ENVIRONMENTAL RESEARCH
CLIMATE

PURPOSE-LED PUBLISHING™

Part of the
ENVIRONMENTAL RESEARCH
SERIES

# Tundra cryogenic land surface processes and $CO_2$–C balance in sub-Arctic alpine environment withstand winter and spring warming

To cite this article: Maria Väisänen *et al* 2023 *Environ. Res.: Climate* **2** 021001

**IOP** Publishing *Environ. Res.: Climate* **2** (2023) 021001 https://doi.org/10.1088/2752-5295/acc08b

ENVIRONMENTAL RESEARCH
CLIMATE

OPEN ACCESS

RECEIVED
17 January 2022

REVISED
15 February 2023

ACCEPTED FOR PUBLICATION
2 March 2023

PUBLISHED
17 March 2023

LETTER

# Tundra cryogenic land surface processes and $CO_2$–C balance in sub-Arctic alpine environment withstand winter and spring warming

**Maria Väisänen**[1,2,3,*], **Jonatan Klaminder**[1], **Henni Ylänne**[4], **Laurenz Teuber**[1], **Ellen Dorrepaal**[1] **and Eveline J Krab**[1,5]

[1] Climate Impacts Research Center, Department of Ecology and Environmental Sciences, Umeå University, SE-981 07 Abisko, Sweden
[2] Ecology and Genetics Research Unit, University of Oulu, PO Box 3000, FI-90 100 Oulu, Finland
[3] Arctic Center, University of Lapland, PO Box 122, FI-96 101 Rovaniemi, Finland
[4] Centre for Environmental and Climate Research, Lund University, PO Box 118, SE-221 00 Lund, Sweden
[5] Department of Soil and Environment, Swedish University of Agricultural Sciences, Lennart Hjelms väg 9, SE-750 07 Uppsala, Sweden
[*] Author to whom any correspondence should be addressed.

**E-mail:** maria.vaisanen@oulu.fi

**Keywords:** non-sorted circle, differential heave, greenhouse gas, snow fence, greenness, light-response, modeling

Supplementary material for this article is available online

## Abstract

Cryogenic land surface processes (CLSPs), such as cryoturbation, are currently active in landscapes covering 25% of our planet where they dictate key functions, such as carbon (C) cycling, and maintain patterned landscape features. While CLSPs are expected to diminish in the near future due to milder winters especially in the southern parts of the Arctic, the shifts in C cycling in these landscapes may be more complex, since climate change can affect C cycling directly but also indirectly via CLSPs. Here, we study the effects of changing winter and spring climate on CLSPs and C cycling in non-sorted circles consisting of barren frost boils and their vegetated rims. We do this by measuring cryoturbation and ecosystem $CO_2$ fluxes repeatedly in alpine subarctic tundra where temperatures during naturally snow covered period have been experimentally increased with snow-trapping fences and temperatures during winter and spring period after snowmelt have been increased with insulating fleeces. Opposite to our hypothesis, warming treatments did not decrease cryoturbation. However, winter warming via deeper snow increased ecosystem C sink during summer by decreasing ecosystem $CO_2$ release in the frost boils and by counterbalancing the negative effects of cryoturbation on plant $CO_2$ uptake in the vegetated rims. Our results suggest that short-term changes in winter and spring climate may not alter cryoturbation and jeopardize the tundra C sink.

## 1. Introduction

Up to 25% of polar and alpine tundra are affected by cryogenic land surface processes (CLSPs), such as cryoturbation, that control energy, water, and carbon (C) cycles as well as soil motions—i.e. frost-induced vertical and lateral soil movement—that maintain patterned landscape features (Walker *et al* 2004, French 2007, Koven *et al* 2009, Aalto *et al* 2017). In these patterned landscapes, the distribution and activity of cryoturbation may differ within short distances due to fine scale variation in topography, soil characteristics, vegetation, and microclimate (Hjort and Luoto 2009, Klaus *et al* 2013). Climate change is particularly pronounced during winter and spring (Thompson and Wallace 2001, Schwartz *et al* 2006, IPCC 2019) and is expected to affect cryoturbation. Whereas in the High Arctic, warming and the associated vegetation expansion could intensify cryoturbation, in the southern parts of the Arctic, warming is expected to dampen cryoturbation (Walker *et al* 2008, Hjort and Luoto 2009). Recent modeling proposes that tundra areas influenced by cryoturbation may decrease as much as 84% by 2040–2069 due to winter warming (Aalto *et al* 2017). Accordingly, ceased cryoturbation due to winter warming is prone to affect tundra C cycling over varying time scales. Over centennial timescales, changes in C cycling may occur, since cryoturbation buries and transfers accumulated organic deposits (Walker *et al* 2004, Kaiser *et al* 2007, Becher *et al* 2013). On the other hand, more contemporary changes in C cycling are also likely, since cryoturbation damages plants limiting root $CO_2$ release and photosynthetic $CO_2$ uptake but may simultaneously intensify microbial C mineralization via mixing mineral soil with organic matter (Klaminder *et al* 2013, Becher *et al* 2015). Thus, even on short term, decreasing cryoturbation could induce varying responses in $CO_2$ uptake and release with currently unpredictable consequences for net ecosystem $CO_2$ balance.

In addition to affecting cryoturbation, the timing and nature of climate changes may also directly affect plant and microbially driven processes in tundra ecosystems (Wipf *et al* 2009, Kreyling 2010, Puissant *et al* 2015). Higher soil temperatures under deeper snow cover may directly increase microbial $CO_2$ release and nutrient mineralization in winter but, on the other hand, may decrease microbial $CO_2$ release during summer, if labile soil C pools are exhausted (Schimel *et al* 2004, Semenchuk *et al* 2015, 2016). Winter warming also improves conditions for plant overwintering and, consequently, for the growing season by protecting plants from winter frost damage (Saarinen and Lundell 2010, Neuner 2014, Palacio *et al* 2015, Krab *et al* 2018) and by increasing nitrogen availability (Blankinship and Hart 2012) that could increase plant $CO_2$ uptake. However, the extent to which photosynthesis can benefit from these conditions may largely depend on the climate in spring since changes in snowmelt timing and increases in spring temperatures may delay or advance the onset of the growing season (Badeck *et al* 2004, Inouye 2008, Saarinen and Lundell 2010, Wipf and Rixen 2010) and alter the susceptibility of plants to freezing damage during spring frost events (Inouye 2008, Wheeler *et al* 2014, Krab *et al* 2018). In ecosystems with naturally shallow snow cover, even small increases in snow cover may have large impacts on mid-winter soil temperatures but increases in spring temperatures may largely control the onset of plant growth and photosynthesis.

Due to these joint effects of decreased cryoturbation-induced disturbances and improved conditions during winter and spring, the responses of C cycling to winter and spring warming in cryogenically active landscapes could differ from the responses of non-cryogenically active tundra (Morgner *et al* 2010, Rogers *et al* 2018). Currently, there is no field experimentation quantifying how increasing winter and spring temperatures (Cronin and Tziperman 2015, Bogerd *et al* 2020) will affect cryoturbation and $CO_2$ fluxes. This lack of experimental work linking climate variables with CLSPs and their intertwined biogeochemical cycles has been identified as a key uncertainty hampering our ability to predict future functioning of tundra landscapes (Aalto *et al* 2017).

