Dominant bryophyte control over high-latitude soil temperature fluctuations predicted by heat transfer traits, field moisture regime and laws of thermal insulation

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Summary

1. Bryophytes cover large territories in cold biomes, where they control soil temperature regime, and therefore permafrost, carbon and nutrient dynamics. The mechanisms of this control remain unclear.

2. We quantified the dependence of soil temperature fluctuations under bryophyte mats on the interplay of bryophyte heat conductance traits, mat thickness, density and moisture regimes.

3. For seventeen predominant bryophytes in six typical subarctic ecosystems, we assessed in situ soil temperature dynamics under bryophyte mats in comparison with bryophyte-removal patches and per-species mat field moisture. In a complimentary laboratory investigation, we studied how per-species bryophyte thermal conductivity and volumetric heat capacity depend on mat density and moisture content. Subsequently, we tested whether heat transfer through bryophyte mats could be modelled as a function of mat thickness, thermal conductivity and volumetric heat capacity, the latter two being determined by mat density and field moisture content.

4. Laboratory assessment revealed that bryophyte thermal conductivity and volumetric heat capacity were independent of mat density, and depended linearly on mat moisture content, but the dependencies were not species-specific. In the field, bryophytes reduced amplitudes of soil temperature fluctuations and freeze–thaw frequency during the growing season, but not mean soil temperature. These effects differed between species and between ecosystems, being strongest in *Sphagnum fuscum*-dominated dry tundra, but were well explained by bryophyte mat thickness and field moisture content as affecting thermal conductivity and volumetric heat capacity.

5. We suggest that reduction in soil temperature amplitudes is a generic feature in (sub) arctic ecosystems and should be considered as an important mechanism of bryophyte control on carbon and nutrient turnover. Although heat transfer through bryophyte mats differs greatly among species and ecosystems, species differences are fully explained by differences in mat thickness and moisture content and generally comply with physical laws, without deviations due to biological processes. These results imply that in global vegetation models of carbon and nutrient cycling, the heat transfer through bryophyte mats can be modelled without taking into consideration bryophyte species composition, but considering bryophyte mat depth and moisture availability only. This will allow us to enhance modelling precision through an improved representation of the soil temperature regime.

Key-words: freeze–thaw regime, moss, plant–soil (below-ground) interactions, soil temperature amplitude, thermal conductivity, thermal diffusivity, thermal insulation, subarctic, tundra, volumetric heat capacity

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Introduction

In cold biomes, soil temperature controls most biological processes, including carbon and nutrient turnover. The functioning of bacteria, fungi and vascular plants is limited by low soil temperatures (Lloyd & Taylor 1994; Chapin *et al.* 1995; Wallenstein, McMahon & Schimel 2009) and depends on temperature alterations, including the frequency of freeze–thaw events (Deluca, Keeney & McCarty 1992; Yergeau & Kowalchuk 2008; Graae *et al.* 2009; Jefferies *et al.* 2010). Activity and survival of soil animals at high latitudes are also largely regulated by soil temperature (Coulson *et al.* 1995; Hodkinson *et al.* 1996; Sjursen, Michelsen & Holmstrup 2005).

Soil temperature regime, in turn, is controlled by climate but can also be strongly affected by plant cover. Cushion-forming vascular plants were shown to reduce diurnal temperature fluctuations at high altitudes and facilitate establishment and survival of vascular plants growing within such cushions (Cavieres *et al.* 2007; Kleier & Rundel 2009). Also bryophyte mats are known to alter soil temperature (Van der Wal & Brooker 2004; Gornall *et al.* 2007; Loffler, Cypionka & Loffler 2008; Cannone & Guglielmin 2009; Blok *et al.* 2011), thereby controlling key ecosystem functions. Bryophytes constitute a large fraction of biomass and cover vast areas in cold biomes (Sonesson & Bergman 1980; Longton 1997; Bates 2000). Permafrost depth depends directly on the thickness of the bryophyte layer (Dyrness 1982; Bonan 1991; Guglielmin, Evans & Cannone 2008). Gornall *et al.* (2007) demonstrated, in a moss transplantation experiment, that, due to altered temperature regime, the levels of soil microbial biomass and activity, and the level of plant available nitrogen under shallow moss layers were higher compared to a deep moss layer.

Understanding the mechanisms of bryophyte control over soil temperature regimes is a prerequisite for predicting future changes in soil temperature and associated soil carbon and nutrient turnover in polar regions. Previous studies on the impacts of the bryophyte layer as regulator of soil temperature regime (Bonan & Shugart 1989; Gornall *et al.* 2007; Cannone & Guglielmin 2009; Yi *et al.* 2009) treated bryophyte mats as a uniform substance and did not consider differences among bryophyte species.

In this study, we assess experimentally how the presence of bryophytes affects soil temperature regime in subarctic ecosystems, focusing on differences between species and between ecosystems. Soil temperature regimes under bryophyte mats are a function of habitat light availability, albedo and heat transfer through the bryophytes. Habitat light availability cannot be modulated by the presence–absence of bryophytes, while the latter processes can. Therefore, in order to mechanistically predict the effects of bryophytes on soil temperature alterations, one should quantify species albedo as well as the mechanisms of heat transfer through bryophyte mats. While albedo values are detectable via remote sensing (e.g. Stoy *et al.* 2012), the processes of heat transfer through bryophyte mats need to be modelled by taking in account bryophyte traits such as mat thickness, thermal conductivity and volumetric heat capacity (Koorevaar, Menelik & Dirksen 1983; for details see the Methods section) but also the potential effects of respiration that might cool bryophyte mats. Here, we aim to unravel whether the heat transfer through bryophyte mats varies among bryophyte species, and among ecosystems, and if so, which bryophyte traits and what mechanisms underpin such variation. The few prior studies conducted on feather mosses only suggested that thermal conductivity of bryophyte mats increases with moisture content (Sharratt 1997; O'Donnell *et al.* 2009) and mat bulk density (Bonan 1991), in ways similar to that of organic soil (Andersland & Anderson 1978; Fauroki 1981). These studies, however, were limited to a few bryophyte species and do not indicate how general or species-specific the reported dependencies may be. Moreover, they considered thermal conductivity only, ignoring the second important constituent of heat transfer, volumetric heat capacity, which to our knowledge has never been investigated for bryophytes. In order to properly understand heat transfer processes from air to soil via bryophyte mats and to incorporate these into current carbon and nutrient turnover models as reviewed by Manzoni & Porporato (2009), we need to quantify both parameters, and clearly understand their dependence on bryophyte mat moisture, density and thickness.

In this study, we aim to answer the following questions:
1. how does the presence of bryophytes affect soil temperature regime under natural field conditions? We hypothesize that (a) bryophyte mats reduce soil temperature, the amplitude of temperature fluctuations and the frequency of freeze–thaw events, (b) the effects differ among individual species and (c) the level of decrease in amplitude of temperature fluctuations under a bryophyte mat differs among ecosystems.
2. which bryophyte traits underpin mechanisms of heat transfer through bryophyte mats? We hypothesized that: (a) thermal conductivity and volumetric heat capacity of a bryophyte mat can be mechanistically and consistently predicted by mat moisture content and mat density; and (b) the reduction in soil temperature amplitude under bryophyte mats, in comparison with open soil patches, is determined by bryophyte mat thickness and thermal diffusivity (being the ratio of thermal conductivity and volumetric heat capacity), while the influence of biological processes like respiration, decomposition and photosynthesis is negligible.

