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Temperature, Heat Flux, and Reflectance of Common Subarctic Mosses and Lichens under Field Conditions: Might Changes to Community Composition Impact Climate-Relevant Surface Fluxes?

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Abstract

Bryophytes and lichens are ubiquitous in subarctic ecosystems, but their roles in controlling energy fluxes are rarely studied at the species level despite large, recent observed shifts in subarctic vegetation. We quantified the surface and subsurface temperatures and spectral reflectance of common moss and lichen species at field sites in Alaska and Sweden. We also used MODIS observations to determine if the removal of *Cladonia* spp. by reindeer overgrazing impacts land surface albedo and temperature. Radiometric surface temperature of a feather moss (*Pleurozium schreberi*) exceeded 50 °C on occasion when dry, up to 20 °C higher than co-located *Sphagnum fuscum* or *C. rangiferina*. Spectral reflectance of *S. fuscum* was on average higher than *Polytrichum piliferum* across the 350–1400 nm range, with substantial within-species variability. MODIS albedo was significantly higher on the Norwegian (relatively undisturbed) side *versus* the Finnish (disturbed) side of a border reindeer fence by an average of 1% during periods without snow cover. MODIS nighttime land surface temperatures were often significantly higher on the Norwegian side of the fence by an average of 0.7 °C despite higher albedo, likely due to poor conductance of heat to the subsurface as observed in *C. rangiferina* in the field. Changes to bryophyte and lichen community composition alter the surface energy balance, and future work must determine how to best incorporate these effects into Earth system models.

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Introduction

Bryophytes and lichens often dominate the surface of boreal and tundra ecosystems (During and Tooren, 1990; Esseen et al., 1997) and as a consequence are commonly associated with permafrost and/or carbon-rich soils (Zimov et al., 2005; Schuur et al., 2008; Tarnocai et al., 2009). The transport of heat from the land surface determines in part the thermal environment of soil, and the partitioning of energy at the land surface determines in part regional climate (Bonan et al., 1990; Beringer et al., 2005; Bonan, 2008). Controls on the subarctic surface energy balance by bryophytes and lichens must be quantified for a comprehensive understanding of the surface and subsurface thermal environment and biosphere-atmosphere energy exchange in a changing climate (Beringer et al., 2001).

In process-based studies of permafrost thaw, mosses are often thought of as an insulating surface layer, whose thermal properties are lost in the instance of fire or other disturbances (Blok et al., 2011). Bryophyte and lichen species are rarely incorporated into models of ecosystem biogeochemistry or physics (Beringer et al., 2001; Cornelissen et al., 2007), due in part to a lack of data and the pronounced spatial variability of the species composition and water content of many subarctic ecosystems (Asner et al., 2003). We hold that the thermal characteristics of bryophyte and lichen species may differ sufficiently to warrant a species-level characterization for modeling studies (Kershaw, 1978; Vogelmann and Moss, 1993; O'Donnell et al., 2009; Elumeeva et al., 2011). Studies of surface and subsurface temperatures and subsurface heat fluxes of bryophytes and lichens at the species level has rarely been undertaken to date despite extensive work on the radiative properties of bryophytes *versus* other surface cover types (Kershaw, 1985; Rees, 1993), transmission of radiation through bryophyte canopies and associated carbon dynamics (Skre et al., 1983), and characterization of bryophyte spectral reflectance (Petzold and Rencz, 1975; Vogelmann and Moss, 1993). A study by Street (2011) however, indicated large differences in surface temperature and heat flux between moss species growing in neighboring patches in subarctic Finland.

To begin progress on bryophyte and lichen energy flux partitioning at the species level, we measured surface and subsurface temperatures and modeled subsurface heat flux in common bryophytes and lichens under field conditions in an area of extensive permafrost degradation in the Innoko National Wildlife Refuge, Alaska. For a more comprehensive study of bryophyte radiative properties, we measured the spectral reflectance of mosses and soils from a tundra ecosystem in Abisko, Sweden. To explore the potential importance of bryophyte and lichen community composition in the Earth system, we investigated differences in albedo and land surface temperature products from the moderate resolution imaging spectroradiometer (MODIS) along a *Cladonia* spp. disturbance gradient on the Norway/Finland border (Kayhko and Pellikka, 1994).

We hypothesize that surface temperatures will differ among bryophyte and lichen species due to differences in albedo, water-holding capacity, and evaporative cooling among species (Nichols

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and Brown, 1980; Kim and Verma, 1996; Liljedahl et al., 2011; Street, 2011). We test this experimental hypothesis using field observations of radiometric surface temperature (T_{surf}), subsurface temperature, spectral reflectance of moss patches, and models of subsurface heat flux (G). We further predict that changes to land surface albedo and temperature from changes in bryophyte community composition as a result of reindeer grazing will be pronounced enough to distinguish from space, and test this prediction using remote sensing data products from MODIS.

Methods

We first describe the study sites and field observations, followed by an explanation of the remote sensing analysis, as well as theoretical considerations regarding G, the surface energy balance, and T_{surf}. Results from multiple sites are used to overcome challenges of data acquisition in remote locations.

