Understanding the drivers of extensive plant damage in boreal and Arctic ecosystems: insights from field surveys in the aftermath of damage

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ABSTRACT

The exact cause of population dieback in nature is often challenging to identify retrospectively. Plant research in northern regions has in recent decades been largely focussed on the opposite trend, namely increasing populations and higher productivity. However, a recent unexpected decline in remotely-sensed estimates of terrestrial Arctic primary productivity suggests that warmer northern lands do not necessarily result in higher productivity. As large-scale plant dieback may become more frequent at high northern latitudes with increasing frequency of extreme events, understanding the drivers of plant dieback is especially urgent. Here, we report on recent extensive damage to dominant, short, perennial heath and tundra plant populations in boreal and Arctic Norway, and assess the potential drivers of this damage. In the High-Arctic archipelago of Svalbard, we recorded that 8-50 % of *Cassiope tetragona* and *Dryas octopetala* shoots were dead, and that the ratios of dead shoots increased from 2014 to 2015. In boreal Norway, 38-63 % of *Calluna vulgaris* shoots were dead, while *Vaccinium myrtillus* had damage to 91 % of shoots in forested sites, but was healthy in non-forested sites. Analyses of numerous sources of environmental information clearly point towards a winter climate-related reason for damage to three of these four species. In Svalbard, the winters of 2011/12 and 2014/15 were documented to be unusually severe, i.e. insulation from ambient temperature fluctuation by snow was largely absent, and ground-ice enforced additional stress. In boreal Norway, the 2013/14 winter had a long period with very little snow combined with extremely low precipitation rates, something which resulted in frost drought of uncovered *Calluna* plants. However, extensive outbreaks of a leaf-defoliating geometrid moth were identified as the driver of *Vaccinium* mortality. These results suggest that weather and biotic extreme events potentially have strong impacts on the vegetation state of northern lands.

Keywords: Winter climate change; Plant mortality; Extreme events; Cryosphere; Pest; Tundra

1. Introduction

Remotely-sensed estimates of vegetation productivity have shown an increasing productivity of northern lands from 1982 to 2011, concurrently with warmer and longer growing seasons (Xu et al. 2013). This process is known as ‘greening’. However, from 2011 to 2014, Arctic regions experienced an overall decline in productivity (Bhatt et al. 2013; Park et al. 2016), in a process known as ‘browning’ (de Jong et al. 2012).

While greening occurs gradually, driven by longer and warmer growing seasons, browning is brought about by different drivers, often as stochastic biotic or weather events, that occur at distinct spatial and temporal patterns in the landscape (Phoenix and Bjerke 2016). Increasing awareness of such events has recently led to more knowledge of their impacts on boreal and Arctic vegetation. The effects of drought and wildfires during summer are among the best-documented events (e.g. Angert et al. 2005; Beck and Goetz 2011; Bret-Harte et al. 2013). However, browning events may take place at any time of the year, and with winters warming more rapidly than summers (Walsh et al. 2011), increased disturbance of northern lands is expected to occur during the cold season: threats to plants associated with reduced snow cover include encasement in ground-ice, which generally develops after rain-on-snow events, freezing damage following extreme winter warming, and desiccation resulting from exposure to light, wind and warmth of plants unable to access frozen soil water, known as frost drought or winter desiccation (Gudleifsson 2009; Bjerke 2011; Bokhorst et al. 2011, 2016; Callaghan et al. 2011; Preece and Phoenix 2013; Williams et al. 2015; Blume-Werry et al. 2016).

Since 2006, several incidents of frost drought following winter warming events have been reported from the sub-Arctic regions of Scandinavia (Bjerke and Tømmervik 2008, Bokhorst et al. 2009, 2012; Bjerke et al. 2014). These reports show that some dominant evergreen and deciduous dwarf shrubs (especially *Empetrum nigrum* and *Vaccinium* *myrtillus*) are vulnerable to such events. However, also conifers, e.g. *Juniperus communis*, *Picea abies* and *Pinus sylvestris*, which are adapted to being exposed during the winter period, occasionally suffer from frost drought after midwinter thaw episodes (Printz 1933; Tranquilini 1982; Kullman 2014; Bjerke et al. 2014).

Leaf defoliation caused by outbreaks of geometrid moths is another driver of widespread damage to northern boreal vegetation (Jepsen et al. 2009, 2011; Callaghan et al. 2013; Karlsen et al. 2013; Bjerke et al. 2014; Bokhorst et al. 2015). These outbreaks have strong effects on both the canopy and the field layer.

Bjerke et al. (2014) reported on 12 additional anomalous events that drove browning during one year in the Nordic Arctic Region, while Callaghan et al. (2013) summarized various weather and biotic events affecting primary production in northern boreal and alpine parts of northernmost Sweden over multiple decades. Hence, although the impacts of some types of events are better documented than others, browning drivers rarely occur in isolation and it is generally not straightforward to identify the causes of plant damage (Sinclair and Lyon 2005; Gunthardt-Goerg and Vollenweider 2007).

While trend changes, such as greening, take place over several years or decades and, hence, can be studied during their progress, the sporadic nature of events in time and space means they cannot be predicted beforehand; it may only be the aftermath of damage that allow us to detect the events and evaluate possible causes (Phoenix and Bjerke 2016). That is the case in the study reported here. During the summers of 2014 and 2015, widespread dieback of shoots of dwarf shrubs and some other cryptophytes was recorded in the Norwegian boreal and Arctic regions (64 °N to 79 °N). Similar types of damage were also recorded in neighbouring regions, as far east as Finland (Salo 2014). Such widespread dieback has major impacts on ecosystem structure and functioning (Bokhorst et al. 2011, 2012; Treharne et al. 2016). Understanding the drivers of this extensive dieback is crucial for assessing the potential recurrence frequency and ecosystem impact, and to evaluate the impacts in a broader, circumboreal and pan-Arctic context. We therefore attempted to quantify the damage ratio at selected sites within the affected regions and to identify the drivers, relying on timing of damage, phytopathological traits, meteorological data, and other environmental data.

As we studied these events retrospectively, we did not test any *a priori* hypotheses. However, based on self-experienced knowledge on the types of extreme events that took place during the study period, and the types of damage occurring, we hypothesized *a posteriori* that hazardous winter weather conditions and insect outbreaks played significant roles. We therefore studied this damage over large areas to assess whether these were the main drivers of the observed plant damage.

2. Materials and methods

2.1 Study area

Our field locations included regions in the boreal and Arctic biomes of Norway. Spitsbergen is the main island of the High-Arctic archipelago of Svalbard (Fig. 1a). It is characterized by large inter-annual variability in air temperatures and steadily increasing precipitation rates and winter temperatures (Førland et al. 2009; van Pelt et al. 2016; Vikhamar-Schuler et al. 2016). We conducted field work at 52 monitoring plots and several additional plots around the settlements of Longyearbyen (78.25° N 15.50° E) and Ny-Ålesund (78.92° N 11.93° E). These areas have experienced some extreme winter temperature anomalies in recent years. For example, mid-winter 2011/12 was associated with a strong positive temperature anomaly, resulting in two weeks of extremely warm weather with prolonged rainfall across most of Spitsbergen (Hansen et al. 2014). Such events have devastating effects on wildlife on the island due to the accumulation of ground-ice following the warming events (Hansen et al. 2013, 2014), but the impacts on the high-Arctic tundra vegetation are poorly understood (Phoenix and Bjerke 2016). Common dwarf shrubs on the tundra at Spitsbergen are *Dryas octopetala* (semi-evergreen, prostrate), *Salix polaris* (deciduous, prostrate) and *Cassiope tetragona* (evergreen, prostrate-erect). *Dryas octopetala* is semi-evergreen, meaning that chlorophyll in active leaves breaks down, and leaves become brown but overwinter attached to the shoots, and chlorophyll is reproduced in the same leaves the next spring (Welker et al. 1997).

For the boreal part of this study we quantified damage at numerous sites along a 610 km long coastal section (Fig. 2), from Flatanger Municipality in Nord-Trøndelag County (64.42° N 10.53° E), via the archipelagos of Lofoten and Vesterålen in Nordland County, to the municipalities of Harstad, Lenvik and Tromsø in Troms County (69.73° N 19.21° E). This coastal section is characterized by a sub-oceanic to oceanic boreal climate with, for these latitudes, mild winters and generally much snowfall (Førland et al. 2009). Much of the lowland is forested, but there are also large areas of human-driven treeless heaths dominated by the erect short to tall shrubs *Calluna vulgaris, Empetrum nigrum, Juniperus communis, Vaccinium myrtillus,* and *V. vitis-idaea*. It has previously been documented that all these species are sensitive to winter warming events, and with the latter species probably being the most tolerant of these (Ögren 1996; Bokhorst et al. 2009, 2012, 2015; Bjerke et al. 2014).

2.2 Estimates of damage ratios in Arctic Norway (Svalbard)

Sampling both in Arctic and boreal Norway was undertaken during the growing seasons of 2014 and 2015. At Spitsbergen, we first observed extensive plant damage across a lowland permanent (marked) vegetation transect dominated by *Cassiope tetragona* (Fig. S1) and

Dryas octopetala (Fig. S2) at Longyearbyen and Ny-Ålesund during 2014. The Longyearbyen transect consisted of seven sites along a 20 km long weak coast-inland gradient, from Indre Bjørndalen to Bolterdalen (Fig. 1b) and the Ny-Ålesund transect consisted of six sites along a 6 km long gradient from Gluudneset to Knudsenheia (Fig. 1c). Four plots of 1 m × 1 m were marked at each site for vegetation surveys. The vegetation plots were established using stratified random selection procedures for general vegetation composition studies. The plots differed slightly with regard to terrain features (flat, sloping, or concave) and aspect. Vegetation composition was analyzed once per year. The cover of the species present was estimated to the nearest 1-5 % (scale used: <1, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 15, 17, 18, 20, 25, 30, 35, 40, 45, 50, … , 95, 100). During cover estimation in 2014 (data collected from 4 to 15 August), we recognized that many plants were grey. That these were dead was confirmed by ecophysiological tests (see below). We therefore discerned between dead and alive plants of the same species during cover estimation. A few shoots also had pale brown leaves, but since the ratio of brown vs. grey leaves was very low, grey and pale brown leaves were not distinguished in the cover estimates in 2014. Health status of shoots was defined according to the colour state of apex leaves, which are always green when shoot is healthy, while older leaves towards the base of shoots naturally turn brown during ageing, though this browning process may be accelerated by external stress factors.