Materials and methods

DATA COLLECTION

Study location and species

The research was conducted in the Abisko area, North Sweden (68°21′N, 18°49′E), about 200 km north of the Arctic Circle, during 2006–2010. We investigated the effects on soil temperature

of 17 bryophyte species: three liverworts and 14 mosses, predominant in six representative subarctic ecosystems (see Supporting Information Table S1 for details). For each bryophyte species, we sampled 3–10 unique sites situated at least 100 m or further from each other where the bryophytes formed mono-specific mats. In these sites, we measured soil temperature, bryophyte mat moisture and collected bryophyte material for measurements of thermal conductivity, volumetric heat capacity, bryophyte mat density and mat thickness and for calibration of moisture sensors. In all sites, soils were organic. While selecting sites, we chose the most typical ecosystem for each species according to Märtensson (1955) and Nyholm (1998), with the exception of *Ptilidium ciliare*, for which we had sites both in alpine meadow and *Sphagnum fuscum*-dominated dry tundra.

Field sampling and measurements

At every site, we selected an intact bryophyte mat where, based on visual estimation, more than 90% of biomass belongs to the same species of at least 100×50 cm. In one half of this mat, we removed the living bryophyte canopy, creating an open soil area of 50×50 cm. The second half of the bryophyte mat, we left intact. Subsequently, at every site, we installed two iButton temperature sensors (1-wire Thermochron, Dallas semiconductors, San Jose, CA, US, accuracy 0·5 °C), one under the intact bryophyte mat and another one into the adjusted open soil patch. The sensors were installed into the same soil layer: in intact bryophyte patches the sensors were installed at $1·5 \pm 0·5$ cm below the living bryophyte mat and in the top $1·5 \pm 0·5$ cm of soil in the open patches. The pairs of sensors were programed to take simultaneous measurements every 4 h. We took such temperature measurements during the periods of mid June 2006–mid June 2007, September 2006–July 2007, October 2007–September 2008, May–September 2008 and June–September 2010. For every new measurement series, new sites were established in order to randomize site effects. Despite loss of or damage to a few sensors, giving differences in the total number of species and per-species replication among the measurement series (Supporting Information Table S1), we generally obtained sufficient replication of measurement series covering the growing season, and for most species, covering the nongrowing season as well.

Measuring temperature once in 4 h with accuracy of 0·5 °C might underestimate the number of freeze–thaw events in case of frequent temperature fluctuations around zero. To check whether and how this could affect the freeze–thaw data, we conducted year-long series of coupled measurements, taking temperature measurements simultaneously 4 hourly by iButton temperature sensors, and by Tinytag Plus temperature sensors (Gemini dataloggers Ltd, Chichester, UK) every minute, recording a min, max and mean temperature every hour with a precision of 0·01 °C. These measurements were conducted from October 2007 to September 2008 in *S. fuscum* and *Tomentypnum nitens* mats and open soil patches. For each species, two mat–open soil pairs were assessed. In a two-way ANOVA with sensor types and species as independent variables, we found that freeze–thaw frequencies did not differ among sensor types; thus, justifying the use of iButton sensors for freeze–thaw data sampling.

In mats of eight bryophyte species, we took hourly field measurements of moisture content with ECH$_2$O EC-5 moisture sensors (Decagon, Hopkins Ct. Pullman, WA, USA, accuracy ± 5%) in August–September 2006 (six species) and June–September 2010 (other two species). The sensors were placed at the median depth of the bryophyte mats in order to minimize the effects of moisture variation along the depth profile of a bryophyte mat. The species names, periods of measurements and replication are shown in the Supporting Information Table S1. We calibrated the sensor data individually for each bryophyte species, using 5–18 bryophyte patches per species and 8–30 measurements per patch (for details see below).

Laboratory measurements of bryophyte heat transfer traits and calibration of field moisture sensors

Heat transfer through a substance is governed by its thermal diffusivity, being the ratio of thermal conductivity and volumetric heat capacity. Thermal conductivity is the quantity of energy transmitted by conduction through a unit of thickness of a material per unit time due to a temperature difference of 1 K between the surfaces of the material. Volumetric heat capacity characterizes the ability of a material to store heat while undergoing a temperature change without undergoing a phase change and is defined as change of heat content by a volume unit of material, divided by the temperature change (Halliday, Resnick & Walker 1997).

To examine how the thermal conductivity and volumetric heat capacity of bryophyte mats depend on mat moisture content, we took for each species 5–18 mat samples of at least 20×20 cm. We cut-off the presumably mostly dead, brown part of the mat with a razor and from the remaining green part cut cylinders of 10 cm in diameter in the top-to-bottom direction. We put the cylinders into open cylindrical plastic containers (diameter = 10 cm, height = 12 cm) keeping the cushion structure intact and minimizing cushion density alterations. For species where the mat was too shallow to allow complete placement of a sensor inside (i.e. *Lophozia lycopodioides*, *Oncophorus wahlenbergii*, *P. ciliare* and *Tetralophozia setiformis*), we prepared two or three cylinders from each mat sample and placed them on top of each other.

We poured water into the containers until the bryophyte samples became fully saturated. Containers had holes in the bottom and were placed on a grid, so that the excess water could drain freely. We kept containers at 12 °C allowing the bryophyte samples to dry slowly. The drying period until air-dry took 4–8 days for most species with the exception of *S. fuscum*, which took three weeks. In order to distribute the water evenly inside cushions, we turned the samples upside down and pressed them every 12 h, gently moving the moisture from the bottom and centre of the sample to the faster drying edges. Every 12 h, we weighed the samples and measured moisture content with ECH$_2$O EC-5 moisture sensors (in order to obtain per-species calibration rules for these sensors), and thermal conductivity and volumetric heat capacity with a KD2 Pro thermal properties analyzer (Decagon, accuracy ±10%). The KD2 Pro sensor conducts three phase measurement cycles that consist of 30 s equilibrium time, 30 s heating time and 30 s cooling time. Every second during heating and cooling, the sensor takes temperature measurements that are subsequently fit into an integral function of heat transfer being dependent on thermal conductivity and volumetric heat capacity.

Once the samples were air-dry, we dried them in the oven at 70 °C for 48 h, as recommended by the Decagon moisture sensors calibration manual (Cobos & Chambers 2009), and weighed them. We subtracted the oven-dry weight from the weight of a drying sample to calculate the mass of moisture at each time we had measured thermal conductivity and volumetric heat capacity. Prior to drying, we had measured the height of the bryophyte mat in each container and calculated the volume occupied by each bryophyte sample. Based on volume and moisture mass data, we postcalculated the volumetric moisture contents of samples.

We derived species-specific calibration curves for the ECH$_2$O EC-5 moisture sensors via simple regression using per-species data of sensor raw measurements as a predictor variable and respective volumetric moisture contents as a response variable (all $R^2 > 0·75$).