INNOKO

Innoko Flats National Wildlife Refuge (hereafter Innoko) is located in interior Alaska (Fig. 1, part A). The study area was located at 63.57378°N, 157.72889°W. Characteristic patches of *Sphagnum fuscum*, *Cladonia rangiferina*, and *Pleurozium schreberi* occupying similar microtopographic positions on the top of hummocks and co-located within meters of each other with minimal shading from the sparse black spruce (*Picea mariana*) overstory were chosen for this analysis. T_{surf} was measured every minute during the study period from day of year (DOY) 149 to 155, 2011, using a SI-111 infrared radiometer (Apogee Instruments, Logan, Utah, U.S.A.) mounted on a tripod. The radiometer was pointed approximately at nadir to all patches, noting microtopographical variability, at a distance of 20–25 cm. The SI-111 has a 22° half angle field of view and is sensitive within a wavelength range of 8 to 14 μm. Measurements made while moving and immediately after moving the tripod to different patches were discarded. Subsurface temperature at 1 cm (T_{1cm}) and 5 cm (T_{5cm}) was measured every minute using Type E (chromel-constantan) thermocouples, and all data were logged using a Campbell CR1000 datalogger (Campbell Scientific, Logan, Utah). A thirty-minute digital filter was chosen for graphical representation of the continuous subsurface temperature measurements.

ABISKO

Spectral reflectance of *Sphagnum fuscum*, *Polytrichum piliferum*, and soil was measured using an ASD Field Spectrometer (ASD Instruments, Boulder, Colorado, U.S.A.) in a subarctic tundra landscape near Abisko, Sweden, centered around 68.301790°N, 18.853610°E. Measurements were made during sunny periods in July 2007 on four plots of *S. fuscum*, three plots of *P. piliferum*, two patches of unsaturated soil, and one patch of saturated soil. Vegetative and edaphic characteristics of the study area are described in Fox et al. (2008), Shaver et al. (2007), Street et al. (2007; 2011b), Spadavecchia et al., (2008), and Williams et al. (2008).

REMOTE SENSING

Reindeer/caribou (*Rangifer tarandus*) overgrazing can sharply diminish the abundance of slow-growing lichen communities (Henry and Gunn, 1991). An area of particular interest for the study of the impacts of reindeer overgrazing on *Cladonia* spp. is a fence on the Norway/Finland border (Fig. 1, part B), where different seasonal reindeer management practices prevail (Kayhko and Pellikka, 1994). Year-round reindeer management on the Finnish side of the border has severely reduced *Cladonia* spp. presence, but winter-only grazing on the Norwegian side has maintained *Cladonia* spp. presence despite higher average annual grazing pressure (Kayhko and Pellikka, 1994). We studied the 25 km^2 area centered around 68.8365°N, 23.8710°E described by the UNEP/GRID-Arendal Maps and Graphics Library (2010).

Albedo and land surface temperature (abbreviated 'LST' for continuity with the MODIS naming conventions) of the Norway/Finland border fence area were explored using the MODIS MCD34A1 and MYD11A2 products. The MCD34A1 product is a 500 m 16-day composite of the Bidirectional Reflectance Distribution Function (BRDF)/Albedo parameters. Actual albedo values

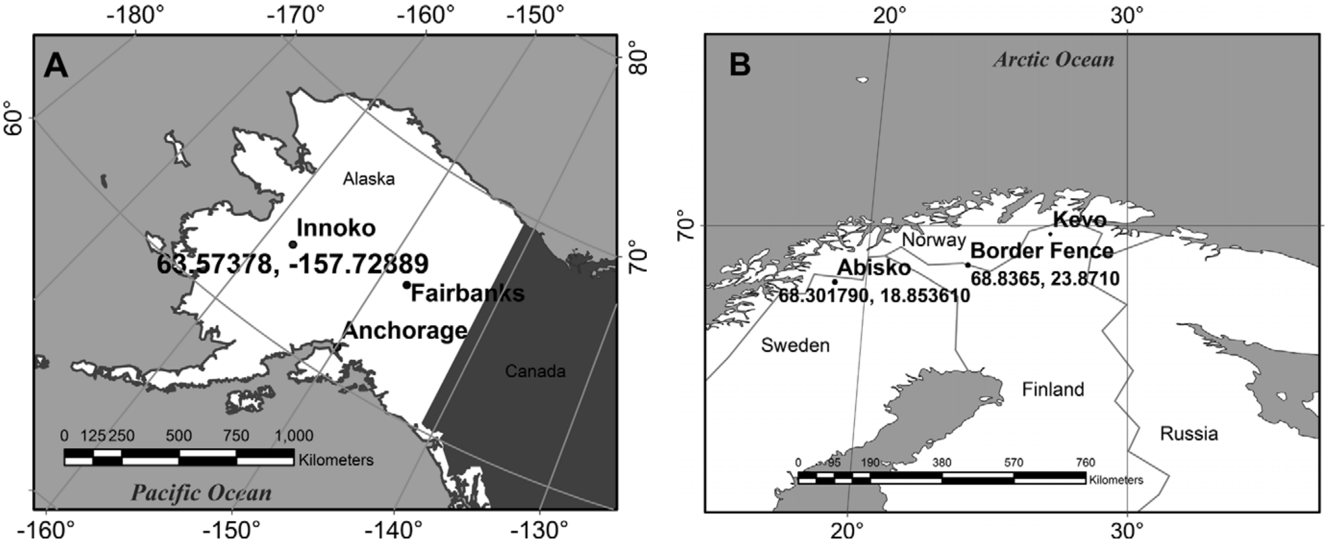

FIGURE 1. Maps of the (A) Innoko, Alaska, study area and the (B) Abisko, Sweden, and Norway/Finland Border Fence study areas.