In 2015, we revisited the same plots and recognized that mats of *C. tetragona* this time consisted of shoots of variable coloration. We identified these as four different health states (Fig. S1): healthy shoots were green, shoots that had been dead for two or more years were grey, shoots that had been dead for less than two years were pale brown, while alive shoots recently stressed were reddish brown due to high accumulation of anthocyanins, probably by a combination of strong solar radiation and cool temperatures (Oberbauer and Starr 2002). Thus, in 2015, we distinguished between these four colour classes of *C. tetragona* during cover estimation (21-26 June and 10-11 August in Longyearbyen, and 6-10 August in Ny-Ålesund).

To explore the variation in damage on a wider scale, we estimated cover of damaged and healthy plants in non-permanent (unmarked) plots outside of our transects, including plots not dominated by *D. octopetala* or *C. tetragona*. This was done on the same dates in 2014 and 2015 as for permanent plots. Unmarked plots were from 10 m to 2500 m from our permanent plots. We studied sites differing from the marked plots in slope, terrain form, cardinal direction and altitude. Easily-reached areas in the vicinities of our marked plots were selected, and within these areas plots were selected using a stratified random approach, ensuring that plots of contrasting microtopography were included. In addition, during a survey from 14 July to 12 August 2015, covering lowland tundra at several sites around Isfjorden – the main fjord at western Spitsbergen, and Sarsøyra, Kaffiøyra and the peninsula Brøggerhalvøya, in the Forlandsundet-Kongsfjorden area, 960 plots dominated by *C. tetragona* and 4145 plots dominated by *D. octopetala* were assessed. This was done along 200 m long transects, within which plots were 2 m × 2 m segments of these transects, delineated with a measuring stick while walking slowly. Transect start was set by an a priori randomly assigned coordinate, and walking direction followed the general direction of the valley or the peninsula, i.e. maintaining the same level in the terrain, and walking towards a point at distance that was set before recording started. Damage was assessed very roughly; values were given as 0 or 1, where 1 represented plots with damage covering more than 5 % of the plot area. This approach, combining continual assessment and minimal recording time per plot, made a large number of assessments possible over a substantial area. The data from the 200 m transects is referred to as “extensive scale”.

2.3 Assessments of damage ratios in boreal Norway

During the early growing season of 2014, we observed, and received information from colleagues and through media, that plants were in a poor state over wide areas in boreal Norway. We therefore initiated surveys to quantify this reduction in health in further detail. We selected five districts along the coast, from Nord-Trøndelag County to Troms County. These districts were Flatanger (between weather stations 1 and 19 in Fig. 2), Flakstad-Vestvågøy (between stations 4 and 5), Vågan (around stations 6, 16 and 20), Vesterålen (around stations 7, 8 and 9), and Troms (around place names Tromsø and Harstad in Fig. 2). At each district, we quantified vegetation damage in plots of 1 m × 1 m with a particular focus on the dominant dwarf shrubs *Calluna vulgaris*, *Vaccinium myrtillus* and *Empetrum nigrum* (see Table S1 for information on plot numbers per district). For the mat-forming *C. vulgaris* and *E. nigrum*, we estimated damage ratios on an area basis, while damage ratios for *V. myrtillus* were based on the erect shoots. Data collection was done during several field campaigns from 23 April to 6 October 2015.

2.4 Additional field and supplementary data

We collected data on inclination, altitude, cardinal slope and plant height in all plots except the plots in Flatanger, the extensive-scale plots and 35 plots at Vestpynten and Longyeardalen near Longyearbyen. In one plot per transect site at Spitsbergen, we collected temperature from August 2014 to June 2015 by using data loggers (UA-001-08 and UA002-64, Onset Computer Co., Bourne, MA, USA) that were attached to the soil surface using a metal rod. Loggers were left exposed, meaning that they were not shaded from direct solar radiation, and readings therefore reflect variation in leaf temperature. In boreal Norway in 2015, we made 181 measurements of vegetation greenness (normalized difference vegetation index, NDVI) with an active optical handheld sensor (GreenSeeker, Trimble Navigation Ltd., California, USA). For the NDVI measurements, we focussed on study plots that had one dominant species covering more than 60 % of the plot, this because it rendered an opportunity to compare damage ratio on species level to NDVI. This sensor did not work well for species-level NDVI at Spitsbergen, because plots generally consist of multiple species; focal species rarely make up uniform patches large enough to render an NDVI value reflecting one species only. At Spitsbergen, we instead measured chlorophyll fluorescence of dark-adapted samples, i.e. maximal quantum efficiency of photosystem II (F_v/F_m) in all permanent plots except for a few due to instrument failure (PEA, Hansatech Instruments, King’s Lynn, Norfolk, UK).

To identify potentially hazardous weather events that could have caused the observed damage, we retrieved daily weather data on temperature, snow depth, precipitation and wind from meteorological stations using the online database eKlima (Norwegian Meteorological Institute 2016). We searched for events within the study period in all seasons that could help to explain the observed plant damage. From Svalbard, we also relied on a detailed report of an extreme event that took place in 2011/12 (Hansen et al. 2014), which may have resulted in damage that was still visible during our field period. Further, during our first surveys of the summer seasons, we searched for evidence of ground-ice, meaning that we checked out remaining snow patches visible in the landscape. If a knife blade was required for cutting, patches were defined as ice (as described in Bjerke et al. 2015). Furthermore, we evaluated how recent winters deviated from previous winters using an index on snow season warming and precipitation intensity calculated for Ny-Ålesund and Longyearbyen. Vikhamar-Schuler et al. (2016) defined this index as the precipitation sum for melt and precipitation days, abbreviated as $\mathrm{MPD}_{\mathrm{sum}}$. In their study of changes in winter warming events, Vikhamar-Schuler et al. (2016) used weather station data until the 2013/14 winter. We updated the time series with data also for the 2014/15 winter.

In boreal Norway, we looked for evidence of outbreaks of caterpillars of geometrid moths, primarily of the species *Epirrita autumnata*. We knew through our own observations, information from colleagues, and from reports in the local media, that there were large outbreaks in the study area. This information was used for selecting field sites. In the field, we evaluated whether the tree canopy and field layer plants had been markedly defoliated. Near-complete leafless tree canopies are the most obvious sign of severe defoliation. Two other indicators of defoliation are caterpillar silk hanging as loose threads from tree branches and occurrences of secondary leaves. These leaves develop from around mid-July after the cessation of caterpillar leaf consumption and are paler, more asymmetric and considerably lighter in weight per unit leaf area than original leaves (Hoogesteger and Karlsson 1992).

Finally, we searched through published reports and online databases for information on types of events that could potentially have caused the declines in health that we recorded in the field. These searches included climatic events, deposition of short- and long-transported air pollution, and signs of other pests than geometrid moths (e.g. outbreaks of fungal pathogens, lemming and other rodents, and leaf-defoliating or bud-mining insects other than geometrid moths). Our primary source was Google Scholar for scientific reports and Google for news reports, but as many reports in Scandinavian languages do not always show up in Google Scholar, we did separate screening of report series in Norwegian and Swedish that could potentially contain relevant information. This includes report series from national authorities (e.g. the Norwegian Environment Agency) and research institutes (e.g. Norwegian Institute for Air Research, NILU). Four sources contained relevant qualitative or quantitative information (Kristiansen et al. 2014; Barstein 2015; Duna 2016; Valt and Salvatori 2016), and this information is incorporated in the treatment of weather data in the Results section, where the weather events are described in brief, and in the Supporting Information, where these events are described in more detail.

2.5 Statistical analysis

Trends from 2014 to 2015, comparisons of samples of contrasting health states, and comparisons of interspecific damage ratio relationships were tested using paired Student's *t*-tests. One-way ANOVA was used to test for differences between sites.

A multiple linear regression analysis with forward stepwise model selection was undertaken to explore potential drivers of damage of *Cassiope tetragona* and *Dryas octopetala* in marked plots. Parameters used were elevation (m above sea level), inclination, heat load, landscape relief using a 5-level ordinal scale (exposed fellfield, upper leeside, middle leeside, lower leeside, depression), average terrain steepness in degrees, ground temperature fluctuations, distance to nearest seashore (m) and distance to open sea (m). Heat load was calculated according to an index developed by Geiger (1966), which takes into account that southwest-facing slopes experience the greatest diurnal heat load because of delayed ground heating. Ground temperature fluctuation was used as a proxy for site-level snow conditions and was calculated for the winter season (November-March) by comparing daily averages of ground temperature with daily air temperature from nearby weather stations (Ny-Ålesund and Svalbard Airport Longyearbyen). Linear Pearson correlation coefficients were calculated for 15-day moving windows. This procedure rendered 139 separate correlation coefficients for each pair of data (first window: 1-15 November, last window: 17-31 March). The mean of these 139 correlation coefficients was included for each site as input data in the model exercise. For two sites where loggers stopped logging during the winter period, data were extrapolated from the nearest site with a complete dataset. Akaike Information Criterion values were used to rank candidate models (Burnham and Anderson 2002). Confidence level for models was set to 95 %. Models were evaluated on their accuracy (0-100 %), and predictors included in the models were evaluated on their relative importance (0-100 %); the sum of all predictors in a model is 100.

Similar model selection procedures were undertaken for damage ratios of *Calluna vulgaris* and *Empetrum nigrum* in boreal Norway. The same physical parameters as used for the Svalbard plants were included, except ground temperature, as such data were not available. Instead, an estimate of snow cover during the winter of 2013/14 was included as a predictor, using average January snow depth retrieved from publicly available snow maps covering mainland Norway (seNorge 2017). These maps are produced daily (1957-present), with a spatial resolution of 1 km × 1 km (Saloranta 2012). Also included as a predictor was average January snow depth measured at the nearest weather station. Sites without information on plot-level plant height were not included in the analyses. This excludes all plots from Flatanger.

