Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland

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Abstract

Climate change scenarios predict an increased frequency of extreme climatic events. In Arctic regions, one of the most profound of these are extreme and sudden winter warming events in which temperatures increase rapidly to above freezing, often causing snow melt across whole landscapes and exposure of ecosystems to warm temperatures. Following warming, vegetation and soils no longer insulated below snow are then exposed to rapidly returning extreme cold. Using a new experimental facility established in sub-Arctic dwarf shrub heathland in northern Sweden, we simulated an extreme winter warming event in the field and report findings on growth, phenology and reproduction during the subsequent growing season. A 1-week long extreme winter warming event was simulated in early March using infrared heating lamps run with or without soil warming cables. Both single short events delayed bud development of Vaccinium myrtillus by up to 3 weeks in the following spring (June) and reduced flower production by more than 80%: this also led to a near-complete elimination of berry production in mid-summer. Empetrum hermaphroditum also showed delayed bud development. In contrast, Vaccinium vitis-idaea showed no delay in bud development, but instead appeared to produce a greater number of actively growing vegetative buds within plots warmed by heating lamps only. Again, there was evidence of reduced flowering and berry production in this species. While bud break was delayed, growing season measurements of growth and photosynthesis did not reveal a differential response in the warmed plants for any of the species. These results demonstrate that a single, short, extreme winter warming event can have considerable impact on bud production, phenology and reproductive effort of dominant plant species within sub-Arctic dwarf shrub heathland. Furthermore, large interspecific differences in sensitivity are seen. These findings are of considerable concern, because they suggest that repeated events may potentially impact on the biodiversity and productivity of these systems should these extreme events increase in frequency as a result of global change. Although climate change may lengthen the growing season by earlier spring snow melt, there is a profound danger for these high-latitude ecosystems if extreme, short-lived warming in winter exposes plants to initial warm temperatures, but then extreme cold for the rest of the winter. Work is ongoing to determine the longer term and wider impacts of these events.

Keywords: Arctic, climate change, Empetrum hermaphroditum, extreme events, flowering phenology, Vaccinium vitis-idaea, V. myrtillus, warming experiment, winter warming

Introduction

Warm periods during winter are predicted to become more frequent in polar regions (Bonsal et al., 2001;
Shabbar & Bonsal, 2003; Liu et al., 2006). In extreme cases, these can manifest as sudden and rapid extreme warming events, where temperatures can rise rapidly (e.g. from −20 °C to +5 °C in just 24 h) and can cause snow melt across whole landscapes (Callaghan et al., 2004b; Phoenix & Lee, 2004). During these events, loss of the snow layer can expose vegetation and soils to warm temperatures for a number of days before the return of freezing temperatures. The returning cold for the rest of the winter may lead to damage by winter desiccation and repeated freeze–thaw cycles and further damage may occur from abrasion by wind-blown ice particles before the system is covered with fresh snow (Walker et al., 2001). These events, therefore, have the potential to impact plant productivity and biodiversity with consequences for herbivore survival (Collins & Smith, 1991; Lee et al., 2000; Pettorelli et al., 2005) and feedback to global climate through changes in ecosystem carbon balance. Furthermore, sudden winter warming events – causing (partial) snow thaw leading to re-freezing and ice-encasement of vegetation (Putkonen & Roe, 2003) – have already been implicated in the population crashes of some plants, and also voles, reindeer and musk ox unable to access their vegetation below ice layers (Forchhammer & Boertmann, 1993; Robinson et al., 1998; Aanes et al., 2002). However, although summer and year-round warming experiments have been conducted in polar regions, the occurrence of extreme and short-lived winter warming events and their impacts on high-latitude ecosystems has been largely ignored (Callaghan et al., 2004a; Phoenix & Lee, 2004). It is of further concern that there is already evidence to suggest that extreme winter warming events are increasing in frequency in some regions: the climate record dating back to 1913 (Johansson et al., in press) from the Abisko Scientific Research Station in sub-Arctic Sweden where this study is based shows a long-term average of one event every 7 years (1913–2000 average) but an unprecedented frequency of approximately one event every year over the last decade.