were computed from the MCD34A1 product following Schaaf et al. (2002). The MYD11A2 product is a one km 8-day composite of day/night land surface temperature and emissivity characteristics. Observations for the time frame of 2001 until 2011 were retrieved using the MODIS server client and were filtered using the associated quality control products. Pixels that intersect the Norway/Finland border, and pixels adjacent to those pixels, were removed from the analysis. To focus on the snow-free season, pixels with albedo values >0.3 that may be contaminated by snow presence were removed from the MODIS albedo and LST analyses.

MODELS FOR SUBSURFACE HEAT FLUX

In the absence of direct measurements, the estimation of subsurface heat flux (G) follows from the continuity equation:

$$\rho_s c_s \frac{\partial T}{\partial t} = -\frac{\partial G}{\partial z} = \frac{\partial}{\partial z}\left(k\frac{\partial T}{\partial z}\right), \tag{1}$$

where t is time, T is temperature, z is depth, ρ_s is soil density, c_s is soil volumetric heat capacity, and k is thermal conductivity. Some inference regarding the soil heat flux parameters is required for an estimate of G, because these are difficult to obtain without resorting to destructive measurements.

Campbell and Norman (1998) offered a simplification for the case of deep soils subject to a sinusoidal temperature forcing:

$$G = \frac{\sqrt{2}Ak\sin[\omega(t-t_0)+\pi/4]}{D}, \tag{2}$$

where A is the amplitude of diurnal T_{surf} fluctuations, t_0 is a phase shift that depends on the time reference, D is damping depth, and ω is the angular frequency which equals $7.3 \times 10^{-5}\ \mathrm{s}^{-1}$ for diurnal fluctuations. D can be estimated using

$$D = \frac{z_1 - z_2}{\ln(A_2) - \ln(A_1)},$$

where A_x represents the amplitude of diurnal soil temperature fluctuations at depth x, here 1 cm and 5 cm. D represents the depth at which the amplitude of temperature changes is 37%, $1/e$, of that at the surface. From the surface and subsurface temperature measurements at Innoko, the only unknown is k, and we explore a range of values between the minimum (ca. 0.05 W $\mathrm{m}^{-1}\ \mathrm{K}^{-1}$) and maximum (ca. 0.55 W $\mathrm{m}^{-1}\ \mathrm{K}^{-1}$ for *Sphagnum* spp. and 0.25 W $\mathrm{m}^{-1}\ \mathrm{K}^{-1}$ for feather mosses) quantified by O'Donnell et al. (2009) to estimate G. *Cladonia rangiferina* was assumed to share a similar range of k as feather mosses.

THEORETICAL CONSIDERATIONS

Explanations for the partitioning of energy toward or away from G follow from the net radiation balance:

$$R_n - G = H + \lambda E + J, \tag{4}$$

where R_n is the net radiation, H is sensible heat flux, λE is latent heat exchange, and J is energy storage, assumed to be negligible here. Expanding the turbulent flux terms H and λE results in:

$$\begin{aligned} H &= g_H c_p (T_s - T_a) \\ \lambda E &= p_a^{-1} g_v \lambda (e_s[T_s] - e_a), \end{aligned} \tag{5}$$

where g_H and g_v are conductances for heat and water vapor respectively, c_p is the specific heat of air at constant pressure, p_a is atmospheric pressure, T_s is aerodynamic surface temperature, T_a is air temperature, λ is the latent heat of vaporization, $e_s[T_s]$ is the saturation vapor pressure of water, and e_a is the partial pressure of water in air. T_{surf} is related to G via Equation 1, and to H and λE through its relationship to T_s (Norman et al., 1995).

Equation (4) can be rewritten to include incident $\downarrow$ and outgoing $\uparrow$ shortwave (SW) and longwave (LW) energy flux:

$$R_n = \downarrow SW - \uparrow SW + \downarrow LW - \uparrow LW, \tag{6}$$

and expanded to incorporate the shortwave albedo, α:

$$R_n = (1-\alpha)\downarrow SW + \downarrow LW - \uparrow LW. \tag{7}$$

Systems with higher albedo will have lower R_n, all else being equal. T_{surf} itself is related to LW via the Stefan-Boltzmann Law for a gray body:

$$LW\uparrow = A\epsilon\sigma T_{surf}^4 \tag{8}$$

where A is surface area, σ is the Stefan-Boltzmann constant, and ϵ is emissivity, often assumed to be ca. 0.97 in natural environments (Campbell and Norman, 1998), but in actuality a function of albedo following Kirchoff's Law of Radiation at equilibrium (see Chen et al., 2002). To summarize, albedo and T_{surf} enter different terms in the surface energy balance, and are therefore determinants of the subsurface and atmospheric energy budget for which the surface represents a boundary.