Measurements of bryophyte cushion morphology

For thickness and density measurements of bryophyte mats, we considered green and fresh (i.e. undecomposed) brown parts of bryophytes to be part of a mat. We measured the thickness of the bryophyte mats in the field with a ruler at four random places upon the removal of the mats from the soil. As these measurements showed that within the same species there was little variability between samples (SE ≤15% of mean value, Supporting Information Table S2), we used average mat thickness per species in further analysis. We measured bryophyte density of each sample studied in the laboratory analysis as dry mass divided by volume.

DATA ANALYSIS

All statistical analyses were conducted using R2.13 and R2.14, Foundation for Statistical Computing, Vienna, Austria.

Bryophyte effects on soil temperature regime

Complicated logistics of temperature measurements and loss of some sensors resulted in multiple sampling gaps. Not all species were measured over exactly the same time period with sufficient replication (see Supporting Information Table S1). Therefore, we restricted our analysis to examining data averaged over time periods. Detailed statistical considerations, which lead to the data analysis described below, are outlined in the Supporting Information Appendix S1.

For each replicate of each measurement series, we calculated averaged values of soil temperature, daily temperature amplitudes and total number of freeze–thaw events (i.e. number of intercepts of 0 °C divided by 2) over all months of the growing season, and the nongrowing season. We have defined the growing season as the core snow-free period, that is, the period starting at least a week after snow melt and finishing at least a week before establishment of stable snow cover (May–September for lowlands, June–September for alpine zones, August–middle September for snow beds). For each of the above described variables, we conducted separate repeated measures ANOVAs for the growing season and nongrowing season with bryophyte species identity as between-subject fixed factor, the presence or absence of a bryophyte mat as within-subject (repeated measures) factor.

For the analysis of the number of freeze–thaw events, the data were log-transformed due to deviations from normality. Furthermore, from this analysis, we excluded the data series of 2010, in which no data were collected in May, when many freeze–thaw events took place. Due to this, we excluded *Rhytidium rugosum* and *O. wahlenbergii* from this analysis, because for these species not enough data were collected in May. For consistency and following the procedure by Yergeau & Kowalchuk (2008) for similar type of measurements, we considered freezing temperature to be 0 °C for all soils below bryophyte mats. In reality, the values for soil freezing temperature may differ among bryophyte species.

We tested whether the impacts of bryophytes on soil temperature regime vary among ecosystems by subjecting the ratio of (growing season averaged) temperature amplitude under bryophyte to the corresponding amplitude in open soil to an ANOVA with species nested within ecosystem type. We used type I sum of squares, species as random factor and ecosystem type as fixed factor. After we detected the significance of ecosystem type, we ran a one-way ANOVA with ecosystem type as independent variable using per-species averages of temperature amplitude ratios as replicates, followed by Tukey post hoc test. We excluded the high altitude rock outcrops and snow bed ecosystems from the analyses because they are represented in our study by only a single species, *Racomitrium lanuginosum* and *Polytrichastrum sexangulare*, respectively.

How do bryophyte mat thermal conductivity and volumetric heat capacity depend on mat moisture content and mat density?

We analysed the dependencies of thermal conductivity and volumetric heat capacity on the mat moisture content and mat density using laboratory-measured data with corresponding measurements within a single bryophyte mat. First, we ran mixed model regression analyses, with the maximum likelihood (ML) method, using thermal conductivity and volumetric heat capacity as response variables, respectively, and bryophyte mat moisture content and density nested within species as independent predictors. We considered the thermal properties of bryophyte mats to be analogous to those of organic soils, for which the dependence of thermal conductivity on volumetric moisture content is known to have sigmoid shape and the dependence of volumetric heat capacity on moisture content to be linear (Andersland & Anderson 1978; Koorevaar, Menelik & Dirksen 1983). Therefore, in this and the following analyses, we modelled thermal conductivity as a fourth-order polynomial of moisture content and volumetric heat capacity as a linear function of moisture content.

We estimated the relative importance of each regression parameter by calculating η^2 as the sum of squares associated with the parameter divided by total sum of squares of the model; the residual sum of squares of the model being associated with species instead of individual observations (i.e., d.f. = 16). In our range of bryophyte mat densities, species mat density was significant neither for thermal conductivity nor for volumetric heat capacity (for details see Results). This allowed us to exclude mat density from the subsequent analyses.

Maximum likelihood methods do not yield a measure of variance explained by the model. To estimate amount of the variance explained by the model, we calculated a ratio of the variance among species explained by the model including fixed effect(s) of volumetric moisture content (and its second, third and fourth power in case of thermal conductivity model) to a 'null' model including only random effect of species, but no fixed effects. Subtracting this ratio from 1, we obtained the fraction of variance associated with volumetric moisture content.

To test whether the dependence of thermal conductivity and volumetric heat capacity on mat moisture depended on species identity, we ran regression analyses for these thermal properties with mat moisture content, bryophyte species identity coded as dummy variables and their interactions as independent predictors. Such method allows testing individual regressions for each species while simultaneously testing whether the confidence intervals for regression slopes overlap (i.e. regression lines are parallel among the species). Overlapping confidence intervals of regression slopes indicate the absence of interaction between the species identity and mat moisture, that is, that the dependence of bryophyte mat thermal conductivity and volumetric heat capacity on moisture is not species-specific, but generic. For calculation details see Quinn & Keough (2002) and Dalgaard (2008).

Can decrease in temperature amplitude under a bryophyte mat be predicted by bryophyte mat thickness and thermal diffusivity?

Based on laws of physics, one would expect that the reduction in soil temperature amplitude under bryophyte mats, in comparison with open soil patches, is determined by bryophyte mat thickness, and thermal diffusivity, the latter being the ratio of

thermal conductivity and volumetric heat capacity only. However, because bryophytes additionally possess active respiration mechanisms, bryophyte mats might cool down faster than open organic soil subsurface. To analyse whether such biological processes affect heat transfer through bryophyte mats, we investigated how well diurnal temperature fluctuations under bryophyte mats could be predicted following purely physical laws.

For this analysis, we used only the site-species combinations where the mat moisture content was measured in the field simultaneously with the series of soil temperature (see Supporting Information Table S1). For each species and each site, we calculated a time series of ratios of the daily temperature amplitude under a bryophyte mat to the daily temperature amplitude on the respective open soil patch and calculated daily averages of mat moisture content per species. From physics, it is known that if temperature changes on the surface of a material have a sinusoidal character, the amplitude of the fluctuations in the inner layers decreases with depth. In case of soil being warmed by the sun at day and releasing energy at night the decrease in soil temperature can thus be calculated as:

$$A = A_0 * \exp(-c * s/\sqrt{d}) \qquad \text{eqn 1}$$

where A is the temperature amplitude at depth s, A_0 is the temperature amplitude at the soil surface, d is soil thermal diffusivity and c is a constant depending on fluctuation frequency, equalling $0.36 \ h^{-1/2}$ for a 24-h cycle (Koorevaar, Menelik & Dirksen 1983). This formula is obtained as an analytical solution for a differential equation, describing one-dimensional sensible heat transfer in a material at constant average air temperature, with thermal diffusivity being independent of depth (Koorevaar, Menelik & Dirksen 1983). We outline the consideration about applicability of this formula in our analysis in the Supporting Information Appendix S2.

