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LETTER

Vulnerability and resilience of the carbon exchange of a subarctic peatland to an extreme winter event

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Abstract

Extreme winter events that damage vegetation are considered an important climatic cause of arctic browning—a reversal of the greening trend of the region—and possibly reduce the carbon uptake of northern ecosystems. Confirmation of a reduction in CO_2 uptake due to winter damage, however, remains elusive due to a lack of flux measurements from affected ecosystems. In this study, we report eddy covariance fluxes of CO_2 from a peatland in northern Norway and show that vegetation CO_2 uptake was delayed and reduced in the summer of 2014 following an extreme winter event earlier that year. Strong frost in the absence of a protective snow cover—its combined intensity unprecedented in the local climate record—caused severe dieback of the dwarf shrub species *Calluna vulgaris* and *Empetrum nigrum*. Similar vegetation damage was reported at the time along ∼1000 km of coastal Norway, showing the widespread impact of this event. Our results indicate that gross primary production (GPP) exhibited a delayed response to temperature following snowmelt. From snowmelt up to the peak of summer, this reduced carbon uptake by 14 (0–24) g C m^{-2} (∼12% of GPP in that period)—similar to the effect of interannual variations in summer weather. Concurrently, remotely-sensed NDVI dropped to the lowest level in more than a decade. However, bulk photosynthesis was eventually stimulated by the warm and sunny summer, raising total GPP. Species other than the vulnerable shrubs were probably resilient to the extreme winter event. The warm summer also increased ecosystem respiration, which limited net carbon uptake. This study shows that damage from a single extreme winter event can have an ecosystem-wide impact on CO_2 uptake, and highlights the importance of including winter-induced shrub damage in terrestrial ecosystem models to accurately predict trends in vegetation productivity and carbon sequestration in the Arctic and sub-Arctic.

Introduction

The frequency of extreme winter warming events is increasing in the Arctic (Vikhamar-Schuler *et al* 2016, Graham *et al* 2017), and these episodes are capable of causing widespread and severe plant damage (Bjerke *et al* 2017). When warm spells melt away snow in the middle of winter, shrubs and other vegetation are left vulnerable to a subsequent return to freezing conditions (Bokhorst *et al* 2011). A partial melt and re-freeze of snow is also damaging due to the formation of thick, hermetic ground ice (Bjerke *et al* 2015, Milner *et al* 2016). These extreme winter events may be an important driver of arctic and subarctic browning

(Phoenix and Bjerke 2016)—reductions in greenness that have been observed by satellites (Bhatt *et al* 2013).

The recent browning of the Arctic appeared as somewhat of a surprise, since satellite data had shown a greening of the region until recently (Bhatt *et al* 2014). Field observations connected these past increases in remotely sensed greenness—expressed as NDVI (normalized difference vegetation index)—to an expansion of shrubs that responded to increases in summer warmth (Myers-Smith *et al* 2011, Elmendorf *et al* 2012). Despite continued warming, large parts of the Arctic have exhibited the contrasting process of browning in recent years, which has been attributed to a multitude of processes that affect vegetation cover including fires, outbreaks of pests and fungi, permafrost degradation, flooding, and changes in grazing pressure (Cohen *et al* 2013, Bjerke *et al* 2014, Phoenix and Bjerke 2016, Lara *et al* 2018). Despite the broad range of possible causes of arctic browning, extreme winter events that affect snow cover and icing are considered the main climatic cause (Bjerke *et al* 2014), and the subsequent impact on the arctic carbon cycle may be large. The widespread vegetation damage indicated by arctic browning implies a reduction in vegetation productivity, and possibly a reduction in the net uptake of CO_2 by affected ecosystems.

However, the vulnerability and resilience of the CO_2 exchange of ecosystems to extreme winter events remains unclear, due to a dearth of flux measurements in damaged areas. While numerous eddy covariance towers have been deployed across the arctic and subarctic in recent years, almost all of them are placed in areas where extreme winter events have not (yet) occurred or—perhaps—have not been detected. The impact on the CO_2 exchange of ecosystems, therefore, has so far been assessed through small-scale manipulation experiments and flux chambers (Bokhorst *et al* 2011, Zhao *et al* 2016, 2017). More commonly, research focuses on phenology and mortality rather than the carbon budget (Bjerke *et al* 2015, Preece *et al* 2012, Jørgensen *et al* 2010, Milner *et al* 2016). Due to these small scales and general lack of flux measurements, it remains largely unknown whether CO_2 fluxes are impacted by extreme winter events at the landscape scale.

In this study, therefore, we present a dataset spanning five summers, from 2010 to 2014, of the CO_2 exchange of a blanket bog located on the island of Andøya in northern Norway. In January 2014, during the last year of measurements, boreal Norway experienced a severe drought combined with a lack of snow and strong frost, which led to widespread vegetation damage along a north-south transect of Norwegian coast about 1000 km in length (Meisingset *et al* 2015, Timmermann *et al* 2015, Bjerke *et al* 2017). The eddy covariance tower on Andøya, where frost drought also damaged shrub vegetation, was the only one to capture this extreme winter event. In connection to this event, this study sets out to answer two questions: did the winter damage to shrub vegetation lead to a substantial reduction in vegetation productivity in the following summer, and if so: how large was this reduction when put in the context of inter-annual variations in CO_2 exchange?

Materials and methods

Site description

This research focuses on a large blanket bog, located on the island of Andøya in northern Norway near the small settlement of Saura (69° 08'N, 16° 01'E, 17 m a.s.l. see figure 1). The Saura bog is located nearly 300 km North of the Arctic Circle, but the climate is mild for this latitude, due to the influence of the nearby Atlantic Ocean. Long-term climate data (1981–2010) from a weather station near the town of Andenes (~17 km to the North), operated by the Norwegian Meteorological Institute, indicate an average temperature of 11.4 °C for July–August and −1.4 °C for January–February. Average annual precipitation is 1030 mm. This classifies the climate as being on the boundary between the subpolar oceanic and subarctic climate zones (Köppen classifications *Cfc* and *Dfc,* respectively). The wet climate and relatively cool summers have been favorable for peat formation on the island, and by comparison to a similar bog a few km to the south-west (Vorren *et al* 2007) it is expected that peat depth at the Saura field site is about 2–3 m.