We examined the effects of winter warming and combined winter and spring warming on cryoturbation and $CO_2$ exchange in a subarctic alpine tundra in Sweden (68°18.030′N, 19°7.262′E, 860 m a.s.l.) with patterned features, non-sorted circles (NSCs), consisting of barren frost boil centers and their vegetated rims that vary in their abiotic and biotic properties and, thus, with the magnitude and drivers of C cycling (Becher *et al* 2015, Väisänen *et al* 2017). These NSC's share similarities to patterned features in the circumpolar region in Scandinavia (Becher *et al* 2013, Aalto *et al* 2017), Siberia, Alaska, and northern Canada (Zoltai and Tarnocai 1981, Walker *et al* 2004, Frost *et al* 2014) in terms of soil properties and vegetation composition. We addressed three research questions. First, how does winter warming and combined winter and spring warming affect cryoturbation (differential heave (DH), cm)? Second, how does winter and combined winter and spring warming affect tundra C balance ($\text{g CO}_2\text{–C m}^{-2}$) during different seasons and annually? Third, how does winter and combined winter and spring warming affect growing seasonal $CO_2$ fluxes ($\text{g CO}_2\text{–C m}^{-2}\text{ h}^{-1}$)—net ecosystem exchange and gross ecosystem production (NEE600 and GEP600, respectively, normalized at a common irradiance, $\text{PAR} = 600\ \mu\text{ mol photons m}^{-2}\text{ s}^{-1}$) and ecosystem respiration ($R_e$, measured in full darkness)—in the frost boils and the rims and does cryoturbation contribute to these C cycles? To answer these questions we used snow fences and insulating fleeces that covered NSCs in autumn, winter and spring (both treatments executed years 2012–2016) that simulated two winter climate change scenarios: snow fences increased soil temperatures during the natural snow-covered period (mid-October to mid-May 2012–2014, *c.* 1 °C), without changing average spring soil temperatures (i.e. winter warming), whereas fleeces increased soil temperatures from October until early June (2012–2014, *c.* 1 °C), thus additionally warming in the spring period after snowmelt (i.e. combined winter and spring warming) (Krab *et al* 2018). During years 2015–2016, we measured DH and $CO_2$ fluxes. We hypothesized that: (1) both warming treatments will decrease cryoturbation and (2) both warming treatments will increase tundra C sink function (i.e. NEE more negative) but the effect will be stronger with combined winter and spring warming, and (3) both warming treatments will affect all growing seasonal $CO_2$ fluxes but the effects will be stronger with combined winter and spring warming and, further, the effects will be different in the frost boils and in the rims.

## 2. Materials and methods

### 2.1. Study site and experimental design

The site was a dry-mesic subarctic alpine tundra heath on Mount Suorooaivi (68°18.030´N, 19°7.262´E) in northern Sweden. The site locates above treeline (860 m a.s.l.) and is densely covered by patterned ground features, *viz.* (NSCs, figure S1) with frost boil centers dominated by barren mineral ground and biological crusts whereas their surrounding tundra is dominated by dwarf shrubs (e.g. *Salix glauca* L. *Empetrum nigrum* L., *Vaccinium vitis-idaea* L., *Betula nana* L., and *Vaccinium uliginosum* L.) above a dense carpet of mosses (e.g. *Polytrichastrum alpinum*) (Makoto and Klaminder 2012, Krab *et al* 2018). The soils are freely draining Turbic Cryosols, and the mineral soil is dominated by sand and silt (63% and 36%, respectively) (Klaminder *et al* 2013). Permafrost is not present in the upper 1 m of the soil as shown by excavation at the site, but the developed cryosolic soils are typically indicating permafrost within the 2 m. A survey on a nearby slope indicates extensive areas of permafrost above 900 m a.s.l and sporadic permafrost down to 400 m a.s.l (Dobiński 2010). The soil depth above the bedrock is typically >1 m but is highly variable and can only be a few decimeters near outcrops. In the vegetated tundra (rims), the humus layer varies from 1 to 8 cm, and the soil bulk density, organic matter and water contents in the top 10 cm soil horizon are 0.15–0.41 g $cm^{-3}$, 14.4–55.9 SOM% and 0.12–0.25 $cm^3$ $cm^{-3}$ of soil, respectively, whereas in the frost boils, the humus layer is absent, and bulk density, organic matter and water contents are 0.93–1.37 $gcm^{-3}$, 0.91–1.83 SOM% and 0.13–0.17 $cm^3$ $cm^{-3}$ soil, respectively (measured in August 2015). In the region, the long-term (1991–2015) mean annual precipitation is 342 mm $y^{-1}$, mean annual air temperatures is 0.3 °C while air temperatures in January and July are −7.1 °C and 12.0 °C, respectively (measured at 321 m a.s.l. at the Abisko Scientific Research Station: www.polar.se/abisko).

The experiment was established in autumn 2012 and the design consisted of 15 NSCs deployed over an area of 100 × 150 m, spatially arranged into six blocks. The NSCs included two habitats: the frost boils, which diameter ranged from 79 to 351 cm (measured in 2015) and their adjacent vegetated rims encompassing a *c.* 40 cm wide zone around the frost boil resulting in a total number of 30 replicates. These NSCs were addressed to control treatment ($n = 6$) and to two winter climate treatments that were applied in the winter seasons from September through May/early June (2012–2016). The treatments were: (1) winter warming with snow trapping fences ($n = 3$, replication limited due to logistics) that increased soil temperatures during the naturally snow covered-period, approx. 6 months, from late autumn to late winter, and (2) combined winter and spring warming with insulating gardening fleeces ($n = 6$, four thin layers of rectangular, white, water-and light-penetrable polypropylene fleece blankets Nelson Garden, Sweden; 17 g $m^{-2}$) that warmed soils for a longer period of time, approx. 8 months ranging from early autumn until late spring (Krab *et al* 2019). In the snow trapping fences, the accumulated extra snow was not removed during snowmelt. During this study, the fleeces warmed soils from 23 September 2014 until 18 May 2015 and from 23 September 2015 until 26 May 2016 and during both springs, the fleeces were removed about 2 weeks after the natural snowmelt.