We calculated the respective species-specific series of daily thermal diffusivity, as the ratio of thermal conductivity to volumetric heat capacity (Koorevaar, Menelik & Dirksen 1983), using the laboratory data for dependencies of bryophyte thermal conductivity and volumetric heat capacity on moisture content. Subsequently, we modelled the ratio of the temperature amplitude under bryophyte mat to the temperature amplitude on open soil patches as a function of bryophyte mat thickness and thermal diffusivity following the eqn 1 modified as:

$$A_b/A_s = \exp(-c * s/\sqrt{d}) \qquad \text{eqn 2}$$

Where A_b is the temperature under the bryophyte mat, A_s is the temperature on open soil, s is the bryophyte mat depth, d is the thermal diffusivity of bryophyte mat and c is a constant as defined for eqn 1.

We applied generalized additive mixed modelling (GAMM) to the natural logarithm of the amplitude ratio time series as response variable and time series of bryophyte mat thickness divided by square root of thermal diffusivity as predictor. Time series of daily values of mat thickness divided by square root of thermal diffusivity were nested within sites, and sites were nested within species. To account for autocorrelation within individual time series, we modelled the residual autocorrelation structure with autoregressive model of order one (AR-1).

The important outcome of this analysis, besides a probability value verifying the presence of a relationship, is the estimation of the constant c. Obtained c being not significantly different from 0.36 (the value derived analytically for heat transfer in soil, in case of daily sinusoidal temperature fluctuations (Koorevaar, Menelik & Dirksen 1983) would indicate that the processes of heat transfer in bryophyte mats are driven by laws of physics only, without locally deviating biological processes.

Results

BRYOPHYTE EFFECTS ON SOIL TEMPERATURE REGIME

We found that all effects of bryophytes on soil temperature regime were pronounced only during the growing season. The data for the nongrowing season are therefore not discussed further, and the results below are based on the ANOVAs with one between-subject factor (species) only.

The effects of the presence–absence of individual bryophyte species on average soil temperature, soil temperature amplitude and number freeze–thaw events are shown in Fig. 1 and Table 1. Average growing season temperatures in the soil under bryophyte mats did not differ from that in open soil, (bryophyte presence effect: $P = 0.897$, $F_{1,80} = 0.17$), neither was there a significant interaction between species and bryophyte presence ($P = 0.301$, $F_{17,80} = 1.18$, Fig. 1a), indicating that bryophytes did not alter average soil temperatures below their own mats as compared to the open soil patches where the mats had been removed. Note that a highly significant species effect (Table 1) indicates differences among soil temperature regimes below mats of distinct bryophyte species. Those are probably due to interspecific habitat and/or albedo differences, which were not a subject of this study.

Amplitude of soil temperature and the number of freeze–thaw events were both reduced by the presence of bryophyte mat ($P < 0.001$, $F_{1,63} = 110$; and $P<0.001$, $F_{14,61} = 71.1$, respectively), and the interaction between species and bryophyte presence were in both cases significant, suggesting that the effects differed among species ($P = 0.005$, $F_{17,63} = 2.49$; and $P = 0.002$, $F_{14,61} = 2.89$, respectively, Fig. 1b,c).

We found significant differences among ecosystems in temperature amplitude ratios under bryophyte mat vs. open soil patches ($P = 0.001$, $F_{3,74} = 15.8$) while species within ecosystem type did not vary significantly. Species of *S. fuscum* -dominated tundra and forest ecosystems had the greatest temperature amplitude dampening effects (amplitude of temperature fluctuations under moss being 57% of that in open soil patches), being significantly higher than those of species of alpine meadows and of fens which had the lowest impact on the amplitude of temperature fluctuations under moss, equalling in both cases 86% of that in open soil patches (Fig. 2).

How do bryophyte mat thermal conductivity and volumetric heat capacity depend on mat moisture content and mat density?

Contrary to our expectations, both bryophyte mat thermal conductivity and volumetric heat capacity were only highly significantly dependent on moisture content but independent of mat density (Table 2, Fig. 3a–d). Volumetric moisture content explained 77% and 83% of the variance in thermal conductivity and volumetric heat capacity. Dummy regressions indicated that neither thermal
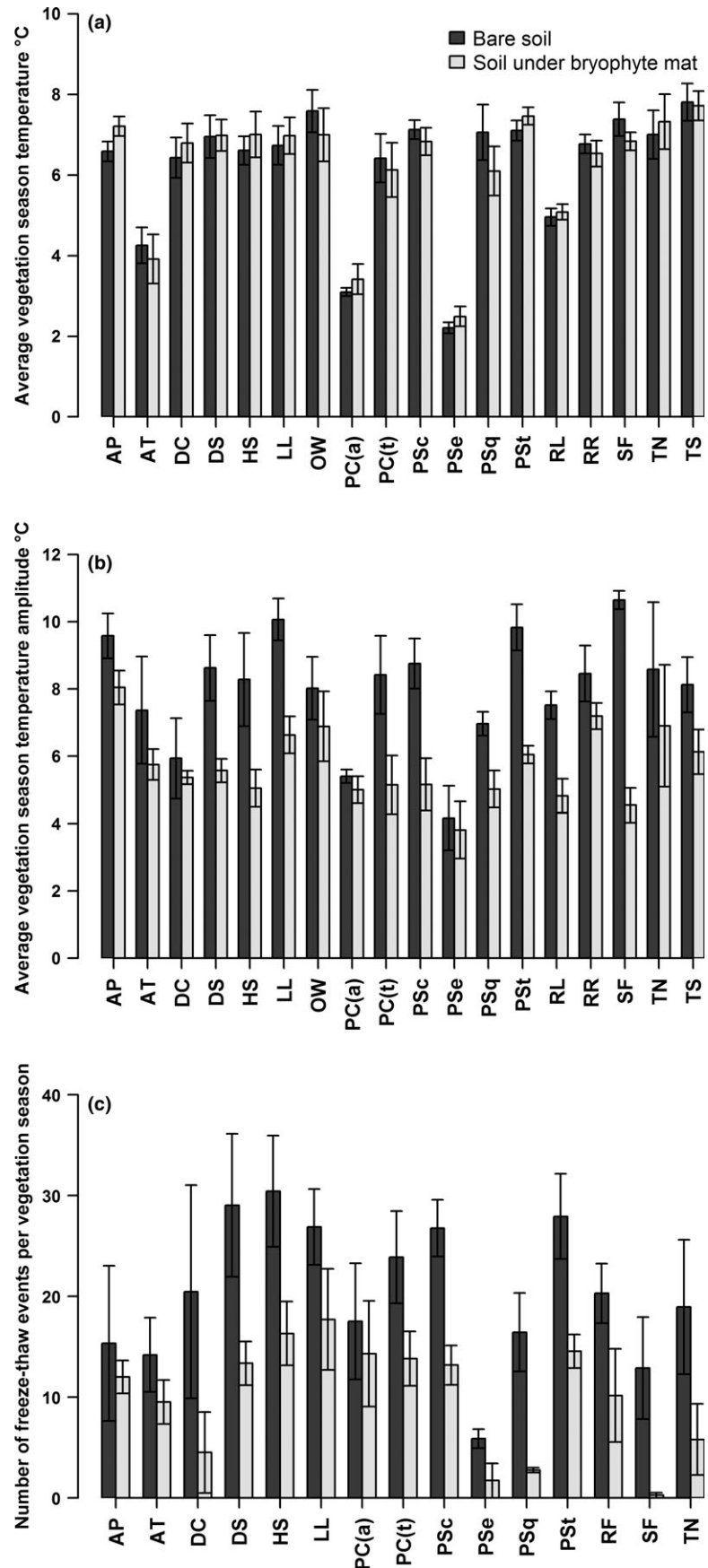
Fig. 1. Effects of bryophyte presence on soil temperature regime: (a) average growing season soil temperature, (b) growing season average temperature amplitudes and (c) total number of freeze–thaw events during the growing season. Note that the analysis for the number of freeze–thaw events was conducted on the log-transformed data, while the graph shows the untransformed values. Replication varies among species ($3 \leq n \leq 10$). The liverwort *Ptilidium ciliare* was sampled in two distinct ecosystems, *Sphagnum fuscum*-dominated tundra ('t') and alpine meadow ('a'). Species names abbreviations: AP-*Aulacomnium palustre*, AT-*Aulacomnium turgidum*, DS-*Dicranum scoparium*, DC-*Drepanocladus cossonii*, HS-*Hylocomium splendens*, LL-*Lophozia lycopodioides*, OW-*Oncophorus wahlenbergii*, PSq-*Paludella squarrosa*, PSc-*Pleurozium schreberi*, PSe-*Polytrichastrum sexangulare*, PSt-*Polytrichum strictum*, PC(a)-*Ptilidium ciliare* in alpine meadow, PC(t)-*Ptilidium ciliare* in *Sphagnum fuscum* dominated tundra, RL-*Racomitrium lanuginosum*, RR-*Rhytidium rugosum*, SF-*Sphagnum fuscum*, TS-*Tetralophosia setiformis*, TN-*Tomentypnum nitens*.