Furthermore, recent studies have shown that several processes are (surprisingly) active during the Arctic winter and may have strong effects on processes during the following growing season (Hobbie & Chapin, 1996; Ögren, 1996; Brooks et al., 1997; Edwards et al., 2006; Grogan & Jonasson, 2006; Larsen et al., 2007). Given that Arctic regions are expected to experience the greatest climatic change during winter months and that higher temperatures during winter and early spring are predicted (Schwartz et al., 2006; Tebaldi et al., 2006; Beniston et al., 2007), there is an urgent need to direct research focus to the responses of ecosystems to winter climatic change.

With these concerns in mind, this experimental study was established to determine the impacts of extreme and short-lived winter warming events on sub-Arctic dwarf shrub heathland in northern Sweden. The experiment uses two types of warming simulation: (1) canopy warming and (2) canopy with soil warming. Soil warming was included to study the potential differences between warming events where soils remain frozen (canopy only) and when soils thaw (canopy and soil warming). This is considered critical for a number of reasons, in particular, plants transpiring through warmed winter-green leaves are likely to have more severe desiccation damage if roots remain frozen and soil warming is likely to cause major increases in net efflux of carbon dioxide (CO2).

We hypothesize that exposure to sub-zero Arctic winter temperatures after an extreme winter warming event will (1) damage vegetative buds leading to reduced growth in the subsequent growing season, (2) reduce flowering and berry production through reduced winter survival of reproductive buds and that (3) impacts will be much greater as a result of canopy warming only compared with canopy with soil warming.

**Materials and methods**

**Site description and warming treatment**

The study was performed in a sub-Arctic heathland community close to the Abisko Scientific Research Station (ANS) in northern Sweden (68°21′N, 18°49′E). The vegetation is dominated by dwarf shrubs, in particular, the evergreen *Empetrum hermaphroditum* Hagerup and *Vaccinium vitis-idaea* L. and the deciduous *Vaccinium myrtillus* L.

The experiment consists of 18 plots (2.1 m × 1.0 m) representing six control plots and six each of two warming treatments, canopy warming and canopy with soil warming. For canopy warming plots, four infrared heating lamps (800 W emitting at 3 μm; HS 2408, Kalgo Electronics Co., Bethlehem, PA, USA) were suspended in parallel (70 cm apart) from wooden frames. This produced a thermal radiation flux of 270 W m−2 to the plots (at zero wind speed). The same setup was also used for canopy with soil warming plots, but these plots were additionally warmed by soil heating cables (LS-TXLP, Nexans, Oslo, Norway, producing 120 W m−2) at 5 cm soil depth and running parallel at 20 cm distance from each other. In the growing season before the winter warming event, cables were carefully threaded through the soil layer using long, arched needles (we have previously found that this method causes minimal disturbance to this vegetation). Control plots received no warming treatment but had wooden frames suspended above them to provide the same (minimal) shading as caused by the frames over the warmed plots. Note that infrared red heating does not
directly warm the air but does simulate warming by warmer air temperatures.

To monitor temperature changes, thermistors were placed in each plot at canopy height and covered by vented funnels covered in reflective aluminum to stop warming by direct irradiance from the lamps. Three additional thermistors were placed at 5 cm soil depth. Temperatures were logged at 6-h intervals starting at midnight and recorded on a data logger (CR10 X Campbell Scientific, Shepshed, Loughborough, UK). Ambient air temperatures were taken from the research station’s automated meteorological station approximately 250 m from the experimental site.

