esa

ECOSPHERE

Snow cover, freeze-thaw, and the retention of nutrients in an oceanic mountain ecosystem

SONJA WIPF,[1,2,5,]† MARTIN SOMMERKORN,[1,6] MARC I. STUTTER,[1] E. R. JASPER WUBS,[3,4] AND RENÉ VAN DER WAL[3]

[1]*The James Hutton Institute, Craigiebuckler, AB15 8QH Aberdeen, Scotland, United Kingdom*
[2]*Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zurcherstrasse 111, 8903 Birmensdorf, Switzerland*
[3]*Aberdeen Centre for Environmental Sustainability (ACES), University of Aberdeen, School of Biological Sciences, Auris, 23 St. Machar Drive, AB24 3UU Aberdeen, Scotland, United Kingdom*
[4]*Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB Wageningen, The Netherlands*

Citation: Wipf, S., M. Sommerkorn, M. I. Stutter, E. R. J. Wubs, and R. van der Wal. 2015. Snow cover, freeze-thaw, and the retention of nutrients in an oceanic mountain ecosystem. Ecosphere 6(10):207. http://dx.doi.org/10.1890/ES15-00099.1

Abstract. As the climate warms, winters with less snow and therefore more soil freeze-thaw cycles are likely to become more frequent in oceanic mountain areas. It is a concern that this might impair the soil's ability to store carbon and nutrients, and lead to increased leaching losses of dissolved C and nutrients and subsequent changes in nutrient cycling and ecosystem productivity.

Through a combination of laboratory and field experiments, we studied short-term effects of changing winter conditions on carbon and nutrient leaching from two plant-soil systems with contrasting snow conditions (shallow/intermittent vs. deep/persistent snow). In the laboratory we exposed cores (soil and vegetation) from sites with either intermittent or persistent winter snow cover to five different freeze-thaw scenarios of realistic frequency and duration. Additionally, we set up a transplant experiment at our field site by reciprocally transplanting soil-plant monoliths between sites with intermittent and persistent snow. Together, the field and laboratory experiments aimed to assess how carbon and nutrient leaching was affected by both historical snow conditions and short-term (through freeze-thaw scenarios and transplantation) changes in snow cover and thermal conditions.

Both a greater number of freeze-thaw cycles and longer duration of sub-zero temperatures increased carbon and nutrient leaching from incubated soil cores. Cores from sites with persistent snow generally had lower nutrient losses under control conditions, but greater losses following induced freeze-thaw cycles than cores from intermittent snow sites. The character of the leached dissolved organic carbon (DOC) suggested fresh organic material, such as live plant roots or microbes, as the source of carbon and nutrients. Nutrient losses from the plant-soil systems in the field were greater at sites with persistent winter snow due to greater volumes of percolating water in spring. This suggests that increasingly severe and frequent soil freeze-thaw events in oceanic mountain ecosystems can enhance the mobilization of C, N and P in labile forms but, in the absence of water fluxes, these nutrients would remain available for in-situ cycling. Thus, under future warmer winter conditions, increased carbon and nutrient losses from oceanic mountain ecosystems could occur if winters with little snow coincide with wet spring conditions.

Key words: climate change; freeze-thaw cycles; moss-sedge heath; nutrient leaching; oceanic mountain range; *Racomitrium lanuginosum–Carex bigelowii;* snow cover; winter ecology; winter soil temperatures.

Received 19 February 2015; revised 14 May 2015; accepted 2 June 2015; **published** 29 October 2015. Corresponding Editor: N. Barger.

[5] Present address: WSL Institute for Snow and Avalanche Research SLF, Fluelastrasse 11, 7260 Davos Dorf, Switzerland.
[6] Present address: WWF Global Arctic Programme, P.O. Box 6784 St. Olavs Plass, 0130 Oslo, Norway.
† **E-mail:** sonja.wipf@slf.ch

Introduction

Increasing winter temperatures and decreased snowfall have been recorded in many mountain regions of the world (IPCC 2013). In many continental mountain ranges with cold winter climate, under projected winter warming most of the precipitation will continue to fall as snow (Knowles et al. 2006, Serquet et al. 2013). In oceanic and temperate mountain ranges (Type C of the Köppen-Geiger climate zones; Kottek et al. 2006) however, thinner and intermittent snow cover is predicted, attributed to more frequent warming spells and an increasing proportion of winter precipitation falling as rain (Brown and Mote 2009, McCabe and Wolock 2010). Decreasing amounts of snowfall and more frequent thaw result in shallow or absent snow cover during extended winter periods (Harrison et al. 2001, McCabe and Wolock 2010). Without insulating snow cover, soil temperatures follow fluctuating air temperatures more closely, leading to greater temperature variability and soil freeze-thaw cycles (Isard et al. 2007, Henry 2008, Robroek et al. 2013). Hence, in oceanic and low temperate mountain ranges, rising winter temperatures are expected to lead to harsher and more variable winter conditions for the plant-soil system.

Freezing and subsequent thawing of soils has large effects on below-ground processes, for instance by physically disrupting soil aggregates (Unger 1991) and plant roots (Tierney et al. 2001, Kreyling et al. 2012), or by lysing microbial cells and therefore decreasing the microbial biomass (De Luca et al. 1992, Yanai et al. 2004, Freppaz et al. 2007). Soil freezing also greatly reduces microbial activity, directly via soil temperatures and water availability, and indirectly through its impact on substrate availability and use by microbes (Mikan et al. 2002, Grogan et al. 2004, Björkman et al. 2010, Kim et al. 2012). Both the severity (i.e., length and minimum temperature) of frost events and increased frequency of soil freeze-thaw cycles are known to have strong effects on below-ground processes, such as microbial and root turnover, as well as gaseous and dissolved carbon and nitrogen losses (see Edwards et al. 2007, Henry 2007, Matzner and Borken 2008, Brooks et al. 2011, and Blankinship and Hart 2012 for reviews or meta-analyses). However, even at temperatures below zero centigrade soil contains a complex mixture of frozen particles and liquid water films, which allow for microbial activity (Mikan et al. 2002, Panikov et al. 2006, Öquist et al. 2009). A decrease in snow cover across large areas together with the linked greater frequency of soil freeze-thaw cycles may impair nutrient retention of soils and increase losses of carbon, nitrogen and phosphorus at thaw. As well as affecting the functioning of mountain ecosystems in-situ, increased losses of nutrients from mountain soils will affect the quality of runoff water in headwaters with implications for downstream receiving waters, both in terms of aquatic ecosystem processes and drinking water quality (Edwards et al. 1986, Brooks et al. 1999, Fitzhugh et al. 2003, Haei et al. 2010).

The majority of studies investigating the effects of changed winter climate on soil biogeochemistry have focused on arctic, boreal or alpine sites (reviews cited above, but see e.g., Kreyling et al. 2011, Groffman et al. 2012, Robroek et al. 2013), where the predicted changes in winter climate mostly result in temperatures overall less cold, but remaining below zero centigrade (Sturm et al. 2005, Isard et al. 2007). Across the widespread oceanic mountain regions, however, the impact of winter climate change and increased freeze-thaw cycles on ecosystem processes remains poorly understood. In the oceanic mountains of the Scottish Highlands, winters have become markedly milder and days with snow cover sparser in recent years (Harrison et al. 2001, Barnett et al. 2006, Van der Wal et al. 2011). Using combined field and laboratory incubation experiments we investigated how this decline in snow cover affects soil temperatures and their variability, nutrient mobilization and nutrient losses from an oceanic mountain ecosystem. To assess how carbon and nutrient leaching was affected by both historical snow conditions and short-term changes, we used a snow fence site, comparing and transplanting plant-soil monoliths between the lee-side of the fence (having experienced 20 winters with deep and persistent snow) and adjacent locations with shallow and intermittent snow in winter. Our hypothesis was that sub-zero soil temperatures mobilize C, N and P in soils, which could potentially be leached, and that such nutrient losses would increase with freeze-thaw cycle frequency. We

Table 1. Vegetation composition and soil characteristics at locations with contrasting snow regimes near and away from the snow fence. Species composition was recorded as % cover (mean ± SE) on 0.3 × 0.3 m on each of 32 subplots. Poaceae comprise the grass species *Agrostis capillaris*, *Avenella flexuosa* and *Festuca ovina*. Other vascular plants comprise *Galium saxatile, Vaccinium myrtillus* and *V. uliginosum*. The pH of humic H horizon material was measured as 1 g soil in 18 ml water, and organic matter content as loss on ignition at 550°C for 1 hour, indicated as g C per kg soil ($N = 5$ per system; mean ± SE).

