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Article type : Research Article

Handling Editor: Amy Austin

**Winter warming effects on tundra shrub performance are species-specific and dependent on spring conditions**

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2745.12872

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Running headline: *Shrub responses to winter and spring climate*

**Author contributions:** ED, JKl. and AM designed and established the winter manipulation experiment with advice from FK, GB, KM and MB. ED, AM, EJK and JKl. maintained the winter manipulation experiment. ED, JKr. and JR planned measurements and design for this study and JR performed all field and laboratory work. EJK, JR and JKr. analysed the data. EJK, JR, GBW and ED wrote the manuscript. All other co-authors commented on the manuscript. JR and EJK contributed equally to the realization of this manuscript.

## Abstract

1. Climate change driven increases in winter temperatures positively affect conditions for shrub growth in arctic tundra by decreasing plant frost damage and stimulation of nutrient availability. However, the extent to which shrubs may benefit from these conditions may be strongly dependent on the following spring climate. Species-specific differences in phenology and spring frost sensitivity likely affect shrub growth responses to warming.

Additionally, effects of changes in winter and spring climate may differ over small spatial scales, as shrub growth may be dependent on natural variation in snow cover, shrub density and cryoturbation.

**2.** We investigated the effects of winter warming and altered spring climate on growing-season performance of three common and widespread shrub species in cryoturbated non-sorted circle arctic tundra. By insulating sparsely vegetated non-sorted circles and parts of the surrounding heath with additional snow or gardening fleeces we created two climate change scenarios: Snow addition increased soil temperatures in autumn and winter and delayed snowmelt timing without increasing spring temperatures, whereas fleeces increased soil temperature similarly in autumn and winter, but created warmer spring conditions without altering snowmelt timing.

**3.** Winter warming affected shrub performance, but the direction and magnitude were species-specific and dependent on spring conditions. Spring warming advanced, and later snowmelt delayed canopy green-up. The fleece treatment did not affect shoot growth and biomass in any shrub species despite decreasing leaf frost-damage in *E. nigrum*. Snow addition decreased frost damage and stimulated growth of *V. vitis-idaea* by approximately 50%, while decreasing in *B. nana* growth ( $P < 0.1$ ). All of these effects were consistent in the mostly barren circles and surrounding heath.

**4. Synthesis.** In cryoturbated arctic tundra, growth of *V. vitis-idaea* may substantially increase when a thicker snow cover delays snowmelt, whereas in longer-term, warmer winters and springs may favor *E. nigrum* instead. This may affect shrub community composition and cover, with potentially far-reaching effects on arctic ecosystem functioning via its effects on cryoturbation, carbon cycling and trophic cascading. Our results highlight the importance of disentangling effects of winter and spring climate change timing and nature, as spring

conditions are a crucial factor in determining the impact of winter warming on plant performance.

**Keywords:** *Betula nana*, cryoturbation, *Empetrum nigrum*, plant phenology, winter climate change, shrubs, snow cover, snowmelt timing, spring climate, *Vaccinium vitis-idaea*

## Introduction

The effects of global change on our climate are particularly pronounced during winter and spring (Thompson & Wallace 2001; Schwartz, Ahas & Aasa 2006; IPCC 2013). The timing and nature of these climate changes may be crucial for its effects on plants and ecosystem processes in seasonal ecosystems (e.g. Sturm *et al.* 2005; Wipf, Stoeckli & Bebi 2009; Kreyling 2010). We know higher soil temperatures in winter generally positively affect conditions for plant overwintering and plant performance during the growing season. Higher soil temperatures in winter due to increased snow cover, for example, protect plants from winter frost damage (Saarinen & Lundell 2010, Neuner 2014, Palacio *et al.* 2015) and increase nitrogen availability (Schimel, Bilbrough & Welker 2004; Blankinship & Hart 2012). However, the extent to which plants can benefit from these conditions may largely depend on the climate in spring. Changes in snowmelt timing and the increases in spring air temperatures may delay or advance the onset of the growing season (Menzel & Fabian 1999; Badeck *et al.* 2004; Menzel *et al.* 2006; Inouye 2008; Saarinen & Lundell 2010; Wipf & Rixen 2010) as well as the susceptibility of plants to freezing damage during spring frost events (Inouye 2008; Wheeler *et al.* 2014). In ecosystems with naturally shallow snow cover, small increases in snow cover in winter may have large impacts on winter soil temperatures whereas increases in spring air temperatures may largely drive plant growth onset. The definitive effects of increases in winter temperature on plant growth may therefore be largely

determined by spring air temperature regime, and this may affect plants with different frost sensitivity and phenology differently (Taschler & Neuner 2004; Wheeler *et al.* 2014). This may be particularly true for shrub-dominated tundra ecosystems at high latitudes, where species differ in their sensitivity to environmental severity during the non-growing season (Saccone, Hoikka & Virtanen 2017) and where spring temperatures largely drive the timing of growth onset (Ernakovic *et al.* 2014).

Changes in winter and spring climate are particularly relevant for shrubs, whose overwintering aboveground structures rely on insulating snow-cover for protection. Generally, harsh winter conditions may cause frost damage to aboveground overwintering plant structures, such as buds, woody stems and evergreen leaves (Sakai & Miwa 1979; Neuner 2014; Palacio *et al.* 2015). Further, the relatively short snow-free period limits seasonal growth (Chapin & Shaver 1985), and cryoturbation (soil frost movement) may mechanically damage roots. Combined with low belowground microbial mineralisation in cold soils (Duran *et al.* 2014), this may reduce plant nutrient uptake and growth the following summer (Jonasson & Callaghan 1992). In arctic and alpine ecosystems, the trend towards shrub expansion due to global change (Myers-Smith *et al.* 2011; Elmendorf *et al.* 2012) might thus be particularly facilitated by changes in winter climate. Shrub cover increases may in turn feed back to higher winter soil temperatures by trapping snow (Sturm *et al.* 2005). However, different shrub species might benefit from changes in winter and spring climate to a different extent, as natural variation in their timing of growth onset (Wipf 2010) and spring frost sensitivity (Pop, Oberbauer & Starr 2000; Inouye 2008; CaraDonna & Bain 2016) may affect their responses to these changes. The combination of the timing and nature of winter climate changes and susceptibility of different shrub species to these changes therefore make the exact impact of winter climate change on shrub encroachment hard to predict.

Cryoturbated soils are landscape features in cold ecosystems that may be particularly sensitive to changes in winter and spring climate (Becher, Olid & Klaminder 2013; Frost *et al.* 2013). These soils cover a substantial area of the arctic and alpine regions (approx. 31% of the permafrost region (Hugelius *et al.* 2014)) and contribute highly to global C-storage (Tarnocai *et al.* 2009; Hugelius *et al.* 2014). In these soils, winter soil temperatures greatly depend on local variation in snow cover, and the resulting differential frost movement leads to continuous burial of organic soil. Non-sorted circle (NSC) tundra represents a common type of cryoturbated soil, consisting of sparsely vegetated soil patches (1-3 m diameter) surrounded by more densely vegetated heath (Washburn 1980; Walker *et al.* 2008; Fig. 1). The interplay of wind and shrub abundance results in shallower snow cover in the centre of NSCs than in the surrounding heath, leading to small-scale variation in soil frost and cryoturbation. However, in recent decades, potentially due to changes in winter climate, large areas of NSCs have experienced shrub encroachment and reduced cryoturbation (Kade, Walker & Raynolds 2005; Becher *et al.* 2013; Frost *et al.* 2013), which may positively feed back onto one another.

