the cranked wire method developed by Clymo (1970). In each experimental and microgradient plot, five (experimental plot) or eight (microgradient plot) cranked wires were randomly put out. Measurements were conducted in the summers of 2005 and 2006 starting at the beginning of May and finishing at the end of September. Along the gradient several wires were damaged due to reindeer trampling. The remaining wires ( $n = 3-8$ ) and the five wires in the experimental plots were averaged before use in the statistical analysis. The temporal differences between sites concerning the measurement of the wires at the beginning and

end of the season were not accounted for, since measurement along the whole gradient always took place within a few days. Furthermore, attributing a growth rate per day would result in a greater error since growth of *Sphagnum* is known to be variable across the growing season and ceases in autumn (own data, not shown, and Dorrepaal *et al.* 2004).

## ABIOTIC FACTORS

### *Temperature*

From mid September 2004 until mid August 2005 soil temperature was measured with temperature buttons (MiniTemp Logger, Photologic Ltd., Cobourg, Ontario, Canada) one placed at each site along the macrogradient and in the experimental treatments AAA and WSW. The buttons were protected from moisture damage by putting them into film canisters, sealed with silicone wax. Furthermore, the canister lid was secured with reflecting tape and a thin layer of the surrounding *Sphagna* was arranged on top thus avoiding both heating-up of the canister and human disturbance of the measurement. The top of the canister was at about the same level as the peat surface, integrating temperature over a depth of 0.5 to 5.5 cm in the randomly chosen position at the Dry + lichen, Dry and Medium plots thus only comparing temperature data among the plots which were raised above the water table level. At each site along the macrogradient (except Annamo) and in the same microgradient plots in which the buttons were used the years before, soil temperature was measured at random positions from end of May 2006 until end of August 2006 with two dataloggers and external sensors (Tinytag Plus TGP-0020, PB-5002-1M5 probe, Gemini Data Loggers, Chichester, UK). At Annamo only one logger could be installed. In the warming experiment each of the treatments AAA and WSW was measured in two randomly chosen plots. Soil temperature was recorded at 1 cm depth since we were interested in the effects of temperature on the uppermost growing parts of the cryptogams. The data were averaged per site and treatment. Values for WAA and WSA plots were calculated from the AAA and WSW plots using the appropriate periods for spring, summer and winter treatment when the OTC positions were changed. We used degree days, i.e. the cumulative number of degrees in the measurement period from autumn 2004 to autumn 2006, as a measure for temperature in this study. The temperature threshold at which both bryophytes and lichens might start to be photosynthetically active was estimated to be at 0°C (Rastorfer 1970; Kappen *et al.* 1996). Consequently, all days of the measurement period with a mean daily temperature exceeding 0°C were summed resulting in a degree day temperature sum.

## *Northern peatland cryptogam composition and scale*

### *Soil moisture and water table level*

Soil moisture was manually measured on several days throughout the season by inserting a handheld Time Domain Reflectometry (TDR) soil moisture meter (Trime FM-2, P2G probe, IMKO GmbH, Ettlingen, Germany) vertically into the peat down to 16 cm depth. On each of the four sides of the plot one measurement was taken and all four measurements were averaged. The resulting soil moisture values were averaged for the summers of 2004 through 2006, to account for seasonal variability in peatlands (water table fluctuations see Appendix S3.2). These values were then calibrated for peat soils (Appendix S3.1).

Water table level was recorded at each plot on several occasions. Soil moisture and water table proved to be closely correlated (details see Appendix S3.2). Since not all plots displayed a measurable water table level, soil moisture was used in the analysis.

### *Nutrient availability*

Soil nutrient availability was measured using ion exchange resins in summer 2004 and 2005 according to Weih (1998). The cation (CEM) and anion (AEM) resins were saturated with  $H^+$  using 0.1 M  $H_2SO_4$  and with  $Cl^-$  using 2 M NaCl, respectively (Giblin *et al.* 1994). We deviated from Weih (1998) by inserting the resins vertically into the peat at approx. 10 cm depth around 28 May 2006 ( $\pm 1d$ ). At the end of the growing season around 16 Sept. 2006 ( $\pm 5d$ ), the resins were returned to the laboratory and extracted with 20 mL of 2 M NaCl in 0.1 M HCl (Giblin *et al.* 1994) by shaking for 2 hours. The extracts were subsequently analysed for nitrate, ammonium and phosphate. Ammonium was measured photometrically with an indicator (Tecator Application note AN 134/91) using a flow injection autoanalyzer (Tecator, FIAstar 5020 Analyzer, 5032 Detector Controller, Foss, Rellingen, Germany). Phosphate was analysed photometrically with the molybdenum-blue method (Tecator Application note AN 146/90) using a flow injection autoanalyser (Tecator, Aquatec 5400 Analyser, Foss, Rellingen, Germany).  $Ca^{2+}$  and  $Mg^{2+}$  were extracted using 2 M HCl. Extracts were subsequently measured by atomic absorption (Varian AAS SpectrAA 220FS, Palo Alto, CA, USA) in an air-acetylene flame under addition of  $LaCl_3$  and  $CsCl$  to suppress spectral and non-spectral interferences. The difference in exposure time to the soil due to temporal differences in burial and excavation time at each site was not taken into account since the resins were buried and excavated within a few days along all the gradients and at the experiment.

Supplementary to the resin assays, soil cores with a cross-sectional area of 7.55 cm<sup>2</sup> and 10 cm depth per plot were taken during the period of late August to early September 2006

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for measurement of extractable nitrate and ammonium. Live roots were removed from the samples before taking an aliquot of soil to be extracted with 1 M KCl solution. The samples were shaken for one hour and subsequently filtered using a Whatman GF/C glass fiber filter. Ammonium and nitrate were measured photometrically by means of the indophenolblue method and the sulfanylamide/naphtyl-ethylene-diamine method, respectively (Skalar SA-40 continuous flow analyzer, Skalar, Breda, The Netherlands). Phosphate was measured photometrically (Shimadzu, UV-1601PC, Shimadzu Corp., Kyoto, Japan) by means of the molybdenum-blue method.

Soil pH was measured in the 1M KCl soil core extracts received for the nutrient analysis using a pH meter (WTW Inolab Level 2 pH meter, Sentix 41 membrane glass electrode, WTW Weilheim, Germany).