Variables	Near snow fence	Away from snow fence
Snow cover conditions	deep, persistent	shallow, discontinuous
Species composition		
Dicranum fuscescens	76.0 ± 4.2	0.3 ± 0.2
Racomitrium lanuginosum	1.1 ± 0.5	93.1 ± 3.4
Carex bigelowii	13.5 ± 2.5	25.1 ± 6.5
Poaceae	36.1 ± 5.5	0.5 ± 0.3
Other vascular plants	1.4 ± 1.8	0
Litter	13.9 ± 4.1	3.4 ± 0.6
Soil pH_{water}	5.0	4.5
Organic matter content	411 ± 36 g kg^{-1}	545 ± 41 g kg^{-1}

further predicted that plant-soil systems with a history of deep and persistent snow would sustain greater nutrient losses from induced freeze-thaw cycle events than those with a history of shallow and intermitted snow.

Methods

Study site

We conducted field experiments on, and obtained samples for laboratory experiments from, Glas Maol (1068 m a.s.l.), a summit plateau in the south-eastern part of the Grampian Mountains, East Scotland, UK (56°53′ N, 3°22′ W). Glas Maol is covered by *Racomitrium lanuginosum–Carex bigelowii* moss-sedge heath (U10b in Averis et al. 2004) growing on alpine podzols over graphite schists (Appendix: Table A1). The site's summer climate is cool and moist, with large amounts of occult precipitation (Pearce et al. 2003). Snow may fall between October and May, but depending on topography, snow cover remains shallow and intermittent in high-altitude and exposed sites due to strong winds, while more protected sites experience mostly persistent snow cover over winter (Dunn et al. 2001). Periodic warm spells and rain can therefore cause large areas to become snow-free at any time in winter. Glas Maol was selected because of the occurrence of snow fences that allowed investigation of the relationships between winter snow regimes, freeze-thaw cycles and nutrient run-off at a single site. To accumulate wind-drifted snow, and therefore make skiing conditions more reliable, 1.3 m tall snow fences (Fig. 1a) were constructed along ski runs in 1986 by the local resort Glenshee. Subsequently, increased snow depth and duration of snow lie, combined with enhanced sheep-grazing during parts of the summer (a side effect of the fences, Scott et al. 2007), have transformed the *Racomitrium lanuginosum–Carex bigelowii* moss-sedge heath in the vicinity of the snow fence into a system dominated by the shallower moss *Dicranum fuscescens* and grasses (Welch et al. 2005; Table 1).

Snow cover in the Scottish mountains has clearly declined since the erection of the snow fences in 1986 (Barnett et al. 2006), but the persistence of snow cover in any one year depends on both the amount of snow fall and subsequent redistribution by frequent strong winds (e.g., Dunn et al. 2001). No time series for snow cover exist for our study site; nearby Mount Cairngorm (1245 m), however, exhibited snow with >50% ground cover on 91 days per year (average 1964–2006), with a declining trend in number of days since the 1960s (Munro 2008). Snow days in winter (December–February) decreased by 43% since the 1980s, leaving plant-soil systems exposed to direct temperature effects more frequently and for longer periods of time (Munro 2008). In a future warmer climate snow cover is likely to become even less persistent as a higher proportion of winter precipitation is predicted to fall as rain instead of snow (Harrison et al. 2001). Our snow fences maintained snow cover throughout winter, thereby

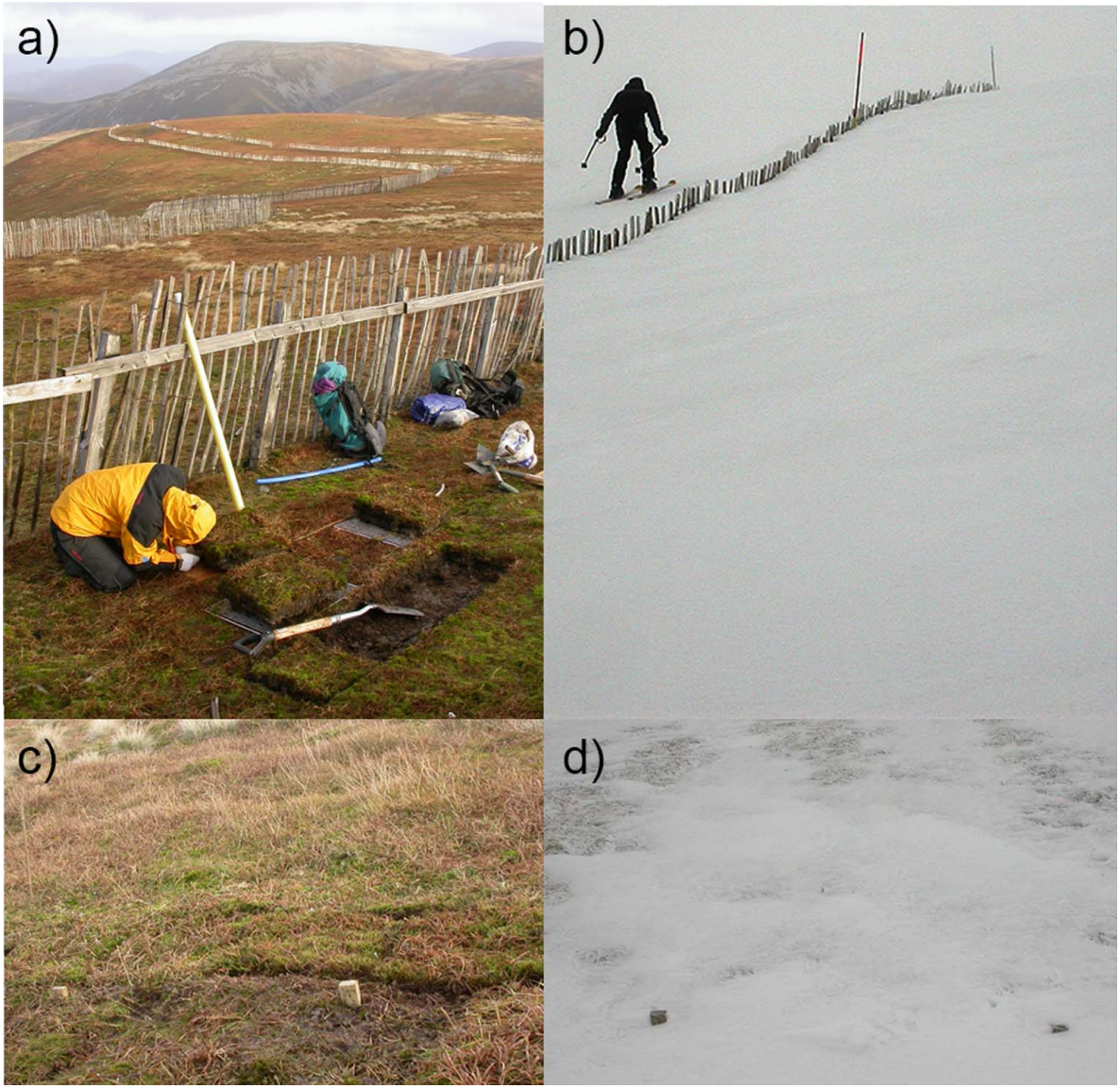

Fig. 1. Locations along the snow fence (a, b) and approx. 40 m away from the snow fence (c, d) in October 2006 (a, c; during setup of the transplant experiment) and January 2008 (b, d). As reference: the height of the snow fence is 130 cm, the height of the plot markers (c, d) 10 cm.

serving as a proxy of snow conditions of the past, whilst areas away from the fence will increasingly have lacked snow cover. The winter 2006/07 in which we conducted our field experiment was one of the mildest on record with monthly mean temperatures constantly above, and snow cover considerably below the long-term average (Met Office 2008, Van der Wal et al. 2011). Therefore, during the study period, the region may have experienced conditions similar to those projected for the future (see Fig. 1d for snow conditions in mid-winter).