Results

INNOKO: SURFACE AND SUBSURFACE TEMPERATURE

Prevailing weather conditions were warm and dry during the earlier part of the measurement period before DOY 152 at Innoko, which was followed by overcast skies with intermittent rain events. T_{surf} reached over 55 °C in *P. schreberi*, but rarely reached over 30 °C in *S. fuscum* or *C. rangiferina* (Fig. 2). T_{surf} of *P. schreberi* exceeded the other bryophytes by nearly 20 °C during warm, sunny periods, but by no more than ca. 5 °C during cool, wet periods (Fig. 2).

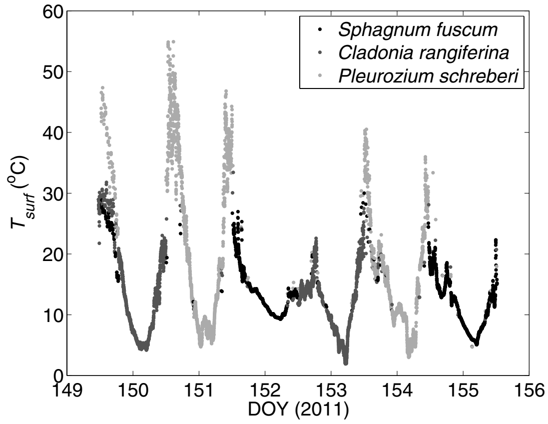

FIGURE 2. Radiometric surface temperature (T_{surf}) of representative *Sphagnum fuscum*, *Cladonia rangiferina*, and *Pleurozium schreberi* patches in the Innoko National Wildlife Refuge, Alaska.

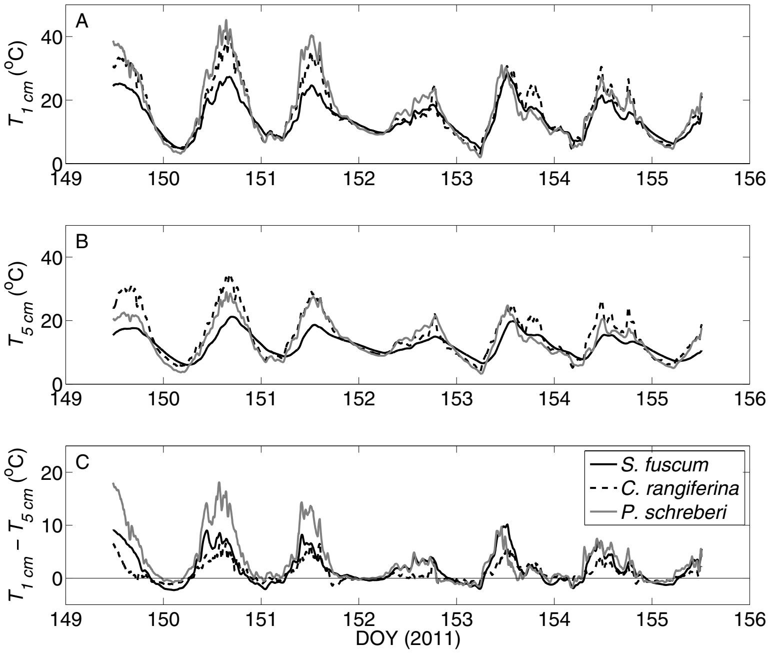

FIGURE 3. Temperature at 1 cm (T_{1cm}, A) and 5 cm (T_{5cm}, B) below the surface of *Sphagnum fuscum, Cladonia rangiferina*, and *Pleurozium schreberi* patches in the Innoko National Wildlife Refuge, Alaska. Subplot C represents the difference between subplots A and B.

T_{1cm} in *P. schreberi* likewise tended to exceed that of *C. rangiferina* and *S. fuscum*, the latter commonly by more than 10 °C, during morning and midday periods (Fig. 3, part A). T_{1cm} among species converged at night and after rain events (Fig. 3, part A). T_{5cm} was often greatest in *C. rangiferina* during dry daytime periods (Fig. 3, part B) such that the difference between T_{1cm} and T_{5cm} was usually lowest in *C. rangiferina* during the day (Fig. 3, part C), with implications for *G* (Fig. 4 and Equation 2). Mean T_{1cm} and T_{5cm} during the study period are significantly different among species (two-sided *t*-test, $p < 0.05$). The mean and standard deviation of T_{1cm} was 14.2 ± 5.8 °C in *S. fuscum*, 16.2 ± 8.5 °C in *C. rangiferina*, and 16.7 ± 9.6 °C in *P. schreberi*. T_{5cm} over the measurement period was 12.4 ± 3.6 °C in *S. fuscum*, 15.2 ± 7.0 °C in *C. rangiferina*, and 13.6 ± 6.0 °C in *P. schreberi*.