Table 1. Effects of bryophyte mats on soil temperature regime (growing season soil temperature averages and amplitudes, and number of freeze–thaw events)

	F	P
Mean soil temperature during growing season		
Bryophyte presence (within-subject factor)	0·17	0·897
Species (between-subjects factor)	9·82	<0·001
Bryophyte presence × Species	1·18	0·301
Soil temperature amplitude during growing season		
Bryophyte presence (within-subject factor)	110	<0·001
Species (between-subjects factor)	1·55	0·105
Bryophyte presence × Species	2·49	0·005
Number of freeze–thaw events during growing season		
Bryophyte presence (within-subject factor)	76·6	<0·001
Species (between-subjects factor)	6·27	<0·001
Bryophyte presence × Species	2·71	0·003

Results (*F* and *P* values) of the repeated measures ANOVAS with bryophyte presence–absence considered as within-subject factor, and bryophyte species identity as between-subjects factor. Note that, although the main effects of species were highly significant in analyses of average growing season temperature and number of freeze–thaw events, this result is not relevant for our research question, because it reflects different soil temperature conditions among the habitats the species grow in.
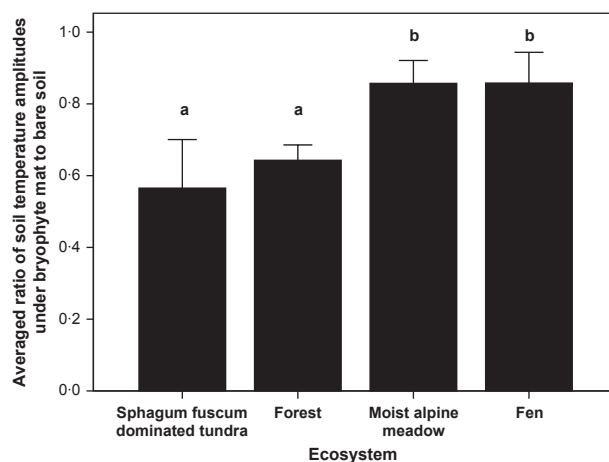
Fig. 2. Differences among ecosystems in field-measured ratio of temperature amplitudes under bryophyte mat and on open soil patches. Different letters indicate significant differences detected by Tukey post hoc test (*P* < 0·05).

conductivity nor volumetric heat capacity was affected by an interaction between species identity and mat moisture content.

Remarkably, although all four terms in the polynomial approximation of bryophyte mat thermal conductivity dependency on mat moisture content were highly significant (see Table 2), the highest coefficient value and by far the highest proportion of the explained variance ($\eta^2 = 0\cdot987$) were associated with the first-order term, that is, the linear moisture content, while the higher-order terms were several orders of magnitude smaller than the first term and had negligible η^2. This strongly suggests that

within the range of values observed for bryophytes, the (generally polynomial) dependency of thermal conductivity on moisture content can be approximated as linear (Fig. 3a).

Based on field measurements of mat moisture content, we calculated per-species average moisture mat content for the studied bryophytes. Using the regression coefficients obtained at the previous step, we calculated bryophyte thermal conductivity and volumetric heat capacity at average field moisture content. These values, together with values of conductivity and heat capacity at maximum and zero moisture content, are reported in the Supporting Information Table S3.

Can decrease in temperature amplitude under a bryophyte mat be predicted by bryophyte mat thickness and thermal diffusivity?

The decrease in amplitude of temperature fluctuations under a bryophyte mat was well predicted by the value of bryophyte mat thickness divided by the square root of thermal diffusivity at field moisture content (GAMM results: P < 0·001, t = −3·9, adjusted R^2 = 0·505, n = 850, Fig. 4). All GAMM smooth terms were nonsignificant indicating the absence of any time-trend beyond the one explained by the predictor variable (thickness divided by the square root of thermal diffusivity). The value of constant *c* in eqn 2 is estimated as 0·356 ± 0·091 (mean ± SE).

Discussion

### NATURE OF INSULATION EFFECTS OF BRYOPHYTE MATS DURING THE GROWING SEASON

Although the importance of bryophyte layers for soil temperature regimes is known (Bonan & Shugart 1989; Gornall *et al.* 2007), our study is the first to assess the complete spectrum of these effects (average temperature, temperature amplitude, freeze–thaw frequency) for many bryophyte species, and for several ecosystems across several years. This regime is a function of (1) habitat light availability, defining how much energy reaches bryophyte mats and which is in principle not altered by bryophytes, (2) albedo, defining how much energy is reflected by bryophytes and (3) heat transfer through the mats.