Relationships between predictor variables and response variables were evaluated using linear Pearson correlation coefficients, except for in one case where scatter plots clearly indicated a non-linear relationship. Curve fitting for this relationship was analyzed in Microsoft Excel by using the add-on XLfit ver. 5.3.1.3 (ID Business Solutions Ltd., Guildford, UK). All other tests were run with SPSS Statistics 22 (IBM Corporation, Armonk, NY, USA). Data were tested for normality and heterogeneity of variance prior to ANOVAs and correlations.

3. Results

3.1 Vegetation damage at Spitsbergen

3.1.1 Results from permanent sites

Physiological shoot measurements clearly show that non-green plants were either stressed or dead. Grey leaves of *C. tetragona* (Fig. S1) and *D. octopetala* (Fig. S2) had no chlorophyll fluorescence. In July 2015, F_v/F_m of pale brown and strongly anthocyanin-containing shoots of *C. tetragona* (Fig. S1) were 39.6 % ($P < 0.001$) and 11.7 % ($P = 0.002$) lower than in pure green shoots. Brown leaves of *D. octopetala* (Fig. S2) with green patches had 28.6 % ($P < 0.001$) lower F_v/F_m than pure green leaves. Some brown shoots of *C. tetragona* also contained leaves which still had some green patches; and this may be the reason why brown shoots had some chlorophyll fluorescence.

In 2014, 36 % of the shoots of *Cassiope tetragona* in the marked plots of the Ny-Ålesund transect were dead (Fig. 3a). Nearly all of these shoots had grey, wilted leaves (Fig. S1). Damage ratio increased to 50 % in 2015 (Fig. 3a). This was a combination of grey shoots (i.e. the same dead shoots as recorded the year before but in 2015 with yet fewer leaves still attached) and shoots with pale brown leaves that were still firmly attached and morphologically similar to normal leaves, except for the colour (Fig. S1). Damage ratios did not differ between sites in the Ny-Ålesund area, neither in 2014 ($P = 0.427$) nor in 2015 ($P = 0.139$).

Fewer shoots of *C. tetragona* were damaged at the Longyearbyen transect (Fig. 3b), but damage ratios doubled from 2014 (grey shoots) to 2015 (combination of grey and brown shoots) ($P = 0.005$, Fig. 3b). Damage ratios did not differ between sites in the Longyearbyen area in 2014 ($P = 0.075$), but in 2015, the two sites IBJ and ISD had higher damage ratios than most other sites ($P < 0.001$). On average, 78 % of the alive shoots of the Longyearbyen transect were strongly anthocyanin-coloured during the late June 2015 survey (Fig. S1).

Dryas octopetala showed a similar increase in damage as *C. tetragona*: from 2014 to 2015, the ratio of damaged shoots increased by 11 percent points ($P = 0.002$) at Ny-Ålesund (Fig. 3c) and by 14 percent points ($P < 0.001$) at Longyearbyen (Fig. 3d). Damage ratios were consistent across all sites at the Ny-Ålesund transect in both years (2014: $P = 0.188$, 2015: $P = 0.532$). In 2014, there were some site differences at the Longyearbyen transect ($P < 0.001$). Damage was not detected at two sites (YBJ and ISD), while maximum damage was 16 % (FLY). In 2015, damage ratios did not differ between the sites at the Longyearbyen transect ($F = 1.30$, $P = 0.299$).

Damage ratios of the two species were not correlated with each other at the Ny-Ålesund transect in any of the two study years ($r < 0.492$, $P > 0.074$). Damage ratios of the two species at the Longyearbyen transect were weakly correlated in 2014 ($r = 0.514$, $P = 0.005$), but not in 2015 ($r = 0.034$, $P = 0.86$).

3.1.2 Results from non-permanent plots

Estimation of damage in areas outside of our permanent transect plots provided additional information on local and regional variation in damage ratios. High variation in damage was found even over short distances. For example, in 36 plots dominated by *C. tetragona* within a 30 m × 20 m square at Vestpynten near Svalbard Airport studied in 2015, damage varied from 23 to 100 %. Thirty-three plots within a slightly larger area in Longyeardalen had damage ratios ranging from 10 to 100 %. Average damage ratios at these two sites were 75 and 80 % (Fig. 4a-b). Damage ratio of *Dryas octopetala* at these two sites was on average lower than for *C. tetragona*, but varied much between plots (Fig. 4b). The high within-site variation in damage ratios is a strong indication that factors acting variably at local scales are major drivers of damage, for example microtopography: highest damage to *C. tetragona* was in depressions and drainage channels (Fig. S3).

3.1.3 Results from the extensive-scale survey

The extensive-scale surveys around Isfjorden (Fig. 4c) and the Forlandsundet-Kongsfjorden (Fig. 4d) areas also detected damage to these two species, but with large species differences between these two areas. Populations of other species were also recorded to have large damage ratios at Spitsbergen (Fig. S4).

3.1.4 Multiple linear regression of results from marked plots

Forward stepwise modelling on data from marked plots provided highly contrasting best models, depending on year, species and transect (Table 1). Accuracy was 58.7 % or higher in six of the eight best models. Ground winter temperature fluctuation (as a proxy for site-level snow conditions) was the variable appearing in most models and was correlated with damage ratios of *C. tetragona* in 2015 (Ny-Ålesund: $r = 0.548$, $P = 0.028$; Longyearbyen: $r = 0.384$, $P = 0.044$), but not with damage ratios of *C. tetragona* in 2014 ($r < 0.330$, $P > 0.131$). Positive relationships mean that damage is associated with high temperature fluctuations and little snow. The response of *D. octopetala* to this predictor is different; relationships were significant only in 2014, for which the relationship is positive in Ny-Ålesund ($r = 0.496$, $P = 0.019$) but negative in Longyearbyen ($r = -0.431$, $P = 0.022$). Distance to open sea appears in four of the best models. It is correlated with *D. octopetala* in Ny-Ålesund in 2014 ($r = -0.468$, $P = 0.028$), indicating a tendency towards higher damage at the westernmost sites, i.e. HAR and MØR (Fig. 1c).

Heat load appears in three models and is the most important predictor for damage of *C. tetragona* in Longyearbyen in 2015, for which there is a good correlation ($r = 0.560$, $P = 0.002$). This suggests that the sloping south- and west-facing sites had the highest damage. A similar relationship is found for *D. octopetala* in Ny-Ålesund in 2014, where this predictor is the second-most important (Table 1; $r = 0.534$, $P = 0.011$).

3.2 Weather and snow at Spitsbergen

Snow accumulation varied much between the two weather stations during the 2013/14 winter. At Svalbard Airport, there was very little snow the entire winter (35 cm-month over the period from January to May), and especially during January and February, while at Ny-Ålesund, cumulative snow cover was 379 cm-month from January to May (Table S2), which is the highest measured for this station. It was an unprecedentedly warm winter, especially in January and February, which were 11.2 and 14.5 degrees warmer than the 1961-1990 norm at Svalbard Airport. February 2014 was 3.9 degrees warmer than the previous warmest February, which was in 2012. There were several freeze-thaw events during the 2013/14 winter, but none as extreme as that described below for the 2014/15 winter.

The Longyearbyen winter of 2014/15 had an extremely shallow snow cover compared to the long-term mean (Table S2) and included much ice. Cumulative snow cover during the 2014/15 winter was closer to normal in Ny-Ålesund (Table S2), but this was largely due to accumulation of snow in late winter (March-May), while average snow depth in January was only 8 cm (Table S2).

Seven warming events occurred in the Longyearbyen and Ny-Ålesund areas between January and April 2015. The most extreme occurred in mid-February when the temperature rose from –23.0 °C to 5.0 °C within 49 h and shortly after returned to freezing (Fig. S5). At Svalbard Airport, the ground was snow-free during this freeze-thaw-freeze event, while at Ny-Ålesund, snow depth declined from 34 to 29 cm during the warming event and increased to 34 cm during the refreezing phase.

Daily mean ground temperature in marked plots during the 2014/15 winter show that there was a strong correlation between air and soil temperatures until mid-March, in both the Ny-Ålesund (Fig. 5a) and Longyearbyen (Fig. 5b) areas, indicating that the snowpack was insufficient to insulate the soil from ambient air temperature fluctuations.

3.3 Precipitation sum for melt and precipitation days during winter at Spitsbergen

The index MPD_{sum}, calculated for every midwinter (December-February) with available meteorological data show that the frequency of mild, wet winters have increased: four of the five winters with highest index value are from the 2006-2015 period, and the winter of 2011/12 has the highest index value in the Ny-Ålesund record and the third highest in the Svalbard Airport record (Fig. 6a). The two following winters (2012/13 and 2013/14) had low index values at both stations, indicating little disturbance to the snowpack. However, the 2014/15 winter had higher MPD_{sum}. These results complement the snow depth and temperature data presented above. In addition to having numerous warming events and little snow, reports and our own observations suggest that ground-ice also accumulated during the 2014/15 winter, both around Longyearbyen and Ny-Ålesund.

3.4 Vegetation damage in boreal Norway

3.4.1 *Calluna vulgaris*

Damage to *Calluna vulgaris* in the 125 study plots in boreal Norway from Lofoten to Troms ranged from 0 to 100 % (38.3 ± 3.0 S.E.). NDVI varied between 0.22 and 0.77 and was strongly related to damage ratios ($r = -0.811$, $P < 0.001$; Fig. 7a). The best model for explaining damage ratios in these 125 plots had an accuracy of 47.8 %. Plant height was by far the most important predictor variable in this model with an importance of 73 %. Plant damage ratios were correlated with plant height ($r = 0.485$, $P < 0.001$). There was a clear height limit for the plant damage with plants higher than 26 cm having damage ratios between 90 and 100 % while below 26 cm damage varied widely (Fig. 8a). However, sampling districts varied in their relationship between damage ratios and plant height. The correlation was strongest at Vågan in Lofoten, which had the plots with the tallest plants (Fig. 8b). The relationship is sigmoid ($r = 0.812$, $P < 0.001$). The relationship was absent at Vesterålen ($r = 0.089$) and weak at Flakstad-Vestvågøy ($r = 0.462$, $P < 0.001$). These two latter districts had little variation in plant height and very few plots with plants taller than 20 cm.