INNOKO: MODELED SUBSURFACE HEAT FLUX

Values of *D* calculated from observations (Fig. 3) and used for the estimation of *G* are listed in Table 1. The ranges of modeled *G* varied between ca. ± 200 W m^{-2} for *S. fuscum*, between ca. ± 100 W m^{-2} for *C. rangiferina*, and between ca. ± 150 W m^{-2} for *P. shreberi* (Fig. 4). Following O'Donnell et al. (2009), *k* was likely low when mosses and lichens were dry before DOY 152, and was likely higher after the precipitation events. Consequently, the magnitude of *G* was likely on the low end of the modeled range

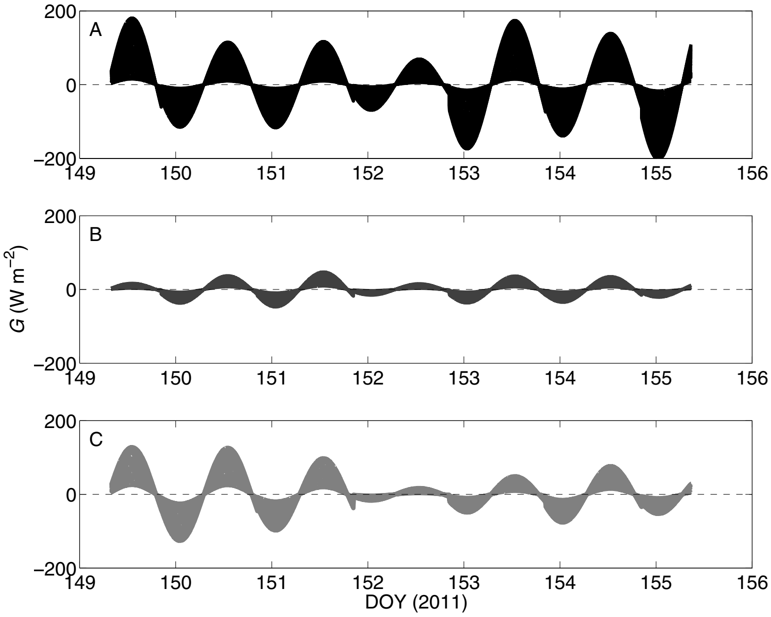

FIGURE 4. Estimated subsurface heat flux (*G*) in representative (A) *Sphagnum fuscum*, (B) *Cladonia rangiferina*, and (C) *Pleurozium schreberi* patches in the Innoko National Wildlife Refuge, Alaska. The line widths reflect uncertainty in thermal conductivity (*k*), which were taken to represent a range of published values (O'Donnell et al., 2009). Positive values reflect energy flux from surface to subsurface.

TABLE 1

Modeled damping depth (m) using Equation (3) as a function of day of year (2011) for the *Sphagnum fuscum*, *Cladonia rangiferina*, and *Pleurozium schreberi* study sites at Innoko, Alaska.

Day of Year	*S. fuscum*	*C. rangiferina*	*P. schreberi*
149	0.05	0.30	0.06
	0.10	0.17	0.08
	0.08	0.10	0.08
	0.08	0.17	0.21
	0.07	0.13	0.14
	0.06	0.18	0.08
	0.04	0.14	0.07
n (s.d.)	0.07 (0.02)	0.17 (0.06)	0.10 (0.05)

for all species during the early part of the measurement period, and on the higher end of the modeled range during the latter part of the measurement period.

ABISKO: SPECTRAL REFLECTANCE

Reflectance in *S. fuscum* tended to be greater than that of *P. piliferum* and bare ground across the visible wavebands and the near infrared wavebands up to ca. 1300 nm (Fig. 5). A spike in reflectance in the red section of the visible spectrum (620–730 nm) was observed in *S. fuscum*. *P. piliferum* reflected on average more radiation than *S. fuscum* across longer wavelengths in the near infrared spectrum, taken here to be 1400–1900 nm. Reflectance of the two moss species was typically $<10\%$ at wavelengths between 1900 and 2400 nm. Bare ground patches reflected less than ca. 20% of radiation across the entire visible to near-infrared spectrum, but reflected more radiation than the bryophytes at wavelengths longer than 1400 nm. Saturated bare ground reflected less radiation than the moss species across the entire observed spectrum.

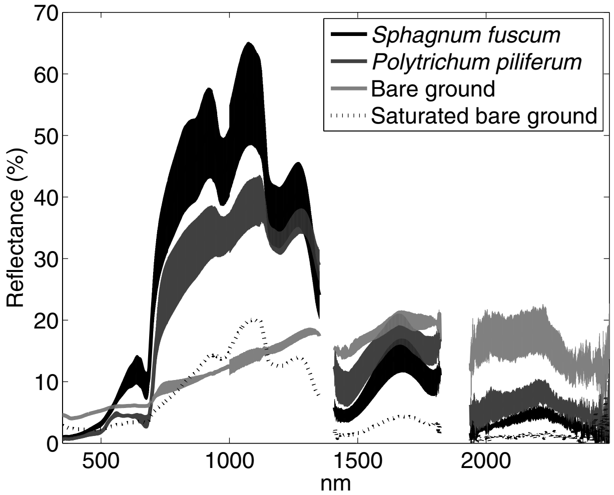

FIGURE 5. The mean and standard deviation of the spectral reflectance of four plots of *Sphagnum fuscum*, three plots of *Polytrichum piliferum*, two representative patches of bare ground, and a patch of saturated bare ground in a tundra ecosystem near Abisko, Sweden.