Though we found considerable differences between average soil temperatures below distinct bryophyte species (Fig. 1a), which could be partly due the interspecific differences in bryophyte albedo (Stoy *et al.* 2012) as well as due to habitat differences, we did not find evidence for a reduction in average soil temperatures under bryophyte mats as compared to bryophyte-removal patches (hypothesis 1a, first statement). This suggests that in our sites, with organic soils having colours rather similar to those of bryophyte mats, albedo differences between open soil patches and bryophyte mats were very small. Respiration, which could cool bryophyte mats more than open organic

Table 2. Results of mixed model regression analyses for dependencies of bryophyte mat thermal conductivity ($n = 365$) and volumetric heat capacity ($n = 364$) on the volumetric moisture content (VMC) and density

	Regression coefficient	SE	d.f.	*t*-value	*P*-value	η^2
Results for thermal conductivity regression						
Intercept	9.18×10^{-2}	0.0090	343	10.1	<0.001	
VMC	9.67×10^{-3}	0.0015	343	6.51	<0.001	0.987
VMC^2	-4.24×10^{-4}	0.0001	343	-3.96	<0.001	0.002
VMC^3	1.09×10^{-5}	0.0000	343	4.18	<0.001	4.99×10^{-5}
VMC^4	-8.03×10^{-8}	0.0000	343	-4.19	<0.001	0.014
Density	-0.28	0.1927	343	-1.43	ns	0.002
Results for volumetric heat capacity regression						
Intercept	0.29	0.07	345	4.27	<0.001	
VMC	0.04	0.00	345	41.3	<0.001	0.998
Density	2.94	1.58	345	1.86	ns	0.001

In both analyses VWC and mat density were nested within species ($n = 17$) as independent predictors. The response variables were thermal conductivity (modelled as being dependent of VWC as a fourth-order polynomial, following an analogy with soil thermal conductivity) and volumetric heat capacity (modelled as linearly dependent on VWC). d.f. – degrees of freedom, η^2 – shows the proportion of variance explained by each factor.
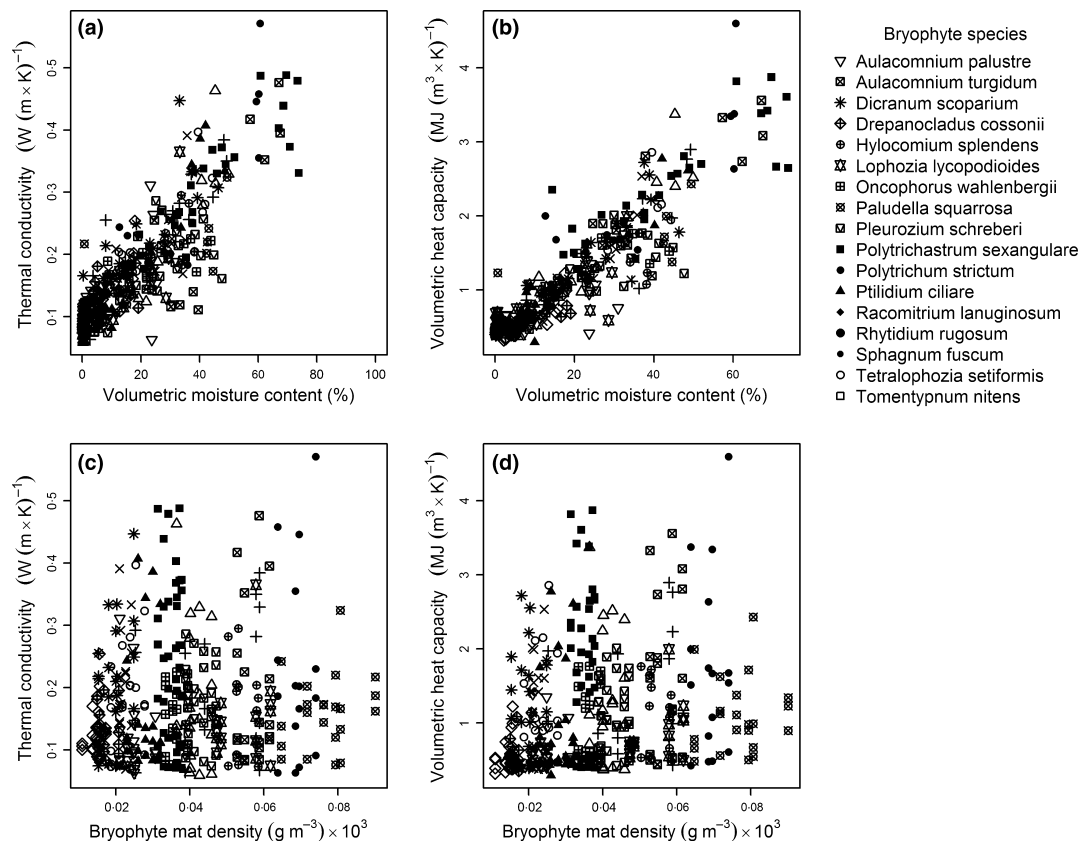
Fig. 3. Dependencies of bryophyte mat thermal conductivity and volumetric heat capacity on (a, b) bryophyte mat volumetric moisture content (%) and (c, d) bryophyte mat density (g m^{-3}). Volumetric moisture content explains 77 and 83% of variance in thermal conductivity and volumetric heat capacity. $N = 366$.

soil patches, does not seem to play a significant role either. Thus, this data suggest that the differences in temperature regimes between soils below bryophyte mats and open soil patches were mostly due to heat transfer mechanisms.

Absence of an overall temperature reduction below bryophyte mats coincides with findings for cushion-forming plants at high latitudes, which have been shown to

also reduce soil temperature amplitudes but not average soil temperatures (Cavieres *et al.* 2007; Cavieres, Quiroz & Molina-Montenegro 2008; Kleier & Rundel 2009). On the other hand, studies of Gornall *et al.* (2007), Guglielmin, Worland & Cannone (2012) and Cannone & Guglielmin (2009) report a reduction in average soil temperatures induced by moss mats in northern and southern high-latitude areas. However,
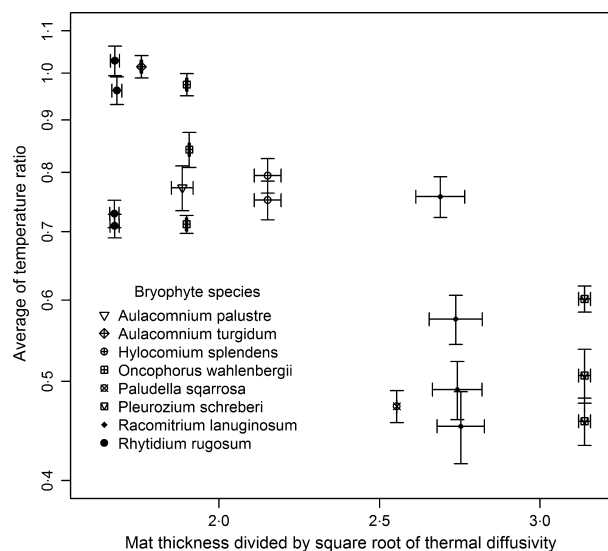
Fig. 4. Empirical relationship between daily reduction in soil temperature amplitude by a bryophyte mat (calculated per species, per site as ratio of daily temperature amplitude under bryophyte mat to amplitude on an adjusting open soil patch) and value of species-specific mat thickness divided by square root of thermal diffusivity at the day-specific field moisture content. $P < 0.001$, $t = -3.9$, adjusted $R^2 = 0.505$, $n = 850$. Y axis has logarithmic scale. Note that the figure does not directly illustrates the statistical analysis, which was not run on species-site averages, but implied nesting of the individual daily measurements within sites, and nesting of sites within species.

these studies mainly reflect a seasonal variation in moss effects on average soil temperature: average soil temperatures are reduced by bryophyte mats at the beginning of the vegetation season but increased at the end of the vegetation season. Integrated over a complete growing season, these effects seem minor.