Simulation of an extreme winter warming event started at the beginning of March for a period of 7 days during which the lamps were kept at 50 cm distance from the snow surface and lowered accordingly as the snow depth decreased (we checked lamp height at least twice daily). This approach ensured gradual snow thaw, taking 3 days to thaw the full depth of snow in each plot (average snow depth, 50 cm). As vegetation became exposed, lamps were kept at 70 cm above the soil surface, and we monitored leaf surface temperatures (Digitron 1408-K with type-K thermocouple, Torquay, Devon, UK) and canopy air and soil temperatures from the thermistors within the plots to ensure that warming was realistic and within the bounds of temperatures recorded for real events. Soil warming cables were switched on 2 days after the lamps to simulate the delay in soil thaw during a real event. Timing, rate and degree of warming were based on real events occurring in the Abisko region (examples shown in Fig. 1). Heating lamps were removed from the frames at the end of the week-long warming treatment to avoid any shading effects of the lamps during the following growing season. Plots were then left untouched for the 3 remaining months of winter before data collection in spring and summer (June–August).

**Impacts of extreme winter warming in the subsequent growing season**

**Vegetative bud phenology, flowering and berry production.** Vegetative bud development and flowering were monitored during the subsequent growing season (early June onwards). For this, 10 randomly selected shoots of the dominant dwarf shrubs *E. hermaphroditum*, *V. vitis-idaea* and *V. myrtillus* were tagged in each plot and surveyed twice weekly for vegetative bud development and the presence of flowers. Vegetative bud development was recorded by noting when the bud had burst and the first leaf had fully expanded (Phoenix et al., 2001). Berry counts were undertaken on the marked shoots of all species in late July.

**Shoot growth and photosynthesis.** Shoot elongation was measured at the end of the season for all three species by measuring the length of the new apical shoot of each marked plant. In late July, rates of light-saturated photosynthesis were measured on leaves of the two most dominant species in the plots, *V. vitis-idaea* and *E. hermaphroditum*. Samples (*n* = 1 from each plot) were collected from control and warmed plots and brought back to the laboratory where their light-saturated photosynthetic rates were measured immediately (GFS 3000 gas exchange system, H. Walz GmbH, Effeltrich, Bavaria, Germany) under standardized conditions (400 μmol m⁻² s⁻¹ photosynthetically active radiation (PAR), temperature 19 ± 2 °C, previous analyses had shown that both species saturate below 400 μmol m⁻² s⁻¹ PAR). Each sample was measured for 25 min in order to gain stable values. Current-year (2007) and second-year (2006) leaves of *V. vitis-idaea* were measured separately. *E. hermaphroditum* shoots included current-year shoots only. Leaf and shoot samples were weighed following drying at 60 °C for 48 h.

**Data analyses.** Flowering phenology and bud development were analyzed by repeated-measures ANOVA. For the flowering phenology, the percentage of plants with flowers (from 10 tagged plants per plot) was used, while for bud development, we used the percentage of plants that had reached fully developed leaves (again, from the 10 tagged plants per plot). Homogeneity of variances was tested with Levene’s test which showed that no transformation of data was required. To test for differences between treatments in the amount of buds that actually burst during the growing season, a one-way ANOVA was used on the data from the last measuring day (July 23, 2007).
A chi-square test was used to test for impacts on the average proportion of shoots with and without berries, the proportions measured in the control plots was used as the expected ratio: we used chi-squared here because the berry count data included too many zero values that made other tests inappropriate. Shoot elongation and net photosynthetic rates were analyzed by one-way ANOVA. All analyses were undertaken using SPSS 14.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results

Simulation of an extreme winter warming event

The temperature changes recorded during the 7-day simulated extreme warming event are comparable with those of real extreme events recorded at the Abisko Scientific Research Station (Fig. 1). Real events are variable in length and temperature (and may include a brief period when temperatures drop below 0 °C). Nonetheless, the field manipulation system does provide a good simulation of an extreme winter warming event comparable with events seen in the past.