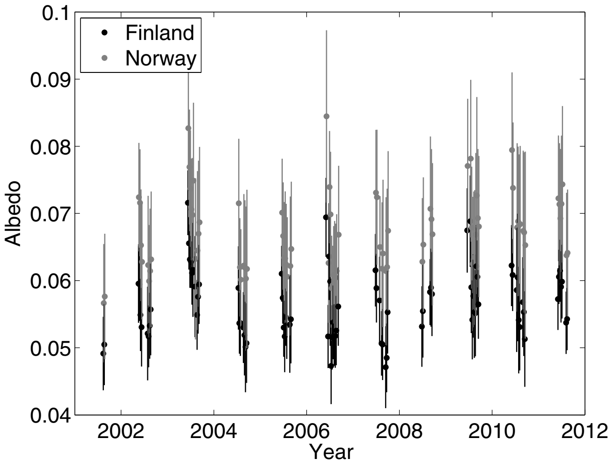

FIGURE 6. The mean and standard deviation of shortwave albedo calculated from the MODIS MCD34A1 product following Schaaf et al. (2002) for Finnish and Norwegian sides of a *Cladonia* disturbance gradient along a border fence.

NORWAY/FINLAND BORDER FENCE: MODIS

Mean MODIS albedo was significantly higher on the Norwegian side of the border fence (0.071) than the Finnish side of the border fence (0.061) during all snow-free periods in the measurement record ($p < 0.05$; Fig. 6).

Across all quality-controlled MODIS pixels (2001–2011), snow-free nighttime LST on the Norwegian side of the border fence (LST_{Norway} 3.2 ± 4.5 °C) was significantly higher than all values from the Finnish side of the fence ($\mathrm{LST}_{Finland}$ 2.5 ± 4.3 °C). Mean nighttime LST_{Norway} was significantly higher than nighttime $\mathrm{LST}_{Finland}$ during 25 of the 63 MODIS observations with sufficient number of pixels that passed quality control criteria to compute statistics, and mean nighttime $\mathrm{LST}_{Finland}$ was significantly higher than mean nighttime LST_{Norway} during 7 of the 63 MODIS observations.

A sufficient number of daytime LST MODIS pixels to support statistical analyses were available on only 14 instances during snow-free periods. The mean of all acceptable daytime LST observations were not significantly different between the Norwegian (6.4 ± 6.4 °C) and Finnish (6.9 ± 7.1 °C) sides of the fence. Mean daytime LST_{Norway} ($\mathrm{LST}_{Finland}$) was significantly higher than daytime $\mathrm{LST}_{Finland}$ on 2 of 14 occasions, and mean daytime $\mathrm{LST}_{Finland}$ was significantly higher than daytime LST_{Norway} on 2 of 14 occasions with sufficient number of pixels to compute statistics.

Discussion

SPHAGNUM FUSCUM

S. fuscum maintained cooler maximum T_{surf} than *P. schreberi* during most of the measurement record at Innoko, and maintained slightly cooler maximum T_{surf} than *C. rangiferina* during the dry early period (Fig. 2). The extremes of modeled G in *S. fuscum* were often larger than those of *C. rangiferina* and *P. schreberi* (Fig. 4), reflecting high potential values of k (O'Donnell et al., 2009). Although *Sphagnum* spp. associated with wetland ecosystems demonstrate large latent heat losses (Kim and Verma, 1996), latent heat flux is often lower than that of vascular plant species despite trivial resistance to latent heat losses (Vogelmann and Moss, 1993; Kim and Verma, 1996) due to the lack of active water transport from deeper layers to the surface (Oechel and van Cleve, 1986; Liljedahl et al., 2011).

Near infrared reflectance of *Sphagnum fuscum* measured in Abisko (Fig. 5) exceeded laboratory observations of other *Sphagnum* species made by Vogelmann and Moss (1993), which did not exceed 40% reflectance across the infrared wavelengths. Vogelmann and Moss (1993) demonstrated that *Sphagnum* spp. albedo is a function of moisture status by observing a strong increase in reflectance across the visible to near-infrared spectrum in *Sphagnum cuspidatum* during a drying experiment. Field-based spectroscopy in Abisko was made during favorable, well-watered periods during the growing season, and reflectance exhibited considerable variability among patches, which may have resulted from landscape position and moisture status. Measuring moisture status non-destructively in mosses and organic soils across both space and time is an ongoing technical challenge.