### STATISTICAL ANALYSIS

Vegetation abundance data from point-intercept recordings were analysed by redundancy analysis (RDA) using CANOCO for Windows 4.5 (Ter Braak & Šmilauer 2002), because the gradients explored in this paper are not sufficiently long to require unimodal methods (gradient lengths for all analyses ranged between 1 and 2). Also, RDA is particularly suited for detecting small systematic changes in the data. Species data were centred and log-transformed prior to analysis. Environmental variables used in the analysis were degree days, soil moisture, *Sphagnum* growth, soil pH,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$  and phosphate concentrations (ion resins) and extractable nitrate and ammonium. Only the variables degree days, soil moisture and *Sphagnum* growth yielded a significant result in the Monte Carlo Permutation Test (9999 permutations) and were thus employed in further analysis. When testing the environmental variables for the experiment the plots were freely permuted. Along the gradient one datalogger (or the mean of two dataloggers) per site was used. The plots at each site were therefore not independent and a split-plot design was applied with the sites being the whole plots and the plots within one site the split plots. When testing for effects of degree days, the whole plots were freely permuted and the split plots kept constant. To test for contributions of moisture and *Sphagnum* growth, the whole plots were kept constant and the split plots freely permuted. Variables were tested on entry in the model in a forward selection. To test the influence of grouping (functional scale) of the vegetation data on the analysis, the data were analysed separately at species and higher grouping levels. These groupings (see above) comprised growth forms, major cryptogam taxa and vascular plant groups, and the grouping according to Chapin III *et al.* (1996). In the latter case vascular cryptogams were neglected since they do not appear in their analysis and were represented here by very few data points.

## Northern peatland cryptogam composition and scale

The dependence of *Sphagnum* growth rate on abiotic and partly biotic factors was tested in linear (multiple) regressions (SPSS 14.0 for Windows). Degree days and soil moisture represented the independent abiotic variables whereas the nominal variable microgradient accounted for not only the abiotic factor soil moisture but also the biotic factor of competition/interaction with other cryptogams/vascular plants given a specific microtopographic position. The microgradient consisted of the four categories Dry + lichen, Dry, Medium and Wet with increasing numbers of 1 to 4. The experimental plots were grouped into the Dry + lichen and Dry microgradient categories according to their soil moisture. Lichen cover along the gradient reached up to two hits per plot in the Dry category. Consequently, experimental plots where lichen cover exceeded two hits were allocated to the Dry + lichen category, whereas plots with two or less lichen hits were attributed to the Dry category.

We applied linear regression to test for relationships between major taxa of cryptogams, vascular plant abundance or overall diversity indices compared to *Sphagnum* abundance. *Sphagnum* itself was excluded when calculating the diversity indices species richness and Shannon Index.

## Results

### TEMPORAL SCALE

There were no significant treatment effects of the 4-yr warming experiment on community composition, as tested in an RDA at species, growth form and major taxa level. However, a trend ( $P = 0.096$ ) could be seen for summer warming when regarding major taxa (Table 2). A further RDA at growth form level showed that the environmental variables moisture and *Sphagnum* growth were significant determinants of community composition ( $P = 0.004$  and  $0.019$ , respectively). Degree days were not significant ( $P = 0.95$ ; Table 3).

**Table 2.** *P*-values of treatment effects on cryptogam and vascular plant composition at different levels of grouping (RDA; Monte Carlo Test: 9999 permutations). Order of the variables entering the model: a – c

Grouping level	Summer warming	Spring warming	Winter snow accumulation
Major taxa	0.096 <sup>a</sup>	0.52 <sup>b</sup>	0.81 <sup>c</sup>
Growth form	0.17 <sup>a</sup>	0.67 <sup>b</sup>	0.89 <sup>c</sup>
Species	0.24 <sup>a</sup>	0.94 <sup>c</sup>	0.65 <sup>b</sup>

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**Table 3.** *P*-values of the first canonical axis and environmental variables (RDA; Monte Carlo Test: 9999 permutations) at species, growth form, major taxa and Chapin III *et al.* (1996) grouping level of the warming experiment and the mesogradient and macrogradient (both including the microgradient). Significant *P*-values are marked with bold letters. Superscript a–c: order of the variables entering the model

Functional scale of diversity		Warming experiment *	Mesogradient (including microgradient) †‡	Macrogradient (including microgradient) †‡
Species	all axes	<b>0.0386</b>	<b>0.0002</b>	<b>0.0001</b>
Growth form		<b>0.0039</b>	<b>0.0005</b>	<b>0.0020</b>
Major taxa		<b>0.0009</b>	<b>0.0003</b>	<b>0.0001</b>
Chapin III <i>et al.</i> 1996		<b>0.0027</b>	<b>0.0005</b>	<b>0.0001</b>
Species	Moisture	<b>0.014<sup>a</sup></b>	<b>0.0004<sup>a</sup></b>	<b>0.0001<sup>b</sup></b>
Growth form		<b>0.004<sup>a</sup></b>	<b>0.0006<sup>a</sup></b>	<b>0.0006<sup>a</sup></b>
Major taxa		<b>0.001<sup>a</sup></b>	<b>0.0004<sup>a</sup></b>	<b>0.0005<sup>a</sup></b>
Chapin III <i>et al.</i> 1996		<b>0.005<sup>a</sup></b>	<b>0.015<sup>b</sup></b>	<b>0.0014<sup>a</sup></b>
Species	<i>Sphagnum</i> growth	0.077 <sup>b</sup>	<b>0.049<sup>b</sup></b>	<b>0.008<sup>c</sup></b>
Growth form		<b>0.019<sup>b</sup></b>	<b>0.015<sup>b</sup></b>	<b>0.006<sup>c</sup></b>
Major taxa		<b>0.0097<sup>b</sup></b>	<b>0.006<sup>b</sup></b>	<b>0.004<sup>c</sup></b>
Chapin III <i>et al.</i> 1996		<b>0.011<sup>b</sup></b>	<b>0.003<sup>a</sup></b>	<b>0.009<sup>c</sup></b>
Species	Degree days	0.94 <sup>c</sup>	0.16 <sup>c</sup>	<b>0.026<sup>a</sup></b>
Growth form		0.95 <sup>c</sup>	0.64 <sup>c</sup>	<b>0.033<sup>b</sup></b>
Major taxa		0.91 <sup>c</sup>	0.68 <sup>c</sup>	<b>0.029<sup>b</sup></b>
Chapin III <i>et al.</i> 1996		0.93 <sup>c</sup>	0.69 <sup>c</sup>	<b>0.045<sup>b</sup></b>