The start of winter warming treatments (first arrow in Fig. 2a) coincided with a brief natural warming of ambient air temperatures. This was not enough to result in any snow melt outside the warmed plots, but probably did assist the lamps in melting snow on the first day. Ambient temperatures then rapidly fell to −12 °C a day later. From the onset of the warming treatments (March 2, 2007), temperatures at canopy height increased to approximately 5 °C over a 48-h period (Fig. 2a) as the snow melted and gradually exposed the vegetation. Plants first became exposed during the second day of warming, and total snow melt to ground level was completed during the third day. Both types of warming treatments (canopy warming and canopy with soil warming) resulted in near-identical warming at canopy height. Once plants became exposed from under the snow, leaf thermocouple measurements showed that average leaf temperatures somewhat tracked the canopy air temperatures and where on average only 0.1 °C warmer than canopy air temperatures over the course of the warming simulation. In any one sweep of measurements, average leaf temperatures could be more than 3 °C warmer or 2 °C cooler than air temperatures (probably due to the considerable influence of sunlight or wind speed, personal observation). This still means leaf temperatures were within the bounds of temperatures recorded for past extreme events and presumably leaf temperatures would equally be prone to the influence of sun and wind in a real warming event.

Compared with control plots, soil temperatures (5 cm depth) were only marginally increased in the canopy warming plots (by ca. 0.3 °C), but increased from 1 to 3 °C in the canopy with soil warming plots during the course of the simulated event (Fig. 2b). After the warming period (second arrow in Fig. 2a), temperatures in the warmed plots immediately declined and returned to ambient.

Following simulation of the events, warmed plots received no snowfall to re-insulate the ground cover, and so canopy temperatures in the exposed plots did not differ from ambient air temperatures. Vegetation and soils within these plots were therefore subject to cold temperatures and three freeze–thaw cycles with temperature fluctuations ranging from −6 to +6 °C. This contrasted sharply with the steady and mild temperatures in the control plot (still insulated below 50 cm of snow) which never fell below −3 °C following the event and did not rise appreciably above 0 °C until the end of April (ca. Julian day 115). Soil temperatures in control plots also showed a steady rise, while in the previously soil warmed plots, there was an initial steady cooling following the abrupt drop in soil

Fig. 2 (a) Canopy air and (b) soil temperatures in control plots and plots subject to simulated extreme winter warming (canopy warming only and canopy with soil warming). The ‘ambient’ air temperature data are taken from the meteorological station of the Abisko Scientific Research Station (at 250 m from our research site). The arrows indicate the start and end of the warming treatment during March 2007; n = 5 for each point, error bars are 1 SE. Ambient air temperatures differ from canopy temperatures before the warming event because the plant canopy within the plots is at that stage naturally covered by a 50 cm layer of insulating snow.
temperatures after the warming cables have been switched off. The exposed previously soil warmed plots did not show any marked diurnal fluctuations in soil temperatures, probably because the low solar angles of the Arctic reduced the sun’s warming influence on the soil which was further buffered by the insulating effect of the litter and bryophyte layer.

**Impacts on vegetative bud phenology**

In the following spring, simulated extreme winter warming (both treatment types) caused an initial delay of bud burst by approximately 1 week for *V. myrtillus*, followed by slower bud development such that complete bud burst was approximately 3 weeks late compared with controls (repeated-measures ANOVA, \( P < 0.001 \); both treatments significantly different from control, Tukey HSD, \( P < 0.05 \)). The amount of buds that actually burst during the growing season was not significantly different between the treatments (mean and SE for control = 97 ± 3%, and winter warming = 85 ± 5%) (Fig. 3a). For *E. hermaphroditum*, warming treatments also delayed the onset and completion of bud burst by almost 1 week (repeated-measures ANOVA, \( P < 0.05 \); canopy and soil warming significantly different from control, Tukey HSD, \( P < 0.05 \)) (Fig. 3b). Percentage of completed bud bursts in this species remained unaffected by the winter warming event. Bud development of *V. vitis-idaea* was not affected by the warming treatments (Fig. 3c). However, there was a nonsignificant indication of a higher percentage of buds that reached full leaf development under the canopy warming treatment (63 ± 7%) as compared with the control (47 ± 6%) and canopy with soil warming treatment (48 ± 6%).