These NSCs provide an excellent study system to disentangle the effects of winter and spring climate change on shrub performance in a heterogeneous landscape. They are small enough to experimentally manipulate within a limited space, and allow us to compare the effects of winter climate change on shrubs in densely vegetated heath to those growing in the mostly barren, cryoturbated soil. In densely vegetated heath, cryoturbation is limited due to relatively higher snow cover. Here, realistic increases in snow cover may not alter soil temperatures dramatically. In mostly barren cryoturbated soil, small increases in the naturally thin snow cover may strongly increase soil temperatures in winter. The ways in which changes in winter and spring climate may impact shrub performance in these small-scale

patches may be fundamentally different, allowing us to investigate by which mechanisms winter climate changes may facilitate shrub encroachment.

In this study, we investigated if winter warming and altered spring conditions differ in their effects on growing-season performance of vegetation in NSCs. We assessed if different shrub species respond differently to two years of altered winter and spring climate change and if these effects differ between densely vegetated heath (outer NSC domains) and mostly barren cryoturbated soil (inner domains). By using snow fences and insulating gardening fleeces that covered NSCs in autumn, winter and spring, we simulated two winter warming scenarios: Snow fences increased soil temperatures during the natural snow-covered period (mid-October - mid-May,  $\sim 1^{\circ}\text{C}$ ), without changing average spring soil temperatures, whereas gardening fleeces increased soil temperatures from October until early June (also  $\sim 1^{\circ}\text{C}$ ), thus additionally warming in early autumn and the spring period after snowmelt. To assess shrub performance, we selected the deciduous shrub *Betula nana* and the evergreen shrubs *Empetrum nigrum* and *Vaccinium vitis-idaea*, as they are common arctic species and the dominant species in both inner and outer domain at the field site (Makoto & Klaminder 2012). Their responses are thus expected to give an indication of how shrubby vegetation of NSCs in general responds to higher winter soil temperatures and changes in spring conditions, while diverging responses of the species can give further insights into species-specific future performance and potential directions of change in community composition of NSCs. Shrub performance was measured as leaf frost damage, shoot length growth and shoot biomass increase. Temporal changes in relative canopy greenness were analysed to test in which way winter climate change affects whole-vegetation phenology.

We expected winter warming through added snow (snow treatment) to delay, and winter warming combined with spring warming (fleece treatment) to advance overall shrub phenology. We expected shrub species to differ in frost sensitivity, and that winter warming

decreases leaf frost damage relative to ambient conditions. More specifically we expected that winter warming through added snow would decrease frost damage more than winter warming combined with spring warming. We hypothesized that winter warming stimulates shrub shoot growth and biomass increase, especially if combined with spring warming and for shrub species that start growing early in spring (*E. nigrum* before *V. vitis-idaea* and finally *B. nana*). We predicted these changes to be most strongly pronounced in the sparsely vegetated inner domains of NSCs.

## Material and methods

### *Site description*

The field site was located ca. 20 km southeast of Abisko, Northern Sweden (68°18'N, 19°10'E). Mean annual temperature and mean annual precipitation in Abisko (385 m a.s.l.) for the period 1990-2013 were 0.3 °C and 337 mm, respectively (Abisko Station Meteorological Data: [www.polar.se/abisko](http://www.polar.se/abisko)). Snow is typically present from October to May. The field site is situated above the treeline at about 850 m a.s.l. and spans an area of 150 x 100 m. The vascular plant canopy is typically less than 10 cm high and the community is characterized by the evergreen dwarf shrubs *Empetrum nigrum* L. and *Vaccinium vitis-idaea* L. and the deciduous dwarf shrubs *Betula nana* L. and *Vaccinium uliginosum* L. The site contains a large number of NSCs that are seen as light grey circles or elongated stripes with a diameter of 1-3 m surrounded by heath vegetation (Fig. 1a). We will from here on refer to the relatively barren circles or stripes as 'inner domain' and the adjacent heath vegetation as 'outer domain'. In the NSC inner and outer domains in this site, *V. vitis-idaea* generally covers 1% and 5% respectively, *B. nana* covers 11 % and 32%, and *E. nigrum* 6% and 30% (Makoto & Klaminder 2012). The site was chosen because NSCs at the site had previously been reported to show strong cryogenic activity (Klaus, Becher & Klaminder 2013).

### *Experimental setup*

The experiment was established in autumn 2012 and insulation manipulations were applied in the winter seasons from September through May in 2012/13 and 2013/14. To increase winter soil temperature from autumn through late winter and extending into spring, six NSCs (Fig. 1a) were covered each with four thin layers of rectangular, white, water- and light-penetrable polypropylene fleece blankets (Nelson Garden, Sweden; 17 g/m<sup>2</sup>) (hereafter: “fleece treatment”). Fleeces were fixed with rocks along the edges. Both the inner and outer domains of the NSCs were covered by the fleeces (Fig. 1b). Fleeces were installed in late September (2012: September 28; 2013: September 18) and removed about two weeks after the natural snowmelt in spring (2013: May 31; 2014: June 3). The fleece manipulation created a novel scenario in which winter warming is combined with warming in spring, which occurs when warmer winters are followed by a warmer spring. This treatment differs from snow removal experiments (by e.g. shovelling) in which winter soil temperatures are ambient or decreased by shovelling (e.g. Wipf & Rixen 2010; Blankinship & Hart 2012).

Six NSCs served as a control. These control NSC were un-manipulated and, therefore, received ambient snowfall and experience ambient soil temperatures.

Furthermore, three snow fences (hereafter: “snow treatment”) were built as low rock walls perpendicular to the dominant (westerly) wind direction near three NSCs to increase soil temperatures from mid-autumn to late winter. Fences were approx. 60 cm in height and 2 m long and followed the upwind side of each NSC in a crescent-shaped pattern, approx. 40 cm outside the boundary between inner and outer domain (Fig. 1ac). The snow fence manipulation created a scenario comparable with snow addition experiments that are regularly conducted in alpine and arctic ecosystems (e.g. Wipf & Rixen 2010; Blankinship & Hart 2012; Johansson *et al.* 2013). Here, increased soil temperatures in winter is followed by delayed snowmelt and ambient spring temperatures, in a system that has relatively little snow

naturally, and where snow is unevenly distributed between inner and outer domain over a small spatial scale.

Treatment and control circles were distributed spatially in six blocks, which were located at least 10 meters apart from each other. Each block contained one replicate of each treatment, except block 4, 5 and 6 that only contained a replicate of the control and fleece treatments. Manipulated circles within blocks were at least 1 m apart. Inner domain diameters ranged from 79 cm to 351 cm (measured in 2015).

#### *Soil temperatures, freeze-thaw cycles and snow depth*

Soil temperatures were measured hourly in the centre (inner domain) of each circle at approx. 1 cm depth in the soil (Tiny Tag Talk 2 temperature loggers with external sensors, Intab Interface-Teknik AB, Sweden). The loggers were installed in autumn 2012 and 2013 and removed in late spring in 2013, whereas in 2014 soil temperatures were also recorded in summer until the peak of the growing season (21<sup>st</sup> of July; Table 1). Soil movement had pushed out four temperature sensors in 2013 (two control, two fleece treatment) and two sensors in 2014 (one control, one fleece treatment), which were excluded from the analyses. For better understanding of the effects of the treatments, and to facilitate comparison to other ecosystems, temperature data were split into five sub-seasons with characteristic patterns of temperature, daylight, and snow conditions (Table 1), i.e. autumn, midwinter, late winter, spring and summer. For each sub-season, we calculated average temperatures and the number of freeze-thaw cycles (FTCs) by counting the number of 0 °C crossings from thaw to freeze (Dale, Reinke & Wright 1980).

Snow depth was measured each year in all treatments at the peak of snow accumulation (late March / early April) at 50-cm intervals along a west-east transect across each plot (i.e. perpendicular to the snow fences). The first measurement point was directly

next to the snow fence (or western plot-edge in the fleece treatment and controls), the next one 50 cm east of the snow fence, and so further until 3 meter east of the snow fence or plot edge. In 2014, an additional snow depth measurement was made at the end of April, following a period of heavy snowfall.