\*: Free permutation

†: Testing of degree days: whole plots permuted at random, split plots constant

‡: Testing of canonical axes, moisture, *Sphagnum* growth: whole plots constant, split plots permuted at random

### SPATIAL SCALE

#### *Microgradient*

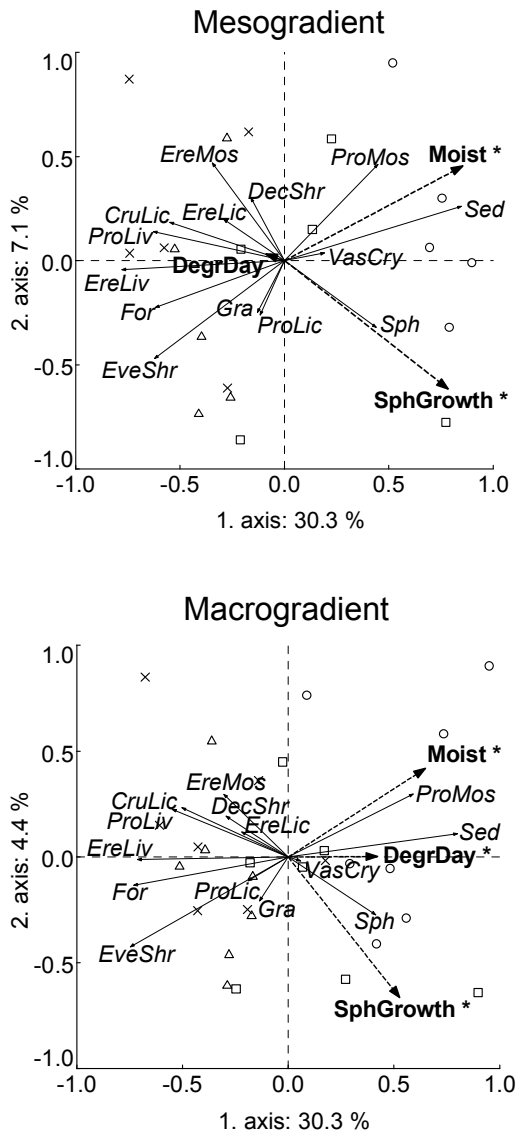
Of the possible independent variables, only the nominal variable, microgradient, explained *Sphagnum* growth significantly ( $P = 0.005$ ;  $R^2 = 0.16$ ), in contrast to moisture ( $P = 0.31$ ;  $R^2 = 0.02$ ) and degree days ( $P = 0.30$ ;  $R^2 = 0.02$ ). In a multiple linear regression, degree days and soil moisture were not related to *Sphagnum* growth ( $P = 0.22$ ;  $R^2 = 0.07$ ) whereas the variables microgradient ( $P = 0.001$ ) and degree days ( $P = 0.035$ ) contributed significantly to the overall significant regression ( $P = 0.002$ ; adjusted  $R^2 = 0.21$ ).

#### *Meso- and macrogradient*

Redundancy analysis revealed that for the meso- and the macrogradient soil moisture and *Sphagnum* growth proved to be significant determinants of community composition.

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Degree days, however, were only significant at macrogradient scale (Table 3). Abundance of prostrate mosses, sedges, vascular cryptogams and *Sphagna* was positively correlated with moisture for the mesogradient, and negatively with forbs, shrubs, erect mosses, liverworts and grasses (Fig. 2). This relationship was reversed for degree days. Sedges, grasses, vascular cryptogams, prostrate lichens, prostrate mosses and *Sphagna* were positively correlated with *Sphagnum* growth, and shrubs, forbs, erect mosses, liverworts and erect and crust-forming lichens negatively. Along the macrogradient a similar picture was revealed. Prostrate mosses, sedges, *Sphagna* and vascular cryptogams were positively correlated to moisture, degree days and *Sphagnum* growth (Fig. 2), while forbs, shrubs, lichens, liverworts and erect mosses corresponded negatively to the environmental variables. Grasses were negatively related to moisture and degree days, but positively to *Sphagnum* growth.



**Fig. 2.** RDA ordination of the mesogradient and the macrogradient (× Dry + lichen, Δ Dry, □ Medium, ○ Wet). Significant environmental variables are marked with an asterisk (Monte Carlo Test: 9999 permutations; Table 3). Growth form, functional group and environmental variable abbreviations: Sph = *Sphagnum*; Sed = sedge; gra = grass; for = forb; ProLic = prostrate lichen; ProLiv = prostrate liverwort; ProMos = prostrate moss; CruLic = crust-forming lichen; DecShr = deciduous shrub; EreLic = erect lichen; EreLiv = erect liverwort; EreMos = erect moss; EveShr = evergreen shrub; VasCry = vascular cryptogam; Moist = moisture; DegrDay = degree days; SphGrowth = *Sphagnum* growth.