CLADONIA RANGIFERINA

C. rangiferina maintained a small gradient between $T_{1\mathrm{cm}}$ and $T_{5\mathrm{cm}}$ below the surface during the measurement period at Innoko compared to other study species (Fig. 3). The extremes of modeled subsurface heat flux were accordingly lower than that of both *S. fuscum* and *P. schreberi* (Fig. 4), noting that representative k values from *P. schreberi* were used here (O'Donnell et al., 2009). In actuality, the magnitude of G may be even lower if stagnant air layers, with a k of ca. 0.025 W m^{-1} K^{-1}, persist in the open areas underneath the *C. rangiferina* surface.

Cladonia species maintain a relatively high albedo when wet or dry (ca. 0.22 *versus* 0.155 for a mesic *Polytrichum juniperinum*–dominated meadow; Petzold and Rencz, 1975), such that R_n of *Cladonia*-dominated surfaces will be lower than that of surfaces with lower albedo, all else being equal. During dry periods, the *C. rangiferina* canopy was crisp to the touch, suggesting that latent heat losses were minimal. The relatively cool radiometric surface temperature of *C. rangiferina versus* that of *P. schreberi* suggests that H was likely lower if one assumes that radiometric and aerodynamic surface temperatures are approximately equal in uniform canopies and that boundary layer and atmospheric resistances to H in the low-statured mats are similar among species (Norman et al., 1995). In summary, R_n in *C. rangiferina* is lower than many other bryophyte and lichen species due to relatively large albedo, but less of this available energy is allocated to G than in the other species studied here. This leaves more energy available for surface heating than may have been expected given its high albedo.

PLEUROZIUM SCHREBERI

T_{surf} of *P. schreberi* often approached temperatures in excess of 50 °C during the dry period (Fig. 2), which meets or exceeds that thought to be damaging to the photosynthetic machinery in vascular plants in subarctic regions (Larcher, 1995) and lies above the long-recognized temperature optima for bryophytes and lichen photosynthesis (e.g. Lange, 1962; Kershaw, 1985). Optimum temperatures for net photosynthesis at light saturation in *Sphagnum* and feather moss species of interior Alaska is on the order of 10–15 °C during late June and on the order of 20–26 °C during mid-August (Skre and Oechel, 1981); the surface temperature of all species measured here meet or exceed these values during a dry period in late May (Fig. 2), noting the difference between leaf internal and surface temperature. T_{surf}, T_{1cm}, and T_{5cm} in *P. schreberi* were often greater than that of *S. fuscum* (Figs. 2 and 3), suggesting that bryophyte species composition, rather than mere presence/absence, plays an important role in the thermal budget of boreal and tundra soils. It is important to note that feather moss species are commonly associated with forest understories (Nilsson and Wardle, 2005) and avoid high radiation loads when shaded in these habitats.

NORWAY/FINLAND BORDER FENCE

T_{surf} (Fig. 2), G (Fig. 3), and albedo (Fig. 5; Petzold and Rencz, 1975) differ among bryophyte and lichen types. Bryophyte and lichen community composition thus may have implications for all energy flux terms in Equation 4, but it is unclear if community composition alone has a discernable impact on land surface characteristics of importance to climate. The Norway/Finland border fence offers a test of the role of bryophyte and lichen community structure in surface-atmosphere energy flux; *C. rangiferina* was for all intents and purposes removed by reindeer from the Finnish side of the fence by grazing management practices (Kayhko and Pellikka, 1994). *Cladonia* spp. and other lichen species are on the decline across the Arctic and subarctic (Joly et al., 2009), due in part to *R. tarandus* grazing pressure (Joly et al., 2007).

Albedo was consistently higher on the Norwegian side of the border fence during the snow-free season (Fig. 6) by ca. 0.01 on average. This figure may appear small, but a 1% difference is substantial given representative ranges of variability in forest albedo, which rarely exceed 0.2 or fall below 0.1 for deciduous forests during the growing season (Hollinger et al., 2010). From this point of view, a 1% change in albedo is approximately a 10% change over the possible ranges of albedo found in deciduous forests during the growing season. Obvious changes in reflectance across the visible bands (Kayhko and Pellikka, 1994) and significant changes to shortwave albedo (Figure 6) from *Cladonia* spp. presence is measurable from space.

From the Earth system perspective, changes to snow extent and duration or tree and shrub cover (Betts, 2000; Chapin et al., 2005; Hollinger et al., 2010) are likely to play a larger role in land surface albedo than changes to bryophyte and lichen community composition in subarctic ecosystems. For example, Euskirchen et al. (2009) found that changes in summer albedo of 0.6% over a 100 year post-fire successional trajectory in Alaskan boreal forests is associated with a -0.9 W m^{-2} decade^{-1} climate forcing, but a 4.3 W m^{-2} decade^{-1} forcing from projected changes in the length of the snow-free season to the year 2100 is predicted. Our observed 1% decrease in surface albedo with *Cladonia* spp. removal corresponds to a >1 W m^{-2} decade^{-1} decrease in climate forcing if these changes occur on the same time scales as those studied by Euskirchen et al. (2009). Bryophyte and lichen species composition may also play an important role in snow capture and melt; Street et al. (2011a) observed that patches of *Polytrichum* spp. at Abisko were the first to thaw in the spring on account of their microtopographical position on the tops of small ridges and their low albedo (Fig. 5). The small-scale patterns of snowmelt and albedo change, on the order of centimeters to meters, lie far below the spatial resolution of MODIS and most other remote sensing products.