The Saura bog is characterized by relatively dry hummocks, with hollows in between. The ratio between the two is about 70:30, with an estimated height difference of 0.15 m. Vegetation on the hummocks consists of dwarf shrubs (*Calluna vulgaris, Empetrum nigrum, Vaccinium uliginosum*, and *Rubus chamaemorus*), mosses (*Dicranum scoparium, Hylocomium splendens, Pleurozium schreberi, Racomitrium lanuginosum, Sphagnum fuscum*), and lichens (*Cladonia* spp.). Hollows are dominated by *Sphagnum* mosses (*S. warnstorfii, S. magellanicum, S. cuspidatum*) and sedges (*Carex rariflora*). In August 2009, a vegetation survey showed that the cover of cryptogams (lichens and bryophytes/mosses) was almost twice as high as the cover of vascular plants (76% versus 44%, when accounting for overlap), and lichens covered 41% of the hummocks on average. Shrub height was very low, with an average of 0.05 m.

Instrumentation

During the summer of 2008, an eddy covariance tower was placed near the center of the Saura bog. A CSAT3 3D Sonic anemometer (Campbell Sci. UK) and a Li-7500 open-path gas-analyzer (Li-Cor, NE, USA) were installed at a height of 2.3 m to measure wind speed and concentrations of CO_2 and H_2O. Data from this setup was collected at 10 Hz on a CR3000 data logger (Campbell Sci. UK). Ancillary meteorological data was measured on a separate tower, at approximately 10 m
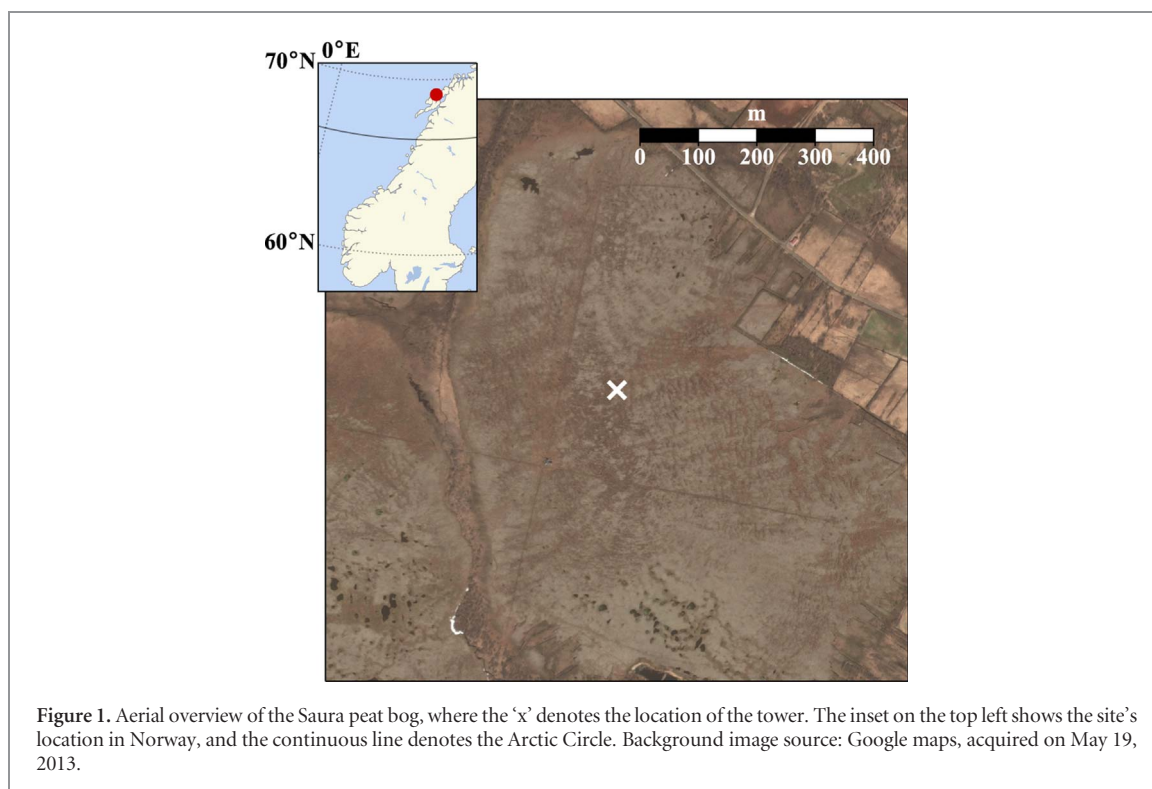
Figure 1. Aerial overview of the Saura peat bog, where the 'x' denotes the location of the tower. The inset on the top left shows the site's location in Norway, and the continuous line denotes the Arctic Circle. Background image source: Google maps, acquired on May 19, 2013.

distance, and averaged for each half hour. This included air temperature at canopy height (5 cm; T_{canopy}) and at 2 m (T_{air}), relative humidity (RH; HMP45C, Vaisala, Finland), photosynthetic photon flux density (PPFD; LI-190, Li-Cor, NE, USA), global solar radiation (R_g; LI-200, Li-Cor, NE, USA), net radiation (R_n; Q*7, REBS, USA), soil temperature (T_{soil}; TCAV-L, Campbell Sci. UK) and soil water content (SWC; CS616, Campbell Sci. UK). Due to large gaps in the data from 2008 and 2009 that preclude detailed time series analysis, this study focuses on the last five summers of the dataset, from 2010 to 2014. The processing of the data was previously described in detail by Lund *et al* (2015), while the partitioning of the fluxes into GPP and R_{eco} followed Lasslop *et al* (2010). Details of these methods are given in the supplementary information available at stacks.iop.org/ERL/13/065009/mmedia.