## FUNCTIONAL SCALE

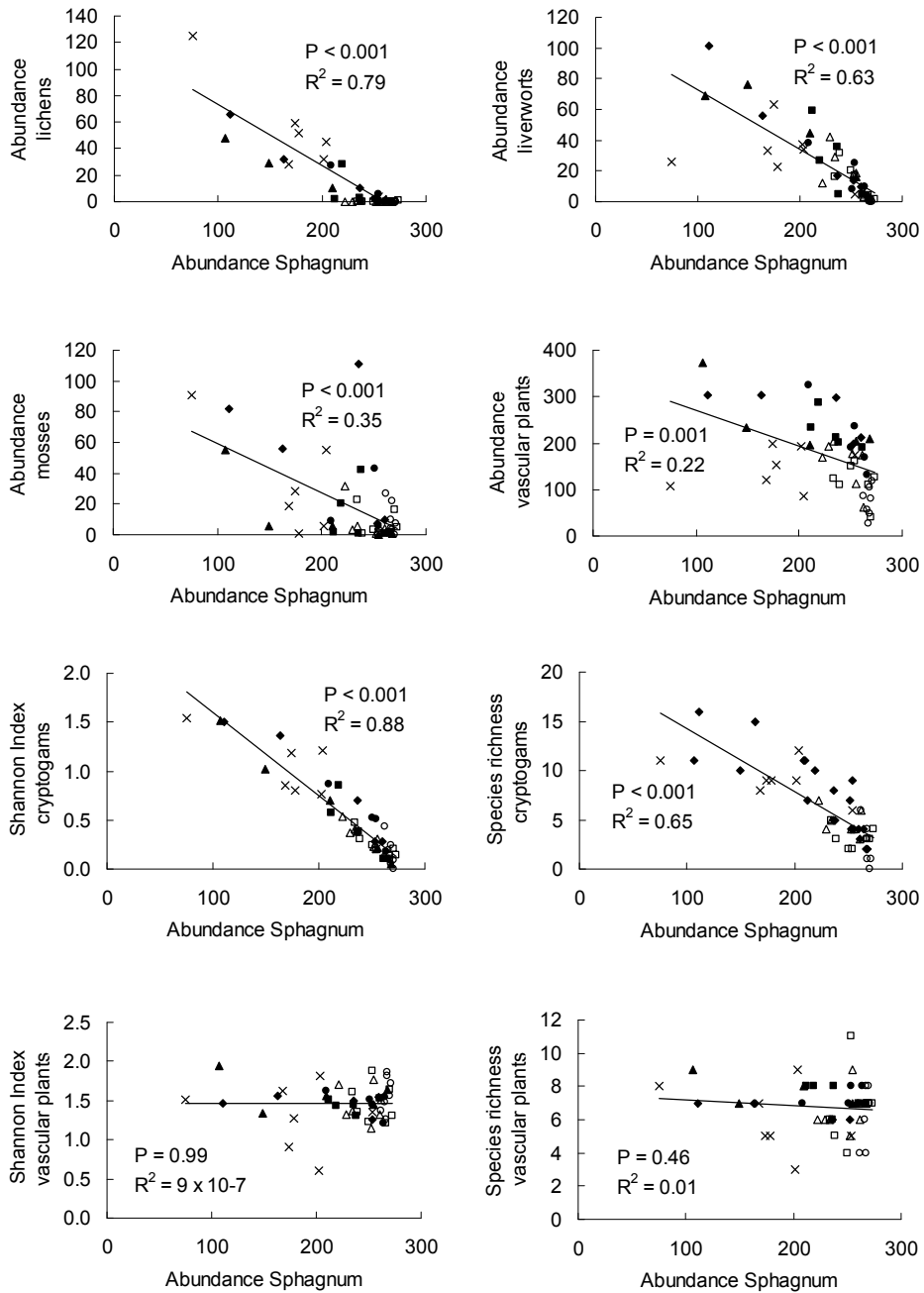
When comparing community composition across different plant functional scales, the canonical axes of the RDA were significant at all levels, but to various extents (Table 3). Moisture as an important environmental factor was significant at all scales from temporal (warming experiment) to spatial (both gradients) and functional (all grouping levels). Except for the warming experiment at species level, *Sphagnum* growth showed significance at all temporal, spatial and functional scales whereas degree days were only significant at the macrogradient scale. Grouping species up to major taxa level enhanced the significance of the variable *Sphagnum* growth at all levels and moisture at the experimental level. At the mesogradient level, the significance of moisture decreased when introducing growth forms and was not influenced at major taxa level. For degree days, introduction of growth forms seemed to decrease the significance of the variable at all levels whereas at major taxa level, significance slightly improved. With the exception of the mesogradient scale, where significance of *Sphagnum* growth improved, all variables showed a decrease in significance when applying the Chapin III *et al.* (1996)-grouping, which excludes liverworts from the analysis.

## RELATION OF ABUNDANCE OF MAJOR TAXA AND DIVERSITY INDICES VS. SPHAGNUM ABUNDANCE

The abundances of all four main taxonomic groups, *viz.* mosses, liverworts, lichens and vascular plants were all highly significantly, negatively correlated with *Sphagnum* abundance (Fig. 3). Dry + lichen plots were located at sites where *Sphagnum* is less abundant whereas plots of high *Sphagnum* abundance tended to be increasingly wet. No clear pattern of the experimental plots concerning treatment was visible.

For the cryptogams, the Shannon diversity and species richness were highly significant and negatively related to the abundance of *Sphagnum* (Fig. 3). With increasing soil moisture, *i.e.* from Dry to Wet plots, *Sphagnum* abundance increased and Shannon Index and species richness decreased. No clear pattern was observed in the experimental plots. Regarding vascular plants, no significant trend could be observed.

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**Fig. 3.** Relationship of mosses, liverworts, lichens, vascular plants, Shannon Index and species richness (indices excluding *Sphagnum*) of cryptogams and vascular plants vs. abundance of *Sphagnum* (× Dry + lichen, Δ Dry, □ Medium, ○ Wet, ◆ AAA, ▲ WAA, ■ WSA, ● WSW, treatment codes see Table 1; n = 48).

## **Discussion**

Our aim was to show how the most important climatic variables (temperature and moisture availability) and the biotic factor *Sphagnum* growth determine the distribution of cryptogams at various spatial, functional and temporal scales in northern peatlands.

We are the first to demonstrate how the importance of these different key determinants of cryptogam composition and diversity in northern *Sphagnum*-dominated peatlands varies according to scales of space and species aggregation. The four-year time scale of our *in situ* climate warming experiment, however, was likely too short to reveal any obvious responses.

### **THE IMPORTANCE OF TEMPORAL SCALE**

The experimental warming treatments did not induce direct changes in vegetation composition (Table 2). However, *Sphagnum* growth, which itself is influenced by temperature, was significant as an environmental driver in the experiment (Table 3). Dorrepaal *et al.* (2004) also showed that *Sphagnum* growth in the same experimental plots increased significantly due to summer warming. The non-responsiveness of the peatland cryptogam composition to summer and spring warming and winter snow accumulation might be due to still prevailing initial heterogeneity among plots (Bates *et al.* 2005), short duration of experimental treatments, growth form and growth rate of cryptogam species and natural succession in mires. The four-year time scale of treatment may have been too short to reveal significant responses of the generally long-lived, slow-growing non-vascular cryptogams. Similarly, in a warming and fertilisation experiment in a boreal mire, there were no responses to experimental treatments over four years, whilst both bryophytes and vascular plants were affected over eight years (Wiedermann *et al.* 2007). Cryptogams growing vertically might have experienced an amplified height increment in response to the experimental treatments. However, proliferation of growing points would take longer to be detectable in the horizontal dimension we measured. Furthermore, the small size of most cryptogams can be expected to result in overall lower growth rates in contrast to vascular plants. Finally, peatlands are subject to natural succession (Gunnarsson *et al.* 2002; Malmer *et al.* 2005), which might impose stronger driving forces on vegetation composition compared to experimental treatments.