In agreement with our expectations (hypothesis 1a, second and third statements), we found that bryophyte mats reduced soil temperature amplitudes and the number of freeze–thaw events. Similar results were reported by Gornall *et al.* (2007) who compared temperature regimes under shallow, intermediate and deep moss layers, and by Cannone & Guglielmin (2009) and Guglielmin, Worland & Cannone (2012) who studied temperature regimes in soils of vegetated vs. unvegetated tundra in Antarctica. Our extended analysis on multiple ecosystems and moss species indicates that this reduction in temperature amplitudes may be a generic feature in (sub) arctic ecosystems. In cold regions, carbon and nutrient turnover is highly sensitive to temperature fluctuations; Especially, the freeze–thaw frequency was shown to affect the composition of microbial communities in soil (Deluca, Keeney & McCarty 1992; Yergeau & Kowalchuk 2008; Muhr, Borken & Matzner 2009; Vestgarden & Austnes 2009; Haei *et al.* 2011), as well as to have a substantial physical effect on soil, causing, for instance physical nutrient release from soil during freezing–thawing cycles (Edwards & Cresser 1992), and therefore to affect carbon and nutrient turnover. Thus,

we suggest that an important but yet often overlooked effect of bryophyte mats is their control on carbon and nutrient cycling via soil temperature stabilization in organic soils. It is important to note that a possibility to extrapolate our findings to the other soil types (e.g. sandy soils, young mineral soils, etc) merits further investigation.

Effects of bryophyte mats on soil temperature amplitude during winter

The bryophyte effects on soil temperature amplitude during winter seem to be site dependent. We found that in our ecosystems bryophytes affected soil temperature amplitude during growing season only, and not during winter. Similar results were reported by Gornall *et al.* (2007) for their study in Spitsbergen, while Kade, Romanovsky & Walker (2006) and Cannone & Guglielmin (2009) reported both winter and summer soil temperature amplitude reductions under tundra vegetation in arctic Alaska and Antarctica, though winter effects were much less pronounced than summer ones. This difference in seasonal impacts could be due to differences in depth of snow cover, which also reduces air temperature fluctuations (Kade, Romanovsky & Walker 2006) and may override soil temperature alterations by bryophyte mats. Our results suggest that in all study sites, there was sufficient snow cover overruling the potential effects of bryophytes on soil temperature.

Difference among bryophyte species in their effects on soil temperature fluctuations

All bryophyte species in our study affected soil temperature regime in the same direction, reducing temperature amplitudes under mats, but, in agreement with hypothesis 1b, the extent of this reduction differed among species. However, these interspecific differences were not underpinned by intrinsic differences in thermal conductivity and volumetric heat capacity but turned out to be functions of moisture content and mat thickness only (see below, under '*Heat transfer traits…*').

Whether and how alterations of soil temperature amplitudes under bryophyte mats affect the plant community merits further investigation. Recently, Gornall *et al.* (2011) and Soudzilovskaia *et al.* (2011) have shown that bryophyte mats structure affects the composition of vascular plant communities via, among other mechanisms, control over soil temperature regimes. Soudzilovskaia *et al.* (2011) suggested that those bryophyte species that show the strongest reduction in soil temperature amplitudes are the most effective suppressors of vascular plant germination. Gornall *et al.* (2011) and Hobbie, Shevtsova & Chapin (1999) have shown that mosses that create thick mats negatively affected biomass production of vascular plants growing in such mats. They also associated this finding with indirect moss effects through the soil temperature regime. As bryophytes are known to compete with vascular plants for light (Jonasson *et al.* 1999; Van der Wal,

Pearce & Brooker 2005), suppression of vascular plant performance via unfavourable soil temperature regime might be an important survival mechanism for many bryophyte species.

Variation among ecosystems in bryophyte effects on soil temperature

We demonstrate that four wide-spread subarctic ecosystems differ in the extent to which bryophytes decrease the amplitude of soil temperature fluctuations. Hypothesis 1c is therefore confirmed. Within ecosystems, however, dominant bryophyte species tend to have similar impacts on the temperature regime. We found that the insulation effects of bryophytes are well explained by mat moisture and thickness. The similarity in the soil temperature amplitude reduction effect among bryophyte species growing in the same ecosystem could thus be a result of similar moisture and light regimes experienced by the bryophytes growing in the same ecosystems, leading to the similar mat moisture content and thickness, or a result of a complex interaction among the effects of moisture and light regime on bryophytes. The set-up of our study does not allow us to distinguish these situations. Neither does our study enable us to assess whether bryophyte field moisture content is mainly due to species traits regulating their water retention capacity (Elumeeva *et al.* 2011) or mainly to site topography and hydrology.

In spite of the unknown underlying mechanisms, our results on the reduction in amplitudes of soil temperature under bryophyte mats in subarctic forests, fens, tundra and alpine meadows may be applied in soil carbon and nutrient cycling studies. Survival and activities of soil micro-organisms and animals in high latitudes are to large extents regulated by soil temperature regimes (Lloyd & Taylor 1994; Sjursen, Michelsen & Holmstrup 2005; Loffler, Cypionka & Loffler 2008; Yergeau & Kowalchuk 2008; Muhr, Borken & Matzner 2009; Wallenstein, McMahon & Schimel 2009; Haei *et al.* 2011). The freeze–thaw regimes and the amplitudes of the fluctuations are known to have distinct effects of fungal, bacterial and arthropod biotas (Sjursen, Michelsen & Holmstrup 2005; Yergeau & Kowalchuk 2008; Haei *et al.* 2011). We show that soils of subarctic bryophyte-dominated wetlands and alpine meadows experience larger soil temperature fluctuations compared to dry tundra and forests, and suggest that the differences in bacterial and fungal activities, and therefore carbon and nutrient pathways and fluxes, among these ecosystems may be partly linked to soil temperature regulation function of bryophytes.

Bryophyte traits underpinning heat transfer through bryophyte mats

To our knowledge, this is the first study to report thermal conductivity for a wide range of bryophytes and ultimately the first to report volumetric heat capacity values for bryophytes. The values of thermal conductivity, measured for multiple species across a range of bryophyte mat moisture contents, ranged from 0.06 W m^{-1} K^{-1} for air-dry *Aulacomnium turgidum* to 0.57 W m^{-1} K^{-1} for maximum water saturated *T. setiformis* (volumetric moisture content 61%). Considering conductivity of individual bryophyte species, our values for *Pleurozium schreberi*, *Hylocomium splendens* and *S. fuscum* are in the range shown previously (e.g. Brown & Williams 1972; Hinzman *et al.* 1991) for Alaskan feather mosses and *Sphagna*. Sharratt (1997) reported lower field-measured conductivity values for mixtures of *P. schreberi* and *Sphagnum* spp, ranging from 0.03 to 0.09 W m^{-1} K^{-1}. Our measurements suggest that thermal conductivity of these species at typical field volumetric moisture content range 0.13–0.18 W m^{-1} K^{-1} for *Pleurozium* and 0.31–0.37 W m^{-1} K^{-1} for *Sphagnum* (see Supporting Information Table S3).