Survey of vegetation damage
In April 2015, shortly after snowmelt, we analyzed the vegetation at the Saura bog in eight stratified randomly selected plots of 40 cm × 60 cm along a 125 m long west-east transect passing 1 m from the tower. At 15 m intervals along the transect, plots were randomly chosen within a radius of 5 m. The two evergreen dwarf shrubs *Calluna vulgaris* and *Empetrum nigrum* showed signs of damage typically caused by winter desiccation (Hancock 2008, Bokhorst *et al* 2011)—i.e. intact, but brown leaves with strongest damage ratio at top shoots and decreasing towards the base. The leaves were pale brown and flat, indicating that leaves had died the year before. Recently dead leaves are inflated and chestnut brown, rather than pale

brown, while leaves that have been dead for longer than a year turn grey and shriveled and easily detach when being touched (Bokhorst *et al* 2009, Bjerke *et al* 2017). Hence, we estimated the green and pale brown cover of both plants to calculate plot-level damage ratios.

Assessment of vegetation development
If large parts of an ecosystem are damaged, we expect that it will take more time following snowmelt and a higher amount of accumulated degree days for photosynthesis rates to develop compared to other years. However, comparisons to other years are complicated by high variations in daily GPP due to changes in incoming solar radiation. Therefore, rather than analyzing GPP rates under observed radiation levels, we use the photosynthetic parameters from the partitioning model of Lasslop *et al* (2010) to calculate GPP rates at light saturation (GPP$_{sat}$). In the case of Andøya, maximum light levels in summer are about 700 W m^{-2}, and GPP$_{sat}$ is calculated as follows:

$$\text{GPP}_{sat} = \frac{\alpha \beta R_g}{\alpha R_g + \beta} \qquad (1)$$

where α (in μmol C J^{-1}) is the canopy light utilization efficiency, which represents the initial slope of the light response curve, and β (μmol C m^{-2} s^{-1}) is the maximum CO$_2$ uptake rate when light availability is non-limiting ($R_g \to \infty$). R_g (W m^{-2}) is the incoming radiation and in this case fixed to 700 W m^{-2} to calculate GPP$_{sat}$ under typical clear-sky conditions.
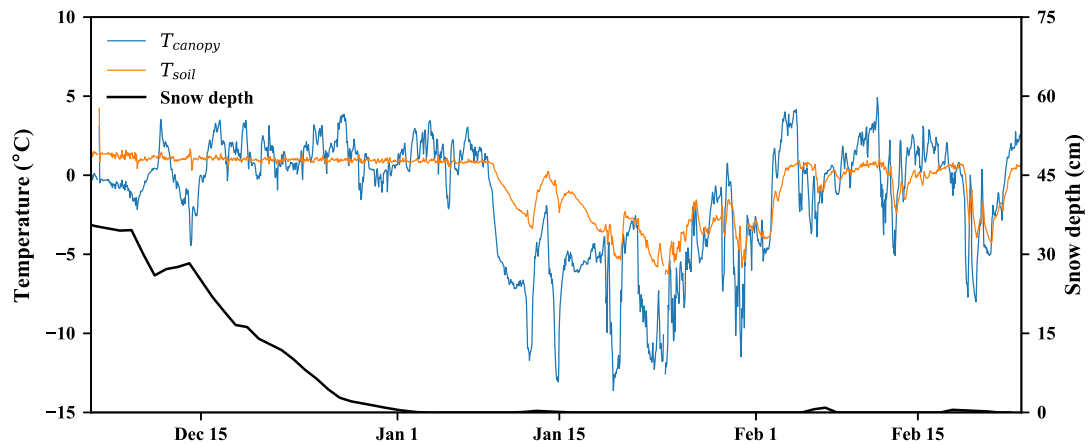
Figure 2. Weather conditions during the frost drought event in the winter of 2013/2014. Hourly measured temperature at canopy height (5 m) is indicated with the blue line, and the orange line shows soil temperature at 5 cm depth. The thick black line denotes modeled snow cover from seNorge (www.senorge.no). Note that the temperature measurement at canopy height may have been inside the snow pack rather than exposed to the outside air before snowmelt completed.

Snow and NDVI datasets

In addition to the data collected by the eddy covariance and meteorological towers, information on snow cover and vegetation productivity was obtained from external datasets to compare the 2014 winter to the long-term record. Snow cover was obtained from The Norwegian Water Resources and Energy Directorate (NVE), which provides maps of snow cover and interpolated air temperature for the whole of Norway, on a daily basis and at a 1 km × 1 km resolution (www.senorge.no). This model performs well for Norway (Saloranta 2012), and snow and temperature data for the location of the tower were retrieved starting in 1963. For each year, the total amount of freezing degree days during snowless periods was calculated as a measure of potential vegetation damage due to frost drought. These totals were calculated separately for polar night (28 November 28–17 January) and the period thereafter until the start of the growing season.