Field experiment

To quantify short- and longer-term ecosystem responses to changed snow and freeze-thaw cycle regimes, we established a reciprocal transplant experiment of intact soil-plant monoliths between locations with either deep and persistent, or shallow and intermittent snow in late

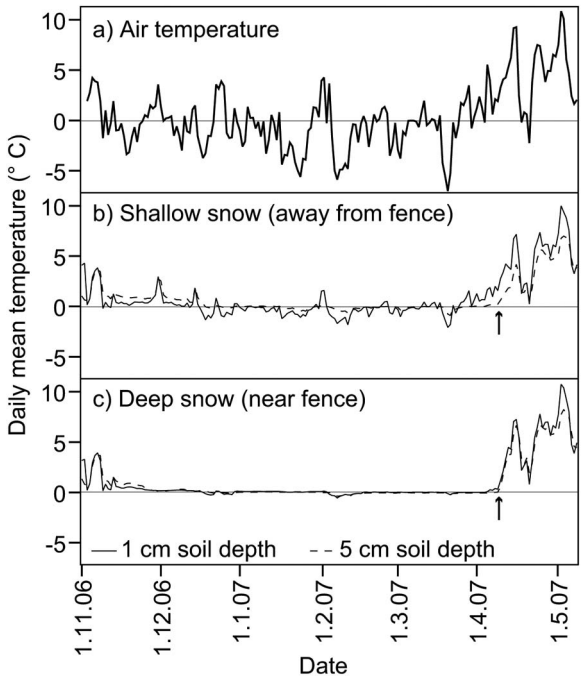

Fig. 2. Temperature course over the winter 2006/2007: (a) air temperatures (measured 1 m above ground) and (b) soil temperatures below shallow snow and (c) below deep snow at 1 cm (solid line) and 5 cm below soil surface (dashed line). Shown are averages of daily means across all plots calculated from hourly measurements. Vertical arrows denote the start of field sampling for soil solutes with passive lysimeters.

October 2006. We chose eight pairs of plots between 980 and 1020 m a.s.l. along a snow fence (outside of the skied area) on the north slope of Glas Maol; each pair comprised one plot with a 20 year history of increased snow depth (at 1.5 m distance from the snow fence; Fig. 1a) and one plot unaffected by the fence (at approx. 40 m distance). Pairs of plots were located in patches with homogeneous vegetation composition and were at least 50 m apart. Within each pair, we transplanted two soil-plant monoliths from one plot to the other (from away to near the snow fence and vice versa) to expose them to a contrasting snow regime. This was accomplished by cutting monoliths of 0.4×0.4 m to a depth of 15 cm with a spade, carefully placing them onto plywood boards, and moving them to their new locations. To control for the effect of transplanting, two monoliths of the same size were transplanted within the plot. In total, we established 8 plot pairs $\times$ 2 snow depth regimes (per pair) $\times$ 2 transplants = 32 subplots.

To characterize winter soil temperatures (Fig. 2) and determine the magnitude and frequency of freeze-thaw cycles at the study site, miniature temperature loggers (iButtons, Maxim, Sunnyvale, California, USA) were installed at 1 cm and 5 cm below the moss-soil interface in each subplot during set-up of the field experiment. Air temperature was logged at two places along the snow fence at 1 m above ground by temperature loggers shaded from direct sunlight. As a proxy for how microbial activity at the soil surface was influenced by the snow cover regime, we determined over-winter decomposition rates by measuring litter mass loss between early November 2006 and early May 2007 using nylon mesh bags (1 mm mesh on the upper side, 0.5 mm on the lower side) fixed to the surface of each subplot and filled with 1g of dry *Carex bigelowii* leaf litter collected on site in October 2006. Six of the 32 bags had been displaced and were excluded from analysis.

To determine the influence of winter snow conditions on nutrient losses following snow melt, passive (zero-tension) lysimeters were installed in all experimental subplots. Lysimeters consisted of a 15×10 cm plastic tray with a 1 cm rim that had an opening on one short edge in which a silicon tube was fitted that connected to a 500 ml PE bottle. The trays were inserted between the organic and mineral soil layer (4–6 cm below the soil surface) during transplanting in October 2006. The bottles were installed on April 10 (i.e., when weather conditions allowed us to reach the site), immediately after, and approximately a fortnight after, snow had disappeared along and away from the fence, respectively. Soils were still mostly frozen at this point, limiting potential nutrient leaching prior to sampling. Soil water was sampled monthly (May 7, June 1, July 9, and August 17, 2007), volumes determined, filtered to <0.45 μm and frozen until further analysis (see below).

Soil sampling and laboratory freeze-thaw treatments

Laboratory experiments were set up to investigate impacts of freeze-thaw scenarios on nutri-

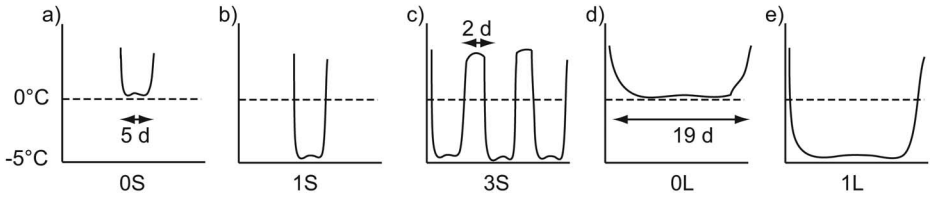

Fig. 3. Freeze-thaw treatments applied in the laboratory to cores from two systems with different snow regimes: (a) 0S–short (5d) control cycle at 0.5°C; b) 1S–short (5d) freeze-thaw cycle; c) 3S–three consecutive short (5d) freeze-thaw cycles interrupted by 2d thawing phases at 5°C; (d) 0L–long (19 d) control cycle at 0.5°C; and (e) 1L–long (19 d) freeze-thaw cycle. $N = 50$ (5 cores per treatment and system).

ent retention in microcosms from sites with different snow cover history. We took great care to avoid common weaknesses of freeze-thaw experiments (Henry 2007), such as inappropriate timing of soil sampling (i.e., summer instead of early winter), exaggerated rates of temperature change and unrealistic amplitudes of freeze-thaw cycles. Also, we worked with intact soil cores rather than homogenized soil, as the latter excludes plant-soil interactions and involves severe disruption of microbial communities and hence artificial carbon and nutrient losses. Samples were collected in early winter before snow cover formation (6 November 2007) when soil biota are less sensitive to cold temperatures than in summer (Lipson et al. 2000). We sampled 25 cores from five locations with persistent snow in winter (near the snow fence) and a further 25 cores from five locations with transient snow (away from the snow fence); all were in the immediate vicinity of our transplant plots. Stainless steel rings, 6 cm in diameter and 6 cm high, were pressed into the ground until flush with the compressed moss surface. Cores were extracted with minimal disruption to soil structure, their base sealed with parafilm and stored to equilibrate in plastic bags at 4°C for two weeks prior to experiments.

The cores were exposed to temperature scenarios simulating the temperatures, rates of temperature change and number of freeze-thaw cycles observed at our persistent and intermittent snow locations in the field (Fig. 2). Using thermostat-regulated growth cabinets (operating without lights) we incubated the cores within rings at the following five temperature regimes (Fig. 3): One short freeze-thaw cycle (1S) and its respective unfrozen control treatment (0S), three consecutive short freeze-thaw cycles (3S), one long freeze-thaw cycle (1L) of the same total duration as 3S, and its respective unfrozen control (0L). Cores were fitted into extruded polystyrene foam so that freezing would proceed from the top downwards, as in the field. The lengths of the individual freeze-thaw cycles were 5 days for 1S, 19 days for 1L, and 3×5 days interrupted by two 2-day thawing phases for 3S. At the start of each freezing phase, the temperature was gradually lowered at a rate of approximately 0.5°C per hour until reaching −5°C, where held constant for the duration of the phase, and resulting in soils freezing within 2 days. During thawing phases and at the end of the incubation, cores were kept at 5°C with the bottom insulation removed, frozen soils thus thawing from top and bottom. Control treatments were kept at a constant temperature of 0.5°C (Fig. 3a, d). We used a replication level of five ($\times$ 5 treatments $\times$ 2 snow regimes = 50 cores).

Soil respiration, leaching and soil solutions

Two days after the incubations (approximately 24 h after final thawing of frozen cores), we measured ecosystem respiration of each core once by quantifying the rate of CO_2 emitted by the core in a dark chamber connected to an infrared gas analyzer (EGM-4, PP-systems, Hitchin, UK). To quantify nutrient mobilization and thus potential nutrient loss induced by freeze-thaw cycle treatments, we simulated an extreme rain event by dripping pH-adjusted water (0.001 M NaCl) at 11 ml/h onto the centre of each core overnight (corresponding to 42 mm of rainfall in ~16 hours), and collected the leachate. The percolated solution was quantified, filtered to <0.45 μm (Millipore cellulose nitrate filters) and analyzed within 48 hours for different N and P forms and DOC. NO_3-N, NH_4-N and

soluble reactive P (SRP) were measured by automated colorimetry, then total dissolved N (TDN), total dissolved P (TDP) and dissolved organic C (DOC) subsequently following an automated UV/persulphate digestion step (Skalar, San++, Breda, NL). Dissolved organic N and P (DON and DOP) were calculated as: DON = TDN − (NO_3-N + NH_4-N); and DOP = TDP - SRP. UV absorbance was determined at $\lambda = 285$ nm wavelength (UV240 spectrometer, Shimadzu, Kyoto, Japan) and normalized to the concentration of DOC to give specific UV absorbance (SUVA-285; L mg^{-1} m^{-1}) as an index of its aromaticity. High SUVA values result from more aromatic DOC indicative of humic soil origins, whereas low SUVA (i.e., less aromatic) values suggest simpler aliphatic structures of more recent biological origin (Chin et al. 1994). The same analyses were performed for all lysimeter samples collected in the field.