Contrary to our expectations, we found that mat density did not affect bryophyte thermal conductivity neither volumetric heat capacity. Mat density was expected to underpin bryophyte species-specificity, based on the positive relationship of material density with thermal conductivity and volumetric heat capacity of organic material (Andersland & Anderson 1978). Bonan (1991) modelled the soil energy budget of Alaskan boreal forests and demonstrated that bryophyte mat thermal conductivity and volumetric heat capacity, in theory, should depend on moss bulk density. We conclude tentatively that the range of bryophyte mat natural densities is too small (ranging 6×10^{-2} mg mm^{-3}, Supporting Information Table S2) to cause species-specificity of bryophyte thermal conductivity and volumetric heat capacity at given soil moisture content (for comparison: density difference between clay and turf soil is two order or magnitude larger). It is also important to consider that in this analysis we used a bulk density measurement, which did not account for mat porosity (i.e. air spaces between the individual shoots: for instance species like feather mosses and *Sphagna* would have smaller pore spaces that would help maintain stagnant air compared to species like *Polytrichum* with very large pore spaces.). Although this is not important in the laboratory study, where air is not turbulent, it could be important in the field. We suggest that some of the unexplained variation in our predictions of temperature amplitude decrease under bryophytes based on thermal diffusivity and mat thickness (Fig. 4) could be due to variation in mat porosity.

We demonstrate that thermal conductivity of bryophyte mat increases with moisture content. Based on an analogy to organic soil, we modelled the dependency of bryophyte mat as a 4th order polynomial. However, our results suggest that, for bryophytes, this dependency is generally linear (Fig. 3a, Table 2). The same conclusion was drawn by O'Donnell *et al.* (2009), who studied thermal conductivity as a function of moisture content for two feather mosses and *Sphagnum* spp. This difference between bryophytes and organic soil could be attributed to higher porosity of the living bryophyte layer compared to soil

and to different water retention characteristics of bryophytes compared to soil (Busby & Whitfield 1978; Elumeeva *et al.* 2011; Michel *et al.* 2011). O'Donnell *et al.* (2009) found that the dependency of bryophyte mat thermal conductivity on moisture content did not differ among three species of Alaskan mosses. Our multispecies data also strongly suggest that the dependency of bryophyte mat thermal conductivity on moisture is not species-specific. We also show that the second constituent of heat transfer, volumetric heat capacity, increases linearly with moisture content and this dependency is not species-specific either. Such absence of species-specificity indicates that thermal properties of bryophyte mat can be modelled based on physics laws, that is, we will not miss any important intervening/confounding factor by ignoring information on the mat species constitution.

It is important to realize that the absence of the species-specificity does not concern the resulting effect of the bryophyte mat on soil temperature amplitudes, but concerns only the thermal conductivity and volumetric heat capacity of mats. In nature, bryophyte mats of distinct species differ in thickness and field moisture content, the latter being a function of site-specific water availability and species-specific conductivity and water holding capacity. Species with thinner mats will affect soil temperature amplitudes less than species with thicker mats, even if they have similar moisture content and therefore the same thermal conductivity and volumetric heat capacity. Also, we stress that the absence of species-specificity relates solely to the mechanisms of transfer of the energy absorbed by the bryophyte mats, while differences in the amount of energy reflected, caused by potentially distinct albedo of different species, fall out of the scope of this investigation.

Implications for global predictions of carbon and nutrient cycling

A critical outcome of the bryophyte thermal conductivity and volumetric heat capacity trait relations reported in this paper is that in cold regions, we can model and quantitatively predict the decrease in soil temperature amplitudes under a bryophyte mat as a function of mat moisture content and mat thickness applying the same physical laws as known for soil (Koorevaar, Menelik & Dirksen 1983). Although we detected this relation in a laboratory experiment, our calculations based on the multiweek field data support it. Unexplained variance in the relationship depicted in Fig. 4 is probably associated with some inaccuracy of moisture measurements and the fact that the laboratory study of heat transfer traits was conducted in stagnant air, while under field conditions air turbulence might have slightly affected heat transfer. However, the value of the constant $c = 0.36 \pm 0.09$ (h$^{-1/2}$) is very similar to the theoretically calculated value of 0·36 for heat transfer in soil (Koorevaar, Menelik & Dirksen 1983). Such relationship suggests that the processes of heat transfer in subarctic bryophyte mats are driven mostly by laws of physics and are similar to the heat transfer in soil indicating that effects of biological processes like decomposition, photosynthesis and respiration on heat transfer through bryophyte mats are negligible. The absence of species-specificity in bryophyte heat transfer considerably simplifies modelling of air–soil heat transfer, allowing to base calculations on bryophyte mat thickness and moisture content only.

These two outcomes should considerably ease the integration of cold region bryophytes in the global vegetation models that are widely used for analyses and predictions of Earth carbon and nutrient cycles. Our results suggest that in global vegetation models of carbon and nutrient cycling (Ostle *et al.* 2009), the cold region bryophyte mats can be modelled as top organic soil layers with possibly distinct albedo, but the thermal properties as determined in this study and depending solely on water availability. Such simplification should not decrease the model output precision. Integration of bryophytes in a global model of carbon cycling, will allow us to quantify the bryophyte input into the Earth's carbon cycle, and additionally considerably increase modelling precision, via improving the representation of soil temperature regime.

Conclusions

This is the first comprehensive study of bryophyte mat effects on soil temperature regime. Based on 17 bryophyte species that prevail in six of the most common ecosystem types in cold biomes, we show that bryophytes stabilize soil temperature and reduce freeze–thaw frequency. We point out that this important, yet often overlooked, effect of bryophyte mats is likely to have important implications for carbon and nutrient turnover in polar regions.

We demonstrate the role of mat thickness and moisture content, as regulators of the extent to which bryophyte mats decrease the amplitude of soil temperature fluctuations and suggest that although the net effects differ among bryophyte species, the mechanisms underpinning the reduction in temperature amplitudes under bryophyte mats are not species-specific. This broadens the possibilities for including vegetation cover effects on soil temperatures regimes in global analyses of carbon and nutrient cycling in cold biomes.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Statistical considerations underlying the analysis of bryophyte effects on soil temperature regime.

Appendix S2. The applicability of soil heat transfer equation for modeling of heat transfer in sub-arctic bryophytes.

Table S1. List of bryophyte species studied, ecosystems where study sites were situated, periods of temperature and moisture measurements and their replication.

Table S2. Depths and densities of bryophyte mats.

Table S3. Specific heat capacity and thermal conductivity of sub-arctic bryophytes at minimum (air dry), maximum and field-average moisture contents.