To ascertain whether the vegetation damage at the Saura bog was visible as a browning event, remotely sensed NDVI data were downloaded from the MODIS Land Product Subsets project (ORNL DAAC 2017), which provides subset data from both the Terra and Aqua satellites at a 250 m × 250 m spatial resolution. The size of a MODIS pixel happens to be very comparable to the footprint of the tower, i.e. the upwind surface area that contributes to the measured flux. The 90% fetch length is typically about 200 m (figure S1). Changes in MODIS NDVI data are therefore expected to provide useful information on the ecosystem at a similar scale to that of the flux tower. Only NDVI data with the highest quality flag was kept, and maps of NDVI were visually inspected for obvious outliers, which were then rejected. Few additional measurements had to be rejected during the summers of 2010–2014, with one invalid measurement in the summers of 2010 and 2013, and two in 2012.
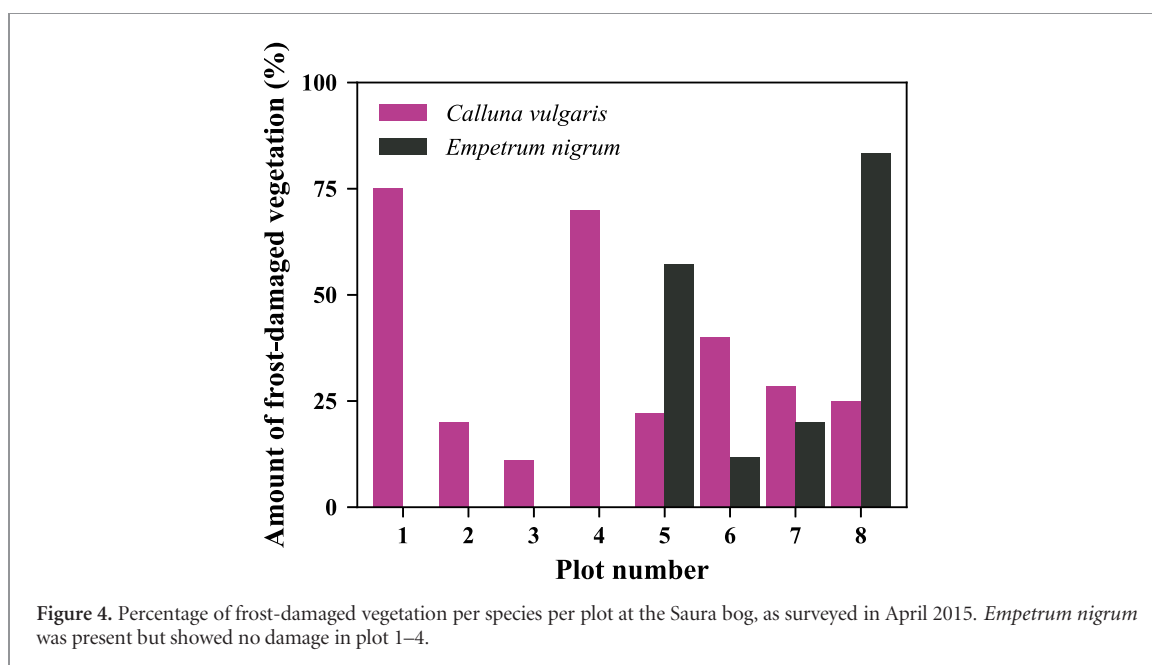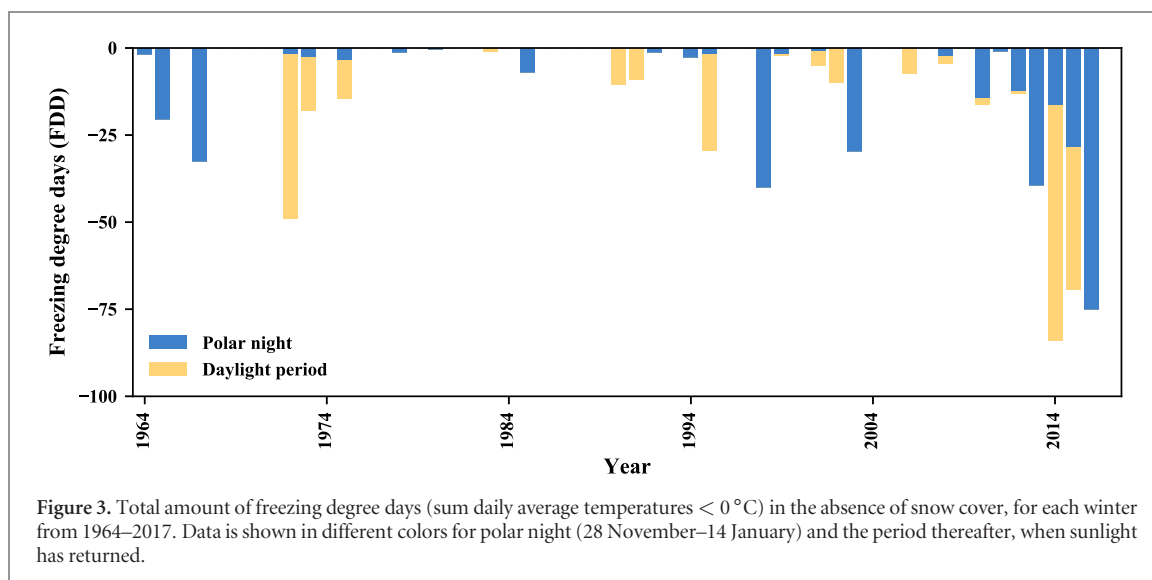
Following this quality check, NDVI values were averaged over the four pixels closest to the location of the tower.

Results

The extreme winter of 2013/2014

In January 2014, large parts of coastal Norway were free of snow following a winter warm spell. Once this event passed, and temperature dropped back below 0 °C, snow cover remained absent and vegetation along large parts of the Norwegian arctic and subarctic coast were exposed to severe frost, leading to wide-spread damage to shrub vegetation due to winter desiccation (Bjerke *et al* 2017). The Saura bog on Andøya was no different in that regard. Remote sensing and data models from the NVE indicate that snow cover was absent during almost all of January and February (figures 2 and S2). The strong drop in soil temperature also indicates that snow cover was absent, while the total amount of precipitation at the nearby meteorological station of Andenes was 1.0 mm in January 2014. From January 9–February 2, temperature at canopy height was well below 0 °C, approaching −15 °C on several occasions, and frost events kept occurring regularly throughout February (figure 2). Although not as strong as in the preceding month, they coincided with clear sky conditions and plenty of incoming sunlight. Such conditions can lead to frost desiccation. While thaw-freeze events may happen occasionally on Andøya, the total amount of freezing degree days, for periods without snow, was unprecedented in the climate data, going back to 1963 (figure 3), and especially high during the part of the winter where sunlight had returned.

The three weeks of frost, combined with intense drought, severely damaged the shrub species *Calluna*

Figure 3. Total amount of freezing degree days (sum daily average temperatures $< 0\,°C$) in the absence of snow cover, for each winter from 1964–2017. Data is shown in different colors for polar night (28 November–14 January) and the period thereafter, when sunlight has returned.