#### *Aboveground vegetation measurements*

Effects of the treatments on whole-canopy green-up and on leaf frost damage, shoot length growth and biomass of new shoots (shoot increment biomass) of typical plant species in NSCs were investigated following two winter seasons of manipulations, between snowmelt and the peak of the growing season, i.e. from the 20<sup>th</sup> of May until the 21<sup>st</sup> of July 2014. For each of these measurements N=6 for each domain/treatment combination, except for the snow treatment (N=3).

We used repeated digital photography to record changes in whole-canopy greenness over the first half of the growing season, as an indication of changes in vegetative phenology (Keenan *et al.* 2014; Toomey *et al.* 2015). In each of the 15 circles, two 50 x 50 cm squares were marked in NSCs, one randomly chosen in the outer domains, and one at a relatively vegetated patch in the inner domains. Pictures of the squares were taken (Canon EOS 1100D) with constant zoom and aperture (f/5.6) from fixed positions using a modified tripod approx. once per week for eight consecutive weeks. White balance and colour balance were standardized for every photo using a diffuse light tent and a grey card. All pictures were cropped to the marked 50 x 50 cm squares to standardize the area covered and green cover was calculated as the percentage of green pixels in the square (using GIMP version 2.8.14). Because of the heterogeneous character of the plant cover in NSC vegetation, total plant cover varied between the marked squares. To be able to compare phenology across plots and treatments, green cover at each date was therefore standardized by calculating the ratio [%] of

green cover at that date relative to the maximum green cover of the same square during the growing season (in most cases as measured on the 21<sup>st</sup> of July), which will further be referred to as: “relative canopy greenness”

We used the relative electrolyte leakage (REL) test (Sutinen, Palta & Reich 1992) to measure frost damage on overwintering leaves of *E. nigrum* and *V. vitis-idaea* and emerging leaf buds of *B. nana*. Evergreen leaves were taken from the inner and outer domain of each plot as soon as possible after snowmelt (May 20). No leaves of *B. nana* were present at that time. One week later (May 27), the sampling was repeated, now also including emerging leaf buds of *B. nana*. This means that at time of sampling (and frost exposure) leaves of different species may have been in different developmental stages. Sufficient leaves for analysis were collected from one individual plant per species per NSC-domain. Immediately upon return to the laboratory, leaves of *V. vitis-idaea* were cut into 0.5 cm long pieces, whereas the smaller leaves of *E. nigrum* and leaf buds of *B. nana* were used whole. Samples were rinsed with deionized water and incubated in 16 ml 0.1% (v/v) Triton X-100 for 24 h. Samples were shaken mechanically at the beginning and end of the incubation for 5 min. After the incubation, initial conductivity was measured (Sevencompact S230, Mettler-Toledo AG, Switzerland), after which the samples were boiled for approx. 55 min. to lyse all cells that had not been damaged by frost. After 24h of resting, samples were shaken hard by hand and final conductivity was measured. Relative electrolyte leakage was calculated as the ratio [%] of the conductivities prior relative to after the boiling.

The temporal dynamics of shoot length growth and shoot increment biomass were measured on *B. nana*, *E. nigrum* and *V. vitis-idaea* shoots by marking main stems (only long shoots for *B. nana*) at a fixed point and measuring shoot length above that point approx. once per week for seven consecutive weeks. One shoot for each species was selected randomly and marked in each domain of each NSC.

At the last measurement date, at the peak of the growing season (July 21), the newly grown shoot parts were cut off at the marking and biomass increment was determined after drying the samples for 48h at 105°C.

### *Statistical analyses*

To assess whether our treatments successfully altered soil temperatures, number of FTCs (freeze-thaw cycles) and snow-depth during the snow-covered period we subdivided the snow-covered season in different sub-seasons (Table 1). Soil temperatures and number of FTCs were analysed using general mixed models (GLMM) and ANOVA. Average soil temperatures and number of FTCs were calculated for each sub-season for each replicate, after which the analyses were run with ‘treatment’ and ‘sub-season’ as fixed factors. We added ‘circle identity’ as a random factor to account for potential spatial autocorrelation between sampling point within a circle. Separate analyses for soil temperature and FTCs were carried out for data from 2013 and 2014. To test how snow was distributed along west-east transects (measurement points) in the NSCs with different treatments, a GLMM was used with fixed factors ‘treatment’ and ‘measurement point’ and random factors: ‘circle identity’ and ‘measurement year’.

We used GLMM to test if our treatments affected frost damage, if this differed for shrubs growing in the inner and outer parts of NSC (domains) and if shrub species differed in their response to the winter and spring climate manipulations. We tested this for fixed factors ‘treatment’, ‘domain’ and ‘species’ and their interactions and ‘circle identity’ was added as a random factor. For this analysis the results of the two sampling days were analysed separately because *B. nana* was only present on the second sampling day (May 27). Similar models were used to test if winter and spring climate changes affected total shoot length growth and biomass as determined at the peak of the growing season.

Shoot length growth and canopy greenness throughout the growing season were analysed using GLMM, testing the effects of fixed factors: ‘treatment’, ‘domain’, ‘species’ and ‘sampling date’ and their interactions and we added ‘circle identity’ as random factor.

Although the experiment was spatially arranged in a randomized block design, ‘block’ was not added in the statistical analyses as random factor because not all treatments were replicated in each block and because of the limited degrees of freedom available for analyses.

All data were tested for normality (qq-plot) and heteroscedasticity (fitted values vs. residuals plot). Data were square root- or log-transformed if model assumptions were not met (see tables in supplementary information). If no interactions were found, models were simplified and the interaction terms removed to increase statistical power. Least square means were used for all post-hoc comparisons. All results are reported with a significance level of  $\alpha < 0.05$ , a statistical trend was indicated for  $\alpha < 0.1$ . All statistical analyses were carried out using the statistical software R (R Development Core Team, version 3.2.3) and Rstudio (RStudio 0.98.1102) with additional packages lmerTest 2.0-11 (function lmer for the linear mixed models and diffslmeans for the post hoc tests) and sciplot 1.1-0 and ggplot2 for graphical illustrations.

## **Results**

### *Snow depth and soil temperatures*

At the peak of the snow accumulation (March-April), about 7 cm deeper snow cover was found in the snow treatment (on average  $10 \pm 13$  cm (se = 1.5)) than in the control plots and the fleece treatment (on average  $3 \pm 5$  cm (se = 0.4)); ( $F = 16.1$ ,  $P < 0.001$ ; Table S1). This effect was greatest close to the snow fence as most snow accumulated directly behind the

snow fences (Fig. 1c, S1). The snow treatment delayed snowmelt for about a week and the fleeces did not delay or advance snow melt timing relative to the control plots.

In both years, mean soil temperatures during the coldest periods of the winter season (autumn, midwinter, late winter) were 1.0 °C warmer in the fleece treatment and 1.4 °C warmer in the snow treatment than in the control plots ( $F = 7.4$ ,  $P < 0.05$  for 2012/13,  $F = 8.43$ ,  $P < 0.01$  for 2013/14; Table 2, Tables S2 and S3, Fig. S2). Treatment and sub-season interacted ( $F = 5.6$ ,  $P < 0.001$  for 2012/13,  $F = 2.8$ ,  $P < 0.05$  for 2013/14, Table S2 and S3), suggesting that our treatments affected soil temperatures differently in different seasons. In 2012/13 and 2013/14, our fleece and snow treatments had strong statistically significant positive effects on soil temperatures in autumn (1.2 °C and 1.4 °C increase for fleece and snow treatment respectively, Table 2) and mid-winter (1.1 °C and 1.8 °C increase for fleece and snow treatment respectively, Table 2). Treatment effects differed over winter sub-seasons (Table S2 and S3): Both treatments warmed soils in autumn and midwinter but in contrast to the fleece treatment the snow treatment increased soil temperatures in the late-winter sub-season (with 1.4 °C in 2013 and 0.9 °C in 2014, Table 2). Contrariwise, in spring 2014 the fleece treatment had a statistically significantly positive effect on spring temperatures (1.3 °C warmer, Table 2), whereas in the snow treatment spring soil temperatures did not differ from ambient. Summer soil temperatures (only measured in 2014) were unaffected by our treatments (Table 2). During a cold spell at the end of June 2014, temperatures dropped to close to 0 °C in all treatments for about a week, including two late-frost events during the night (Fig. S2).