### 2.2. Differential frost heave

As an index of cryoturbation we used differential (frost) heave (Klaus *et al* 2013). We measured DH four times (17 September 2014, 18 March and 9 September 2015, 1 April 2016) with a theodolite (Wild NAK-0, Preisler Instrument, Preisler Instrument AB Klostergatan 10 222 22 Lund Sweden) that was located at a central area of the study site. At each frost boil, the heights were recorded (cm) from the frost boil center (two measurements) and the southern (S), northern (N), western (W) and eastern (E) corners of the rim and used to calculate mean values for the center and the rim per each frost boil. DH for the two winter periods (17 September 2014–18 March 2015; 9 September 2015–1 April 2016) were calculated as (Becher *et al* 2015):

$$\mathrm{DH} = (h_{\mathrm{w,fb}} - h_{\mathrm{s,fb}}) - (h_{\mathrm{w,r}} - h_{\mathrm{s,r}})$$

where $h$ indicates the height of frost boil (fb) and rim (r) during late winter (w) and late summer (s). DH is generally positive since the freezing-induced expansion of ice lens underneath frost boil centers induces upward movement (heaving) during winter that exceeds the movements in their adjacent vegetated rims. During summer, the thawing-induced collapse of the ice lens induces downward movement and, thus, the frost boil centers subsidize (collapse) more relative to their rims resulting in a generally negative 'DH'. To describe this soil subsidence and the associated physical disturbances that could influence biota and $CO_2$–C fluxes during growing season, we calculated DH over summer 2015 (18 March–9 September 2015) as:

$$\mathrm{DH_{summer}} = (h_{\mathrm{s,fb}} - h_{\mathrm{w,fb}}) - (h_{\mathrm{s,\,r}} - h_{\mathrm{w,r}})\,.$$

In this paper, we consider that frost-induced soil movements over winter or summer are more intense when |DH| increases and, thus, over summer, more negative DH indicates intensified soil movement and less negative DH dampened soil movement.

### 2.3. Soil and surface air temperature and freezing degree days (FDDs)

Soil temperature was recorded at 1 cm depth at each experimental replicate ($n = 30$, 23 September 2014–31 May 2016, Tiny Tag Talk 2, Intab Interface-Teknik AB, Sweden) and used to calculate monthly mean soil temperatures (figure S3). We also calculated cumulative FDDs, i.e. the sum of mean daily soil temperatures $<0$ °C (23 September 2014–31 May 2015; 24 September 2015–31 May 2016). Surface air temperatures at 10 cm height were recorded at central locations of the site ($n = 3$, 18 June–23 September 2015, Tiny Tag Talk 2, Intab Interface-Teknik AB, Sweden, insulated with radiation shields), and the average air temperatures over 18–30 June, in July, August and over 1–23 September were 8.1 °C, 9.6 °C, 11.1 °C, and 6.2 °C, respectively.

### 2.4. $CO_2$ fluxes, vegetation greenness and modeling $CO_2$ exchange

Ecosystem $CO_2$ fluxes were measured over one year with portable infrared gas analyzer (EGM-4, PP Systems, USA) using a closed system chamber (diam. 14.6 cm, height 14.5 cm, with attached PAR and air temperature sensors, CPY-4, PP Systems, USA) on permanently marked spots representative of the frost boil and the rim habitats of each NSC. During the snow-free period in 2015, $CO_2$ fluxes were measured 12 times (table S2(a)) usually under sunny conditions between 9:00–16:00 h. Each time, we conducted one measurement with the transparent chamber (NEE), followed by a measurement in complete darkness (opaque chamber placed to cover CPY-4; $R_e$). In addition, the light responsiveness of photosynthesizing organisms was determined by three gradual shading measurements (1-layer, 2-layered, and 4-layered mosquito mesh) in between full light and darkness (21 June–11 September 2015). Measurements (30 s, values recorded at 5 s intervals) were conducted by placing the chamber on the marked spot and sealed to the ground with bubble plastic. Final flux rates were calculated using quadratic fitting and GEP (flux rates reported as negative values) was calculated by subtracting $R_e$ (flux rates reported as positive values) from NEE (under full light). Here, positive NEE indicates net C source whereas negative NEE indicates net C sink.

During winter 2015–2016, we measured $R_e$ eight times (table S2(b)) from the same spots as in summer by placing the covered chamber on top of an undisturbed snow cover. This floating chamber technique is considered reliable for detecting winter $CO_2$ release with shallow snow cover (Björkman *et al* 2010), such as our study site. In March 2016, snow depths (average based on 3–5 measurements) at close proximity to the $CO_2$ spots were as follows: (i) in the frost boils, $0.6 \pm 0.2$ cm, $0.5 \pm 0$ cm and $8.7 \pm 5.8$ cm in the control, fleece and snow fence, respectively (mean ± S.E.) and (ii) in the rims, $4.9 \pm 2.9$ cm, $2.5 \pm 0.4$ cm and $17.5 \pm 2.7$ cm in the control, fleece and snow fence, respectively. To confirm $CO_2$ diffusion through the fleeces, we measured $R_e$ in the fleece treated NSCs twice, first with the gardening fleeces on and then, immediately after removing the fleece, during the last measurement campaign (table S2(b)). $CO_2$ concentrations were measured for 3–5 min at 5 s intervals and flux rate was calculated using quadratic fitting.

During the snow-free season 2015, the seasonal development of vegetation greenness at permanently marked spots (i.e. the $CO_2$ spots in the rims) was measured by repeated digital photography (Canon EOS 350D Digital, Japan, 8.20 megapixels, 35 mm focal length) 11 times (18 May–11 September 2015) and from June 18 onwards in synchrony with $CO_2$ fluxes following prescribed protocol (Sonnentag *et al* 2012, Blume-Werry *et al* 2016). From each picture, green, red, and blue channels were extracted (software ImageJ 2006.02.01) and used to calculate green chromatic coordinate (gcc). The measured ecosystem $CO_2$ fluxes were used for normalizing growing seasonal $CO_2$ fluxes at a common irradiance and for modeling seasonal and annual $CO_2$–C sums (information S1).

### 2.5. Statistics

The responses of cryoturbation (DH, DH over summer), soil temperature and FDD, seasonal and annual $CO_2$–C sums, growing seasonal $CO_2$ flux rates (NEE600, GEP600 and $R_e$) and vegetation community greenness (gcc) to the warming treatments (control, snow-trapping fences, insulating fleeces) were tested with linear mixed regressions with the *lme* function (*nlme*-package, Pinheiro *et al* 2021) using restricted maximum likelihood and additional fixed terms that varied by parameter. To evaluate significant main and interaction effects of the warming treatments, we used a Tukey's post hoc test (*emmeans*-package, Lenth 2021). For cryoturbation, the model included warming treatment as a fixed term and spatial block as a random term—all other statistical models included NSC plot identity as the random term. For soil temperature, the model included the fixed main and interaction effects of warming, habitat (frost boil *vs.* rim) and month while for FDD, 'winter' was used instead of month. We analyzed the fixed effects of warming treatments, habitat, and season (summer *vs.* winter) on seasonal C sums, whereas annual C sum was

**Table 1.** Differential heaving (DH) over winters 2014–2015 and 2015–2016 and over summer 2015 at the NSCs. DH was measured in control treatment ($n = 6$, $n = 5$ for winter 2014/2015 and summer 2015), combined winter and spring warming and winter warming treatments that were carried out with insulating fleeces ($n = 6$) and snow-trapping snow fences ($n = 3$), respectively. Values present mean (cm) with standard error within the parenthesis. The effect of warming treatments on DH over the different periods was analyzed using linear mixed effects regressions (block identity as a random factor) followed by ANOVA, which output including *F*-values, degrees of freedom and *P*-values are reported.