**Flowering phenology and berry production**

Simulation of an extreme winter warming event considerably reduced the flower production in both *V. myrtillus* (repeated-measures ANOVA, \( P < 0.001 \); both treatments significantly different from control, Tukey HSD, \( P < 0.01 \)) by up to 89% with canopy warming and 90% with canopy and soil warming. *V. vitis-idaea* flowering was also considerably reduced by the warming treatments (repeated-measures ANOVA, \( P < 0.05 \); canopy warming significantly different from control, Tukey HSD, \( P < 0.05 \)) by up to 77% with canopy warming and up to 54% with canopy and soil warming. Flowering of *E. hermaphroditum* remained unaffected (chi-squared values: 0.2 and 0.4, df = 1). For *V. vitis-idaea*, the canopy warming treatment was associated with a reduction in berry production (chi-squared value: 14.1, df = 1, \( P < 0.05 \)), but as shown in Fig. 5, the decrease in berry production associated with the combined canopy and soil warming was not significant (chi-squared value: 2.5, df = 1).

**Shoot growth and net photosynthesis**

Summer shoot elongation remained unaffected for any of the three species by the winter warming treatment. *V. myrtillus* shoot elongation was 4.0 ± 0.3, 3.9 ± 0.3 and 4.3 ± 0.4 mm for the control, canopy warming
and canopy and soil warming plots, respectively; 19.3 ± 2.0, 17.6 ± 1.3 and 15.0 ± 1.1 for *V. vitis-idaea* and 17.4 ± 1.2, 18.1 ± 3.1 and 14.3 ± 2.6 for *E. hermaphroditum* (± values are SE). Rates of light-saturated photosynthesis in current-year leaves of *V. vitis-idaea* and *E. hermaphroditum* were not affected by simulation of an extreme winter warming event. However, there was a marginally nonsignificant (*P* = 0.062) decrease in photosynthetic rates of second-year leaves of *V. vitis-idaea* resulting from the canopy warming treatment. Mean photosynthesis values were 0.0215 ± 0.002, 0.0130 ± 0.002 and 0.0171 ± 0.002 μmol g⁻¹ s⁻¹ from the control, canopy warming and canopy and soil warming, respectively.

There were no signs of visible damage to the plants (e.g. leaf chlorosis or necrosis) during the event, and no such damage became apparent in the growing season when the above measurements were being made.

**Discussion**

Here, we have reported findings from the first study to simulate impacts of an extreme and short-lived winter warming event. The results indicate that even just one such event, which leads to complete snow melt during winter, exposure to warm, and then cold (ambient) winter temperatures, can negatively impact plant development and reproduction in the following growing season and also impacts on growth through changes in the number of vegetative buds that burst. In contrast, however, there were no clear effects of this single extreme warming event on photosynthesis and apical shoot growth.

**Impacts of extreme winter warming events in the following growing season**

In sharp contrast to warming experiments that lengthen the growing season by continued warming in spring (Dunne *et al.*, 2003; Aerts *et al.*, 2004), there was a delay in bud development in two of the dominant dwarf shrubs, *V. myrtillus* and *E. hermaphroditum*, with the response in *V. myrtillus* being particularly strong. This may in part be due to *V. myrtillus* being an early bud burst/early flowering species with a strategy of producing new leaves and flowers rapidly in spring (Molau, 1993; Kudo & Suzuki, 2002). It is possible that the short winter warming event was enough to trigger
the development of buds which were then exposed to the following cold period and freeze–thaw cycles (Ögren, 1996; Tolvanen, 1997). Indeed, initialization of bud burst in some V. myrtillus plants was observed in some warming plots toward the end of the warming event (but time constraints meant we were unable to survey for this at the time).