Our treatments significantly altered FTCs in different sub-seasons ( $F = 3.9$ ,  $P < 0.01$  (2012/13),  $F = 11.1$ ,  $P < 0.001$  (2013/14); Tables S4 and S5). In autumn 2012, no FTCs were recorded after the late installation of the loggers on 14 October, but there were no significant effects of the treatments on the FTCs in autumn 2013 either. Generally, no FTCs were found

during midwinter and late winter. In spring 2013, the snow treatment reduced the number of FTCs significantly ( $P < 0.001$ , post-hoc test, Table 2). In contrast, in the spring of 2014, statistically significant increases in FTC frequency in the fleece treatment relative to the control and snow treatments were found ( $P < 0.001$ ; Tables S4 and S5 and post-hoc test), most likely because ambient temperatures stayed just below 0 °C in April 2014 and the fleece treatment frequently increased temperatures above 0 °C (Fig. S2).

#### *Vegetation responses*

The fleece treatment had a significant effect on relative canopy greenness ( $F = 5.6$ ,  $P < 0.05$ ; Table S6 and post-hoc test) and accelerated the temporal development of the relative canopy greenness compared to the control and snow treatments (interaction between treatment and date:  $F = 2.5$ ,  $P < 0.01$ ). In both domains, 50% of maximum canopy greenness was reached earlier in the fleece treatments than in control plots (3 days earlier in inner domains, 6 days earlier in outer domains) whereas in the snow addition treatment it was delayed by 3 days in the inner domains (Fig. 2). The vegetation in the fleece treatment continued to have higher relative canopy greenness throughout most of the spring and early summer season compared to the other treatments. All treatments showed a decline in relative greenness during the cold spell between 19 and 26 June in 2014, but recovered soon afterwards. The inner and outer domain did not show any difference in relative canopy greenness or response to the treatments.

Snow disappeared from the control and fleece treatment in the week of 12-18 May, (in between site-visits), whereas the snow in the snow addition treatment disappeared just before the 20<sup>th</sup> of May. Straight after the last snowmelt (May 20) there was a significant difference in leaf frost damage between the two evergreen shrub species ( $F = 24.7$ ,  $P < 0.001$ ; Table S7), but there was no treatment effect, nor an interaction. One week after snowmelt (May 27),

leaf frost damage was highest for *B. nana* (mean  $\pm$  SE across treatments and domains:  $32.6 \pm 1.0$  %), followed by *E. nigrum* ( $17.6 \pm 0.8$  %) and *V. vitis-idaea* ( $15.2 \pm 1.0$  %,  $F = 55.1$ ,  $P < 0.001$ ; Fig. 3, Table S8). Leaf frost damage was reduced by the fleece treatment in *E. nigrum* and the snow addition treatment reduced frost damage in *V. vitis-idaea* (interaction between treatment and species:  $F = 3.8$ ,  $P < 0.01$ ; Table S8 and post-hoc test). There was a trend towards lower leaf frost damage in the outer domain than in the inner domain ( $F = 4.0$ ,  $P < 0.1$  (May 20),  $F = 3.8$ ,  $P < 0.1$  (May 27)), but domain did not interact with the treatment or species effects.

Shoot length growth of the three species was differentially affected by the treatments (interaction between treatment and species:  $F = 5.6$ ,  $P < 0.001$ ; Table S9). This difference between the species in shoot length growth response to the treatments was most pronounced later in the growing season (interaction between treatment, species, and date:  $F = 2.2$ ,  $P < 0.001$ ; Fig. 4, Table S9). No significant effect of the fleece treatment on shoot length growth was found. *V. vitis-idaea* responded to the snow treatment with enhanced length growth ( $P < 0.05$ , post-hoc test), especially after a cold spell in mid June 2014 (Fig S2, Fig. 4). In contrast, the snow treatment tended to negatively affect *B. nana* ( $P < 0.1$ , post-hoc test), which shoots almost ceased growing after the cold spell (Fig 4.). The negative effects of the snow treatment on *B. nana* seemed most pronounced in the inner domain, where length growth during the last three weeks of the measurement period averaged only 0.05 cm. *Empetrum nigrum* length growth did not respond significantly to any of the treatments. Shoot length growth was slightly lower in the inner domain than the outer domain ( $F = 4.5$ ,  $P < 0.05$ ; Table S9), especially for *B. nana* (interaction between domain and species:  $F = 2.9$ ,  $P < 0.1$ ). There were no significant interactions between domain and treatment. Total shoot length growth until the peak of the growing season also showed a significant interaction between

treatment and species ( $F = 2.7$ ,  $P < 0.05$ ; Table S10), reflecting the different effect of the snow treatment on *B. nana* and *V. vitis-idaea*.

As with the shoot length growth, shoot increment biomass seemed to be reduced by the snow treatment for *B. nana* and enhanced for *V. vitis-idaea* (Fig. 5). However, while shoot biomass correlated significantly with total shoot length growth ( $P < 0.001$ , Fig. S3), the treatments, species or domain effects did not induce statistically significant differences in shoot biomass (Table S11).

## Discussion

We showed that winter warming affects shrub performance substantially, but that the direction and magnitude of its effects are species-specific and dependent on spring conditions. Both winter warming (by snow addition) and the combination of winter soil and spring warming (by fleeces) affected shrub phenology, however higher temperatures in spring advanced canopy green-up, whereas later snowmelt and ambient late-spring temperatures delayed green-up. Surprisingly, warmer winters in combination with increased spring temperatures did not lead to increased shoot growth and biomass in any of the shrub species despite the advance in phenology and observed decreased frost-damage in *E. nigrum*.

Winter warming due to increased snow cover, in contrast, stimulated the growth of *V. vitis-idaea*, which corresponded to decreased leaf frost-damage in *V. vitis-idaea*, and it decreased *B. nana* growth ( $P < 0.1$ ), despite an absence of changes in leaf-frost damage in *B. nana*.

Shrub performance was overall higher in the vegetated outer domains of non-sorted-circles (NSC) than in the mostly barren inner domains, but the treatment effects were similar regardless of location, suggesting winter and spring warming affect shrub performance to a similar extent in different microhabitats in a heterogeneous landscape. Below we will further discuss the causes of these findings and their potential implications.

### *Warmer winters and altered spring temperature and freeze-thaw cycle regimes*

Our manipulations of climate outside the growing season increased mean soil temperatures comparably in the snow and the fleece manipulation during periods with natural snow cover (autumn until late winter). Soil temperature increased on average 1.4 °C in the snow and 1.0 °C in the fleece treatment (Table 2), i.e. an effect comparable to what has been found in other snow manipulation studies in similar ecosystems (Dorrepaal *et al.* 2004; Johansson *et al.* 2013). During this period the freeze-thaw cycle regime was not affected by any of the treatments, such that the snow and fleece treatment manipulated winter soil climate in a similar way and that differences in shrub performance between these treatments can be attributed to differences in spring conditions.