Figure 4. Percentage of frost-damaged vegetation per species per plot at the Saura bog, as surveyed in April 2015. *Empetrum nigrum* was present but showed no damage in plot 1–4.

vulgaris and *Empetrum nigrum* (heather and crowberry), as surveyed on April 26 2015, and shown in figure 4. Both shrub species had large amounts of damaged vegetation: dieback of *Calluna vulgaris* was recorded in all plots, ranging from low to high, while *Empetrum nigrum* was only affected in four plots, albeit severely ($>50\%$ of dead vegetation) in two. No damage to *Empetrum* was observed in the other four plots. On average, 43% of *Calluna vulgaris* and 27% of *Empetrum nigrum* was damaged or dead.

Year-to-year variations in summer weather conditions and CO_2 budgets

Summer weather conditions (June–August) differed considerably among the years studied (table 1). The summers of 2010 and 2012 were cold, with an average temperature of 9.0 and 9.1 °C, and temperature never exceeded 20 °C in both years. 2011 was considerably warmer at 10.7 °C, with a maximum at 24.1 °C.

The summers of 2013 and 2014 were the warmest, with average temperatures of 11.5 and 11.4 °C and maximum temperatures of 24.9 °C and 25.6 °C, respectively. The wettest summers occurred in 2010 and 2013, although 2012 was nearly as wet. Precipitation in 2011 and 2014 was ~30% to ~45% lower. The sunniest summer of these five years occurred in 2014, although 2011 was not that dissimilar with 5% less incoming radiation. The other three summers received ~20% less radiation than in 2014. Detailed plots of temperature, radiation and vapor pressure deficit are shown in figure S3.

In figure 5, the fluxes of GPP, R_{eco} and *NEE* are shown for the years 2010–2014 and split up for the months of June to August. June is normally the month in which green-up occurs, and maximum GPP rates are reached in the first half of July. By mid-July, days shorten and light conditions begin to decline, which gradually lowers GPP over the rest of the summer.

Table 1. Average air temperature at 2 m (T_{air}), maximum recorded air temperature (T_{max}), average global radiation (R_g), total precipitation (P), and cumulative CO_2 fluxes (*NEE*, GPP and R_{eco}) at the Saura bog from 1 June–31 August, during 2010–2014. All data was recorded at the site, apart from P, which was measured ∼17 km away at the weather station near the local town of Andenes. Standard deviations of T_{air} and R_g are determined on daily values. The ranges given for the carbon fluxes represent random flux uncertainty rather than ordinary standard deviations. Due to model uncertainties, the sum of GPP_{mod} and $R_{eco,mod}$ does not exactly equal NEE_{obs}.

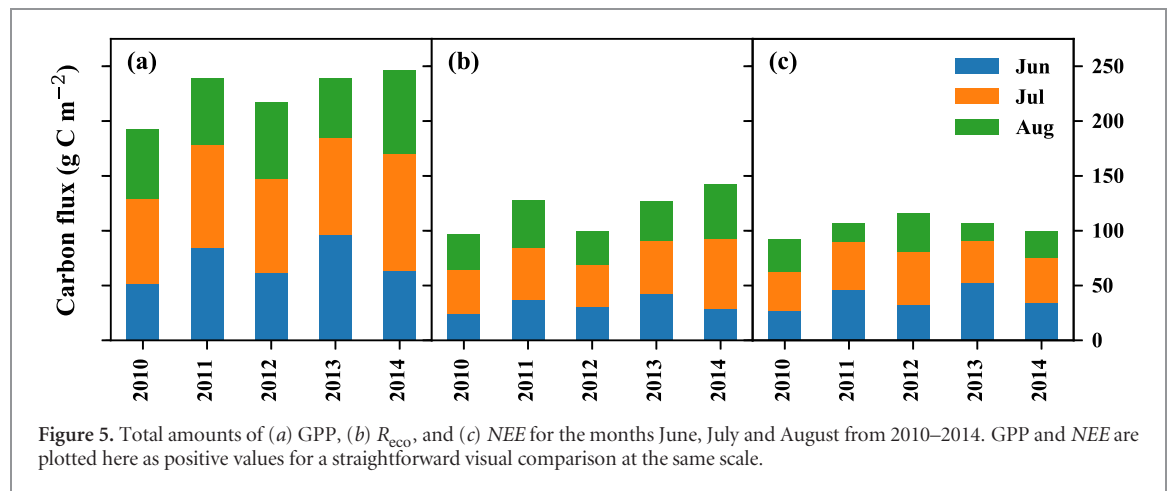|	$T_{air}(°C)$	$T_{max}(°C)$	$R_g\,(Wm^{-2})$	$P\,(mm)$	$NEE_{obs}(g\,C)$	$GPP_{mod}(g\,C)$	$R_{eco,mod}(g\,C)$
2010	9.0 ± 2.3	19.8	153.6 ± 67.5	214.5	-92.0 ± 1.5	-192.3 ± 2.2	97.1 ± 2.1
2011	10.7 ± 2.4	24.1	179.5 ± 88.6	142.3	-106.6 ± 1.7	-239.1 ± 2.4	128.1 ± 2.4
2012	9.1 ± 2.0	19.8	158.1 ± 79.1	186.9	-115.7 ± 1.8	-216.8 ± 2.5	99.3 ± 2.6
2013	11.5 ± 2.4	24.9	154.0 ± 76.1	210.2	-106.2 ± 1.8	-239.0 ± 2.5	127.0 ± 2.5
2014	11.4 ± 3.7	25.6	187.2 ± 83.0	116.0	-99.9 ± 1.7	-246.4 ± 2.6	142.3 ± 2.5

Figure 5. Total amounts of (*a*) GPP, (*b*) R_{eco}, and (*c*) *NEE* for the months June, July and August from 2010–2014. GPP and *NEE* are plotted here as positive values for a straightforward visual comparison at the same scale.

Figure 5 clearly shows that 2010 had the lowest GPP. In that year, snowmelt didn't occur until the first week of May—two to four weeks later than in the other years (table S1). Moreover, that summer was also the coldest with the least amount of incoming radiation (table 1), limiting vegetation development. The following year was much warmer and sunnier, with snowmelt in early April, and GPP in June and July was high. 2012 also had less GPP in June, but July and August were similar to the other years. Photosynthesis rates in June 2013 were exceptionally high, but August of that year had the lowest cumulative flux of all five years. Finally, 2014 started off slowly, but had very high photosynthesis rates in July and August due to warm and sunny weather, which provided exceptional growing conditions.