The dataset from Flatanger, consisting of 142 plots, did not contain data on plant height and was therefore not included in the modelling exercise. Only two Flatanger plots had no signs of shoot damage, while 42 % of plots had damage ratios of 80 % or higher. The average damage ratio here was 62.6 % (± 2.4 S.E.).

3.4.2 *Empetrum nigrum*

Average damage ratio of *Empetrum nigrum* in 111 plots distributed from Lofoten to Troms was 22.4 % (± 3.0 S.E.) and was correlated both with plant height ($r = 0.546$, $P < 0.001$) and *Epirrita* occurrence ($r = 0.383$, $P < 0.001$). These two predictor variables were also inter-correlated ($r = 0.670$, $P < 0.001$) and were the most important variables in the best model, which had an accuracy of 38.5 %. These two predictors explained 88 % of the model. NDVI was negatively correlated with damage ratios ($r = -0.666$, $P < 0.001$; Fig. 7b). *Empetrum nigrum* co-occurred with *C. vulgaris* in 132 of the study plots in Flatanger, and average damage ratio in these plots was 4.8 % (± 1.1 S.E.). Plant height was not measured in these plots, and therefore not included in the modelling exercise.

3.4.3 *Vaccinium myrtillus* and *Juniperus communis*

The 19 *Vaccinium myrtillus* plots studied had damage ratios ranging from 0 to 100 %. Average damage ratio of the 16 sites in forests with recent *Epirrita* outbreaks was 90.7 % ± 2.2 S.E. The three locations from non-forested areas had damage ratios of 0 % (alpine), 0 % (bog) and 30 % (coastal heath). The damage at the latter site differed from those of forests, by having branches being dark brown in the top 5 cm and green close to the base (Fig. S6). Damaged branches in *Epirrita* forests were pale brown and not green towards the base (Fig. S6). We measured frequency of *V. myrtillus* annually over three years at one of these sites (Håkøya in Fig. 2); the frequency of alive *V. myrtillus* declined by 80.3 % from 2013 (prior to outbreak) to 2015 (second season of outbreak). The year-to-year declines were 64.4 % (2013-14) and 44.4 % (2014-15). *Juniperus communis* was in general green and undamaged in the study area, with an average damage ratio in 61 plots of 2.2 % (± 1.6 S.E.).

3.5 Weather and snow in boreal Norway

The only weather event that we identified as potentially hazardous occurred during the 2013/14 winter. Maximum snow depth during this winter was reached in November-December (Table S3), a situation not recorded for any of these stations previously. Snow cover maps retrievable at senorge.no show that the entire coastal lowland northwards to ca. 69.32° N was free of snow from 1 January to 15 March 2014, i.e. for 75 consecutive days in a period when these land areas normally are covered by snow. January was extremely dry. None of the stations received more than 10 % of the monthly mean precipitation for January, and several stations received less than 1 % (Table S3). Daily mean temperature was above freezing already from 2 February at most stations, only interrupted by short periods of colder weather, and this type of weather prevented any significant increase in snow depth.

4. Discussion

Our environmental and phytopathological data point towards a winter climatic reason for most of the observed damage reported here. We did not find any evidence of outbreaks of plant pathogens, nor did we find any reports indicating unusual dispersal of air pollution. We also evaluated whether any climate-related aspects of the growing seasons could have caused damage, but we did not find any such indications. However, we did observe outbreaks of geometrid moths in boreal birch forests, and some of the plant damage observed was clearly associated with these outbreaks.

Boreal regions of north-western Europe are frequently exposed to moisture advection from the North Atlantic Ocean, which leads to long shoulder seasons (autumn-winter and winter-spring transitions), and even midwinters, with temperature close to 0 °C (Førland et 2009; Groisman and Stewart 2014; Groisman et al. 2016; Vikhamar-Schuler et al. 2016). This situation is becoming more pronounced also for western Spitsbergen, which is subject to the most rapidly warming winter climate in the world (Hansen et al. 2014; van Pelt et al 2016; Vikhamar-Schuler et al. 2016). In regions with long cold-season periods characterized by mean temperature close to 0 °C, even minor changes in temperature will have large impacts on the ground environment. In such regions, colder-than-normal winter seasons are generally associated with a long-lasting, stable snow cover, while normal winters may be characterized by fluctuating snow cover in shoulder seasons and permanent snow cover in midwinter, and warmer-than-normal winters may have a strongly fluctuating snow cover, accumulating during short cold periods and thawing during warmer periods. Thus, such areas may experience extensive year-to-year variation in mean winter temperature, snow cover and ground-ice accumulation (Førland et al. 2009; Bjerke et al. 2015; Groisman et al. 2016; Vikhamar-Schuler et al. 2016).

It could be expected that vegetation in boreal and Arctic Norway would be tolerant to changing winter climate, since winters are naturally very variable. However, several recent winters have had anomalous warm periods followed by a return to freezing temperatures, which have resulted in frost drought-induced plant dieback over large scales (Bokhorst et al. 2009; Bjerke et al. 2014). During the 1920s and 1930s, which was the previous period with average winter temperature higher than the long-term average (Vikhamar-Schuler et al. 2016), extensive frost-drought-induced plant damage was reported (e.g. Langlet 1929; Printz 1933; Bathen 1935). However, this is, to the best of our knowledge, the first report of such extensive plant damage from High-Arctic areas. For Svalbard, there may be several reasons why this is the first such report; in previous warm periods, like the 1930s, there were not many plant biologists surveying the vegetation on the archipelago. Moreover, previous periods with warm winters were not as warm as the most recent period (Vikhamar-Schuler et al. 2016), thereby probably not having a similarly severe impact on snow cover and ground-ice conditions.

Several recent winters at Svalbard resulted in extensive accumulation of ground-ice (Hansen et al. 2014). Our data and models from Svalbard suggest that plants were indeed killed during winters with little snow and moderate to thick ground-ice. At some sites (both marked and unmarked) and for some species, we recorded higher plant damage in depressions, such as along small drainage channels and at the bottom of leeside slopes, than in nearby leesides. These are habitats where ice tends to accumulate during rain-on-snow events as the water travels to the most low-lying parts of the terrain and freezes when temperature drops below 0 °C. It has recently been shown that *C. tetragona* is vulnerable to experimental icing (Milner et al. 2016). The lowest damage ratios were often in the middle of leesides where some snow probably remained during thaw periods, and where ice probably did not accumulate to such thickness as in depressions. The many grey shoots recorded in 2014 suggest that it was not the most recent winter that induced the dieback; these grey shoots had been dead for some years. The winter of 2011/12 had a very high $\mathrm{MPD}_{\mathrm{sum}}$ index value and shallow snow cover with extensive ground-ice (Hansen et al. 2014), while the winters of 2012/13 and 2013/14 had much lower index values. These lines of evidence strongly suggest that the grey shoots recorded in 2014 died as a result of the extreme ground icing conditions of the 2011/12 winter.

At Svalbard in 2015, we recorded both fresh and old damage, seen as pale brown and grey shoots, respectively. There was also a high ratio of strongly anthocyanin-coloured shoots, a phenomenon not recorded during the 2014 surveys. Our analysis of climatic data show that the 2014/15 winter was in all respects similar to the 2011/12 winter. There is therefore little doubt that the fresh damage recorded in summer 2015 was caused by the severe conditions of the 2014/15 winter. However, it is generally not clear whether plants in specific plots were damaged by encasement in ground-ice or exposure to ambient temperature fluctuations. Probably both factors caused extensive plant damage, and microtopography of plots with the highest damage ratios clearly suggests that ice encasement was a primary driver for damage to *C. tetragona*. The relative low accuracy of the best linear model may be due to the fact that we only had three marked plots in depressions. On the other hand, fluctuations in ground temperature (which correlates with air temperature) suggest that plants at several sites were exposed to ambient temperature fluctuations for long periods of time. The high anthocyanin content of *C. tetragona* in 2015 indicates that these conditions caused stress in this species, probably via a combination of exposure to high light and cool temperature under reduced snow cover (Oberbauer and Starr 2002). The high anthocyanin content this year was also detected by another monitoring study in the Longyearbyen area (Anderson et al. 2016). The large spatial variation in damage rates may be related to local and regional variation in snow cover and rain-on-snow events. A spatial rain-on-snow model suggests that such events are more frequent in south-western Spitsbergen (van Pelt et al. 2016). This indicates that damage rates might have been even higher slightly further to the south from our study areas.

The larger midwinter discrepancy in Ny-Ålesund than in Longyearbyen between temperature at 2 m above the ground measured at the weather station and nearby ground temperature measured using loggers is peculiar. However, the Ny-Ålesund weather station is located behind some of the tallest buildings in the settlement. A photograph in March 2016 (Duna 2016) shows that this area is characterized by a distinctive snow drift caused by the "snow fence effect" of the buildings. This may explain the discrepancy between station snow depth and our ground temperature data. Hence, it is likely that the ground temperature series from our study sites better reflect the dominating snow cover of the 2014/15 winter than does the snow depth measured at the weather station.

The series of weather events that took place in boreal Norway during the 2013/14 winter were unusual. In particular, the dry weather in January combined with snow-free landscapes is unprecedented in the historical record (Kristiansen et al. 2014). All environmental information suggests that the very extensive damage to *Calluna vulgaris* in boreal Norway was caused by frost drought following this extreme weather event. The higher survival of plants shorter than 26 cm suggest that a very shallow snow cover provided some protection from ambient air, light and temperature, while the large variation in damage ratios at plant heights lower than 26 cm indicate that the prevailing snow depth differed within and between districts. The abundance of wilted shoots, without development of new shoots from the ground, clearly suggests that both roots and shoots died in many populations. Similar extreme damage to *C. vulgaris* has been reported in Scotland after winters where similar weather situations with dry weather and frozen ground caused dramatic declines in moisture content of plants (Watson 1966; Hancock 2008; Davies et al. 2010). The large amount of dead biomass makes these heaths more fire-prone (Davies et al. 2010), and indeed, there have been reports in Norwegian media of wildfires in coastal heaths after the 2013/14 winter (e.g. Jensen and Haugen 2016). This same event also led to damage to *Empetrum nigrum* at several sites, although damage ratios were much lower in this species, especially in Flatanger.