In our snow treatment, snowmelt was delayed about one week in comparison to ambient conditions, which is slightly less compared to other studies using snow fence manipulations (Wipf & Rixen 2010; Johansson *et al.* 2013; Rumpf *et al.* 2014) due to the overall thin snow cover. Average spring temperatures in the snow treatment did not differ from ambient conditions, but decreased the number of FTCs in spring. Snow-addition did not alter spring soil moisture conditions (mid-June, *unpublished data* 2015), most likely due to the thin layer of snow even in the snow treatment. Fleeces warmed the soils in the period after snowmelt for approximately two more weeks, increasing the upper soil temperatures compared to control and snow treatment by 1.0 °C. This corresponds to observed warming trends during springtime in the arctic of 1-2 °C per decade in the last 20 years (Rigor, Colony & Martin 2000). Even though spring temperature increased relative to ambient conditions, the fleece treatment showed a significant increase in FTCs in spring in 2014. High solar irradiation combined with the fleece warming caused temperatures to more frequently rise above 0 °C during the daytime than under ambient conditions in May 2014 (average ambient

Abisko temperature:  $2.9 \pm 4.0$  °C) while nights were still cold, increasing FTCs. In contrast, in the relatively warm May of 2013 warming did not increase FTCs (average ambient Abisko temperature:  $7.4 \pm 5.4$  °C, average temperature 1990-2012:  $3.5 \pm 3.2$  °C, Abisko Station Meteorological Data: [www.polar.se/abisko](http://www.polar.se/abisko)), as ambient day and night temperatures were both above 0 °C. This implies that despite higher spring temperatures shrubs may have experienced more stress from frost during warmer springs than under ambient ‘colder’ springs, a phenomenon that has been observed in earlier studies (Inouye 2008; Wipf *et al.* 2009; Wheeler *et al.* 2014).

*Impact of warmer winter soil temperatures on canopy green-up and leaf frost damage depend on spring conditions*

In correspondence with previous snow addition experiments in shrub-dominated tundra (Wipf & Rixen 2010; Cooper, Dullinger & Semenchuk 2011), a slightly thicker snow cover that persisted a week longer in combination with ambient average spring temperatures, delayed canopy green-up by 3 days in the inner domains. In contrast, winter warming in combination with additional spring warming advanced canopy green-up by 3-6 days. Earlier canopy green-up in the northern hemisphere has been observed as a consequence of snow removal in previous experimental manipulation studies (e.g. Wipf 2010; Rosa *et al.* 2015; Blume-Werry, Jansson & Milbau 2017) as well as a result of decreasing snowpack and higher spring temperatures in natural observations (Menzel & Fabian 1999; Penuelas & Filella 2001). Our result suggests that higher spring soil temperatures specifically drive this advanced green-up rather than the earlier snowmelt, since the fleece treatment did not advance snow melt timing.

Shrub phenology is tightly linked to the extent to which shrubs are vulnerable to spring frost-events (Inouye 2008; Wheeler *et al.* 2015, 2016), whereby species with later

phenology seem to exhibit higher frost sensitivity compared to species with earlier phenology (CaraDonna & Bain 2016). The deciduous *B. nana* which naturally has a later bud break and growth onset than the evergreens *V. vitis-idaea* and *E. nigrum* (Wipf 2010; Blume-Werry *et al.* 2017) showed highest frost-damage overall. We expected leaf frost damage in shrubs to be generally lower with winter warming due to less severe autumn-to-late winter frost (Saarinen & Lundell 2010; Palacio *et al.* 2015), which could have been counteracted by the increased number of FTCs in the spring warming treatment. However, this treatment did not increase leaf frost damage in any of the species. This is in contrast with studies that found increased frost damage under spring conditions with multiple frost events, however in these studies snowmelt timing was advanced thereby exposing plants to FTCs earlier in spring than in our manipulations (Inouye 2008; Gerdol *et al.* 2013; Wheeler *et al.* 2014). The effects of winter warming on frost damage depended on spring scenario and were species-specific: Although *B. nana* was most damaged by frost in general, this was unaffected by increases in winter soil temperatures or altered spring conditions, despite potential earlier bud break under spring warming (Pop *et al.* 2000). Delayed snowmelt in combination with ambient spring conditions reduced frost damage in *V. vitis-idaea*, which is in accordance with findings of Saarinen & Lundell (2010). Winter warming in combination with warmer springs reduced leaf frost damage in *E. nigrum*. *Empetrum nigrum* is generally one of the first shrub species to start growing in spring (Wipf *et al.* 2009; Blume-Werry *et al.* 2017), but is relatively frost resistant (Neuner 2014) therefore it may have benefitted most from the increased spring temperatures despite the increased number of spring FTCs in the fleece treatment. Warmer winters and/or decreases in leaf frost damage may, along with effects on reproductive strategy (Wheeler *et al.* 2015, 2016) and root phenology (Blume-Werry *et al.* 2017), have significant impacts on aboveground shrub growth and biomass.

*Winter warming effects on shrub growth are dependent on spring regime and are species-specific*

Earlier green-up and decreased leaf frost damage due to changes in winter and spring climate could underlie shrub expansion in arctic tundra, yet, for shrubs to expand these effects should consequently lead to higher production. However, the effects of our spring warming manipulation on shrub growth onset and reduction in frost damage did not lead to significant changes in growth in any of the species. In accordance, *B. nana* and *V. vitis-idaea* growth have been reported to be unaffected or somewhat decreased by spring warming in previous studies (Keuper *et al.* 2011; Livensperger *et al.* 2016). Although our fleece treatment decreased frost damage in *E. nigrum*, it did not advance its growth or biomass, which supports similar findings by Dorrepaal *et al.* (2006). However, in exceptionally warm years (Wipf 2010) or after multiple years of increased winter soil temperatures in combination with spring warming (Keuper *et al.* 2011) *E. nigrum* did show substantially increased growth, suggesting that reduced spring frost damage may in the longer-term positively affects its growth.

Our snow addition treatment seemed to reduce *B. nana* growth despite the lack of treatment-induced changes in frost damage on its emerging buds. Delayed green-up of *B. nana* may have been responsible for this effect, as the timing of leaf emergence has been reported to be linked to growth-season production (Livensperger *et al.* 2016). In contrast to *B. nana*, *V. vitis-idaea* showed a strong positive response to winter warming, by increasing its shoot length growth by over 50%. *Vaccinium vitis-idaea* prefers thicker snow packs (Rasmus, Lundell & Saarinen 2011) and is photosynthetically active under the snow (Starr & Oberbauer 2003; Saarinen *et al.* 2016), this may enable it to take advantage of altered N dynamics with warmer winters (Welker *et al.* 2005) while still benefitting from the insulating capacities of the snow. Even though this growth increase was not followed by significant

increases in biomass, we expect that *V. vitis-idaea* will increase its vegetation cover under snowier winters which might, in longer term, lead to increased net C uptake due to increased plant biomass as shown by Natali, Schuur & Rubin (2012).

#### *No domain-specific plant responses to winter climate change*

The shrubs in outer domains of NSC, which naturally experience a thicker snow cover, showed a trend towards being less damaged by frost and shoots had a slightly higher shoot length growth. Shrubs in the outer domains of NSCs were expected to benefit less from increased winter soil temperatures than in the inner domains, because of the already higher thermal protection by snow and denser vegetation (YanTao *et al.* 2013). In the mostly barren inner domains, warmer soil temperatures may have had a larger direct impact on shrubs and additionally reduce cryoturbation. However, the patterns of treatment effects on the measured plant parameters were generally very consistent for inner and outer domains. Although the negative effects of the winter warming by snow addition on *B. nana* shoot length growth seemed somewhat higher in the inner domain, there was no domain-specific treatment effect. Shrubs in both inner and outer domains of NSCs are thus affected by winter warming and spring regime to a similar extent. This suggests that our winter climate manipulations did not affect shrub performance by inducing major changes in cryoturbation in the inner domain, and that the effects of the treatments on soil temperatures were comparable between the two sampling locations.