| Warming treatment | DH 2014–2015 | $DH_{summer}$ 2015 | DH 2015–2016 |
|---|---|---|---|
| Control | 2.1 (1.0) | −2.5 (1.1) | 0.6 (1.7) |
| Fleece | 1.4 (0.8) | −4.8 (3.1) | 5.0 (2.9) |
| Snow fence | 3.3 (0.5) | −7.2 (4.7) | 6.7 (4.7) |
| ANOVA | $F_{2,6} = 0.9988$<br>$P = 0.4222$ | $F_{2,6} = 0.7926$<br>$P = 0.4949$ | $F_{2,7} = 1.1827$<br>$P = 0.3610$ |

analyzed using warming and habitat as fixed terms. For growing seasonal radiation normalized $CO_2$ fluxes, the model included the fixed effects of warming, habitat, and DH over summer (did not respond to warming treatments, table 1) and, as an additional random term, day of the year (DOY). Since these tests showed significant habitat-dependent interactions with warming treatments and DH over summer (table S6), we split the data and tested the effects of warming and DH over summer separately for the frost boils and the rims (table S7). Vegetation greenness (measured only at the rims) was analyzed using warming and DH over summer as the fixed terms and DOY as an additional random term. All data were inspected for normality using qq-plots and residual plots and Ln-transformed data was used for annual and seasonal C sums to ensure model fit. For visualizing data, we used *ggplot2*-package (Wickham 2016) and *Hmisc*-package (Harrell *et al* 2021) and for PAR-normalized $CO_2$ fluxes and gcc we used loess smoothed (0.70) data. All statistical analyses were run using the statistical software R.

## 3. Results

Both warming treatments increased soil temperatures from November until February during winters 2014–2015 and 2015–2016: fleeces increased soil temperature on average by 0.9 °C and snow-trapping fences by 1.7 °C in comparison to control, although during winter 2015–2016, fleeces had a stronger warming effect in the frost boils (table S1, figure S2). In the frost boils, FDDs turned less negative in the fleece ($-1048 \pm 53$; mean ± S.E.) and in the snow fence ($-970 \pm 72$) treatments in comparison to the control ($-1253 \pm 51$) while in the rims, FDDs turned less negative only with the snow fences (table S4, figure S3). Warming treatments did not affect soil temperatures during summer (table S1, figure S2).

Neither the snow fence treatment, nor the fleece treatment affected DH during winters 2014/2015 and 2015/2016 or over summer 2015 (table 1).

Only the snow fence treatment affected tundra C balance during summer; the ecosystem C sink was stronger (i.e. less positive) in the NSCs with the snow fences in comparison to control and the fleece treatment, and these effects were the same in the frost boils and in the rims (figure 1, table S5). The winter and annual tundra C balance did not differ significantly between the treatments (table S5).

In the frost boils, growing seasonal NEE600 tended to decrease (i.e. more negative, stronger C sink) with the snow fences in comparison to the fleece and control, and NEE600 also decreased significantly as DH over summer intensified (i.e. turned more negative; figure 2(a), table S7). Growing seasonal GEP600 increased (i.e. turned less negative) in the snow fence treatment in comparison to the control (figure 2(b)) whereas $R_e$ was smaller in the snow fence treatment in comparison to both fleece and control that did not differ from each other, and $R_e$ also decreased as DH over summer intensified (figure 2(c), table S7).

In the rims, growing seasonal NEE600 did not respond to any of the warming treatments or to DH over summer (figure 3(a), table S7). On the other hand, the relationship between DH over summer and GEP600 differed depending on the warming treatment (table S7). In the control, GEP600 increased (i.e. approached zero) as DH over summer intensified whereas in both warming treatments, GEP600 remained stable as DH over summer intensified (figure 3(b)). The fleeces increased $R_e$ in comparison to control and, in addition, the relationship between DH over summer and $R_e$ differed depending on the warming treatment (table S7). In the control, $R_e$ decreased whereas in both of the warming treatments, $R_e$ remained stable as DH over summer intensified (figure 3(c)). The snow fence and fleece treatments did not have any main effect on vegetation greenness, gcc (effect of warming; $F_{2,143} = 2.23$, $P = 0.1108$), which declined as DH over summer intensified (effect of DH over summer; $F_{1,143} = 6.24$, $P = 0.0136$). This decline further varied depending on the warming treatment (warming × DH over summer; $F_{2,143} = 6.49$, $P = 0.0020$) and was steeper in the control in comparison to both warming treatments (figure 4).

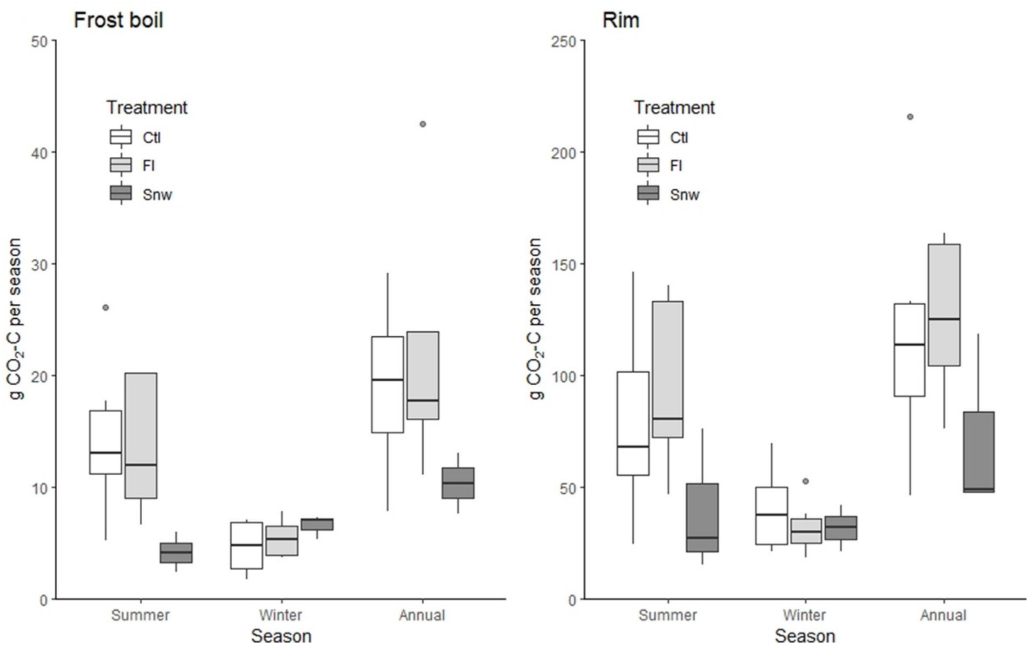

**Figure 1.** Modeled ecosystem $CO_2$–C sums during summer 2015 (Summer), winter 2015–2016 (Winter) and annually (Annual) in the barren frost boil and vegetated rim habitats of the NSCs under different warming treatments—the non-manipulated control (Ctl), combined winter and spring warming with insulating fleeces (Fl) and winter warming with snow-trapping snow fences (Snw). The filled boxes represent the 2nd and 3rd quartile with median lines while whiskers represent 1st and 4th quartile, and circles indicate outliers. Note different scales for the frost boil and the rim habitats.