It is also clear that a single extreme winter warming event can cause major reductions in flowering and berry production. Again, V. myrtillus was found to be particularly sensitive here with the single warming event eliminating flowering almost entirely. As with the impact on vegetative bud phenology, it is possible that the short warming event instigated flower bud burst in this early flowering species, leaving it prone to the returning cold temperatures and freeze–thaw cycles. If this resulted in bud damage, such a mechanism may also drive the lower flowering of V. vitis-idaea (a plant which also showed some indications of damage through the marginally nonsignificant lower rates of light-saturated photosynthesis). Whether the reduction in flowering resulted from freezing damage to flower buds after the warming event, or from flower buds beginning to develop but then permanently stopping on cessation of warming cannot be interpreted from the current results. However, it is unlikely that the warming event reduced flowering by reducing the number of buds on a shoot because buds are set in the previous growing season (i.e. before the warming event). It seems most likely that the reduction in flowering is a result of impacts on existing buds, rather than production of new buds in the first instance.

That there were different responses between species indicates that there might be different mechanisms behind responses to this event. These changes in flowering are likely to have been responsible for the subsequent large reductions in berry production, although at present, we cannot rule out resource limitation due to the reduced period with fully developed leaves. Such major reduction in berry production by a single extreme warming event may actually have only limited impacts on the stability of V. myrtillus or V. vitis-idaea populations because reproduction from seed is rarely successful in these communities (Callaghan & Emanuelsson, 1985). Instead, there may be major implications for the vertebrate herbivores and local human populations that use these berries as an important food source (Anderson, 1985).

There is some evidence to suggest that V. vitis-idaea may somewhat compensate for the disturbance by producing more vegetative growth (seen as a statistically nonsignificant increase in the numbers of vegetative buds that actively grew, as seen under the canopy warming treatment). This species is known to instigate vegetative reproduction if the snow-free period is too short (Kudo, 1991), and it is possible that the short period of physiological activity during the warming event may have triggered a similar response.

Interestingly, there was no such effect in the combined canopy and soil warming treatment. While it is difficult to suggest a mechanism for this difference between the two warming treatments (though the thawing of soil and roots must hold the answer), this does indicate that the extent of soil thaw may impact on the response of some components of the system to the extreme warming event (i.e. through supplying the plants with water from thawed soils). Some studies have suggested that Arctic plant phenology is influenced by soil temperatures (Holway & Ward, 1965; Walker et al., 2001), indicating that above zero soil temperatures might be necessary for proper onset of bud development. Given this, the increase in soil temperatures above 0°C from the combined canopy and soil warming plots may have triggered bud development that did not occur in the canopy-only warming plots. These buds may then have survived the following cold period due to the freeze hardiness of this species (Sakai & Otsuka, 1970). There was little additional soil warming in the canopy warming plots, because there is a reasonable dense dwarf shrub understorey and deep bryophyte layer which both act as a good insulator and prevented further soil warming in this treatment.

It is perhaps surprising, however, that not more differences were seen between the two different warming treatments. Indeed, we hypothesized greater impacts from the canopy-only warming as a result of desiccation from warmed (and transpiring) vegetation unable to access water in the frozen ground. Only in the case of V. vitis-idaea flowering and berry production were greater impacts of the canopy-only warming treatment observed and suggests that the extent of soil thaw may play a lesser role in mediating phenology, reproduction and growth responses to extreme warming events than we anticipated.

In contrast to the large differences seen in phenology and reproduction, there were only weak indications of impacts on apical shoot growth and photosynthesis. This is particularly surprising for V. myrtillus which showed such considerable delays in vegetative bud development: the 1–3-week delay seen in this species is large under any circumstance, but particularly so against the background of the short (approximately 12 weeks) growing season in this sub-Arctic region. This anomaly suggests that this species is able to compensate for the late bud development with accelerated growth, but further work is needed to investigate this. This potential compensation might have resulted in decreased resources necessary for flower and berry...
production. For *V. vitis-idaea* at least, the trend of a single extreme winter warming event reducing growth and photosynthesis may indicate that greater impacts and reduced productivity could occur from either a more extreme event (longer, with larger temperature fluctuations), or repeated events.