This type of dieback is heavily reminiscent of the widespread dieback to dwarf shrubs and conifers that was observed in Norwegian lowlands after the mild 1931/32 winter (Printz 1933). The mild weather of that winter also affected uplands in Scandinavia, causing snowmelt and accumulation of ground-ice, which led to a crash in reindeer populations (Riseth et al. 2016).

Although *Vaccinium myrtillus* is vulnerable to winter stress (Ögren 1996; Bokhorst et al. 2009, 2011, 2012, 2015; Blume-Werry et al. 2016), our data suggest that winter weather was not the primary cause for most of the damage to this shrub reported here. Instead, it was severely affected by defoliation from moth larvae, its cover being reduced by 80 % at one site from before to after a multiyear larval outbreak. Following damage, *V. myrtillus* often produces numerous new shoots that may compensate for parts of the biomass loss (Tolvanen 1997; Bokhorst et al. 2011). However, despite extensive compensatory growth, larval leaf defoliation of the severity shown in this study, may result in major compositional changes, from dwarf shrub-dominated (*V. myrtillus, E. nigrum*) to grass-moss dominated vegetation (e.g. Karlsen et al. 2013; Bokhorst et al. 2015). Larval outbreaks are expected to increase in frequency and intensity in northern Scandinavia with ongoing climate change due to range expansions of native species and increased establishment of non-native species (Jepsen et al. 2011). A decline in the abundance of *V. myrtillus* may therefore be expected, given its vulnerability to both frost drought and leaf defoliation.

Overall, these results provide further evidence that climatic and biotic extreme events will have significant impacts on vegetation state in rapidly changing northern regions. Most reports of the types of damage outlined here are from maritime regions with relatively mild winters. However, it has been hypothesized that the recent remotely sensed observations of reduced productivity in many regions of the Arctic (Epstein et al. 2015) is related, at least in part, to widespread plant damage driven by hazardous events (Phoenix and Bjerke 2016) like the ones we have reported here. It has also been suggested that winter-related plant damage has contributed to the recent weakening of the relationship between growing season temperature and remotely sensed vegetation productivity in central parts of Spitsbergen (Vickers et al. 2016). Remote sensing of the vast northern ecosystems provides much knowledge on major greening and browning trends, but this study underlines the critical importance of complementary field-based assessments to fully understand observed ecosystem changes. Winter ecology remains underrepresented in northern climate change studies despite the particularly rapid changes taking place in the cold season (Bokhorst et al. 2016; Phoenix and Bjerke 2016), and an increasing appreciation of its importance in determining landscape function is further demonstrated by this study.

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Figure captions

Fig. 1. Study areas at Spitsbergen, Svalbard. (a) Overview map including main geographical names used in text; white-grey colours: glaciers; yellow surfaces: unglaciated land; open rectangles: locations of the main study areas in Ny-Ålesund and Longyearbyen; crosses: sites assessed for damage during the 2015 extensive-scale survey. Site abbreviations: Forlandsundet-Brøgger area: ENG = Engelskbukta, KAF = Kaffiøyra, KON = Kongsfjorden, SAR = Sarsøyra; Isfjorden area: ADV = Adventdalen, ALK = Alkhornet, BJØ = Bjørndalen, COL = Colesbukta, DIC = Dicksonfjorden, SAS = Sassendalen. (b) Detailed map of the Longyearbyen area; filled circles: sites with permanent (marked plots); site abbreviations: BOL = Bolterdalen, HOT = Hotellneset, IBJ = Indre Bjørndalen, ISD = Isdammen, LON = Longyeardalen, SVH = Svalbardhytta, YBJ = Ytre Bjørndalen; open squares: areas with unmarked plots mentioned in the text. (c) Detailed map of the Ny-Ålesund area; filled circles: sites with permanent (marked plots); site abbreviations: GLU = Gluudneset, NAN = Nannestadelva, SMI = Smithelva, LEI = Leirhaugen, HAM = Hamnerabben, KNU = Knudsenheia.

Fig. 2. Map of coastal, boreal Norway showing the main study sites, which includes place names used in the main text. Weather stations are numbered; see Table S3 for station names.

Fig. 3. Damage ratios recorded in permanent sites. *Cassiope tetragona* at the Ny-Ålesund (a) and Longyearbyen (b) transects; *Dryas octopetala* at the Ny-Ålesund (c) and Longyearbyen (d) transects. Error bars are ±1 SEM.

Fig. 4. Damage to *Cassiope tetragona* and *Dryas octopetala* recorded in non-permanent plots. Damage ratio at Vestpynten (a) and Longyeardalen (b) areas; error bars are ±1 SEM. Frequency of plots with recorded damage in the Isfjorden area (c) and in the

Forlandsundet-Kongsfjorden area (d). Total number of plots with observed plants were for Isfjorden 928 (*C.t.*) and 3684 (*D.o.*), and for Forlandsundet-Brøgger area 32 (*C.t.*) and 461 (*D.o.*).

Fig. 5. Relationship between ground and air temperature. (a) Ny-Ålesund area; (b) Longyearbyen area. Air temperature is from the Ny-Ålesund and Svalbard Airport Longyearbyen weather stations. Site names as in Fig. 1.

Fig. 6. Midwinter (December-February) values for the index precipitation sum for melt and precipitation days (MPD_{sum}) from Ny-Ålesund and Longyearbyen. Winters are denoted with the last year of the winter, e.g. “2015” is the winter of 2014/15. Correlation (*r*) between Ny-Ålesund and Longyearbyen is 0.798.

Fig. 7. Relationship between damage ratios and NDVI measured using a handheld optical sensor. (a) *Calluna vulgaris*, (b) *Empetrum nigrum*.

Fig. 8. Relationship between plant height and damage ratio of *Calluna vulgaris*. (a) All plots with plant height data. (b) Plots in the Vågan district, where the tallest plant were recorded.

Table caption

Table 1. Best linear models for damage ratios of *Cassiope tetragona* and *Dryas octopetala* measured in 2014 and 2015 in permanent sites in the Ny-Ålesund and Longyearbyen areas. The variation explained by of the best model (accuracy) and the most important predictors is given in the range from 0 (worst) to 100 (best). All presented models and predictors are significant at *P*-level of 0.05. Only predictors in the best models with importance higher than 15 are included.

Table 1.

(a) *Cassiope tetragona*	Longyearbyen		Ny-Ålesund	
Year	2014	2015	2014	2015
Model accuracy (%)	40.6	75.9	73.0	70.5
Predictors in best model (no.)	7	7	8	7
Predictors (relative importance, %)				
Snow		24	28	48
Distance	18		31	
Heat load		47		
Plant height	36			
Elevation				21

(b) *Dryas octopetala*	Longyearbyen		Ny-Ålesund	
Year	2014	2015	2014	2015
Model accuracy (%)	58.7	37.1	75.7	65.3
Predictors in best model (no.)	8	8	7	7
Predictors (relative importance, %)				
Snow	42		24	
Distance			21	19
Heat load			23	
Slope	25			35
Aspect	21	22		
Microtopograhpy		43		

Supporting Information

Understanding the drivers of extensive plant damage in boreal and Arctic ecosystems: insights from field surveys in the aftermath of damage

by

Jarle W. Bjerke et al.

HEALTH STATES OF ARCTIC PLANTS

Health states with associated contrasting leaf colours of *Cassiope tetragona* and *Dryas octopetala* are shown in Figs S1 and S2. *Cassiope tetragona* growing under variable microclimatic conditions is shown in Fig. S3. Damage ratios of three other species recorded in the field is shown in Fig. S4.

THE 2014/15 WINTER AT SPITSBERGEN

Time series of snow cover at Spitsbergen are short, starting in the 1970s, and lacking data from 1994 to 2008. However, available data from Svalbard Airport Longyearbyen suggest a declining trend of snow cover, and the winter of 2014/15 had an extremely shallow snow cover (Table S1a). Cumulative snow cover for January to May in 2015 was 21 cm-month, which is only 24 % of the average cumulative snow cover for the years with data between 1977 and 1993. Notably, February had extremely little snow with an average of 1 cm. Cumulative snow cover during the 2014/15 winter was closer to normal in Ny-Ålesund (Table S1b), but this was largely due to much fresh snow in late winter (March-May). Mean snow cover in January was 8 cm, which was only 33 % of average January snow cover for the available years between 1975 and 2014. The temperature evolution during the warm period in February 2015 is shown in Fig. S5.

Daily mean ground temperature in marked plots during the 2014/15 winter follow the fluctuations in air temperature to various extents. Until mid-January, the correlation between daily mean ground and air temperature was very strong for most sites at both transects (15-d windows, $r > 0.9$; Fig. 5). This strong correlation continued for some sites (e.g. MØR at the Ny-Ålesund transect and BOL at the Longyearbyen transect) until ca. 8 March, albeit with some fluctuation. At other sites (e.g. SMI at the Ny-Ålesund transect and HOT at the Longyearbyen transect), ground temperature fluctuations were more damped, and correlation with air temperature was mostly below 0.8. These comparisons with air temperature show that vegetation had no to very little protection from snow. Even if the snowpack of the Ny-Ålesund weather station was more than 20 cm deep from February onwards (Table S1), the ground temperature data from the Ny-Ålesund transect suggests that some sites had very little snow until mid-March (Fig. 5a). NAN and SMI, the two sites with the lowest correlation with air temperature from 15 January onwards, are both situated close to the foot of a steep hillside, and hence probably less wind-exposed than most other sites, something which led to more snow accumulation at these sites. However, even for these sites, correlation with air temperature was high ($r > 0.7$) during shorter periods in February and March (Fig. 5a), indicating that snow depth occasionally was reduced, thereby not insulating well.