### **THE IMPORTANCE OF SPATIAL SCALE**

As we expected, each spatial scale contributed its own environmental variation to the microclimate experienced by a given *Sphagnum* bog community, so that differences between two adjacent communities have come about in a consistently different way than

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differences between two distant communities. Despite our efforts to choose sites homogeneous in abiotic factors, the possibility remains that environmental variables other than temperature may have contributed to the overall temperature effect. Differences in salt and N deposition or bedrock geology, although below detection limit, could be influencing vegetation composition. Also, different glacial histories might have influenced re-colonisation, the Caledonian mountain chain in our macrogradient being a possible barrier for spreading plants, shaping plant distribution as we know it today. However, at least the predominant species in our study are of widespread distribution in both Sweden and Norway and, unlike establishment which might be a limiting factor for species distribution, dispersal is unlikely to have put a major biogeographical constraint on present-day vascular plant community composition (cf. Alsos *et al.* 2007).

At the microgradient scale, *Sphagnum* growth depended mainly on microtopography, this factor including moisture and possible species interactions, and, to a lesser extent, on temperature. Correspondingly, Asada *et al.* (2003) reported that growth of *S. fuscum* on hummocks is mainly influenced by precipitation and less by temperature, unless temperatures fall below 0°C. The positive effect of temperature on growth of *S. fuscum* at low temperatures (as opposed to at higher temperatures; see Robroek *et al.* 2007), has been reported from the Subarctic previously (Sonesson *et al.* 2002; Dorrepaal *et al.* 2004). The importance of microtopography and related soil moisture on the performance of *Sphagna* has been shown in various studies (e.g. Pederson 1975; Rydin 1993). Also, studies of species composition (e.g. Kvillner & Sonesson 1980; Bragazza & Gerdol 1996) recognised microtopography and/or related soil moisture/water table level as the most important factor for bryophyte distribution. Climate change-induced temperature increases can, under subarctic conditions, result in increased growth rates of *S. fuscum* if soil moistures are high enough and the peat mosses are in a favourable topographical position.

As shown for the warming experiment, soil moisture and *Sphagnum* growth were also significant determinants of species distribution at the mesogradient scale in Abisko (Table 3). The altitudinal gradient in Abisko comprises the area of present-day *S. fuscum* distribution here. Temperatures can be expected to vary from 0.9 - 2.3 K on the chosen altitudinal gradient of 230 m (0.4-1K per 100m, Körner 1999), well within predicted climate change scenarios for this century (ACIA 2005). This small temperature range is unlikely to have a clear direct impact on species composition. However, temperature-driven growth enhancement of *Sphagnum* may lead to expansion of small *Sphagnum* islands at the border of present peatland distribution if soil moisture is sufficient. Within current peatlands in Abisko, long-term changes in vegetation composition are likely to be

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mainly influenced by hydrology and *Sphagnum* growth which in turn is influenced mainly by microtopography and partly by temperature. Locally, on palsas, temperature-induced permafrost degradation may further influence vegetation composition (Camill 1999; Malmer *et al.* 2005).

At the macrogradient scale, including both the Swedish and Norwegian sites, temperature as an abiotic driver gains significance for species distribution. The 5 K difference in annual mean temperatures between Abisko and Andøya corresponds with the upper end of climate-warming predictions for this century (ACIA 2005). As suggested by our results and previous studies at the climatic macrogradient scale (e.g. Gignac *et al.* 1991; Vitt *et al.* 1995), such a temperature range may well cause changes in cryptogam species composition. Combining the above patterns, we are the first to reveal how the relative contributions of different environmental drivers to cryptogam composition vary with spatial scale.

### THE IMPORTANCE OF FUNCTIONAL SCALE

The various functional classification schemes in this study show that species aggregation affects and even enhances the relationships between environmental drivers and cryptogam composition, up to the major taxa level where lichens, liverworts, mosses and *Sphagna* are distinguished within the cryptogam group (Table 3, Fig. 3). Cryptogam species are often single finds in a specific habitat. Summarising similar growth forms can therefore reveal functional responses of species groups with regard to environmental factors which otherwise would remain hidden. For instance, *Sphagnum* growth in the warming experiment only gains significant explanatory power of cryptogam composition when species are aggregated into growth forms (Table 3). Excluding liverworts from the analysis according to the grouping by Chapin III *et al.* (1996) slightly reduces this power. Since identifying cryptogams is a time-intensive and often difficult task, our suggested minimum requirement for understanding peatland cryptogam composition is the distinction of the easily recognised major taxa: lichens, liverworts, mosses and *Sphagna*.

### SPHAGNUM DRIVES PEATLAND CRYPTOGRAM SPECIES DIVERSITY AND ABUNDANCE

Increasing *Sphagnum* abundance strongly reduces the performance of lichens, liverworts and mosses (Fig. 3). Furthermore, *Sphagnum* growth is a strong driver of cryptogam composition in peatlands (Table 3). Vasander (1981) reported lower growth rates for reindeer lichens than for *Sphagna* (Pakarinen 1978), indicating that lichens can only persist in places where *Sphagnum* ceases growing. The Dry + lichen plots with low

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*Sphagnum* growth rates (Appendix S1.2), likely due to frost disturbance during winter when the hummocks are blown snow-free, confirm this reasoning. Similarly, liverworts can only invade hummocks when *Sphagnum* growth is reduced (Pakarinen 1978; Hugonnot *et al.* 2003). We observed a strong reduction of liverwort abundance in fast-growing *Sphagnum* hollows in Abisko. Mosses, e.g. *Dicranum elongatum*, a typical companion of *S. fuscum* in subarctic mires in the Abisko area, are outcompeted in growth when precipitation increases (Sonesson *et al.* 2002). Accordingly, the highest abundances for non-*Sphagnum* mosses are found in the driest locations (Fig. 3). Negative relations between vascular plants and *Sphagna* (Heijmans *et al.* 2002; Malmer *et al.* 2003) are in our study mainly driven by deciduous and evergreen shrubs compensating for the positive relationship of sedges and vascular cryptogams.