Statistical analyses

We used linear mixed models with restricted maximum likelihood to test for differences in nutrient fluxes and concentrations between snow regimes (persistent vs. intermittent snow), freeze-thaw treatments and interactions between them. In the laboratory experiment, we used sampling site as a random effect and snow regime and freeze-thaw treatment as fixed effects. Specific contrasts were formulated to test for differences between the effects of one short freeze-thaw cycle treatment and its unfrozen control treatment (1S vs. 0S), between one long freeze-thaw cycle treatment and the respective control treatment (1L vs. 0L), between one short and three short freeze-thaw cycles (1S vs. 3S), and between one long and three short freeze-thaw cycles (1L vs. 3S). In the field experiment, we used plot pair as a random effect, and monolith origin (persistent or intermittent snow) and plot location after transplant (adjacent to/away from fence) as fixed effects. Analyses were performed in R 2.7.1 using the nlme library (Pinheiro et al. 2012).

Results

Environmental conditions at the field site

Soil temperatures in plots experiencing unmanipulated snow conditions (away from the fence) remained above 0°C until mid-December, when soil temperatures dropped below zero. Until March, four warm spells (i.e., two or more consecutive days with air temperatures above 0°C) were recorded, followed by cold spells with air temperatures as low as −8°C (Fig. 2a). During and after the warm spells, soil temperatures in plots away from the fence closely followed the course of the air temperature (Fig. 2a, b), suggesting that snow cover was lacking for extended periods during winter. During these, the surface soils went through at least three low-temperature events, one of which was intense enough to affect deeper soil layers (i.e., loggers at 5 cm soil depth indicated sub-zero temperatures). In plots along the snow fence (Fig. 2c), soil temperatures decreased to 0°C by late November, suggesting accumulation of snow. The snow remained sufficiently deep for most of winter to decouple air and soil temperatures. Soil surface temperatures reached a minimum of −1°C in some plots after two warm spells, suggesting that snow cover had partly melted, but temperatures returned to 0°C within days and deeper soil layers remained at temperatures >0°C at 5 cm soil depth.

Laboratory freeze-thaw cycle experiments: carbon fluxes

Cores from locations with both deep and shallow snow that were subjected to freeze-thaw cycles similar to those measured at the field site showed significant differences in gaseous carbon losses among freeze-thaw cycle treatments ($F_{4,32} = 17.6$, $P < 0.0001$; Fig. 4). In comparison to unfrozen controls (0S and 0L), respiration rates were almost doubled after one short (1S) or one long (1L) freeze-thaw cycle treatment, respectively (all $P < 0.0001$; Fig. 4, top panels). However, three consecutive freeze-thaw cycles (3S) decreased respiration rates compared to one short or one long freeze-thaw cycle (1S: $F_{1,32} = 13.2$, $P = 0.001$ and 1L: $F_{1,32} = 6.1$, $P = 0.019$), especially in cores from locations with shallow snow (Fig. 4).

The increased respiration rate in response to freeze-thaw cycles was likely fuelled by a higher quantity of labile dissolved organic carbon (DOC) available to soil microbes. The DOC leachate concentrations more than doubled after one short freeze-thaw cycle (1S) compared to the

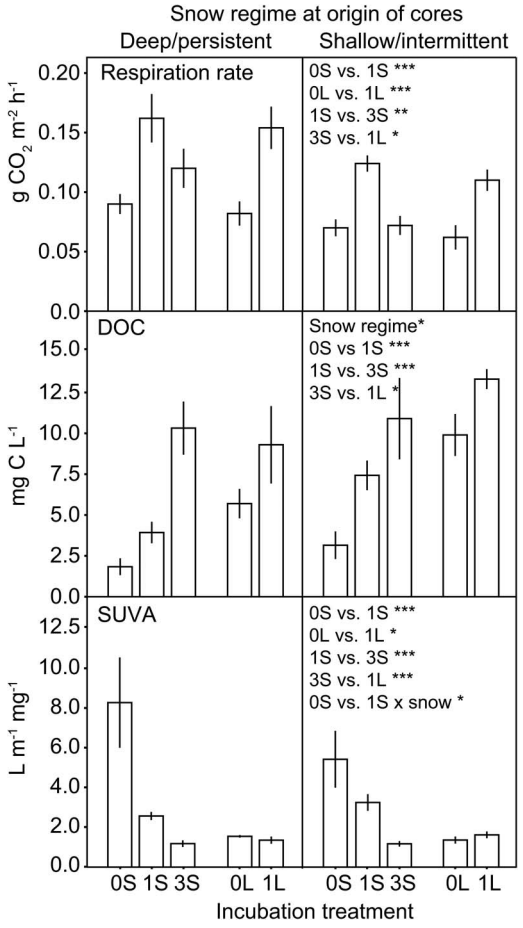

Fig. 4. Respiration rates, DOC concentrations (dissolved organic C) and specific UV absorbance (SUVA) of leachate from cores sampled at locations with contrasting winter snow cover and exposed to different freeze-thaw cycle regimes (see Fig. 3 for treatments). Bars show means of 5 cores per site of origin and treatment ± SE. Significant differences between snow regimes and pre-defined contrasts are given as *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

0S control treatment (+128%, $F_{1,32} = 18.3$, $P < 0.001$; Fig. 4). Three short freeze-thaw cycles (3S) strongly increased DOC loss compared to one short cycle (1S) (by 87%; $F_{1,32} = 28.8$, $P < 0.0001$), becoming similar to that observed for one long freeze-thaw treatment (1L; Fig. 4). Longer incubation (0L, 1L and 3S) generally induced higher DOC leachate concentrations than shorter incubation, but treatment differences were not statistically significant (Fig. 4). Multiple freeze-thaw cycles, as well as longer incubation periods, lowered specific UV absorbance (SUVA), indicating that the DOC released was of less aromatic character under these conditions. The leachate of 0S cores showed markedly high concentrations of aromatic DOC (Fig. 4), with SUVA more than twice that of 1S cores, and more than four times that of 0L, 1L, and 3S cores (all $P < 0.0001$; Fig. 4).

When comparing treatment responses between snow regimes, respiration rates under controlled laboratory conditions were generally found to be higher in cores originating from deep snow sites compared to those from shallow snow sites ($F_{1,8} = 10.0$, $P = 0.013$; Fig. 4), but DOC concentrations and DOC character (SUVA) did not differ between the snow regimes. As hypothesised, cores from sites that were historically protected against freeze-thaw cycles by a thick snow layer were more sensitive to freeze-thaw-induced DOC losses in the laboratory (freezing treatments vs. control treatments: +108% in cores from deep snow but +62% in cores from shallow snow sites).

Laboratory freeze-thaw cycle experiments–N and P fluxes

Compared to DOC, leaching losses of nitrogen and phosphorus generally showed greater variability within treatments (see greater error bars in Fig. 5 vs. Fig. 4). Total dissolved N (TDN) leaching was enhanced by 188% compared to controls after one short freeze-thaw cycle (0S vs. 1S; from 1.1 to 3.2 mg N l^{-1}; $F_{1,32} = 16.2$, $P = 0.0004$). TDN leaching was further increased by three consecutive short freeze-thaw cycles (3S vs. 1S; $F_{1,32} = 6.5$, $P = 0.007$). There was a tendency for one single long freezing event (1L) to increase TDN concentrations compared to controls (0L to 1L; on average from 2.1 to 3.0 mg N l^{-1}) but not significantly so ($F_{1,32} = 2.2$, $P = 0.15$). Generally, different N forms were released from the soil cores in different amounts (NO_3-N > NH_4-N > DON), but patterns differed somewhat among freeze-thaw treatments and snow cover regimes. In cores from deep snow locations, increasing freeze-thaw frequency appeared to mobilize increasing amounts of all three N-compounds. Yet, DON, NO_3-N and NH_4-N leaching from shallow snow locations did not significantly increase with multiple, compared to single freeze-thaw cycles.