The 2014/15 winter had high $\mathrm{MPD_{sum}}$ index values for both stations (Fig. 6a), being ranked as the fourth highest value in the Ny-Ålesund record and the fifth highest in the longer Longyearbyen record. Ground-ice also accumulated during the 2014/15 winter, both around Longyearbyen (Barstein 2015) and around Ny-Ålesund (Valt and Salvatori 2016). This is also evident from our own field observations in early June 2015 (Fig. S7), and from landscape photographs. For example, one photograph from 28 January shows that the area around Ny-

Ålesund was covered in ground-ice (Duna 2016). A thaw event in the days before the photograph was taken reduced snow cover at the weather station from 6 cm to 0 cm, and this photograph shows that snow became icy in areas without complete thaw. Overall, this assembly of information strongly suggests that the 2014/15 winter had an anomalously shallow snow cover, much ground-ice accumulation and high number of days with thaw temperatures, probably being quite similar to the extreme 2011/12 winter, as reported on by Hansen et al. (2014) and van Pelt et al. (2016).

HEALTH STATES OF *VACCINIUM MYRTILLUS*

Shoots of *Vaccinium myrtillus* damaged by caterpillar-induced defoliation and winter frost-induced top wilting differ in morphology, as shown in Fig. S6.

THE WINTER OF 2013/14 IN BOREAL NORWAY

In the study area, from Nord-Trøndelag to Troms, the winter of 2013/14 was at first very wet (November in Table S2a) with temperatures only slightly above the norm (Table S2b), causing much of the precipitation to fall as snow, and leading to higher-than-normal snow depths for most of the stations (Table S2c). The wet weather continued in December (Table S2a), but with temperatures more than 2 degrees above normal (Table S2b). Despite the mild weather, temperatures were close to freezing, and this led to increasing snow depths at most stations (Table S2c). Snow accumulation was highest at the most northerly meteorological stations. Numerous stations experienced the driest January ever recorded (Kristiansen et al. 2014). Temperatures in January were close to normal (Table S2b). Snow depth decreased during January and were below 9 cm at most stations, which was 21 % or less of normal snow depth for this month (Table S2c). Snow cover maps retrievable at senorge.no show that the entire coastal lowland northwards to ca. 69.32° N was free of snow from 31 December 2013 to 15 March 2014, i.e. for 75 consecutive days in a period when these land areas normally are covered by snow. Much of this area was also free of snow for several weeks before and after this period.

February was from 3 to nearly 5 degrees warmer than the norm (Table S2b), and still quite dry with many stations receiving less than 50 % of the normal precipitation (Table S2a). The station Laukhella had the driest February month in a time series running from 1998, precipitation rates being only 38 % of the previous low record (Kristiansen et al. 2014). Precipitation mostly fell as rain on days with temperatures above freezing. This led to continued reduction of snow depth; monthly averages being close to 0 cm and 7 % or less of the norm for most stations, except for some of the most northerly stations (Table S2c). March was wet and mild. For ca. three continuous weeks (from ca. 22 February to 14 March), daily mean temperatures at most stations were above the daily normal, and also above freezing. During March, a few centimeters of snow accumulated at the southerly stations – still less than 25 % of the norm – while snow depth declined slightly at the most northerly stations to between 19 and 41 % of the norm (Table S2c). April was also mild and wet, leading to minor changes in snow depth. Consequently, all stations had the highest snow cover already in November or December, a situation not recorded for any of these stations previously. Daily mean temperatures were spring-like already from 2 February at most stations, only interrupted by short periods of colder weather.

The period from December to February as a whole was close to average in terms of $\mathrm{MPD}_{\mathrm{sum}}$. It is ranked as 74 of 146 winters in the long Tromsø weather station data series; the winter of 1890/91 having the highest index value (Fig. S8). However, very wet weather in December nullified the extreme dry weather in January and February. Thus, as a whole, December 2013-February 2014 was close to normal. This index is so far not calculated for single months, and not for other weather stations in coastal boreal Norway.

Photo credits

All photos presented in this document were taken by Jarle W. Bjerke, except photo in Fig. 1f, which was taken by Rachael Treharne.

SUPPLEMENTARY FIGURES AND TABLES

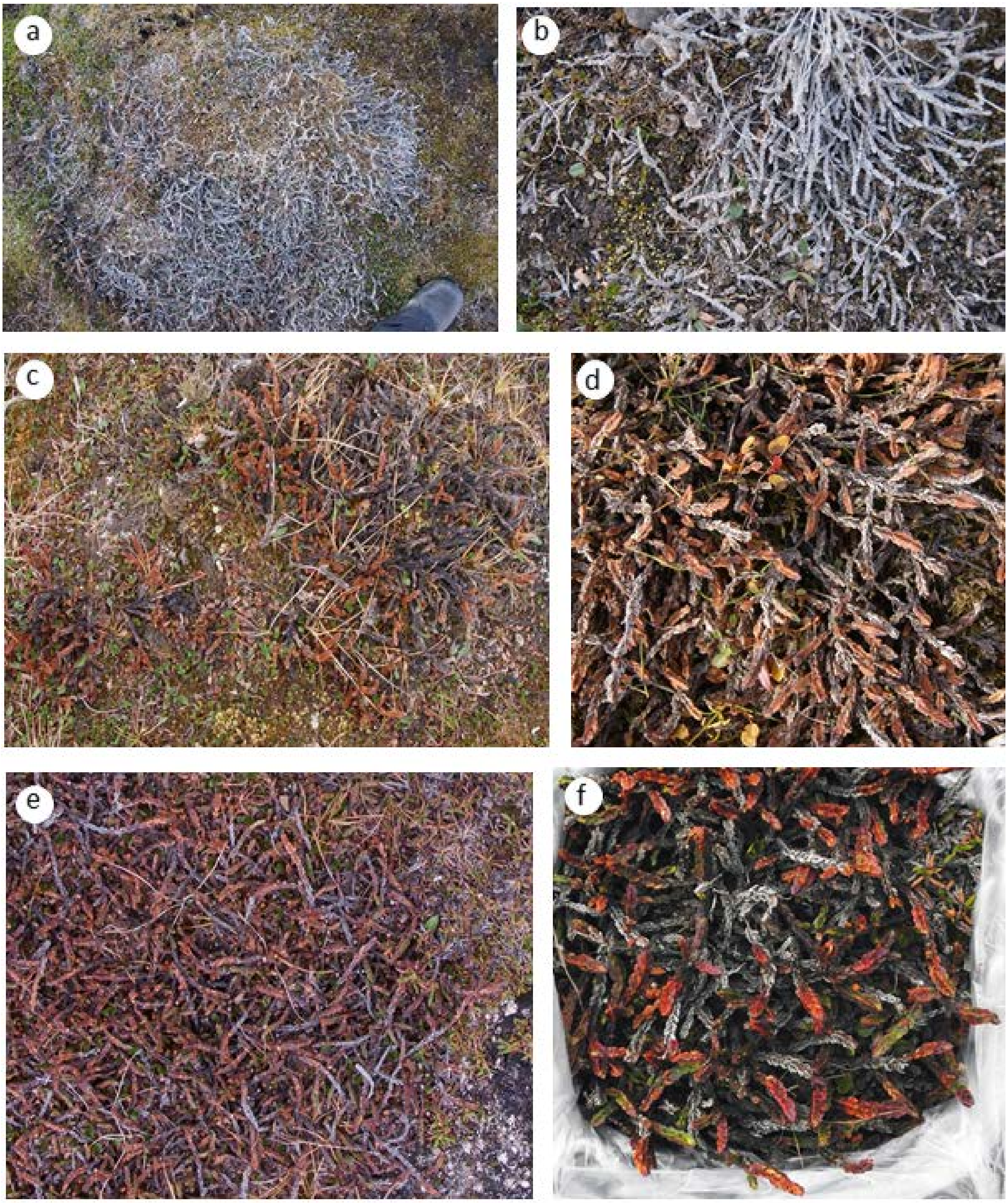

Fig. S1. Health categories of *Cassiope tetragona*. (a) Completely dead patch with grey leaves and stems; (b) Detail showing dead, grey shoots; (c) recently dead patch with brown leaves (green leaves at this image are *Salix polaris*); (d) detail showing individual brown shoot apices and mostly grey basal leaves; (e) alive patch with leaves strongly violet-red due to accumulation of anthocyanins (intermixed with some grey and brown shoots); (f) detail showing strongly anthocyanin-coloured shoots intermixed with some green and grey shoots. Note colour of anthocyanin-rich shoots ranging from violet-burgundy at tips to orange-red towards base.

Fig. S2. Health categories of *Dryas octopetala*. (a) Completely dead mat with grey leaves only; (b) Detail of mostly dead mat, but with some surviving shoots at the more vertically-inclined edge of the mat; (c) partly dead mat with grey dead leaves, stressed anthocyanin-containing leaves with red and brown colours, and healthy, green leaves; (d) first stage of autumn yellowing, some leaves being completely yellow, others only yellow at the tips.