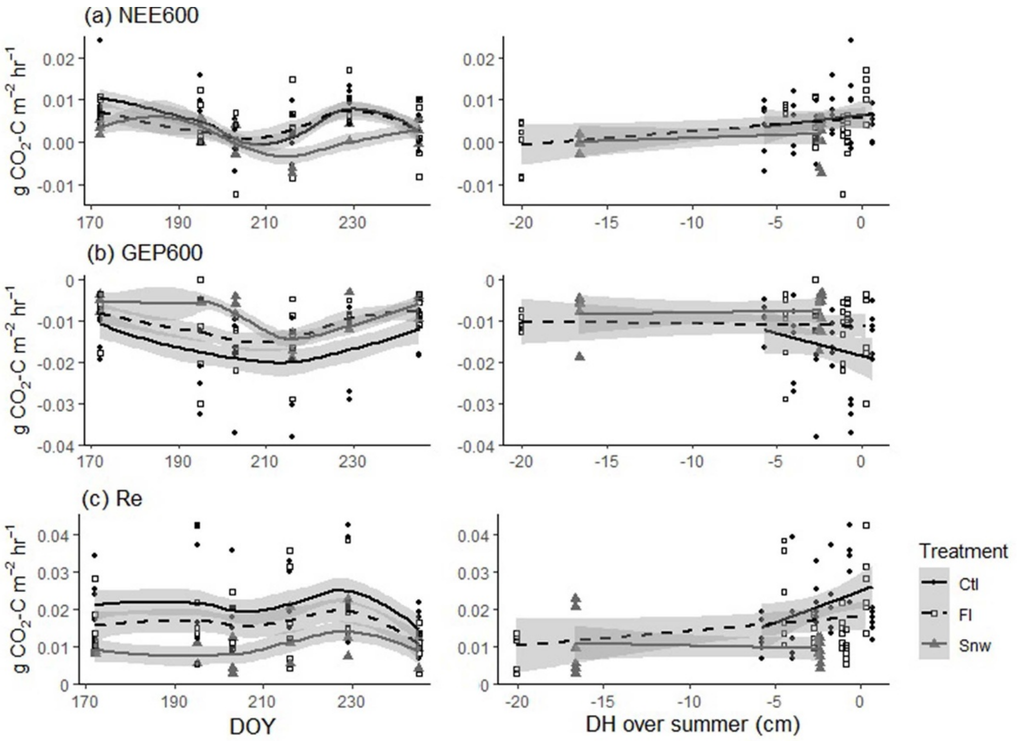

**Figure 2.** $CO_2$ flux rates in the barren frost boil habitats (a) NEE600 stands for net ecosystem exchange at a common radiation level of PAR 600 with negative values indicating C sink and positive values C source, (b) GEP600 stands for gross ecosystem production at a common radiation level of PAR 600, and (c) $R_e$ stands for ecosystem respiration measured in complete darkness in different warming treatments—the non-manipulated control (Ctl, $n = 6$), combined winter and spring warming with insulating fleeces (Fl, $n = 6$) and winter warming with snow-trapping snow fences (Snw, $n = 3$). The left-hand panels show $CO_2$ flux rates as a function of day of the year (DOYs 172–254 i.e. 21 June–11 September 2015) with each measurement as an individual point with loess smoothed (0.70) lines. The right-hand panels show the $CO_2$ flux rates as a function of differential heave (DH) over summer and show each measurement as an individual point with a fitted linear regression line and 95% CI indicated with grey.

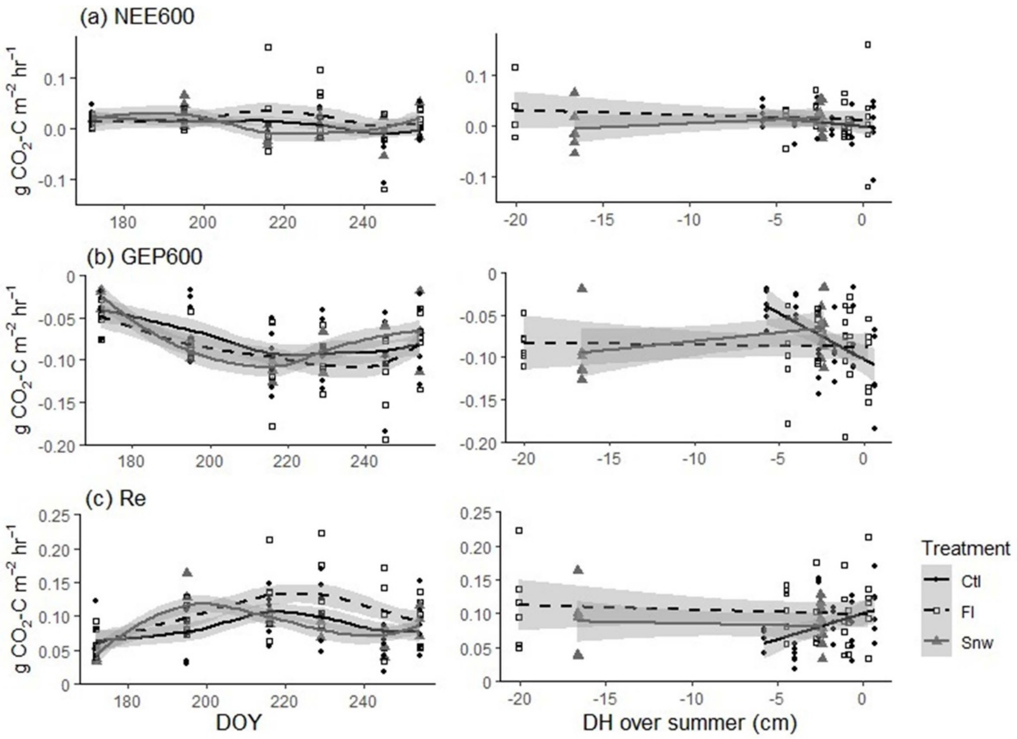

**Figure 3.** CO$_2$ flux rates in the vegetated rim habitats (a) NEE600 stands for net ecosystem exchange at a common radiation level of PAR 600 with negative values indicating C sink and positive values C source, (b) GEP600 stands for gross ecosystem production at a common radiation level of PAR 600, and (c) $R_e$ stands for ecosystem respiration measured in complete darkness in different warming treatments—the non-manipulated control (Ctl, $n = 6$), combined winter and spring warming with insulating fleeces (Fl, $n = 6$) and winter warming with snow-trapping snow fences (Snw, $n = 3$). The left-hand panels show CO$_2$ flux rates as a function of day of the year (DOYs 172–254 i.e. 21 June–11 September 2015) with each measurement as an individual point with loess smoothed (0.70) lines. The right-hand panels show the CO$_2$ flux rates as a function of differential heave (DH) over summer and show each measurement as an individual point with a fitted linear regression line and 95% CI indicated with grey.