#### *Outlook*

It is still mostly unknown how plants within topographically complex landscapes will respond to climatic changes (Spasojevic *et al.* 2013; Schweiger & Beierkuhnlein 2016). In our heterogeneous NSC landscape, the effects of the winter soil temperature and spring

climate regimes in plant performance were consistent in locations that strongly differ in vegetation cover, nutrient availability, physical disturbance (by cryoturbation) and natural snow cover. Winter climate change thus impacted equally in already encroached areas and in barren areas, contradicting observations that shrubs expand mainly into these barren areas (Tape *et al.* 2012). The effects of winter warming and associated spring regime thus mainly seem to depend on individual plant characteristics and less on their location within a heterogeneous landscape.

The importance of the spring season for arctic ecosystem processes is well established (Aerts, Cornelissen & Dorrepaal 2006; Ernakovich *et al.* 2014), and evidence is rising that warming at different periods in the cold-season (Olsson *et al.* 2003) and its sequence may determine the net effects for ecosystem functioning (Aerts *et al.* 2009; Wipf & Rixen 2010; Blok, Elberling & Michelsen 2016). We showed that the effect of soil winter warming on shrub performance is not only species-specific but also dependent of subsequent spring conditions. This might explain why different winter and/or spring manipulation studies on the same species have found contradicting results (e.g. Wipf 2010; Wipf & Rixen 2010; Wheeler *et al.* 2014; Livensperger *et al.* 2016), and underlines the importance of disentangling effects of winter and spring temperatures and snowmelt timing. For shrubs in NSC-tundra this means that *V. vitis-idaea* may increase their cover, and expand into the barren circle inner domains, but only in a scenario where delayed snowmelt and ambient spring temperatures follow higher winter soil temperatures. Instead, in a scenario with warmer spring temperatures *E. nigrum* may be favoured and increase its cover in longer-term (Keuper *et al.* 2011). This highlights the need for accurate model predictions of how winter climate change will affect the interplay of snow and soil temperatures experienced by plants, such that empiricists can evaluate their consequences with higher certainty. Increased shrub height and cover may lead to a strong positive feedback effect on winter soil temperatures and plant growth via snow

trapping (Williams & Smith 1989; Sturm, Racine & Tape 2001), which will have substantial consequences for C dynamics in these globally important ecosystems, e.g. via its effects on respiration (Liptzin *et al.* 2009; Semenchuk *et al.* 2016), cryoturbation (Kade & Walker 2008; Hjort 2014) and C-sequestration into plant biomass (Epstein *et al.* 2012). Additionally, changes in plant growth onset timing and biomass after altered winter and spring conditions may significantly affect plant-herbivore interactions in these systems (Pettorelli *et al.* 2005; Olofsson *et al.* 2009) and biotic cascades into the soil system (Wookey *et al.* 2009). Despite which winter and spring climate change scenario would dominate in a future climate, our results underpin that increased winter temperatures are likely to affect aboveground plant growth, and that conditions in the spring season seem to be critical for its directional effects on plant performance.

### **Acknowledgements**

The authors wish to thank Laurenz Teuber for assistance during field- and laboratory work, Johan Olofsson for helpful comments on our data analysis and the staff of the Abisko Scientific Research Station for their hospitality and practical help. This research was financially supported by grants from VR (621-2011-5444) and Formas (214-2011-788) and a Wallenberg Academy Fellowship (2012.0152) to ED and an Erasmus student exchange grant to JR.

### **Conflict of interest**

The authors declare they have no conflict of interest.

### **Data accessibility**

Data are deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.90d2g>

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### Supporting information

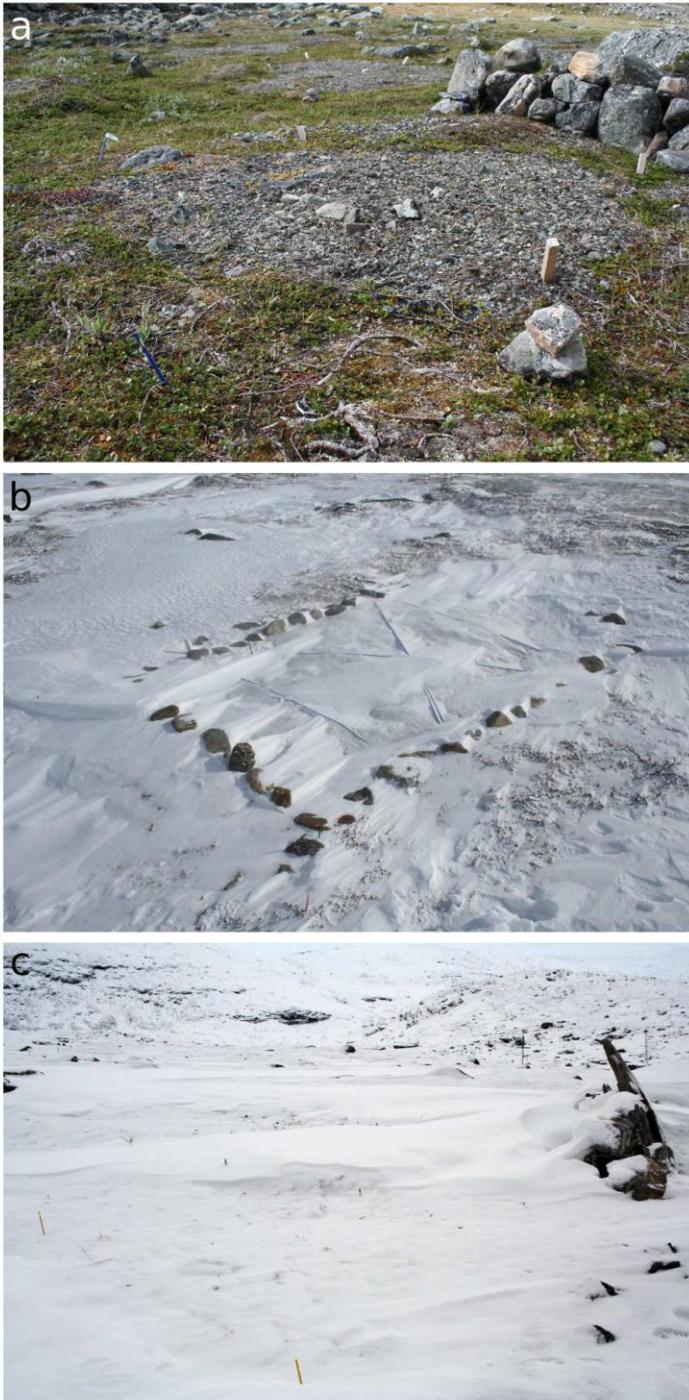
**Figure S1.** Average snow depth patterns over non-sorted circles at peak snow depth (2012-2014)

**Figure S2.** Daily mean soil temperature at 1 cm depth in (manipulated) non-sorted circles in 2012-2013 and 2013-2014.

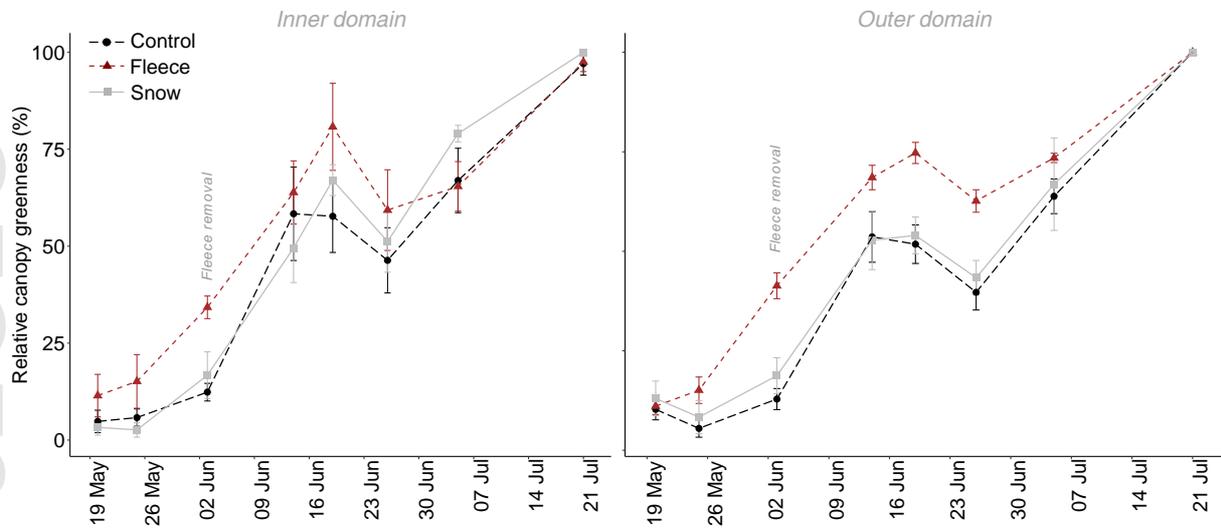
**Figure S3.** Linear regression of shoot increment biomass vs. total shoot length growth of *B. nana*, *E. nigrum*, and *V. vitis-idaea*.