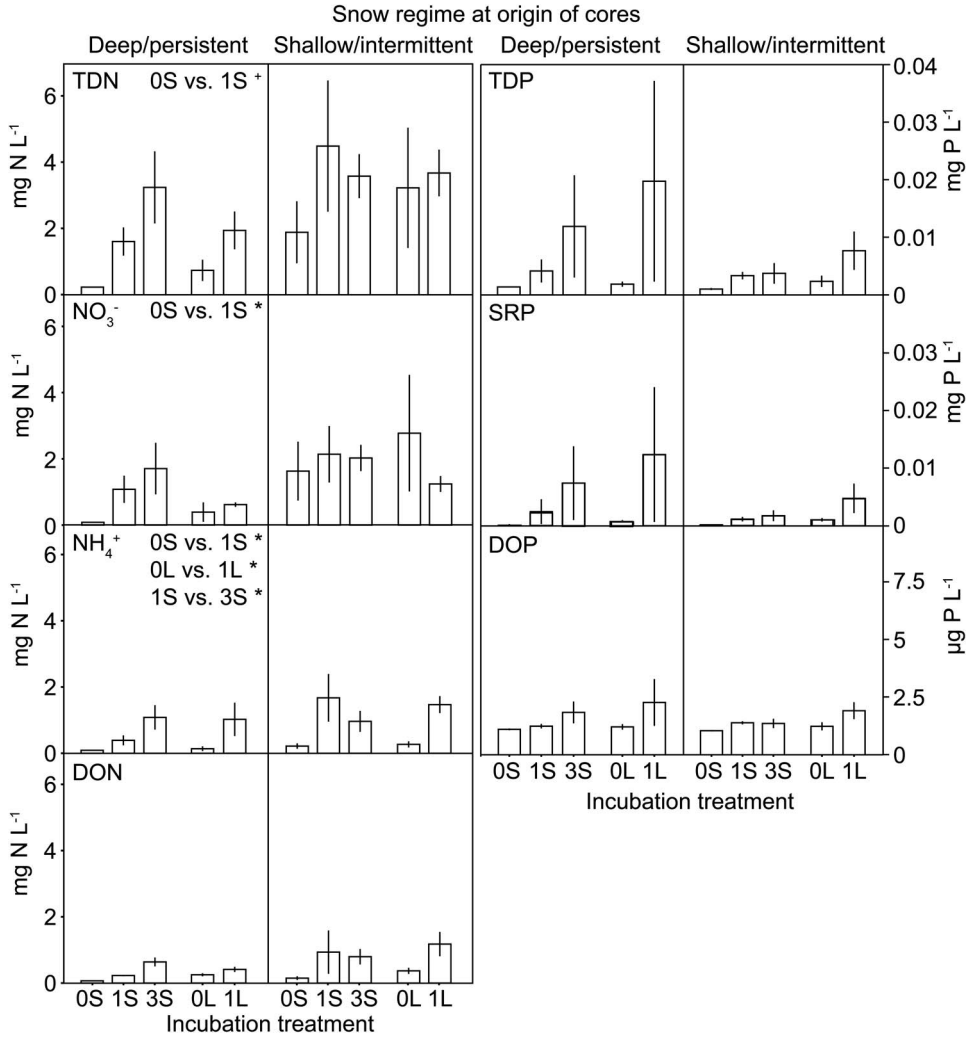

Fig. 5. Concentrations of N forms (total dissolved nitrogen (TDN), nitrate (NO_3^-), ammonium (NH_4^+) and dissolved organic N (DON)) and P forms (total dissolved P (TDP), solubilized reactive P (SRP ≈ phosphate), and dissolved organic P (DOP)) in leachate from cores sampled at sites with contrasting winter snow cover and exposed to different freeze-thaw cycle regimes (Fig. 3 for treatments). Significant differences between snow cover and pre-defined contrasts between incubation treatments are given as * $P < 0.05$, and $^+P < 0.1$.

Leachate phosphorus concentrations (Total P, dissolved organic P and phosphate) differed strongly between the two snow regimes (Fig. 5) and were generally far greater from cores originating from deep than shallow snow locations. Although mean concentrations suggested that cores from deep snow locations were more sensitive to freeze-thaw events than those from shallow snow locations, none of these apparent differences were statistically significant due to large variation within treatments.

Cores from unfrozen controls and longer duration treatments lost slightly more water during incubation (as evidenced by soil mass changes) and subsequently produced less leachate during leaching. However, results for carbon and nutrient fluxes were very similar as for concentrations (Appendix: Table A2).

Nutrient fluxes in the field experiment

Patterns of over-winter litter mass loss of *Carex bigelowii* illustrate that at the soil surface in-situ

conditions for decomposition were impaired by the lack of snow cover. The litter mass loss rates were 26% lower in plots with shallow snow compared to deep snow (7.4% vs. 10.0% of the overall litter mass was decomposed; $F_{1,7} = 12.6$, $P = 0.009$). There was no significant difference in decomposition rates between subplots originating from locations with different snow regimes (i.e., with different vegetation type; $F_{1,7} = 2.4$, $P = 0.18$). Despite a measurable impact of winter snow regime on decomposition at the surface, there were few effects on soil nutrient concentrations or fluxes observed in the field. Initially, total N (TDN) concentrations derived from in-situ lysimeters were slightly greater from monoliths transplanted from deep to shallow snow locations compared to other monoliths (Sampling date × community type × location: $F_{3,60} = 2.5$, $P = 0.066$; Appendix: Fig. A1), which may indicate a negative effect of freeze-thaw cycles (Fig. 2) on the nutrient holding capacity of a system adapted to deep snow. Throughout the lysimeter sampling period following snowmelt (May–Aug), however, monoliths originating from shallow snow locations lost approximately 3–6 × more nutrients and carbon when transplanted to the fence than when transplanted within their location of origin, while there was no such effect on monoliths originating from microhabitats with deep snow (Fig. 6). Overall, these patterns of nutrient fluxes were strongly driven by plot hydrology: the more water leached through the monoliths, the more nutrients were lost over the season (strong and significant relationships between amount of water and nutrient losses; $R = 0.57–0.94$; $P < 0.05$ for all compounds; Fig. 6; Appendix: Fig. A1).

Discussion

Through a combination of laboratory and field experiments, we demonstrated that over-winter freeze-thaw cycles occur under shallow and intermittent snow cover at an oceanic temperate mountain site, and that these have the potential to enhance the mobilization of C, N and P into labile form. Importantly, such freeze-thaw induced losses (determined in laboratory experiments that employed freeze-thaw cycles of realistic magnitude and frequency) were greatest in plant-soil systems that originated from sites with deep and persistent over-winter snow cover. However, field measurements during the subsequent growing season indicated that a location's specific water fluxes eventually determine nutrient loss from oceanic mountains.

Most previous field and laboratory studies found that soils from cold biomes exhibit increased mobilization and losses of carbon and nutrients when exposed to freeze-thaw (see Matzner and Borken 2008, and Brooks et al. 2011 for reviews), but there is large variability between different nutrient forms and sites. In our incubation study, freezing and subsequent thawing enhanced mobilization and created similar response patterns across all C, N and P compounds studied (Figs. 4 and 5). Several other experimental studies with soils from temperate ecosystems reported similar freeze-thaw induced increases in DOC, DON and NH_4^+ fluxes (Fitzhugh et al. 2001, Austnes and Vestgarden 2008, Reinmann et al. 2012, but see Hentschel et al. 2008), whilst NO_3^- or total nitrogen fluxes were unaffected or decreased after freezing-thawing. Brooks et al. (2011) suggest a strong coupling of carbon and nutrient cycling during winter and spring, and different mechanisms that could influence their interaction and cause varying patterns. For instance, increased DOC mobilization can increase NO_3^- immobilization or denitrification, or reduced oxygen diffusion in frozen soils could enhance denitrification. Part of the observed variability in response to freeze-thaw among studies will be due to how such biological factors play out in the various studied ecosystems (due to differences in edaphic and climatic conditions). However, we suspect that differences in methodology (see below) are a strong driver of apparent contradictions between studies, as observed for freeze-thaw induced fluxes of different nutrient forms.