## 4. Discussion

We hypothesized that warming during winter and during winter and spring would decrease cryoturbation but neither of the warming treatments decreased cryoturbation (here, the intensity of DH) over two winters (2014/2015, 2015/2016) or over summer 2015. Cryoturbation may show threshold dynamics with increasing winter temperatures (i.e. less negative FDDs) and, instead of a gradual dampening, it may rapidly cease after the threshold FDD has been surpassed (Aalto *et al* 2017). Also, in the frost boils and in the rims, FDDs turned less negative in the warming treatments in comparison to the control but, plausibly, these changes in FDDs did not yet surpass a potential threshold to affect DH. Although overall our warming treatments did not affect DH, we observed two outstanding values for DH over summer from NSCs with a snow-fence or with a fleece both located within the same spatial block. Indeed, the occurrence of cryoturbation has been predicted to increase due to increased snowfall (Aalto *et al* 2017) and, in general, may also respond to changes in precipitation and soil moisture (Hjort and Luoto 2009, Klaus *et al* 2013). However, we did not observe extreme soil moisture conditions or snow depth in this spatial block to explain these outstanding DH values. We propose that cryoturbation may withstand moderate short-term winter and spring warming and increased snowfall in subarctic tundra.

We also hypothesized that both warming treatments will increase tundra C sink function (i.e. NEE more negative) but that combined winter and spring warming with insulating fleeces would increase C sink more. Partially supporting our second hypothesis, winter warming via snow-trapping fences (winter warming effect *c.* 1.7 °C) turned summer NEE less positive and, thus, increased ecosystem C sink function up to 50%–70% in comparison to control and these effects were consistent in frost boils and rims. On the other hand, warming with fleeces (winter warming effect *c.* 0.9 °C) did not increase the C sink indicating that the harsh mid-winter conditions control the subsequent summer CO$_2$ fluxes more than the (late) spring conditions. These observations may have been stochastic as modeling of the summer C budgets did not succeed for all experimental replicates (tables S3(a) and (b)). In contrast to the effects observed in summer, winter warming with snow fences did not change the winter or annual C sink function significantly. Work from other tundra systems has shown that snowier and warmer winters increase winter C mineralization (Jefferies *et al* 2010,

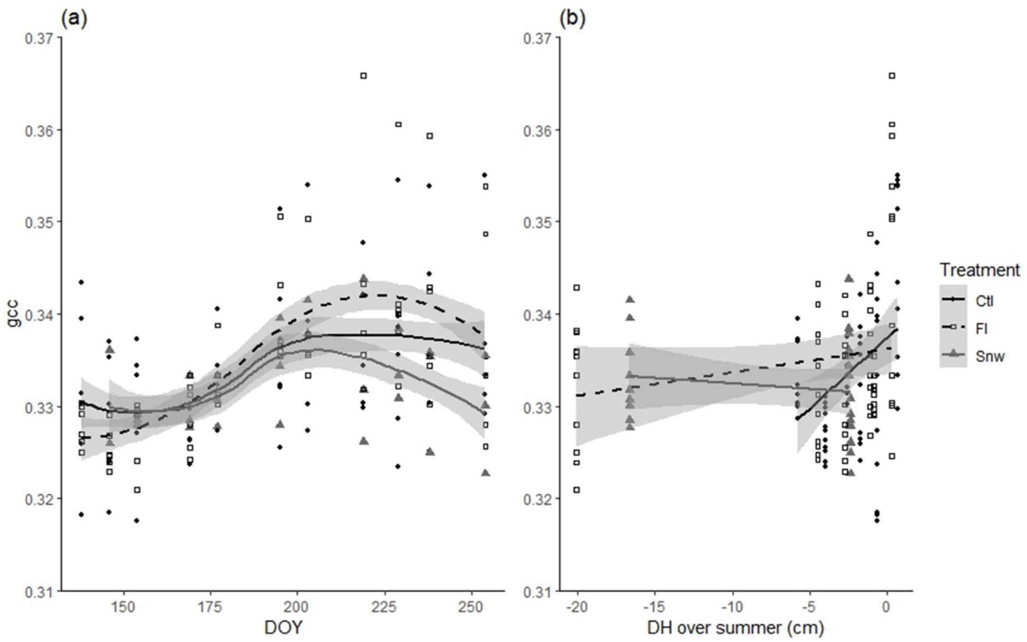

**Figure 4.** The vegetation greenness (green chromatic coordinate, gcc) at the vegetated rims (a) as a function of day of the year (DOY) and (b) as a function of differential heave (DH) over summer 2015 in different warming treatments—the non-manipulated control (Ctl, $n = 6$), combined winter and spring warming with insulating fleeces (Fl, $n = 6$) and winter warming with snow-trapping snow fences (Snw, $n = 3$). The left-hand panel shows gcc as a function of day of the year (DOYs 172–254 i.e. 21 June–11 September 2015) with each measurement as an individual point with loess smoothed (0.70) lines. The right-hand panel shows the gcc as a function of DH over summer and shows each measurement as an individual point with a fitted linear regression line and 95% CI indicated with grey.

Semenchuk *et al* 2016) but, indeed, only when exposed to deep (>1 m) snowpack and near or above zero soil temperatures. Our study area has shallow snowpack and subzero winter soil temperatures across all treatments and, therefore, at windswept cryogenic tundra habitats, moderate increases in winter temperatures and/or snowfall may not influence winter C release. Below, we expand on how the increasing summer C sink function is driven by GEP600 and $R_e$ which responses to warming treatments and cryoturbation, in line with our third hypothesis, differ between the frost boil and the rim habitats.

In the barren frost boils, NEE600 was more negative in the snow fence treatment in comparison to the control and this pattern was paralleled by the dampening of GEP600 and, especially, $R_e$. The snow fences decreased production in comparison to ambient conditions (GEP600 *c.* 0.0082 g $CO_2$–C $m^{-2}$ $h^{-1}$ less negative) suggesting that photosynthesizing biological crusts covering the frost boils may suffer from reduced photoactive period due to longer laying snow (Hui *et al* 2018). Snow fences also decreased $R_e$ (*c.* 0.0119 g $CO_2$–C $m^{-2}$ $h^{-1}$ less positive) in comparison to ambient conditions. Previous studies with perpetually deeper snow have found decreased growing seasonal $CO_2$ release ($R_e$ and microbial respiration), which has been attributed to soil warming-induced increase in winter C mineralization and, consequently, depletion of labile soil C pools (Semenchuk *et al* 2016, 2019, Monteux *et al* 2018). Since our snow fences did not significantly increase winter $CO_2$ release, growing seasonal $R_e$ may have decreased due to greater volumes of melting waters rapidly flushing soil $CO_2$ (Lupascu *et al* 2014). The warming treatments did not affect the seasonal relationship between DH and $CO_2$ fluxes and, as DH over summer became more intense, NEE600 turned consistently more negative due to decreasing $R_e$, which may be caused by decreased root respiration (Becher *et al* 2015). Our findings suggest, firstly, that in frost boils the increasing C sink in response to snowier and warmer winters may be driven by the pronounced dampening of $R_e$. Secondly, our findings highlight that cryoturbation and winter warming may, independent of each other, contribute to $CO_2$ fluxes in frost boils.