Increases in vegetation greenness and shrub abundance have contributed to a net warming of the land surface in the Arctic (Jia et al., 2003; Chapin et al., 2005), but studies to date have only focused on vascular vegetation. Along the Norway/Finland border fence, LST_{Norway} was often higher than $\mathrm{LST}_{Finland}$, especially at night, suggesting a slight surface cooling from *C. rangiferina* overgrazing. These observations are consistent with the observation that T_{surf} of *C. rangiferina* was often higher than in *S. fuscum*, which can be explained in part by the reduced transport of heat to the subsurface in *C. rangiferina* (Figs. 3 and 4). In other words, the counterintuitive result that a decrease in albedo was accompanied by a decrease in LST can be understood by considering the entire surface energy balance (Equation 4) and differences in G between *Cladonia* spp. and other surface types. The finding that a decrease in albedo led to a decrease in LST is not unprecedented; studies of temperate forest management have found that darker forests maintain lower surface temperatures than brighter fields due to increases in latent and sensible heat flux (Juang et al., 2007). An early study by Kershaw (1978) found that the *Cladonia stellaris* phase of a post-wildfire lichen recovery time series had high albedo and large longwave radiation losses (related to T_{surf} via Equation 8) compared to post-burn surfaces and the climax *Stereocaulon paschale*, although both lichen species are characteristically white/off white. The energy balance, cool subsurface, and relatively warm surface of *Cladonia* spp. should be further investigated, especially with respect to its unique morphology, miniature white canopy, and important interaction with wildlife and reindeer herd management (Joly et al., 2007, 2009).

MODELING IMPLICATIONS

Our results demonstrate that the biophysical properties of different bryophyte and lichen species can impact surface-atmosphere and surface-subsurface energy flux to a degree that is relevant for climate forcing scenarios. Moss layers are commonly included in process-based models of arctic ecosystem function (e.g. BIOME-BGC; Engstrom et al., 2006; Engstrom and Hope, 2011) and are required for an accurate description of energy and water flux (Beringer et al., 2001). Correctly accounting for moss impacts on subsurface energy flux is critical for models of permafrost thaw; empirical evidence demonstrates that the presence of a moss layer can delay permafrost thaw by about a month in the high Arctic (Gornall et al., 2007), but the role of individual species on permafrost thaw has yet to be examined. Improving existing maps of plant communities in boreal, subarctic, and arctic ecosystems (e.g. Walker et al., 2005) to include estimates of moss and lichen species composition is a logical starting point for building species-level effects into ecosystem models.

Modeling the role of bryophyte and lichen species on ecosystem processes must also take into account multiple feedback processes that dictate high-latitude ecosystem change (Wookey et al., 2009). Bryophytes and lichens are generally expected to respond negatively to climate warming at subarctic latitudes, often due to shading by dwarf shrubs (Cornelissen et al., 2001; van Wijk et al., 2004; Walker et al., 2006; Wookey et al., 2009). Bryophyte cover has also increased in response to experimental warming and nutrient addition at high arctic latitudes (Gordon et al., 2001; Hudson and Henry, 2010). Improving the representation of vegetation, including non-vascular vegetation in climate and ecosystem models, is a complex and ongoing challenge that is critical for understanding vegetation-climate interactions in an era of global change.

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Albedo, T_{surf}, and G are important components of the surface energy balance (Equations 4–7) and can differ significantly among bryophyte and lichen species both temporally (e.g. Figs. 1 and 4) and spatially (e.g. Fig. 6). Future work should investigate the full surface energy balance across different bryophyte and lichen species, noting that partitioned energy flux measurements using radiometers (Equation 6) and G measurements using heat flux plates are likely to be more defensible than eddy covariance or Bowen ratio methodologies in most cases (Kim and Verma, 1996; Liljedahl et al., 2011), owing to the complex spatial structure of bryophyte and lichen communities (Asner et al., 2003). Furthermore, the open stature of *Cladonia* canopies may challenge conventional measurements of subsurface heat flux using soil heat flux plates if the instrument receives a direct solar radiation load under the miniature canopy. Regardless of methodological difficulties, understanding surface-subsurface and surface-atmosphere energy exchange in Arctic and subarctic ecosystems is a priority to better understand feedbacks between vegetation change, permafrost dynamics, and climate (Zimov et al., 2005; Chapin et al., 2008; Schuur et al., 2008).

Despite methodological challenges, careful remote sensing applications and detailed radiometric and micrometeorological measurements can offer insights into the role played by different bryophyte species in the energy budget of the land surface. We suggest that future research should explicitly consider species composition when studying the thermal budget of boreal and arctic ecosystems and corresponding heat flux into permafrost-dominated soils.

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