The respiration by the ecosystem, R_{eco}, followed a predictable pattern for all years, where the warmest summers had the highest amounts of respiration and the coldest summers the lowest (figure 5, table 1). The summer with the highest *NEE* (difference between GPP and R_{eco}), therefore, occurred in 2012 when both low temperatures and wet conditions suppressed respiration. Such behavior is not uncommon for high latitude ecosystems, where changes in R_{eco} and GPP can be more pronounced than changes in *NEE* (Parmentier *et al* 2011). A detailed overview of GPP, R_{eco} and *NEE* is given in figure S4.

Response of GPP to environmental forcing
The observations of vegetation damage (figure 4) appear to be at odds with the large increase in GPP in

2014 (figure 5). Despite the documented frost damage, ecosystem functioning seems to have been unaffected. However, the exceptional growing conditions in July and August of 2014, when compared to the other years, obscures any reductions in vegetation productivity due to winter damage. To assess the effect of winter damage on GPP, the interannual variability in fluxes due to differences in radiation and temperature should first be removed.

In figure 6(*a*), the potential photosynthesis rate at 700 W m^{-2} (GPP_{sat}) has been plotted against the amount of days following snowmelt, up until peak summer (day of year 200). In this figure, it becomes clear that in 2010 and 2013 plant growth started very quickly following snowmelt, and GPP_{sat} increased to more than 3 μmol m^{-2} s^{-1} within the first month. In both years, snowmelt was immediately followed by a period of warm and sunny weather and vegetation developed promptly. In the other years, temperatures following snowmelt stayed low, vegetation development took longer, and photosynthesis rates did not increase beyond 3 μmol m^{-2} s^{-1} until ∼60 days after snowmelt. However, when we plot GPP_{sat} against the amount of accumulated degree days, the differences between years strongly reduce in the period up to ∼300 °D, as shown in figure 6(*b*).

At values greater than ∼300 °D, however, there are clear divergent patterns: in 2011, 2012 and 2013, GPP_{sat} continued its linear response to accumulated degree days, and in all three years GPP_{sat} reached its maximum value after another two or three weeks. In 2014, this linear response to temperature increases halted,
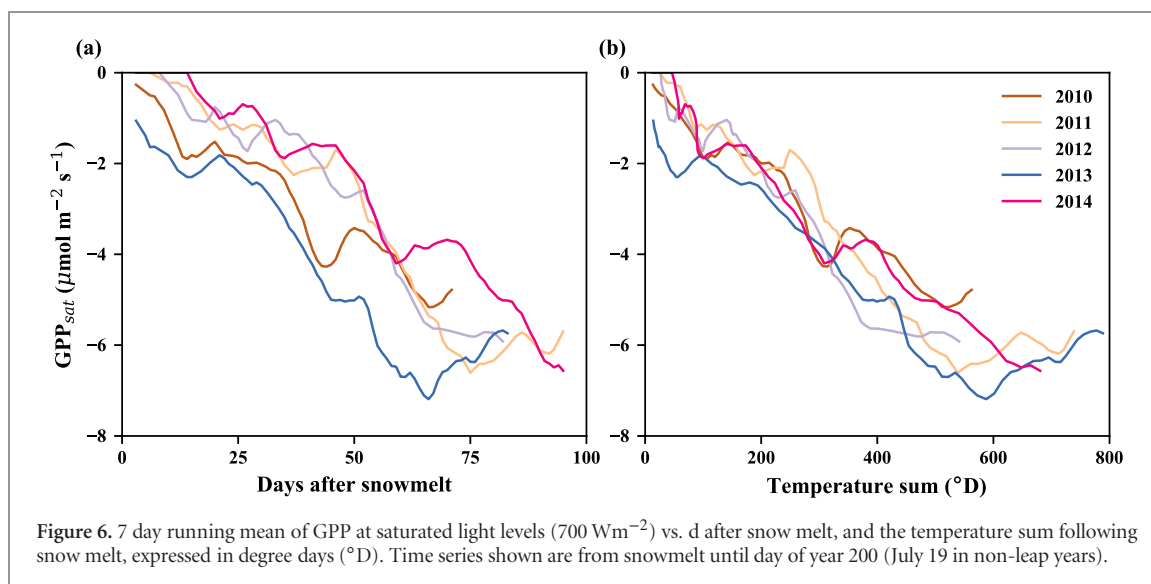
Figure 6. 7 day running mean of GPP at saturated light levels (700 Wm^{-2}) vs. d after snow melt, and the temperature sum following snow melt, expressed in degree days (°D). Time series shown are from snowmelt until day of year 200 (July 19 in non-leap years).

only to pick up at a later time. Vegetation development took another five weeks, up until the second half of July. Of all snow-free seasons, only 2010 showed a degree-day response similar to that of 2014. However, a simple comparison of these two years is problematic since weather conditions in 2010 were vastly different from 2014: snowmelt occurred 3.5 weeks later and incoming radiation and temperature were much lower (table 1, figure S3).

A delayed response in 2014, similar to a cold and cloudy year, is the kind of behavior that would be expected when a high number of shrubs are damaged and their contribution to GPP is lowered (Bokhorst *et al* 2011). It appears, therefore, that the capacity of the ecosystem to take up carbon was reduced during the summer of 2014.

To quantify this reduction, we interpolated the photosynthetic parameters α and β of the years 2010–2013, obtained from the partitioning model (Lasslop *et al* 2010), to specific dates in 2014 by using the temperature sum as a lookup table—similar to figure 6(*b*). This interpolation approximates what the photosynthetic parameters α and β would have been in 2014, if the vegetation had developed with temperature as in the other years. Subsequently, GPP was calculated with the observed radiation in 2014, following equation 1, from the day that 300 °D was reached (day of year 159) up until the peak of summer (day of year 200). The period following the peak of summer is omitted to avoid an influence due to varying onsets of senescence (the whole time series is shown in figure S4). A median of these estimates showed that the vegetation could have photosynthesized an additional 14 g C m^{-2} in 2014, with an upper estimate of 24 g C m^{-2} (when compared to 2013) and a lower estimate of 0 g C m^{-2} (when compared to 2010)—if there had been no net effect from the damaged vegetation. Since cumulative GPP was 116 g C m^{-2} during the same period in 2014, this flux could have been ~12% higher, with a lower and upper estimate of 0% and 21%.