In the vegetated rims, NEE600 did not respond significantly to the warming treatments and DH over summer (figure 3(a)). This stability in NEE600 was, however, driven by pronounced shifts in GEP600 and $R_e$. Firstly, the warming treatments changed the seasonal relationship between DH and $CO_2$ fluxes, and as DH over summer intensified, GEP600 turned steeply less negative under ambient conditions whereas remained stable with the fleeces or even turned more negative with the snow fences. Ecosystem productivity depends on the overall leaf area and vegetation greenness (Shaver *et al* 2013), and at our site, greenness (gcc) varied, similar to GEP, depending on the warming treatment and the intensity of DH over summer. Deeper snow often increases plant productivity through heightened plant nitrogen (*sensu* greenness) (Semenchuk *et al*

2015, Rogers *et al* 2018) but at our study site, both warming treatments (fleeces and snow fences) may have also increased productivity through decreasing the frost damages of the dominating dwarf shrubs (Krab *et al* 2018). Like GEP600, also $R_e$ decreased under ambient conditions as DH over summer intensified but stayed stable in the warming treatments. In addition, warming with the fleeces increased $R_e$, which opposes findings from High Arctic tundra (no cryoturbation) where short-term increases in winter soil temperature have not affected growing seasonal $R_e$ (Semenchuk *et al* 2016, Rogers *et al* 2018). It is possible that spring warming with fleeces decreased the frost damages of plants roots and, thus, induced greater root respiration. Our findings are the first to suggest that the negative effects of cryoturbation on plant production (Becher *et al* 2015) may be buffered by warmer and snowier winters. Changes in winter conditions under a future climate may thus be an important factor affecting plant encroachment success into barren frost boils.

## 5. Conclusions

Our study provides the first evidence that cryoturbation, an example of CLSPs feared to decline due to climate warming especially in the Low Arctic (Walker *et al* 2008, Hjort and Luoto 2009, Aalto *et al* 2017) does not dampen in response to short-term experimentally increased winter and combined winter and spring temperatures. However, we found that in these cryogenic landscapes, snowier and warmer winters may enhance growing seasonal net ecosystem C uptake but via different mechanisms depending on the habitat: Winter warming enhances C sink in the barren frost boils by decreasing ecosystem C release while in the vegetated rims, winter warming supports C sink by buffering plant production against seasonal cryoturbation-induced disturbances. We conclude that the future of CLSPs in the climate change-sensitive subarctic tundra may not be as sinister as recently suggested (Aalto *et al* 2017), but that interplay between CLSPs and climate are decisive for C sink function in patterned landscapes across the circumpolar tundra region.

## Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors. Data will be available from 31 March 2023.

## Acknowledgments

Reiner Giesler and Johan Olofsson helped with logistics. Tuukka Mäkiranta and Jacob DeKraai helped in conducting $CO_2$ flux measurements. Konstantin Gavazov, Björn Robroek and Erik Lundin provided valuable ideas for conducting wintertime $CO_2$ campaigns. Patrick Saccone helped with $CO_2$ modeling and Matthias Peichl and Gesche Blume-Werry with vegetation image analyses. Frida Keuper, Ann Milbau, Kobayashi Makoto and Marina Becher contributed to the design of the experimental set up. We thank the Swedish Polar Research Secretariat, logistical support and hospitality. This project was funded by Grants from Vetenskapsrådet (Decision Number 621-2011-5444), Formas (Decision Number 214-2011-788), and a Wallenberg Academy Fellowship (Decision Numbers KAW 2012.0152 and KAW 2017.0298) to Ellen Dorrepaal and Formas (Decision Number 2017-01182) to Eveline Krab.

## Author contributions

E D and J K designed the experiment. E D, J K, E K, M V and L T maintained the experiment and measured differential heave. M V and H Y designed the $CO_2$-flux measurements. M V did the $CO_2$ flux measurements and vegetation imaging, processed the raw data and modeled winter $CO_2$ sums. H Y modeled light responses and growing seasonal $CO_2$ sums. L T processed temperature data. M V analyzed the data and wrote the paper to which all co-authors contributed.

## Conflict of interest

Authors declare no conflict of interest.

## ORCID iD

Maria Väisänen https://orcid.org/0000-0001-9055-8443

## References

Aalto J, Harrison S and Luoto M 2017 Statistical modelling predicts almost complete loss of major periglacial processes in Northern Europe by 2100 *Nat. Commun.* **8** 1–8

Badeck F W, Bondeau A, Bottcher K, Doktor D, Lucht W, Schaber J and Sitch S 2004 Responses of spring phenology to climate change *New Phytol.* **162** 295–309

Becher M, Olid C and Klaminder J 2013 Buried soil organic inclusions in non-sorted circles fields in northern Sweden: age and paleoclimatic context *J. Geophys. Res. Biogeosci.* **118** 104–11

Becher M, Olofsson J and Klaminder J 2015 Cryogenic disturbance and its impact on carbon fluxes in a subarctic heathland *Environ. Res. Lett.* **10** 114006

Björkman M P, Morgner E, Cooper E J, Elberling B, Klemedtsson L and Björk R G 2010 Winter carbon dioxide effluxes from Arctic ecosystems: an overview and comparison of methodologies *Glob. Biogeochem. Cycles* **24** n/a

Blankinship J C and Hart S C 2012 Consequences of manipulated snow cover on soil gaseous emission and N retention in the growing season: a meta-analysis *Ecosphere* **3** 1–20

Blume-Werry G, Wilson S D, Kreyling J and Milbau A 2016 The hidden season: growing season is 50% longer below than above ground along an arctic elevation gradient *New Phytol.* **209** 978–86

Bogerd L, Linden E C, Krikken F and Bintanja R 2020 Climate state dependence of Arctic precipitation variability *J. Geophys. Res. Atmos.* **125** e2019JD031772

Cronin T W and Tziperman E 2015 Low clouds suppress Arctic air formation and amplify high-latitude continental winter warming *Proc. Natl Acad. Sci. USA* **112** 11490–5

Dobiński W 2010 Geophysical characteristics of permafrost in the Abisko area, northern Sweden *Pol. Polar Res.* **31** 141–58

French H M 2007 *The Periglacial Environment* (New York: Wiley)

Frost G V and Epstein H E 2014 Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s *Glob. Change Biol.* **20** 1264–77

Harrell F E J, Dupont C and Al E 2021 Hmisc: Harrell miscellaneous *R package version 4.5–0* (available at: https://CRAN.R-project.org/package=Hmisc)

Hjort J and Luoto M 2009 Interaction of geomorphic and ecologic features across altitudinal zones in a subarctic landscape *Geomorphology* **112** 324–33

Hui R, Zhao R M, Liu L C, Li Y X, Yang H T, Wang Y L, Xie M and Wang X Q 2018 Changes in winter snow depth affects photosynthesis and physiological characteristics of biological soil crusts in the Tengger Desert *Photosynthetica* **56** 1304–12

Inouye D W 2008 Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers *Ecology* **89** 353–62

IPCC 2019 Technical summary *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate* ed H-O Pörtner *et al* (Cambridge University Press)

Jefferies R L, Walker N A, Edwards K A and Dainty J 2010 Is the decline of soil microbial biomass in late winter coupled to changes in the physical state of cold soils? *Soil Biol. Biochem.* **42** 129–35