There is also disparity among studies in terms of how nutrient cycling responds to the number and magnitude of freeze-thaw cycles. For example, for DOC, DON and NH_4^+ mobilization our incubation experiment revealed remarkably similar patterns between several consecutive short and one single long freeze-thaw cycle of the same duration. By contrast, in three Norwegian mountain sites (Vestgarden and Austnes 2009), DOC, DON and NH_4^+ leaching did not greatly increase after multiple freeze-thaw cycles compared to

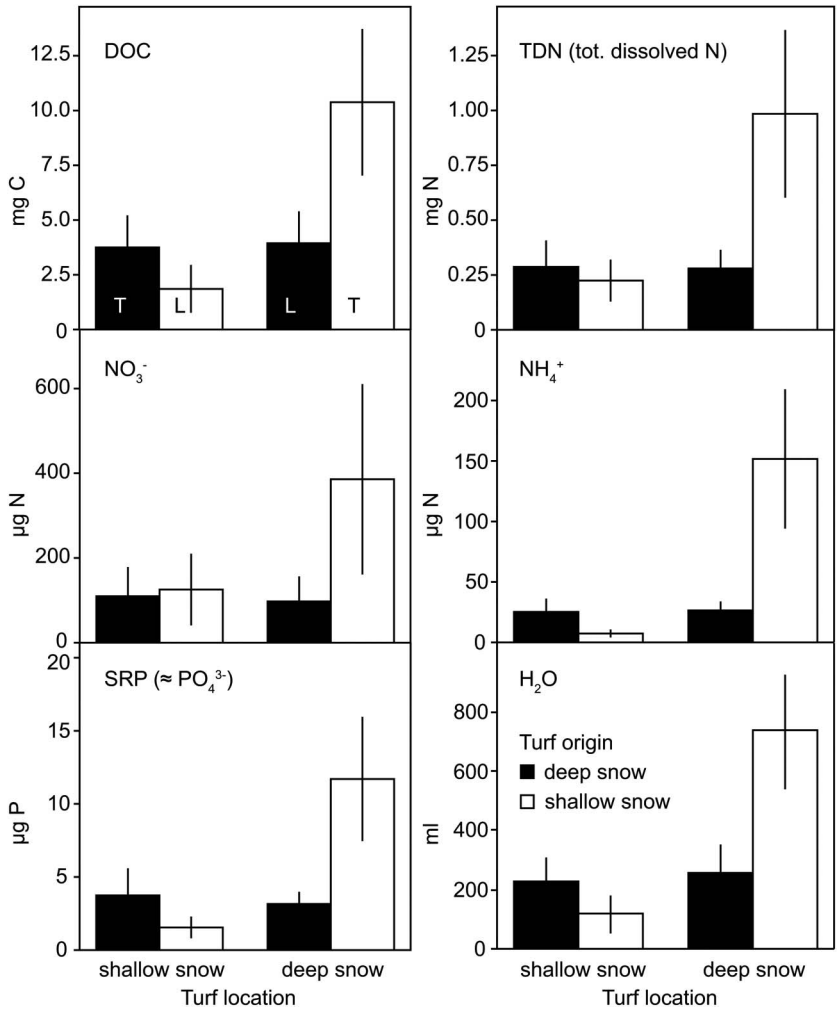

Fig. 6. Efflux of DOC and nutrients as measured in soil water percolated through monoliths and trapped by passive lysimeters at sites with contrasting snow cover. Monoliths (i.e., patches of soil and vegetation) originating from sites with deep snow (black, near snow fence) and shallow snow (white, away from a snow fence) were either moved within (L = Local) or transplanted between (T = Transplant) these locations.

17, 2007).

unfrozen controls, but losses were greatest from cores that had gone through one long freeze-thaw cycle. Differences in methodological aspects, such as the use of deeper soil cores (6 cm depth in our study, compared with 15 cm deep soil cores used by Vestgarden and Austnes (2009)) might have mitigated the effects of freeze-thaw cycles occurring in the biologically active top-soils by including nutrient immobilization processes in sub-soils (Hentschel et al. 2008).

By using intact and vegetated soil monoliths in our experiment, all three possible origins of carbon and nutrients, namely soil organic matter, soil microbes and plants (i.e., live roots, rhizomes, above-ground parts, and/or litter; Henry 2007, Matzner and Borken 2008, Jefferies et al. 2010, Brooks et al. 2011, Templer 2012), could have contributed to the observed leaching losses in our experiment. The evidence from our study that DOC of low aromatic character (low SUVA) was leached after freeze-thaw suggests recent biological origin (plant or microbial cells) of mobilized carbon and nutrients. Three lines of

evidence point to microbes as the main source of labile carbon and nutrients in the current study. First, there was no relationship between DOC leaching and plant biomass in the cores, thus a greater root or leaf mass was not associated with greater carbon mobilization. Second, although multiple experimentally-induced freeze-thaw cycles mobilized additional carbon and nutrients (compared to one short freeze-thaw cycle), soil respiration after thawing was not stimulated accordingly, suggesting that microbial biomass was most reduced in the 3S treatment. Finally, an earlier observational study in the same type of ecosystem found that microbial C and N declined strongly over winter (Bardgett et al. 2002), attributed to microbial dieback due to repeated freeze-thaw cycles. Tracer methodologies, such as stable isotopes, would help to confirm whether the labile nutrients mobilized by freeze-thaw are indeed mainly of microbial origin.

Because winter soil microbial communities in ecosystems with shallow snow and thus naturally occurring soil frosts, e.g., from arctic, alpine and boreal regions, generally proved to be fairly resistant to freeze-thaw cycles (Grogan et al. 2004, Koponen et al. 2006, Sharma et al. 2006, Elliott and Henry 2009, Männistö et al. 2009), we hypothesized that soils from locations with shallow snow cover would be less sensitive to freeze-thaw induced nutrient losses than from historically deep snow cover locations. Although we found that the microbial community overall was negatively affected by freeze-thaw (see previous paragraph), the controlled laboratory experiment did indeed confirm that cores from deep snow locations showed greater nutrient leaching due to freeze-thaw treatments than cores from locations with shallow snow. Similar findings by Vestgarden and Austnes (2009) were attributed to soil micro-organisms from shallow snow sites being adapted to fluctuating winter temperatures. That microbial communities differ in composition along natural snow cover gradients (Zinger et al. 2009, Shahnavaz et al. 2012), and in general show a higher resistance to freezing-thawing processes in cold regions (Henry 2007, Matzner and Borken 2008) has been shown in studies along steep environmental gradients. Our study system with a snow lie history that was modified due to the snow fence relatively recently suggests that the winter microbial community composition can adapt to changes in snow cover over much shorter time periods.

In contrast to our laboratory results, which suggest that increased freeze-thaw cycles associated with reduced snow cover can lead to higher C and nutrient mobilization, monoliths that had been transplanted from deep to shallow snow sites in the field showed nutrient losses that were not significantly different to those from controls transplanted within the same location. However, transplants from shallow to deep snow locations showed increased nutrient fluxes following snow melt, associated with greater water volumes collected in lysimeters. This divergence in nutrient flux between a controlled hydrological regime (i.e., fixed leaching volumes in the laboratory) and natural hydrology in the field experiment shows the overriding importance of local hydrological conditions. In our study, for logistical reasons, snow had already melted when soil water sampling commenced. As soils away from the fence were still frozen when we installed the lysimeters, we likely trapped a representative fraction of nutrients mobilized and leached during thaw. Although infiltration was very heterogeneous, both percolating water volumes and nutrients captured by lysimeter samplers (Appendix: Fig. A1) were generally greater in monoliths transplanted from shallow to deep snow. This finding of coupled water and nutrient fluxes controls is in line with previous field experiments (Austnes et al. 2008, Austnes and Vestgarden 2008, Kaste et al. 2008), but contrasts with others (Groffman et al. 2001*a, b*). In early summer, plot locations near the snow fence were wetter than those at greater distance, which might have facilitated water infiltration in general. Why monoliths transplanted from shallow to deep snow exhibited far higher water fluxes than the local monoliths at the same location remains unclear. Possibly the thick and open moss carpets of *Racomitrium lanuginosum* collected a higher amount of occult precipitation (Van der Wal et al. 2005) than the short but dense moss carpets formed by *Dicranum fuscescens*. Also, cores from the *R. lanuginosum* community contained 35% less root mass than the *D. fuscescens* community (S. Wipf, *personal observation*), which could decrease water and nutrient uptake by plants and increase leaching losses.

The existence of a snow fence for 20 years at our site allowed us to compare plant-soil systems subject to contrasting winter snow regimes. However, other effects caused by this fence may have influenced our results. During the first years after construction, the fence was a barrier to sheep roaming the mountain during summer, resulting in greater sheep presence near the fence. In fact, the rapid vegetation transition from *Racomitrium–Carex* heath to a *Dicranum*-grass community near the fence has been attributed to both the combined effects of elevated snow and sheep density (Welch et al. 2005). Over time, gaps in the fence developed, and certainly by summer 2000 (but likely earlier, Van der Wal, *personal observation*), the snow fence was no barrier to sheep anymore. Thus, during the past decade, the fence primarily accumulated snow and not sheep. Yet, greater amounts of phosphorous lost from cores sampled along the fence (Fig. 5) might be a legacy of higher sheep presence in the past. Phosphorous is usually rapidly immobilized and complexed in a variety of organic and inorganic compounds (Turner et al. 2004) and is generally tightly cycled in soil-plant-microbial systems. Our results indicate that a fraction of phosphorus compounds is mobilized by freeze-thaw cycles, as was found in incubation studies with homogenized soil (Vaz et al. 1994, Freppaz et al. 2007). In the absence of experimental leaching, as applied in our laboratory study, this excess P would likely be immobilized rapidly (Olde Venterink et al. 2002, Freppaz et al. 2007). Also, the soil-plant monoliths transplanted from away to near the fence in 2006 for our field experiment shifted from *Racomitrium-Carex* heath to a *Dicranum*-grass community over the following 6 years without elevated sheep presence (Van der Wal, *personal observation*). We therefore do not believe that past sheep presence, as a potential confounding factor associated with the snow fence, has unduly influenced our results.