Comparison to remote sensing data

In figure 7, a time series is plotted of the maximum and average NDVI value for each summer (day of year 175–225) from 2000–2017, which shows that 2014 had the lowest value in a decade—up to that point. The average value for the summer of 2010 was nearly as low, but with a higher maximum. The peak season was missed in 2013, due to bad coverage (figure S5), and NDVI values are probably underestimated for that year since GPP was high (figure 5). Average NDVI values in 2014 are lower than in the other measurement years, but not unprecedented in the long-term satellite record. This is probably due to the excellent growing conditions in the summer of 2014, which boosted vegetation growth after mid-summer (figures 5 and S4).

However, the maximum NDVI value reached in 2014 was the second-lowest until then (after 2003), and it took much longer than normal to reach the maximum (table S2, figures 7 and S5). On average, peak NDVI values are reached on day of year 207 ± 11 days, but the maximum in 2014 was on day of year 222 (August 10). The low NDVI—a browning event—and the delayed peak were probably due to the large amount of damaged vegetation. The only years with a later time-to-peak were 2007 (223) and 2017 (225), although considerable uncertainty exists on these dates due to cloud cover and their average values are much higher (figures 7 and S5).

Interestingly, average NDVI values were at their all-time lowest in 2015—the year following the extreme winter event. The browning event worsened, indicating no recovery of the ecosystem, and this was possibly due to another extreme winter (figure 3). Unfortunately, flux measurements at the Saura peat bog had ceased by 2015, and we do not know how this was reflected in the ecosystem fluxes. The same goes for the upwards return of NDVI levels in 2016. However, NDVI shows a reasonable agreement with GPP_{sat} (Figure S5) and it is therefore likely that photosynthesis rates in 2015 were lower than in 2014.
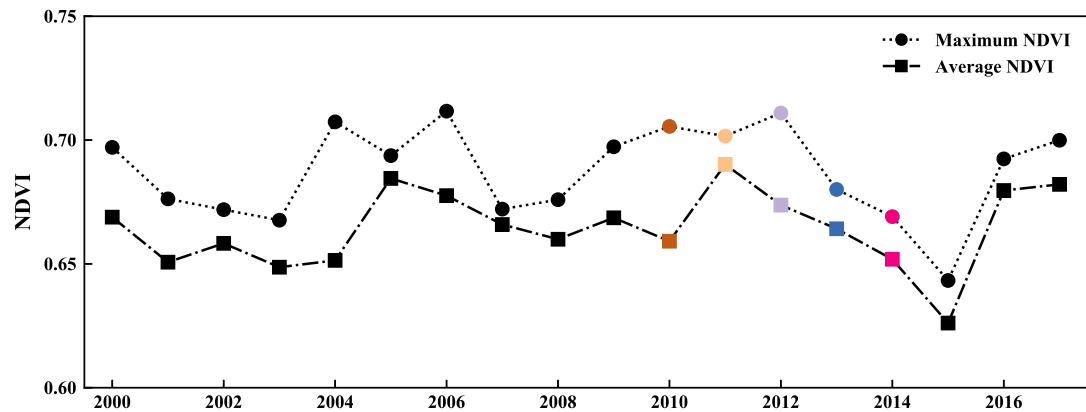
Figure 7. Maximum and average NDVI values for the summer (day of year 175–225) from 2000–2017, obtained from MODIS (v6), averaged over the four pixels closest to the position of the eddy covariance tower. The years covered in this study are shown in color. The values for 2013 are probably underestimated due to a coverage gap during peak summer. A more detailed NDVI time series is shown in figure S5.

Discussion

Impact of the 2013/2014 winter on summer CO_2 exchange

This study shows that the severe frost drought event of January and February 2014, unprecedented in the climate record on Andøya, led to the strong dieback of the shrub species *Calluna vulgaris* and *Empetrum nigrum*. Cumulative GPP, however, was higher in 2014 than in other summers. This contradictory result can be explained by the fact that 2014 also had the sunniest and warmest summer of the 5 years in this dataset (table 1). This provided ideal conditions for growth of undamaged plants.

However, when interannual variability in radiation and temperature is compensated for, it is clear that vegetation productivity showed a delayed response following snowmelt when compared to other years (figure 6). This indicates a vulnerability of this ecosystem to the extreme winter event. While briefly following a similar development for GPP_{sat} as for the other years, a clear departure occurred at two months following snowmelt, at a point when shrub bud break normally would occur. Although a period of colder weather may have contributed to this delayed response, this pattern remained present when GPP_{sat} was compared to accumulated degree days. Vegetation development was lagging behind other years, most likely due to the large number of winter-damaged shrubs.

After the initial anomaly in GPP_{sat}, the ecosystem showed high photosynthesis rates later in the summer (figures 5 and S4), indicating some resilience to the extreme winter event. A possible explanation for this may be that the ecosystem partly recovered its carbon uptake through compensatory growth (Bokhorst *et al* 2011), spurred on by the exceptionally warm and sunny weather of July and August 2014. Higher temperatures, however, also stimulated ecosystem respiration, with record high respiration in July and

August 2014 (figure 5). It is possible that part of these high respiration rates was related to decomposing dead plant material, limiting *NEE*, but a separation of ecosystem respiration into autotrophic and heterotrophic respiration rates is not possible with this dataset. In future studies of the impact of extreme winter events, such effects on respiration need to be taken into account during field campaigns.