The negative relation of overall Shannon Index and species richness with *Sphagnum* abundance (data see Appendix S1.2) is strongly driven by decreasing cryptogam abundance (Fig. 3). The wetter the plots the fewer cryptogam species are able to compete with *Sphagnum*. In the case of lichens, direct negative effects of substrate moisture are also likely to play a role, since most northern lichens tend to be found in relatively dry (micro-)sites (Robinson *et al.* 1989; Williams & Rastetter 1999). Vascular plant species richness and Shannon Index, however, are unaffected by increasing *Sphagnum* abundance (Fig. 3) as the increasing numbers of sedge species compensate for the decreasing numbers of shrub species in wetter plots. The importance of microtopography for species richness of mosses and liverworts has also been found in swamp forests, where vascular plants were hardly affected by relief either (Økland *et al.* 2008). Thus, in subarctic regions a warmer and wetter climate might locally, depending on microtopography, trigger *Sphagnum*-mediated declines in species diversity. Permafrost thaw and intense rain events, however, may lead to an increase in surface cover of wet graminoid dominated vegetation (Christensen *et al.* 2004) and open water bodies, so that an altogether different vegetation pattern can be expected.

### Conclusions

The relative contributions of different climatic (temperature, hydrology) and biotic (*Sphagnum* growth) determinants of peatland vegetation composition in the European Subarctic strongly depend on the scale at which a study is conducted. Soil moisture and *Sphagnum* growth operate as determinants at all spatial scales, whereas temperature only discriminates in a cross-regional comparison. Responses of *Sphagnum* growth or abundance in turn impact strongly on cryptogam diversity and species richness. Peatland cryptogam responses to field manipulations of climate are too slow to reveal substantial

shifts in species composition in short-term (4-yr) experiments. Aggregating species groups at various functional scales helps to summarize the driving forces of cryptogam and vascular plant composition in *Sphagnum*-dominated peatlands. Combining responses and variation of species composition at different temporal, spatial and functional scales will turn out to be most helpful for extrapolating vegetation responses to climate change from the plot to the landscape or regional scale.

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### Appendix S1. Site descriptives, environmental variables and abundance measurements

#### 1.1. Site descriptives

Site	Experiment	Abisko 1	Abisko 2	Abisko 3
Altitude [m a.s.l.]	340	370	400	480
Latitude	68°21'N	68°21'N	68°20'N	68°20'N
Longitude	18°49'E	18°48'E	18°48'E	18°49'E
Site	Abisko 4	Abisko 5	Annamo	Andøya
Altitude [m a.s.l.]	520	600	150	40
Latitude	68°20'N	68°19'N	68°32'N	69°07'N
Longitude	18°50'E	18°51'E	17°13'E	15°52'E

## Northern peatland cryptogam composition and scale

1.2. Mean (SE) of independent, dependent variables and abundance measures along the microgradient and warming experiment. Treatment codes see Table 1 (main manuscript). Measurement of samples at detection limit: d.l.

	Dry + lichen	Dry	Medium	Wet
<b>Explanatory variables</b>				
pH	2.84 (0.03)	2.85 (0.02)	3.02 (0.08)	3.17 (0.11)
Ca [mg/l]	58.18 (16.42)	39.60 (13.09)	53.49 (16.13)	64.71 (14.82)
Mg [mg/l]	27.75 (4.70)	17.94 (3.04)	25.87 (4.82)	35.64 (9.81)
NH4-N [mg/core]	0.0483 (0.0098)	0.0422 (0.0077)	0.0406 (0.0062)	0.0473 (0.0047)
NH4-N [ $\mu$ g/l]	d.l.	d.l.	d.l.	d.l.
NO3-N [mg/core]	0.0012 (0.0005)	0.0010 (0.0002)	0.0014 (0.0004)	0.0013 (0.0002)
NO3-N [ $\mu$ g/l]	d.l.	d.l.	d.l.	d.l.
PO43-P [mg/core]	0.0925 (0.0332)	0.0409 (0.0261)	0.1172 (0.0303)	0.0583 (0.0218)
PO43-P [ $\mu$ g/l]	85.61 (38.16)	90.21 (50.36)	65.08 (29.86)	254.23 (127.40)
Moisture [vol-%]	56.38 (4.47)	52.55 (4.78)	68.89 (5.00)	90.65 (2.35)
Degree days (sum of 2 years)	2112.64 (102.06)	2112.64 (102.06)	2112.64 (102.06)	2112.64 (102.06)
<i>Sphagnum</i> growth [cm]	0.50 (0.10)	0.65 (0.09)	0.98 (0.15)	0.99 (0.13)
<b>Abundance</b>				
<i>Sphagna</i>	179.29 (20.55)	245.00 (6.17)	255.29 (5.81)	267.43 (1.11)
Prostrate mosses	3.57 (3.57)	0.29 (0.29)	3.71 (2.10)	7.86 (3.28)
Erect mosses	25.29 (11.84)	7.43 (3.83)	3.43 (1.82)	2.57 (1.43)
Prostrate liverworts	13.29 (6.76)	2.57 (0.75)	1.29 (0.36)	1.14 (0.55)
Erect liverworts	18.29 (3.64)	15.71 (4.89)	11.86 (4.22)	1.14 (0.99)
Prostrate lichens	0.14 (0.14)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Erect lichens	20.00 (10.63)	0.29 (0.29)	0.14 (0.14)	0.00 (0.00)
Crust-forming lichens	29.14 (8.66)	0.14 (0.14)	0.00 (0.00)	0.00 (0.00)
Deciduous shrubs	7.71 (3.88)	15.94 (6.10)	10.29 (6.19)	5.91 (3.51)
Evergreen shrubs	101.57 (13.88)	118.29 (15.28)	72.26 (10.25)	38.57 (8.67)
Grasses	0.00 (0.00)	0.00 (0.00)	0.51 (0.33)	0.00 (0.00)
Sedges	1.80 (0.96)	1.29 (1.02)	5.40 (2.04)	20.83 (3.24)
Forbs	36.77 (6.52)	20.83 (4.86)	28.29 (6.67)	7.97 (2.00)
Vascular cryptogams	0.00 (0.00)	0.00 (0.00)	0.51 (0.51)	1.03 (1.03)
<b>Diversity<sub>overall</sub></b>				
Species richness	16 (1)	12 (1)	11 (1)	12 (1)
Shannon Index	1.86 (0.13)	1.41 (0.09)	1.27 (0.10)	1.73 (0.06)