Conclusions

Our field experiment coincided with one of the warmest and least snowy winters on record (Met Office 2008), thus plots with shallow snow may have experienced conditions similar to those projected for the future: mid-winter warm spells inducing snowmelt, followed by cold spells that cause large soil temperature fluctuations, while snow accumulation along the fence prevented these soil temperature fluctuations almost entirely. Our laboratory trials showed that freeze-thaw cycles in soil induce substantial nutrient loss under controlled hydrological flushing and, furthermore, that soils usually covered by a thick layer of snow in winter were especially vulnerable to such nutrient loss. The microbial community, which is the supposed source of DOC and nutrients, may thus be less adapted to subzero conditions in soils from snow protected locations. Combined, the laboratory findings point to greater carbon and nutrient losses from oceanic mountain ecosystems under future conditions of reduced winter snow lie. Under field conditions, however, factors associated with localized hydrology and infiltration gain dominance and decouple the links between freeze-thaw processes, mobilization and nutrient loss. Still, due to the importance of hydrology, there remains potential for enhanced nutrient loss from oceanic ecosystems under predicted future winter conditions (i.e., less snow and corresponding harsher soil temperatures), especially if winters with little snow coincide with a wet spring. Our study illustrates that combined laboratory and field experiments are needed to understand both winter mineralization processes and superimposed processes of nutrient leaching. Moreover, divergent responses to freeze-thaw conditions in laboratory and/or field research across temperate and oceanic ecosystems call for a concerted research approach to unravel winter biogeochemical cycling and its carry-over effects on summer ecosystem processes.

Acknowledgments

Many thanks to C. Rixen, R. Gwatkin, S. Palacio, and R. Castillo for help in the field and to A. Sim for help in the laboratory, the British Atmospheric Data Centre (BADC) for providing hourly precipitation data (http://badc.nerc.ac.uk/), and two reviewers for constructive comments on this manuscript. S. Wipf was funded by Swiss National Science Foundation grant PBZHA—117043 and the de Giacomi and HH Schaefer foundations.

Literature Cited

Austnes, K., O. Kaste, L. S. Vestgarden, and J. Mulder.

2008. Manipulation of snow in small headwater catchments at Storgama, Norway: Effects on leaching of total organic carbon and total organic nitrogen. Ambio 37:38–47.

Austnes, K., and L. S. Vestgarden. 2008. Prolonged frost increases release of C and N from a montane heathland soil in southern Norway. Soil Biology and Biochemistry 40:2540–2546.

Averis, A. M., A. B. G. Averis, H. J. B. Birks, D. Horsfield, D. B. A. Thompson, and M. J. M. Yeo. 2004. An illustrated guide to British upland vegetation. JNCC, Peterborough, UK.

Bardgett, R. D., T. C. Streeter, L. Cole, and I. R. Hartley. 2002. Linkages between soil biota, nitrogen availability, and plant nitrogen uptake in a mountain ecosystem in the Scottish Highlands. Applied Soil Ecology 19:121–134.

Barnett, C., J. Hossell, M. Perry, C. Procter, and G. Hughes. 2006. Patterns of climate change across Scotland: Technical Report. Scotland & Northern Ireland Forum for Environmental Research, Edinburgh, Scotland, UK.

Björkman, M. P., E. Morgner, R. G. Björk, E. J. Cooper, B. Elberling, and L. Klemendtsson. 2010. A comparison of annual and seasonal carbon dioxide effluxes between sub-Arctic Sweden and High-Arctic Svalbard. Polar Research 29:75–84.

Blankinship, J. C., and S. C. Hart. 2012. Consequences of manipulated snow cover on soil gaseous emission and N retention in the growing season: a meta-analysis. Ecosphere 3:1.

Brooks, P. D., D. H. Campbell, K. A. Tonnessen, and K. Heuer. 1999. Natural variability in N export from headwater catchments: snow cover controls on ecosystem N retention. Hydrological Processes 13:2191–2201.

Brooks, P. D., P. Grogan, P. H. Templer, P. Groffman, M. G. Öquist, and J. Schimel. 2011. Carbon and nitrogen cycling in snow-covered environments. Geography Compass 5:682–699.

Brown, R. D., and P. W. Mote. 2009. The response of Northern Hemisphere snow cover to a changing climate. Journal of Climatology 22:2124–2145.

Chin, Y.-P., G. Aiken, and E. O'Loughlin. 1994. Molecular weight, polydispersity and spectroscopic properties of aquatic humic substances. Environmental Science and Technology 28:1853–1858.

De Luca, T. H., D. R. Keeney, and G. W. McCarty. 1992. Effect of freeze-thaw events on mineralization of soil nitrogen. Biology and Fertility of Soils 14:116–120.

Dunn, S. M., S. J. Langan, and R. J. E. Colohan. 2001. The impact of variable snow pack accumulation on a major Scottish water resource. Science of the Total Environment 265:181–194.

Edwards, A. C., J. Creasey, and M. S. Cresser. 1986. Soil freezing effects on upland stream solute chemistry. Water Research 20:831–834.

Edwards, A. C., R. Scalenghe, and M. Freppaz. 2007. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. Quaternary International 162:172–181.

Elliott, A., and H. Henry. 2009. Freeze–thaw cycle amplitude and freezing rate effects on extractable nitrogen in a temperate old field soil. Biology and Fertility of Soils 45:469–476.

Fitzhugh, R. D., C. T. Driscoll, P. M. Groffman, G. L. Tierney, T. J. Fahey, and J. P. Hardy. 2001. Effects of soil freezing disturbance on soil solution nitrogen, phosphorus, and carbon chemistry in a northern hardwood ecosystem. Biogeochemistry 56:215–238.

Fitzhugh, R. D., G. E. Likens, C. T. Driscoll, M. J. Mitchell, P. M. Groffman, T. J. Fahey, and J. P. Hardy. 2003. Role of soil freezing events in interannual patterns of stream chemistry at the Hubbard Brook experimental forest, New Hampshire. Environmental Science and Technology 37:1575–1580.

Freppaz, M., B. L. Williams, A. C. Edwards, R. Scalenghe, and E. Zanini. 2007. Simulating soil freeze/thaw cycles typical of winter alpine conditions: Implications for N and P availability. Applied Soil Ecology 35:247–255.

Groffman, P. M., C. T. Driscoll, T. J. Fahey, J. P. Hardy, R. D. Fitzhugh, and G. L. Tierney. 2001*a*. Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. Biogeochemistry 56:191–213.

Groffman, P. M., C. T. Driscoll, T. J. Fahey, J. P. Hardy, R. D. Fitzhugh, and G. L. Tierney. 2001*b*. Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry 56:135–150.

Groffman, P. M., et al. 2012. Climate change effects are manifest in complex and surprising ways in the northern hardwood forest. BioScience 62:1056–1066.

Grogan, P., A. Michelsen, P. Ambus, and S. Jonasson. 2004. Freeze-thaw regime effects on carbon and nitrogen dynamics in sub-arctic heath tundra mesocosms. Soil Biology and Biochemistry 36:641–654.

Haei, M., M. G. Öquist, I. Buffam, A. Ågren, P. Blomkvist, K. Bishop, M. Ottosson Löfvenius, and H. Laudon. 2010. Cold winter soils enhance dissolved organic carbon concentrations in soil and stream water. Geophysical Research Letters 37:L08501(1-5).

Harrison, J., S. Winterbottom, and R. Johnson. 2001. Climate change and changing patterns of snowfall in Scotland. The Scottish Executive Central Research Unit Report, Edinburgh, Scotland, UK.

Henry, H. A. L. 2007. Soil freeze-thaw cycle experiments: trends, methodological weaknesses and

suggested improvements. Soil Biology and Biochemistry 39:977–986.

Henry, H. A. L. 2008. Climate change and soil freezing dynamics: historical trends and projected changes. Climatic Change 87:421–434.