Possibility of moisture limitations

In addition to the documented damage to the shrubs, other causes of the lower vegetation productivity at the Saura bog need to be considered. Droughts and heatwaves in particular can reduce the carbon uptake of an ecosystem when plants close their stomata to conserve water (Lund *et al* 2012, van der Molen *et al* 2011). This behavior is taken into account by the partitioning method used in this study, where GPP is reduced for high vapor pressure deficit values (Lasslop *et al* 2010). Minor events did occur in early July 2014, as in other years, but at a very low level and for only a few days, which cannot explain the observed differences (figure S3). Low soil moisture could be another limiting factor but 2014 was not exceptionally dry (table 1, figure S6), and significant reductions in soil moisture occurred after the deviation in GPP rates. Moreover, a previous study of the Saura bog by Lund *et al* (2015) showed that dry conditions had a low impact on the ability of this ecosystem to store carbon. It is therefore unlikely that summer drought conditions caused the divergent pattern of GPP as shown in figure 6.

Extreme winter events and remotely sensed browning

Although the Saura bog has experienced multiple winters with strong frost in the absence of snow, as shown in figure 3, many of these did not lead to strong reductions in NDVI. It is striking that the strong frost event that occurred during polar night in the winter of

2015/2016, did not negatively affect NDVI values. To the contrary, after two years of browning, NDVI values jumped back up to a normal value. A possible explanation for this may lie in the timing of these events. The extreme winter events in early 2014 and 2015 occurred when the sunlight had returned, after one and a half month of darkness. Under sunny conditions, plants may attempt to transpire but cannot access the frozen soil water, and they desiccate (Bjerke *et al* 2017). The absence of sunlight during the frost event in the winter of 2015/2016 probably prevented extensive plant damage due to frost drought. This shows that the damage of an extreme winter event varies depending on its timing within the cold season. Other factors, such as interannual variation in the amount of frost resistance that was built up, may also have played a role.

Resilience and vulnerability of ecosystem functioning to wintertime impacts

Our results show a considerable delayed response of the vegetation to temperature, as shown in figure 6(*a*), but the estimated impact on GPP varies strongly: from 24 g C m^{-2} to no effect at all when compared to 2010. This appears to suggest that the impact of the frost event on CO_2 fluxes could have been negligible, but this is unlikely since weather conditions in the summers of 2010 and 2014 were strongly dissimilar. In 2010, snowmelt occurred almost three and a half weeks later than in 2014, and values of 300 °D weren't reached until June 18, compared to June 8 for 2014 (table S1). Besides this difference in the length of the growing season, there was also a stark contrast in the amount of incoming radiation up to the peak of summer: 432 MJ in 2010 vs. 763 MJ in 2014. The highly unfavorable growing conditions in 2010 are reflected in the GPP$_{sat}$ values, which by mid-summer had not reached the same maximum uptake as in the other years, and average summer NDVI values were among the lowest recorded. The similar vegetation development in 2014 and 2010—one of the warmest and sunniest years vs. the shortest, coldest and cloudiest growing season in this dataset—is in fact a strong indication that the extreme winter event reduced GPP—comparable in size to interannual variations in summer weather. Fully accounting for large differences in weather remains challenging, which is why a large uncertainty remains on our estimate of the impact of the extreme winter event on ecosystem carbon exchange.

Besides these uncertainties, the CO_2 uptake of the ecosystem may have been somewhat resilient to the frost drought due to a contribution from vegetation types other than shrubs. About 30% of the surface area of the Saura bog consists of hollows, where shrubs are absent and *Carex* spp. is abundant—which could have responded to the warm weather. Moreover, the Saura bog has a large abundance of lichens and mosses. These functional vegetation groups were not strongly affected by the frost drought event, and the warm

and sunny weather may have boosted their photosynthesis rates. In other words: while the CO_2 exchange of this bog was vulnerable at the species level (i.e. shrubs), to a certain degree it was resilient at the ecosystem level. The 2014 frost drought event may have had a much larger impact on the net CO_2 exchange at other affected areas along the Norwegian coast, in places where the fraction of shrubs vs. mosses and sedges would have been higher—e.g. in dry heathlands (Bokhorst *et al* 2009, Bjerke *et al* 2014).

While the further decline in NDVI in 2015 shows that the peatland did not recover in the following year, possibly due to an additional extreme winter event, the return to normal NDVI values in 2016 shows that this ecosystem can recover from an extreme winter event in a relatively short time. Such behavior has been reported before for a browning event in northern Scandinavia caused by a winter warming event (Bokhorst *et al* 2012). If, however, extreme winter events will increase in frequency, e.g. every other year, subsequent browning events may constitute a browning trend. In that case, the species distribution of an ecosystem may change, with a lasting effect on CO_2 and energy exchange.

Conclusions

The extreme winter event in January 2014 severely damaged shrubs at the Saura bog, and reduced both vegetation CO_2 uptake and NDVI in the following summer. A comparison with the photosynthetic parameters of other years indicates that the ecosystem could have taken up an additional 14 (0–24) g C m^{-2} (~12% of GPP) from day 159 to 200 if it had not been damaged. This means that the reduction in GPP caused by the winter event of 2014 was similar in size to interannual differences due to summer weather conditions (table 1).

Vegetation damage from extreme winter events should be included in model simulations. Current land surface models project an increase in arctic vegetation productivity following high latitude warming (Xia *et al* 2017, Zhang *et al* 2014, Sitch *et al* 2007), despite recent browning trends showing the opposite (Phoenix and Bjerke 2016). This suggests an overestimation of GPP in areas prone to winter damage. However, species that are more resilient to extreme winter events may compensate the impact of extreme winter events on the net CO_2 exchange of ecosystems. Observations and modeling studies that focus on the impact of extreme winter events on CO_2 exchange, therefore, should not exclusively focus on vulnerable species, such as shrubs, but determine the resilience of the ecosystem as a whole.

This study focused on one extreme winter event in one particular year but when such events increase in frequency, and vegetation is damaged more often, this may lead to shifts in ecosystem composition.

Vulnerable species such as shrubs may decline, in favor of more resilient mosses and sedges, which alters the net carbon uptake and albedo. The likelihood of which remains unknown. Continued monitoring of the CO_2 exchange of ecosystems subject to extreme winter events, and the improved modelling of their response to these instances, is essential to project how the carbon exchange of high latitude ecosystems and associated climate-feedbacks will respond to further arctic winter warming.

Acknowledgments

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