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1.2. continued

	AAA	WAA	WSA	WSW
<b>Explanatory variables</b>				
pH	2.89 (0.03)	2.87 (0.05)	2.89 (0.06)	2.88 (0.09)
Ca [mg/l]	17.43 (2.87)	16.19 (6.78)	22.32 (7.29)	25.29 (8.96)
Mg [mg/l]	16.77 (1.98)	14.88 (4.39)	21.23 (5.51)	21.56 (6.22)
NH4-N [mg/core]	0.0293 (0.0025)	0.0312 (0.0032)	0.0296 (0.0038)	0.0306 (0.0047)
NH4-N [ $\mu$ g/l]	d.l.	d.l.	d.l.	d.l.
NO3-N [mg/core]	0.0012 (0.0002)	0.0010 (0.0005)	0.0011 (0.0002)	0.0007 (0.0002)
NO3-N [ $\mu$ g/l]	d.l.	d.l.	d.l.	d.l.
PO43-P [mg/core]	0.0555 (0.0337)	0.1228 (0.0574)	0.1068 (0.0334)	0.1559 (0.0920)
PO43-P [ $\mu$ g/l]	132.50	132.50	3.38	106.68
Moisture [vol-%]	39.18 (2.21)	30.22 (3.37)	33.02 (3.19)	34.95 (1.62)
Degree days (sum of 2 years)	1754.67	1799.19	1819.85	1872.19
<i>Sphagnum</i> growth [cm]	0.56 (0.12)	0.77 (0.25)	0.91 (0.06)	0.99 (0.10)
<b>Abundance</b>				
<i>Sphagna</i>	204.60 (29.06)	197.80 (30.80)	233.20 (8.53)	248.80 (10.35)
Prostrate mosses	1.00 (0.63)	0.60 (0.40)	0.00 (0.00)	1.40 (0.93)
Erect mosses	52.20 (20.03)	13.00 (10.09)	13.20 (8.06)	10.80 (6.91)
Prostrate liverworts	30.40 (19.23)	22.80 (12.79)	7.40 (3.33)	11.20 (5.86)
Erect liverworts	9.20 (2.33)	18.80 (8.79)	19.00 (8.26)	5.80 (0.58)
Prostrate lichens	0.60 (0.40)	0.20 (0.20)	0.60 (0.60)	0.60 (0.60)
Erect lichens	19.80 (10.84)	16.60 (9.47)	6.00 (4.79)	6.20 (4.34)
Crust-forming lichens	1.40 (1.40)	0.80 (0.80)	0.00 (0.00)	0.20 (0.20)
Deciduous shrubs	34.20 (12.88)	30.24 (9.48)	19.80 (7.76)	23.40 (10.09)
Evergreen shrubs	192.60 (15.52)	170.64 (27.31)	164.88 (19.77)	148.32 (20.18)
Grasses	1.44 (1.05)	5.76 (2.51)	4.68 (0.72)	3.96 (1.84)
Sedges	3.60 (3.17)	0.36 (0.36)	0.36 (0.36)	3.24 (1.19)
Forbs	31.32 (6.80)	34.92 (6.82)	34.92 (7.30)	31.68 (3.72)
Vascular cryptogams	0.00 (0.00)	1.08 (1.08)	0.36 (0.36)	0.00 (0.00)
<b>Diversity<sub>overall</sub></b>				
Species richness	17 (3)	16 (2)	15 (2)	15 (2)
Shannon Index	1.91 (0.20)	1.88 (0.21)	1.68 (0.12)	1.58 (0.16)



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Appendix S2. Division of species into growth forms (cryptogams) and functional groups (vascular plants)

Growth form	Species	Growth form	Species
<i>Sphagna</i>	<i>Sphagnum angustifolium</i>	Prostrate liverworts	<i>Lophozia binsteadii</i>
	<i>Sphagnum balticum</i>		<i>Lophozia ventricosa</i>
	<i>Sphagnum fallax</i>		<i>Ptilidium ciliare</i>
	<i>Sphagnum fuscum</i>	Erect liverworts	<i>Riccardia latifrons</i>
	<i>Sphagnum lindbergii</i>		<i>Mylia anomala</i>
	<i>Sphagnum magellanicum</i>	Prostrate lichens	<i>Alectoria nigricans</i>
	<i>Sphagnum nemoreum</i>		<i>Cetraria aculeata</i>
	<i>Sphagnum papillosum</i>	Erect lichens	<i>Flavocetraria nivalis</i>
	<i>Sphagnum riparium</i>		<i>Cetraria islandica</i>
	<i>Sphagnum russowii</i>		<i>Cladonia arbuscula</i> ssp. <i>arbuscula</i>
<i>Sphagnum subnitens</i>	<i>Cladonia arbuscula</i> ssp. <i>mitis</i>		
<i>Sphagnum subsecundum</i>	<i>Cladonia</i> cf. <i>amaurocraea</i>		
<i>Sphagnum warnstorffii</i>	<i>Cladonia</i> cf. <i>maxima</i>		
Prostrate mosses	<i>Hylocomium splendens</i>		<i>Cladonia gracilis</i>
	<i>Pleurozium schreberi</i>		<i>Cladonia squamosa</i>
	<i>Loeskygnum badium</i>		<i>Cladonia stygia</i>
	<i>Warnstorfia fluitans</i>		<i>Cladonia uncialis</i>
	<i>Scorpidium scorpioides</i>		<i>Flavocetraria cucullata</i>
	<i>Straminergon stramineum</i>		<i>Sphaerophorus globosus</i>
Erect mosses	<i>Aulacomnium turgidum</i>	Crust-forming lichens	<i>Cladonia borealis</i> or <i>C. pleurota</i>
	<i>Dicranum fuscescens</i> (incl. <i>Dicranum flexicaule</i> )		<i>Cladonia</i> sp.
	<i>Dicranum elongatum</i>		<i>Cladonia sulphurina</i>
	<i>Dicranum groenlandicum</i>		<i>Icmadophila ericetorum</i>
	<i>Dicranum leioneuron</i>	Deciduous shrubs	<i>Ochrolechia frigida</i>
	<i>Pohlia nutans</i>		<i>Betula nana</i>
	<i>Polytrichum strictum</i>		<i>Vaccinium myrtillus</i>
<i>Racomitrium lanuginosum</i>	Evergreen	<i>Vaccinium uliginosum</i>	
Prostrate liverworts	<i>Anastrophyllum minutum</i>	shrubs	<i>Andromeda polifolia</i>
	<i>Calypogeia sphagnicola</i>		<i>Calluna vulgaris</i>
	<i>Cephalozia bicuspidata</i>		<i>Empetrum nigrum</i> ssp. <i>hermaphroditum</i>
	<i>Cephalozia leucantha</i>		<i>Vaccinium microcarpum</i>
	<i>Cephalozia loitlesbergeri</i>		<i>Vaccinium vitis-idea</i>
	<i>Cephalozia lunulifolia</i>	Grasses	<i>Calamagrostis lapponica</i>
	<i>Cladopodiella fluitans</i>	Sedges	<i>Carex canescens</i>
	<i>Kurzia pauciflora</i> or <i>K.</i> <i>trichoclados</i>		<i>Carex chordorrhiza</i>
	<i>Lophozia atlantica</i>		<i>Carex lasiocarpa</i>
			<i>Carex limosa</i>