Hentschel, K., W. Borken, and E. Matzner. 2008. Leaching losses of nitrogen and dissolved organic matter following repeated freeze/thaw events in a forest soil. Journal of Plant Nutrition and Soil Science 171:699–706.

IPCC. 2013. Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.

Isard, S. A., R. J. Schaetzl, and J. A. Andresen. 2007. Soils cool as climate warms in the Great Lakes region: 1951-2000. Annals of the Association of American Geographers 97:467–476.

Jefferies, R. L., N. A. Walker, K. A. Edwards, and J. Dainty. 2010. Is the decline of soil microbial biomass in late winter coupled to changes in the physical state of cold soils? Soil Biology and Biochemistry 42:129–135.

Kaste, O., K. Austnes, L. S. Vestgarden, and R. F. Wright. 2008. Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of inorganic nitrogen. Ambio 37:29–37.

Kim, D.-G., R. Vargas, B. Bond-Lamberty, and M. R. Turetsky. 2012. Effects of soil rewetting and thawing on soil gas fluxes: a review of current literature and suggestions for future research. Biogeosciences 9:2459–2483.

Knowles, N., M. D. Dettinger, and D. R. Cayan. 2006. Trends in snowfall versus rainfall in the western United States. Journal of Climatology 19:4545–4559.

Koponen, H. T., T. Jaakkola, M. M. Keinänen-Toivola, S. Kaipainen, J. Tuomainen, K. Servomaa, and P. J. Martikainen. 2006. Microbial communities, biomass, and activities in soils as affected by freeze thaw cycles. Soil Biology and Biochemistry 38:1861–1871.

Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263.

Kreyling, J., G. Jurasinski, K. Grant, V. Retzer, A. Jentsch, and C. Beierkuhnlein. 2011. Winter warming pulses affect the development of planted temperate grassland and dwarf-shrub heath communities. Plant Ecology and Diversity 4:13–21.

Kreyling, J., D. Peršoh, S. Werner, M. Benzenberg, and J. Wöllecke. 2012. Short-term impacts of soil freeze-thaw cycles on roots and root-associated fungi of *Holcus lanatus* and *Calluna vulgaris*. Plant and Soil 353:19–31.

Lipson, D. A., S. K. Schmidt, and R. K. Monson. 2000. Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. Soil Biology and Biochemistry 32:441–448.

Männistö, M., M. Tiirola, and M. Häggblom. 2009. Effect of freeze-thaw cycles on bacterial communities of arctic tundra soil. Microbial Ecology 58:621–631.

Matzner, E., and W. Borken. 2008. Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review. European Journal of Soil Science 59:274–284.

McCabe, G. J., and D. M. Wolock. 2010. Long-term variability in Northern Hemisphere snow cover and associations with warmer winters. Climatic Change 99:141–153.

Met Office. 2008. UK climate and weather statistics. Monthly mean temperatures and anomaly maps for snow lie, Nov 2006 to Apr 2007. http://www.metoffice.gov.uk/climate/uk/summaries

Mikan, C. J., J. P. Schimel, and A. P. Doyle. 2002. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. Soil Biology and Biochemistry 34:1785–1795.

Munro, J. R. C. 2008. The Cairngorm climate, 1964-2006, and its impact on local tourism. Thesis. Univeristy of Edinburgh, Edinburgh, Scotland, UK.

Olde Venterink, H., T. E. Davidsson, K. Kiehl, and L. Leonardson. 2002. Impact of drying and re-wetting on N, P and K dynamics in a wetland soil. Plant and Soil 243:119–130.

Öquist, M. G., T. Sparrman, L. Klemedtsson, S. Harrysson-Drotz, H. Grip, J. Schleucher, and M. Nilsson. 2009. Water availability controls microbial temperature responses in frozen soil CO_2 production. Global Change Biology 15:2715–2722.

Panikov, N. S., P. W. Flanagan, W. C. Oechel, M. A. Mastepanov, and T. R. Christensen. 2006. Microbial activity in soils frozen to below −39°C. Soil Biology and Biochemistry 38:785–794.

Pearce, I. S. K., S. J. Woodin, and R. van der Wal. 2003. Physiological and growth responses of the montane bryophyte *Racomitrium lanuginosum* to atmospheric nitrogen deposition. New Phytologist 160:145–155.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar, and R Development Core Team. 2012. nlme: linear and nonlinear mixed effects models. R Foundation for Statistical Computing, Vienna, Austria.

Reinmann, A. B., P. H. Templer, and J. L. Campbell. 2012. Severe soil frost reduces losses of carbon and nitrogen from the forest floor during simulated snowmelt: a laboratory experiment. Soil Biology and Biochemistry 44:65–74.

Robroek, B. J. M., A. Heijboer, V. E. J. Jassey, M. M.

Hefting, T. G. Rouwenhorst, A. Buttler, and L. Bragazza. 2013. Snow cover manipulation effects on microbial community structure and soil chemistry in a mountain bog. Plant and Soil 369:151–164.

Scott, D., D. Welch, R. van der Wal, and D. A. Elston. 2007. Response of the moss *Racomitrium lanuginosum* to changes in sheep grazing and snow-lie due to a snow-fence. Applied Vegetation Science 10:229–238.

Serquet, G., C. Marty, J. P. Dulex, and M. Rebetez. 2013. Seasonal trends and temperature dependence of the snowfall/precipitation-day ratio in Switzerland. Geophysical Research Letters 38:L07703.

Shahnavaz, B., L. Zinger, S. Lavergne, P. Choler, and R. A. Geremia. 2012. Phylogenetic clustering reveals selective events driving the turnover of bacterial community in alpine tundra soils. Arctic, Antarctic, and Alpine Research 44:232–238.

Sharma, S., Z. Szele, R. Schilling, J. C. Munch, and M. Schloter. 2006. Influence of freeze-thaw stress on the structure and function of microbial communities and denitrifying populations in soil. Applied Environmental Microbiology 72:2148–2154.

Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock, and V. E. Romanovsky. 2005. Winter biological processes could help convert arctic tundra to shrubland. BioScience 55:17–26.

Templer, P. H. 2012. Changes in winter climate: soil frost, root injury, and fungal communities. Plant and Soil 353:15–17.

Tierney, G. L., T. J. Fahey, P. M. Groffman, J. P. Hardy, R. D. Fitzhugh, and C. T. Driscoll. 2001. Soil freezing alters fine root dynamics in a northern hardwood forest. Biogeochemistry 56:175–190.

Turner, B. L., R. Baxter, N. Mahieu, S. Sjögersten, and B. A. Whitton. 2004. Phosphorus compounds in subarctic Fennoscandian soils at the mountain birch (*Betula pubescens*)—tundra ecotone. Soil Biology and Biochemistry 36:815–823.

Unger, P. W. 1991. Overwinter changes in physical properties of no-tillage soil. Soil Science Society of America Journal 55:778–782.

Van der Wal, R., A. Bonn, D. Monteith, M. Reed, K. Blackstock, N. Hanley, D. Thompson, M. Evans, and I. Alonso. 2011. Mountains, moorlands and heaths. Pages 105–159 *in* U. N. E. Assessment, editor. The UK National Ecosystem Assessment Technical Report. UNEP-WCMC, Cambridge, UK.

Van der Wal, R., I. S. K. Pearce, and R. W. Brooker. 2005. Mosses and the struggle for light in a nitrogen-polluted world. Oecologia 142:159–168.

Vaz, M. D. R., A. C. Edwards, C. A. Shand, and M. S. Cresser. 1994. Changes in the chemistry of soil solution and acetic-acid extractable P following different types of freeze/thaw episodes. European Journal of Soil Science 45:353–359.

Vestgarden, L. S., and K. Austnes. 2009. Effects of freeze-thaw on C and N release from soils below different vegetation in a montane system: a laboratory experiment. Global Change Biology 15:876–887.

Welch, D., D. Scott, and D. B. A. Thompson. 2005. Changes in the composition of *Carex bigelowii-Racomitrium lanuginosum* moss heath on Glas Maol, Scotland, in response to sheep grazing and snow fencing. Biological Conservation 122:621–631.

Yanai, Y., K. Toyota, and M. Okazaki. 2004. Effects of successive soil freeze-thaw cycles on soil microbial biomass and organic matter decomposition potential of soils. Soil Science and Plant Nutrition 50:821–829.

Zinger, L., B. Shahnavaz, F. Baptist, R. A. Geremia, and P. Choler. 2009. Microbial diversity in alpine tundra soils correlates with snow cover dynamics. ISME Journal 3:850–859.

Supplemental Material

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/ES15-00099.1.sm