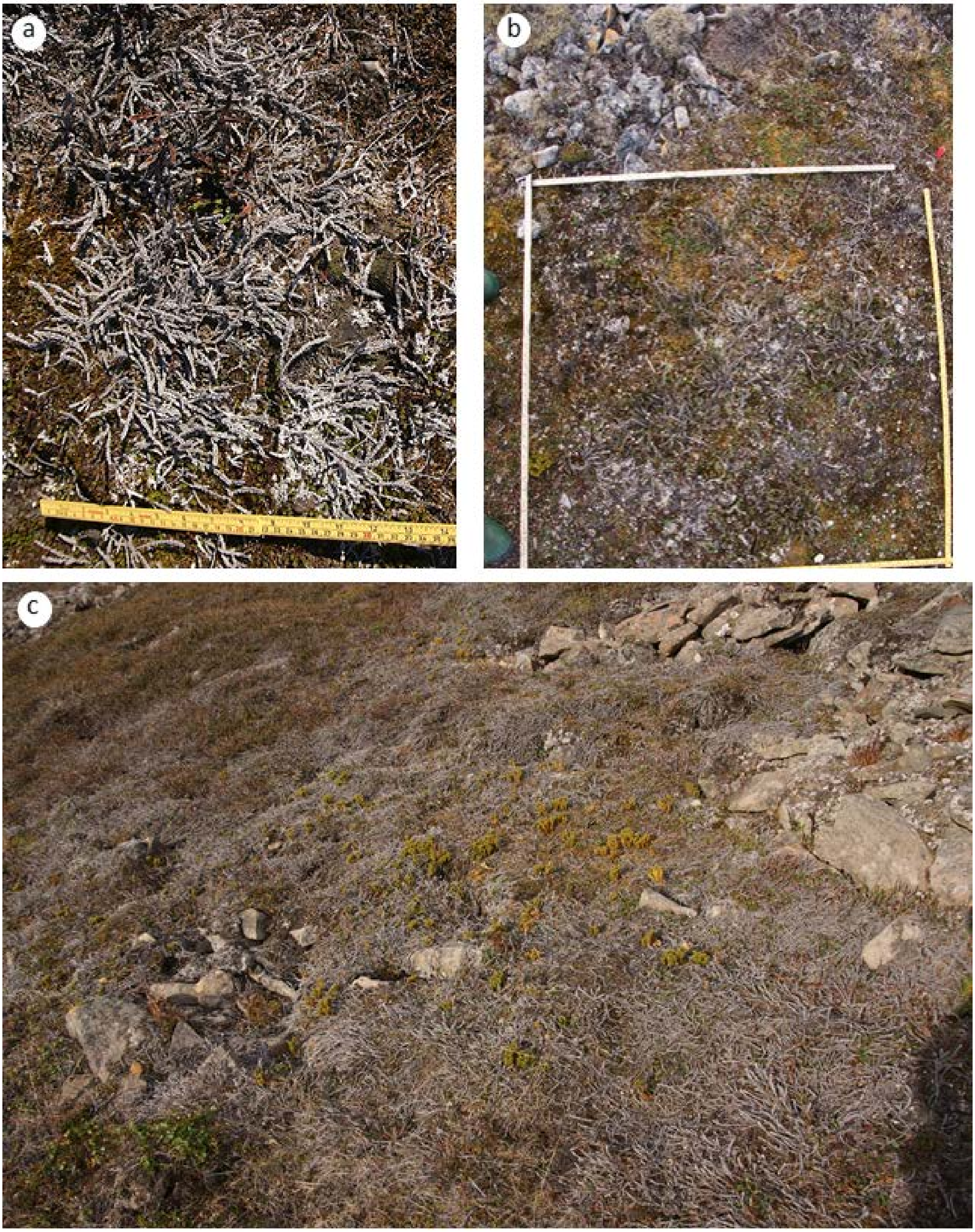

Fig. S3. Damage to *Cassiope tetragona* under variable microtopographic conditions. (a) Snowbed at foot of hill at Hamnerabben; (b) exposed ridge at Leirhaugen; (c) drainage channel in steep terrain in Endalen near Longyearbyen. Note the surviving, green shoots of

Huperzia arctica in between the dead shoots of *C. tetragona*. The slope in the upper left corner of the image is slightly raised compared to the drainage channel, and there most shoots of *C. tetragona* were alive. Green leaves in lower left and lower right corners are *Salix polaris*.

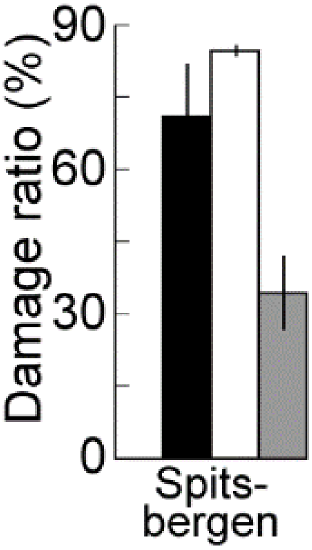

Fig. S4. Damage ratio of *Empetrum nigrum* (black), *Equisetum arvense* ssp. *boreale* (white) and *Saxifraga oppositifolia* (grey) at Spitsbergen. Data for *E. nigrum* from Longyeardalen only, while data for the two other species are from sites both in the Longyearbyen area and Ny-Ålesund. Error bars are ± 1 SEM.

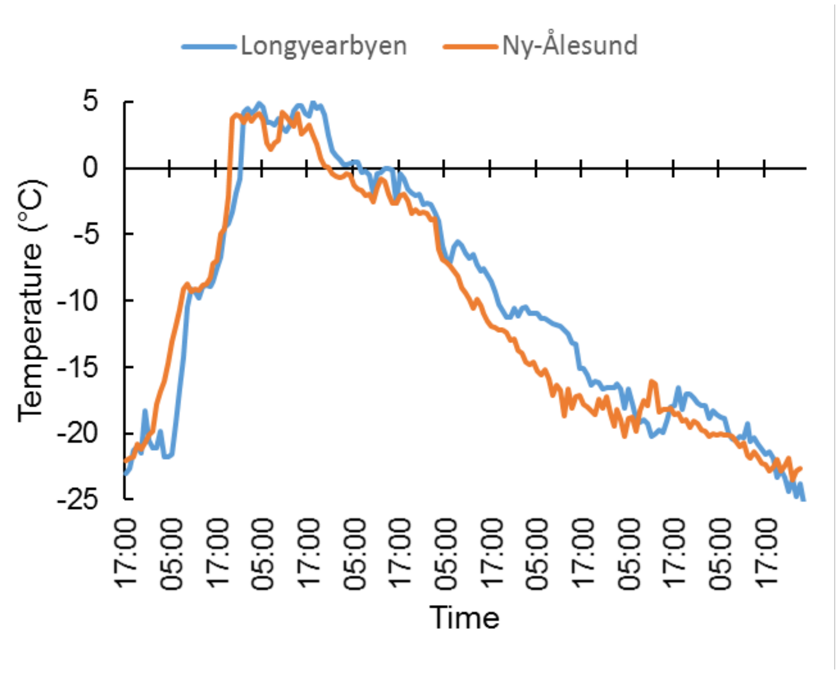

Fig. S5. Temperature development during an extreme freeze-thaw event at Spitsbergen in 2015 from 14 February 17:00 to 22 February 04:00.

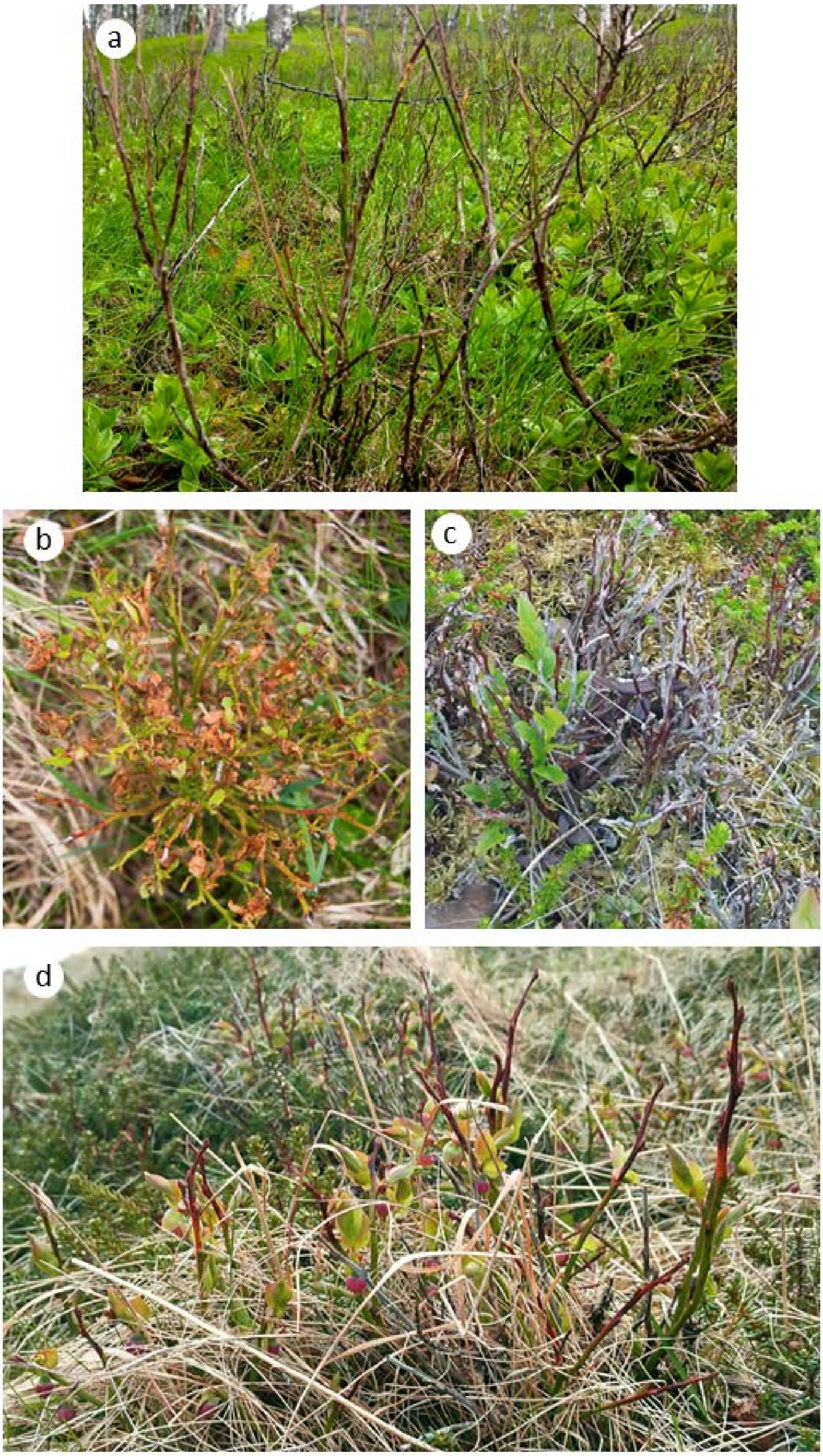

Fig. S6. Types of damage to *Vaccinium myrtillus* detected in the field. Complete (a) and partial (b) leaf defoliation caused by larvae of *Epirrita autmnata*; note brown leaves that were not browsed completely, but were too damaged to sustain growth; (c) old (grey) and fresh (brown) frost drought-damaged shoots at a wind-exposed coastal site where snow is absent during long parts of winter; note that a few shoots survived; (d) frost drought damage to upper half of shoots, lower half survived due to partial snow protection during winter. Associated green plants are *Cornus suecica* and *Avenella flexuosa* (a), *Agrostis capillaris* (b and d), *Empetrum nigrum* (c and d), and *V. vitis-idaea* (c).