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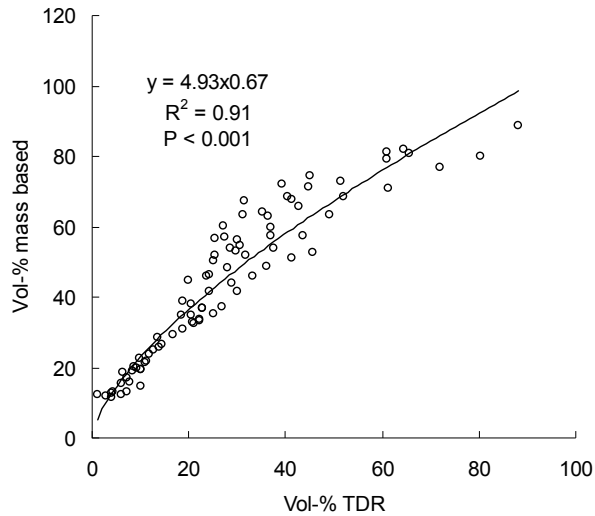
continued

Growth form	Species	Growth form	Species
Sedges	<i>Carex magellanica</i> ssp. <i>irrigua</i>	Forbs	<i>Comarum palustre</i>
	<i>Carex rostrata</i>		<i>Drosera rotundifolia</i>
	<i>Carex rotundata</i>		<i>Pinguicula villosa</i>
	<i>Eriophorum angustifolium</i>	Vascular cryptogams	<i>Rubus chamaemorus</i>
	ssp. <i>angustifolium</i>		<i>Equisetum arvense</i> s.l.
	<i>Eriophorum vaginatum</i>		
	<i>Trichophorum cespitosum</i> ssp. <i>cespitosum</i>		

**Appendix S3. Measurement and relations of soil moisture and water table level**

**3.1 Calibration of the Time Domain Reflectometry (TDR) soil moisture meter**

For calibrating the TDR soil moisture meter *Sphagnum fuscum* and *Sphagnum riparium* peat of different densities was collected from peatlands in the Abisko area in 2005 and 2006 and transferred into a bucket of known volume. The peat was saturated with water, where-after soil moisture and weight were measured weekly until the peat had completely dried out. The peat was dried at 105°C. With known volume, weight and an assumed density of water of 1g/cm<sup>3</sup>, the mass based volume-% could be calculated for each point of the calibration (Fig S1).



**Fig. S1.** Calibration: TDR versus mass based measurements of soil moisture (n = 85).

### 3.2 Measurement of water table level and its relationship to soil moisture

Water table level and soil moisture were recorded simultaneously at each plot. Water-permeable plastic pipes were inserted 40-50cm into the ground in October to guarantee a maximum depth of unfrozen ground. For measuring the water table level a self-made device was used. One wire was connected to the ground, the other attached to a ruler being inserted into the pipe. When touching the water table in the pipe the electric circuit was closed, whereby a beeping sound was produced. The water table level could be calculated as a subtraction of outer distance of the pipe above ground level minus inner distance to water table level.

The water table level in the experiment proved to be too low to be measurable. Thus we tried to predict water table level from soil moisture measurements. Where soil moisture and water table level were measured simultaneously they were included in a dataset to plot soil moisture against water table level. This relationship proved to be significant (Fig S2).

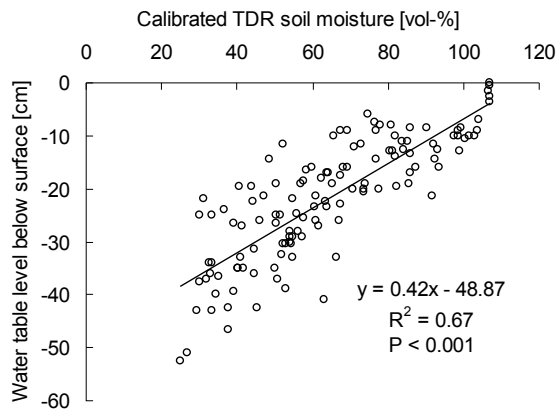
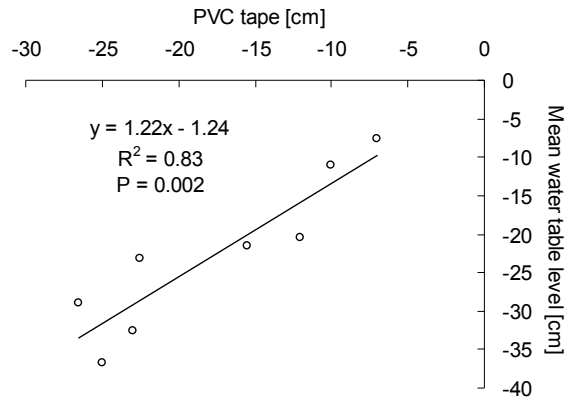


Fig. S2. Relationship water table level – calibrated soil moisture (n = 126).

At the more remote sites in Norway water table level measurements could not be conducted on a regular basis, therefore depth of water table level was mainly measured passively following a modified method developed by Belyea (1999). Plastic sticks onto which PVC tape was attached were put into the ground in October 2005 when the ground was unfrozen and retrieved in the following year in October 2006. The humic acids of the peat water stain the PVC tape at water table level where conditions are anoxic. Often the border between heavily stained and non-stained tape consists of a less stained and spotted zone according to changes in water table depth. This distance was measured with a ruler and the middle point taken as average water table level for one year. PVC tape measurements were in good accordance with water table measured manually during the rest of the year (Fig S3).

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**Fig. S3.** Relationship of manually measured versus passively measured water table level.

Since calibrated soil moisture is related to water table (Fig S2) and, furthermore, manually and passively measured water table levels are correlated (Fig S3) we assumed that even if measurements of soil moisture could not be conducted at all sites simultaneously, it is valid to take a mean of soil moistures as an estimate of water relations in these peatlands.

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