Kaiser C, Meyer H, Biasi C, Rusalimova O, Barsukov P and Richter A 2007 Conservation of soil organic matter through cryoturbation in arctic soils in Siberia *J. Geophys. Res.* **112** G02017

Klaminder J, Giesler R and Makoto K 2013 Physical mixing between humus and mineral matter found in cryoturbated soils increases short-term heterotrophic respiration rates *Soil Biol. Biochem.* **57** 922–4

Klaus M, Becher M and Klaminder J 2013 Cryogenic soil activity along bioclimatic gradients in Northern Sweden: insights from eight different proxies *Permafr. Periglac. Process.* **24** 210–23

Koven C, Friedlingstein P, Ciais P, Khvorostyanov D, Krinner G and Tarnocai C 2009 On the formation of high-latitude soil carbon stocks: effects of cryoturbation and insulation by organic matter in a land surface model *Geophys. Res. Lett.* **36** L21501

Krab E J, Monteux S, Weedon J T and Dorrepaal E 2019 Plant expansion drives bacteria and collembola communities under winter climate change in frost-affected tundra *Soil Biol. Biochem.* **138** 107569

Krab E J, Roennefarth J, Becher M, Blume-Werry G, Keuper F, Klaminder J, Kreyling J, Makoto K, Milbau A and Dorrepaal E 2018 Winter warming effects on tundra shrub performance are species-specific and dependent on spring conditions *J. Ecol.* **106** 599–612

Kreyling J 2010 Winter climate change: a critical factor for temperate vegetation performance *Ecology* **91** 1939–48

Lenth R V 2021 emmeans: estimated marginal means, aka least-squares means *R package version 1.6.0* (available at: https://CRAN.R-project.org/package=emmeans)

Lupascu M, Welker J M, Seibt U, Xu X, Velicogna I, Lindsey D S and Czimczik C I 2014 The amount and timing of precipitation control the magnitude, seasonality and sources (14C) of ecosystem respiration in a polar semi-desert, northwestern Greenland *Biogeosciences* **11** 4289–304

Makoto K and Klaminder J 2012 The influence of non-sorted circles on species diversity of vascular plants, bryophytes and lichens in sub-Arctic tundra *Polar Biol.* **35** 1659–67

Monteux S, Weedon J T, Blume-Werry G, Gavazov K, Jassey V E J, Johansson M, Keuper F, Olid C and Dorrepaal E 2018 Long-term *in situ* permafrost thaw effects on bacterial communities and potential aerobic respiration *ISME J.* **12** 2129–41

Morgner E, Elberling B, Strebel D and Cooper E J 2010 The importance of winter in annual ecosystem respiration in the High Arctic: effects of snow depth in two vegetation types *Polar Res.* **29** 58–74

Neuner G 2014 Frost resistance in alpine woody plants *Front. Plant Sci.* **5** 654

Palacio S, Lenz A, Wipf S, Hoch G and Rixen C 2015 Bud freezing resistance in alpine shrubs across snow depth gradients *Environ. Exp. Bot.* **118** 95–101

Pinheiro J, Bates D, DebRoy S, Sarkar D and Team R C 2021 nlme: linear and nonlinear mixed effects models *R Package Version 3.1–152* (available at: https://CRAN.R-project.org/package=nlme>)

Puissant J, Cecillon L, Mills R T E, Robroek B J M, Gavazov K, de Danieli S, Spiegelberger T, Buttler A and Brun J-J 2015 Seasonal influence of climate manipulation on microbial community structure and function in mountain soils *Soil Biol. Biochem.* **80** 269–305

Rogers M C, Sullivan P F and Welker J M 2018 Evidence of nonlinearity in the response of net ecosystem $CO_2$ exchange to increasing levels of winter snow depth in the High Arctic of northwest Greenland *Arctic, Antarct. Alpine Res.* **43** 95–106

Saarinen T and Lundell R 2010 Overwintering of *Vaccinium vitis-idaea* in two sub-Arctic microhabitats: a reciprocal transplantation experiment *Polar Res.* **29** 38–45

Schimel J P, Bilbrough C and Welker J M 2004 Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities *Soil Biol. Biochem.* **36** 217–27

Schwartz M D, Ahas R and Aasa A 2006 Onset of spring starting earlier across the Northern Hemisphere *Glob. Change Biol.* **12** 343–51

Semenchuk P R, Christiansen C T, Grogan P, Elberling B and Cooper E J 2016 Long-term experimentally deepened snow decreases growing-season respiration in a low- and high-arctic tundra ecosystem *J. Geophys. Res. Biogeosciences* **121** 1236–48

Semenchuk P R, Elberling B, Amtorp C, Winkler J, Rumpf S, Michelsen A and Cooper E J 2015 Deeper snow alters soil nutrient availability and leaf nutrient status in high Arctic tundra *Biogeochemistry* **124** 81–94

Semenchuk P R, Krab E J, Hedenström M, Phillips C A, Ancin-Murguzur F J and Cooper E J 2019 Soil organic carbon depletion and degradation in surface soil after long-term non-growing season warming in High Arctic Svalbard *Sci. Total Environ.* **646** 158–67

Shaver G R, Rastetter E B, Salmon V, Street L E, van de Weg M J, Rocha A, van Wijk M T and Williams M 2013 Pan-Arctic modelling of net ecosystem exchange of $CO_2$ *Phil. Trans. R. Soc.* B **368** 20120485

Sonnentag O, Hufkens K, Teshera-Sterne C, Young A M, Friedl M, Braswell B H, Milliman T, O'Keefe J and Richardson A D 2012 Digital repeat photography for phenological research in forest ecosystems *Agric. For. Meteorol.* **152** 159–77

Thompson D W J and Wallace J M 2001 Regional climate impacts of the Northern Hemisphere annular mode *Science* **293** 85–89

Väisänen M, Krab E J and Dorrepaal E 2017 Carbon dynamics at frost-patterned tundra driven by long-term vegetation change rather than by short-term non-growing season warming *Biogeochemistry* **136** 103–17

Walker D A *et al* 2004 Frost-boil ecosystems: complex interactions between landforms, soil, vegetation and climate *Permafr. Periglac. Process.* **15** 171–88

Walker D A *et al* 2008 Arctic patterned-ground ecosystems: a synthesis of field studies and models along a North American Arctic transect *J. Geophys. Res.* **113** G03S01

Wheeler J A, Hoch G, Cortes A J, Sedlacek J, Wipf S and Rixen C 2014 Increased spring freezing vulnerability for alpine shrubs under early snowmelt *Oecologia* **175** 219–29

Wickham H 2016 *ggplot2: Elegant Graphics for Data Analysis* (New York: Springer)

Wipf S and Rixen C 2010 A review of snow manipulation experiments in Arctic and alpine tundra ecosystems *Polar Res.* **29** 95–109

Wipf S, Stoeckli V and Bebi P 2009 Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing *Clim. Change* **9** 105–21

Zoltai S C and Tarnocai C 1981 Some nonsorted patterned ground types in Northern Canada *Arctic Alpine Res.* **13** 139–51