Fig. S7. Melting ice covering a mat of *Dryas octopetala*, Adventdalen, June 2015. The pale green dots are shoots of the moss *Polytrichum juniperinum*.

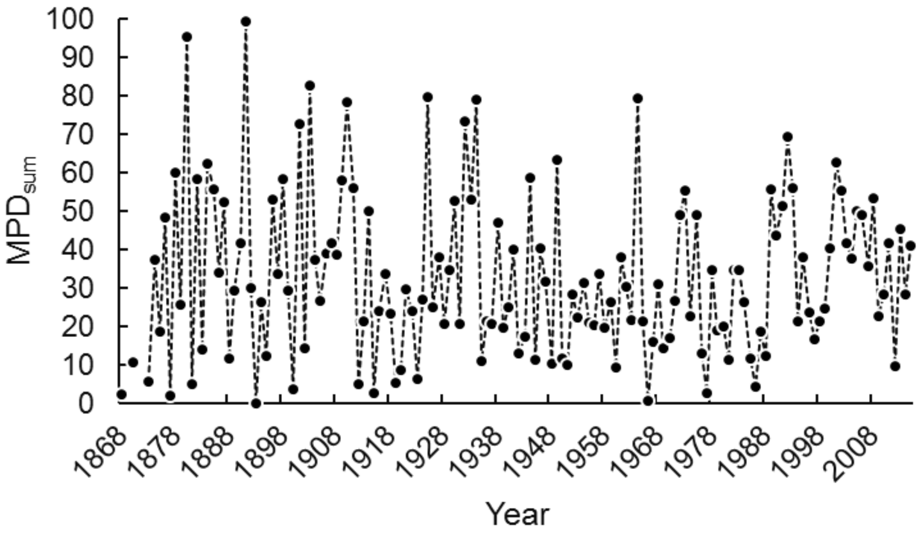

Fig. S8. Midwinter (December-February) values for the index precipitation sum for melt and precipitation days (MPD_{sum}) from Tromsø. Winters are denoted with the last year of the winter, e.g. “1868” represents the winter of 1867/68. Temperature records are lacking for some of the first years in the time series.

Table S1. Number of studied plots per district in boreal Norway.

District	Plot number
Flatanger	142
Flakstad-Vesvågøy	29
Vågan	18
Vesterålen	34
Troms	9
Overall	231

Table S2. Mean monthly snow depth (cm) at the weather stations Ny-Ålesund (a) and Svalbard Airport Longyearbyen (b) during the study period compared to previous periods. At Svalbard Airport, snow depth was measured from 1977 to 1993, and from 2009 onwards, but not from 1994 to 2008. At the Ny-Ålesund station, snow depth was measured in 1975, 1976 and 1979 (“1970s”), and from 2009 onwards. Cumulative snow depth has the unit cm-month referring to the sum of monthly means for the period from January to May.

(a) Ny-Ålesund	1970s	2009-2011	2012	2013	2014	2015
January	29	24	13	10	47	8
February	32	31	24	21	57	29
March	43	46	25	26	95	34
April	50	52	26	24	90	46
May	31	43	20	22	90	42
Cumulative snow	185	197	108	103	379	159

(b) Longyearbyen	1977-1993	2009-2011	2012	2013	2014	2015
January	13	12	5	18	7	5
February	18	13	6	21	4	1
March	22	16	6	19	9	4
April	24	20	5	17	10	8
May	12	7	6	9	5	3
Cumulative snow	89	68	28	84	35	21

Table S3. Weather and snow data for the 2013/14 winter from selected lowland weather stations close to our study sites in mainland Norway. Municipality names with station names and altitude (m a.s.l.) in parentheses are given. Numbers refer to numbers in map in Fig. 2. (a) Precipitation sum; (b) temperature; (c) snow cover. Values are monthly means for snow cover and temperature. Values in parentheses are deviations from monthly normal values (1961-90) for precipitation and temperature and from monthly average snow cover for the period from 2000 to 2016. Deviations are expressed in percentage for snow depth and precipitation (100 = 2013/14 value identical to long-term value), and in degrees for temperature. NA = data not available. For some stations, data were lacking for a few days during the 2013/14 winter. Daily values for these days were estimated by using day-to-day variation in daily temperatures from nearby stations.

Table S3.

(a) Precipitation	Nov	Dec	Jan	Feb	Mar	Apr
1 Osen (Buholmråsa)	157 (182)	134 (149)	7 (9)	21 (33)	85 (139)	78 (139)
2 Bodø (Kjerringøy)	172 (158)	215 (179)	<1 (0)	56 (71)	119 (155)	114 (178)
3 Hamarøy (Tømmerneset)	238 (165)	245 (139)	1 (1)	107 (85)	235 (226)	139 (172)
4 Moskenes (Reine)	458 (148)	383 (152)	11 (4)	131 (51)	286 (125)	NA
5 Vestvågøy (Leknes)	260 (184)	173 (112)	14 (10)	98 (88)	164 (167)	155 (221)
6 Vågan (Kvitfossen)	526 (185)	345 (120)	3 (1)	177 (88)	325 (145)	374 (220)
7 Sortland (Sortland)	250 (170)	210 (147)	4 (2)	70 (59)	250 (266)	114 (137)
8 Øksnes (Alsvåg)	254 (181)	140 (99)	2 (2)	45 (39)	169 (167)	124 (142)
9 Andøy (Andøya)	182 (167)	110 (100)	<1 (1)	47 (54)	167 (211)	105 (155)
10 Lenvik (Laukhella)	127 (116)	112 (101)	5 (6)	19 (21)	177 (253)	103 (171)
11 Tromsø (Langnes)	149 (142)	113 (108)	<1 (1)	28 (32)	151 (219)	110 (180)
12 Karlsøy (Grunnfjord)	120 (115)	99 (90)	<1 (0)	40 (45)	115 (165)	99 (164)

(b) Temperature	Nov	Dec	Jan	Feb	Mar	Apr
1 Osen (Buholmråsa)	NA	4.7 (3.1)	NA	4.4 (3.7)	4.2 (2.3)	5.6 (1.6)
13 Bodø (Helligvær)	3.6 (1.1)	3.1 (2.8)	-0.8 (0.0)	3.2 (3.9)	2.4 (1.9)	4.0 (1.2)
14 Tysfjord (Drag)	0.9 (NA)	0.6 (NA)	-3.6 (NA)	2.0 (NA)	0.9 (NA)	2.7 (NA)
15 Værøy (Værøy)	4.0 (0.5)	3.9 (2.4)	1.1 (0.5)	3.5 (3.0)	3.0 (1.9)	4 (1.5)
5 Vestvågøy (Leknes)	2.0 (0.7)	2.1 (2.8)	-1.5 (-0.1)	2.2 (3.7)	1.7 (2.5)	3.2 (1.2)
16 Vågan (Svolvær)	2.3 (0.6)	2.0 (2.3)	-1.0 (0.1)	2.4 (3.8)	1.6 (2.2)	3.0 (1.1)
7 Sortland (Sortland)	1.2 (0.4)	0.8 (2.2)	-2.6 (-0.3)	1.5 (3.6)	1.3 (2.3)	2.8 (1.0)
8 Øksnes (Alsvåg)	2.7 (NA)	2.6 (NA)	-0.7 (NA)	2.4 (NA)	2.0 (NA)	3.3 (NA)
9 Andøy (Andøya)	1.2 (0.3)	0.9 (2.1)	-2.5 (-0.4)	1.2 (3.4)	0.7 (2.1)	2.5 (1.4)
17 Lenvik (Hekkingen)	1.6 (0.6)	1.3 (2.4)	-2.8 (-0.6)	1.5 (3.6)	1.0 (2.1)	2.6 (1.0)
11 Tromsø (Langnes)	-0.2 (0.4)	-0.5 (2.2)	-5.9 (-2.1)	-0.1 (3.6)	-0.4 (1.9)	1.3 (0.6)
18 Karlsøy (Torsvåg)	1.9 (0.3)	2.0 (2.3)	-0.5 (0.6)	2.3 (3.5)	0.9 (1.4)	2.1 (0.7)

Table S3 continued

(c) Snow depth	Nov	Dec	Jan	Feb	Mar	Apr
19 Namsos (Otterøy)	3.0 (114)	4.0 (51)	0 (0)	0 (0)	7 (43)	0 (0)
2 Bodø (Kjerringøy)	2.3 (110)	7.3 (101)	0 (0)	0.1 (1)	0.3 (4)	0 (0)
3 Hamarøy (Tømmerneset)	16.8 (259)	15.1 (110)	2.5 (11)	0.3 (1)	5.3 (16)	3.7 (21)
4 Moskenes (Reine)	2.5 (67)	4.4 (35)	0 (0)	0 (0)	1.8 (7)	0 (0)
5 Vestvågøy (Leknes)	3.5 (105)	1.1 (12)	0 (0)	0 (0)	3.7 (24)	1.9 (34)
20 Vågan (Kongsmarka)	13.5 (113)	21.8 (111)	8.2 (21)	10.0 (16)	12.2 (15)	7.5 (11)
7 Sortland (Sortland)	NA	NA	0.9 (NA)	0.1 (NA)	1.7 (NA)	4.0 (NA)
8 Øksnes (Alsvåg)	10.3 (194)	7.3 (62)	1.7 (8)	0.3 (1)	3.9 (16)	3.5 (22)
10 Lenvik (Laukhella)	16.9 (214)	44.0 (308)	39.1 (138)	30.2 (66)	10.5 (19)	17.2 (37)
11 Tromsø (Langnes)	2.9 (56)	7.5 (88)	0.8 (7)	1.4 (7)	4.4 (18)	7.8 (71)
12 Karlsøy (Grunnfjord)	8.2 (143)	30.8 (231)	23.0 (93)	21.6 (68)	13.4 (41)	11.5 (46)