**Table S1-11.** ANOVA results of performed statistical analyses.

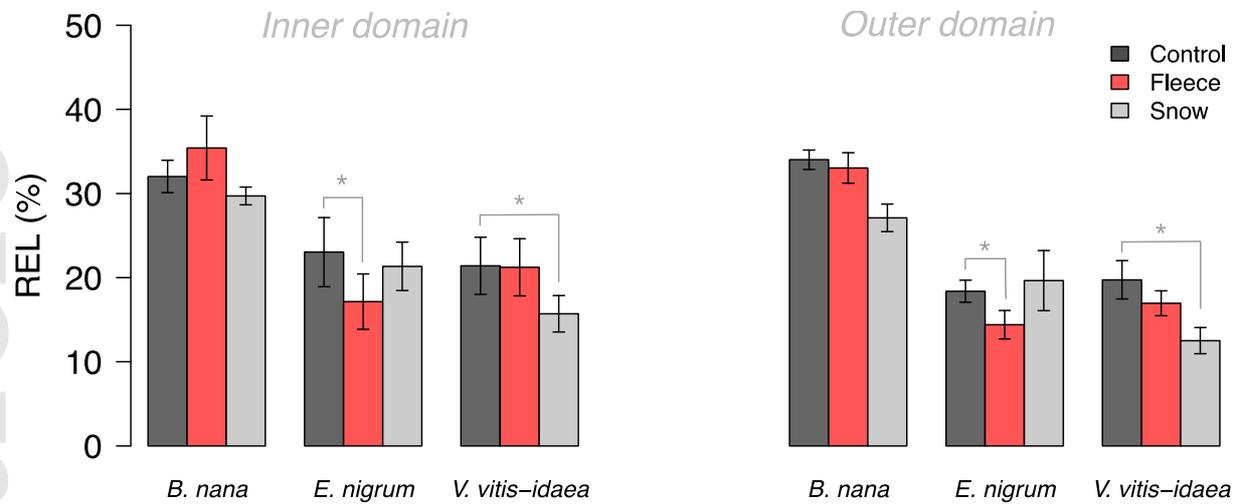
## Figures



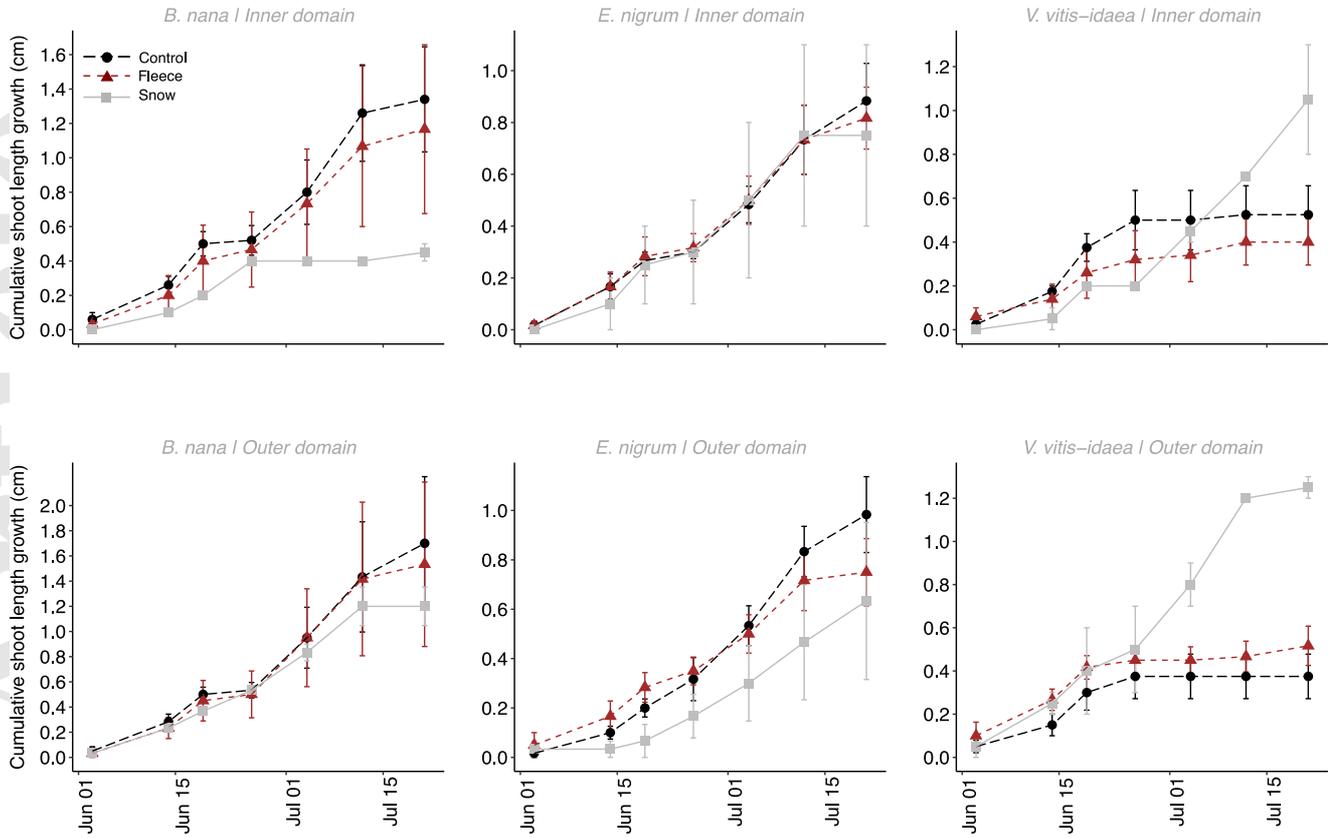
**Fig. 1.** Non-sorted circles in a) summer, b) under an insulating gardening fleece in early spring and c) behind a snow fence in late winter/spring. Snow fences and their effects are depicted in photo a and c.