Overall, the deciduous *V. myrtillus* was generally more sensitive to warming than the evergreen species (*E. hermaphroditum* and *V. vitis-idaea*). This is consistent with a recent meta-analysis of Arctic climate manipulation experiments that showed deciduous dwarf shrubs (possibly) more sensitive (i.e. show a greater positive response) to summer warming than evergreen dwarf shrubs (van Wijk et al., 2004). However, the overall responses of deciduous and evergreen dwarf shrubs in that meta-analysis were seen as trends rather than being statistically significant. Further, some caution is advisable in comparing these studies because an extreme winter warming event is more likely to make an impact through damage to plants rather than through enhancing growth, for example through freezing damage on return of ambient temperatures following the warming event. Plant frost hardiness – which may well be an important driver of interspecific differences in sensitivity to winter warming – does not appear to follow clear plant functional type separation (Taschler & Neuner, 2004).

Interspecific differences in sensitivity to an extreme warming event might be a result of interspecific differences in timing of flowering or bud burst. Early flowering species tended to benefit from early snow melt in several studies (Dunne et al., 2003; Aerts et al., 2004) because they can respond to warming most rapidly. In our study, the greater sensitivity of *V. myrtillus* may relate to this being the species with the earliest bud burst and flowering, such that it too may respond most readily to a warming event with initiation of bud development. Unlike in early snow melt studies, however, this may then result in the observed greater sensitivity because bursting buds would then be exposed to the returning cold following the event.

*Natural phenomena and climate change*

While this study was motivated by concern over increases in warming events observed in the climate record and predicted to occur in a warmer Arctic, it must also be remembered that these events are natural phenomena. For instance, events lasting 5 days or more with temperatures reaching over 5°C have occurred approximately once every 7 years between 1913 and 2000 at Abisko (Abisko Station, unpublished data). Given the interspecific differences in plant sensitivity to these events, they may play an important role in maintaining the structure and composition of sub-Arctic heathland, with the system going through cycles of damage and recovery. We suggest, therefore, that irrespective of their changing frequency under climatic change, understanding the impacts of these winter events is an important part of understanding the regulatory effects of winter climate on Arctic and sub-Arctic ecosystems.

Overall though, given that just a single event can have major impacts on the phenology and reproductive output of some sub-Arctic species, an increase in frequency of these events may have major implications for these ecosystems. Repeated damage to species without an adequate period for recovery may lead to changes in the community structure and diversity of these systems and ultimately lead to reduced productivity. Furthermore, the wider ecosystem responses during the extreme event may also be of considerable consequence: thawed and warmed soils, for example, are likely to have considerable net efflux of CO2, while lack of snow cover denies small mammals insulation and protection from predators. With these concerns in mind, work is now underway to determine the wider ecosystem consequences and long-term impacts of annual events in consecutive years, and the direct impacts of extreme winter warming during the event itself.

**Conclusion**

This study of the impacts of sudden extreme winter warming has revealed some striking responses in the phenology and reproductive output of dominant sub-Arctic heathland species in response to just a single event. Furthermore, considerable interspecific differences in sensitivity were seen. There was also some evidence that the extent of soil thaw can mediate plant responses to extreme winter warming, but the importance of this for the specific plant variables measured was much less apparent than hypothesized. Our findings suggest that should further events in following years continue to produce these responses, changes in the productivity of plant species and ultimately community shifts may occur. Clearly, there is a pressing need to better understand wider aspects of ecosystem structure and function. Although climate change may lengthen the growing season by earlier spring snow melt, there is a profound danger for these high-latitude ecosystems if extreme warming induces premature plant development, interrupted by return of freezing winter temperatures.

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