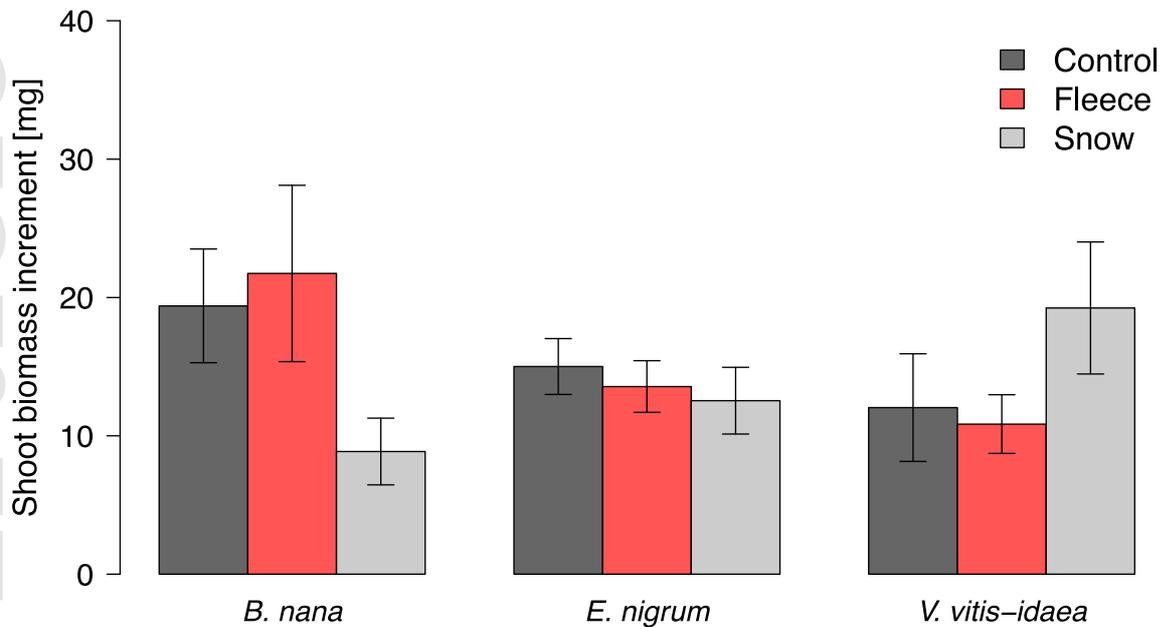
**Fig. 2.** Development of mean ( $\pm$  SE) relative canopy greenness of vegetation subjected to two winters of manipulation with fleece insulation (n=6), snow addition (n=3) or control conditions (n=6) in inner and outer domain of non-sorted circles, derived from repeated digital photography in spring and summer 2014.



**Fig. 3.** Mean ( $\pm$  SE) leaf frost damage measured by relative electrolyte leakage (REL) for *B. nana*, *E. nigrum*, and *V. vitis-idaea* subjected to two winters of manipulation with fleece insulation (n=6), snow addition (n=3) or control conditions (n=6) in the inner and outer domain of non-sorted circles (sampling on the 27<sup>th</sup> of May). A higher percentage indicates more frost damage. *Betula nana* buds had overall a statistically significantly higher REL % than leaves of *E. nigrum* and *V. vitis-idaea*. Species-specific treatment effects are indicated with a grey asterisk.



**Fig. 4.** Mean ( $\pm$  SE) shoot length growth of *B. nana*, *E. nigrum*, and *V. vitis-idaea* subjected to two winters of manipulation with fleece insulation (n=6), snow addition (n=3) or control conditions (n=6) in the inner and outer domain of non-sorted circles. Total number of individuals on which shoot growth measurements were performed for all seven weeks for inner|outer domains was: 10|15, 14|15, and 11|12 for *B. nana*, *E. nigrum*, and *V. vitis-idaea*, respectively.



**Fig. 5.** Mean ( $\pm$  SE) shoot biomass increase until the peak of the growing season of *B. nana*, *E. nigrum*, and *V. vitis-idaea* subjected to two winters of manipulation with fleece insulation (n=6), snow addition (n=3) or control conditions (n=6) in non-sorted circles. Data for inner and outer domain were combined as no significant domain effect or domain:treatment interaction effect was found. The observed differences were not statistically significant. Total number of shoots collected was 28, 29, and 27 for *B. nana*, *E. nigrum*, and *V. vitis-idaea*, respectively.

## Tables

**Table 1.** Sub-seasons used for analyses of temperature data and their climatic and treatment characteristics.

Sub-season	Period	Characteristics
Autumn	2012: 28 September <sup>†</sup> – 31 October 2013: 18 September – 31 October	Decreasing temperatures and sunlight Little snowfall; fleece insulation present
Midwinter	1 November – 15 January	Low temperatures; no sunlight Snow and fleece insulation present
Late winter	16 January – 31 March	Low temperatures; increasing sunlight Most snowfall; fleece insulation present
Spring	2013: 1 April – 31 May 2014: 1 April – 3 June	Increasing temperatures and sunlight Snow disappearing; fleece insulation present
Summer	2014: 4 June – 21 July <sup>‡</sup>	Highest temperatures; maximum sunlight Snow and fleece insulation not present

<sup>†</sup> No temperature data recorded before 14 October 2012.

<sup>‡</sup> Summer temperatures only recorded in 2014 (until the end of vegetation measurements).

**Table 2.** Mean soil temperature (°C) and number of freeze-thaw cycles (crossings from thaw to freeze) ( $\pm$  SE) at 1 cm depth in non-sorted circles receiving control, fleece insulation or snow addition treatments. See Table 1 for details of the sub-seasons and treatment durations. Significant differences between the treatments are marked with different letters in each row. If values are not marked with letters they are not significantly different from each other.

Sub-season	Variable	Control	Fleece	Snow
Autumn	Temperature 2012	-2.9 $\pm$ 1.6 <sup>a</sup>	-1.6 $\pm$ 1.1 <sup>b</sup>	-1.2 $\pm$ 1.0 <sup>b</sup>
	Temperature 2013	0.0 $\pm$ 3.0 <sup>a</sup>	1.0 $\pm$ 2.6 <sup>b</sup>	1.0 $\pm$ 2.2 <sup>b</sup>
	FTC 2012	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6
	FTC 2013	5.0 $\pm$ 1.6	3.8 $\pm$ 0.8	2.7 $\pm$ 1.2
Midwinter	Temperature 2012/13	-7.5 $\pm$ 3.1 <sup>a</sup>	-6.2 $\pm$ 2.7 <sup>b</sup>	-5.8 $\pm$ 2.9 <sup>b</sup>
	Temperature 2013/14	-4.9 $\pm$ 2.0 <sup>a</sup>	-4.1 $\pm$ 1.8 <sup>b</sup>	-3.1 $\pm$ 1.9 <sup>c</sup>
	FTC 2012/13	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
	FTC 2013/14	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.7 $\pm$ 0.6
Late winter	Temperature 2013	-9.6 $\pm$ 3.4 <sup>a</sup>	-8.9 $\pm$ 2.7 <sup>ab</sup>	-8.2 $\pm$ 2.4 <sup>b</sup>
	Temperature 2014	-8.2 $\pm$ 4.1 <sup>a</sup>	-7.6 $\pm$ 3.4 <sup>ab</sup>	-7.3 $\pm$ 3.6 <sup>b</sup>
	FTC 2013	0.3 $\pm$ 0.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
	FTC 2014	0.0 $\pm$ 0.0	0.4 $\pm$ 0.5	0.0 $\pm$ 0.0
Spring	Temperature 2013	0.3 $\pm$ 6.5 <sup>ab</sup>	1.1 $\pm$ 6.7 <sup>b</sup>	0.0 $\pm$ 6.4 <sup>a</sup>
	Temperature 2014	-0.7 $\pm$ 4.5 <sup>a</sup>	0.6 $\pm$ 5.1 <sup>b</sup>	-0.3 $\pm$ 4.1 <sup>a</sup>
	FTC 2013	34.5 $\pm$ 2.5 <sup>b</sup>	30.0 $\pm$ 5.7 <sup>b</sup>	22.0 $\pm$ 6.2 <sup>a</sup>
	FTC 2014	9.4 $\pm$ 3.6 <sup>a</sup>	26.6 $\pm$ 8.9 <sup>b</sup>	6.3 $\pm$ 5.9 <sup>a</sup>
Summer	Temperature 2013	n.a.	n.a.	n.a.
	Temperature 2014	10.5 $\pm$ 6.4	10.9 $\pm$ 6.8	10.7 $\pm$ 6.4
	FTC 2013	n.a.	n.a.	n.a.
	FTC 2014	2.8 $\pm$ 1.8 <sup>b</sup>	3.0 $\pm$ 2.2 <sup>b</sup>	0.0 $\pm$ 0.0 <sup>a</sup>