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Persistent reduction of segment growth and photosynthesis in a widespread and important sub-Arctic moss species after cessation of three years of experimental winter warming

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Summary

1. Winter is a period of dormancy for plants of cold environments. However, winter climate is changing, leading to an increasing frequency of stochastic warm periods (winter warming events) and concomitant reductions in snow cover. These conditions can break dormancy for some plants and expose them to freeze-and-thaw stress.
Mosses are a major component of high latitude ecosystems, yet the longer-term impacts of such winter warming events on mosses remain unknown.

2. In order to determine the longer-term legacy effects of winter warming events on mosses, we undertook a simulation of these events over three consecutive winters in a sub-Arctic dwarf shrub-dominated open woodland. The mat-forming feathermoss Hylocomium splendens (the most abundant cryptogam in this system), is one of the most widespread Arctic and boreal mosses and plays a key functional role in ecosystems. We studied the ecophysiological performance of this moss during the summers of the experimental period (2007-2009) and in the following years (2010-2013).

3. We show that the previously reported warming-induced reduction in segment growth and photosynthesis during the experimental years was persistent. Four years after the last event, photosynthesis and segment growth were still 30 and 36 % lower than control levels, which was only a slight improvement from 44 and 43 % four years earlier. Winter warming did not affect segment symmetry. During the years after the last simulated event, in both warmed and control plots, chlorophyll fluorescence and segment growth, but not net photosynthesis, increased slightly. The increases were probably driven by increased summer rainfall over the study years, highlighting the sensitivity of this moss to rainfall change.

4. Overall, the legacy effects shown here demonstrate that this widespread and important moss is likely to be significantly disadvantaged in a future sub-Arctic climate where frequent winter warming events may become the norm. Given the key importance of mosses for soil insulation, shelter and carbon sequestration in high-latitude regions, such persistent impacts may ultimately affect important ecosystem functions.
Introduction

Understanding the impacts of climate change on ecosystems is complex for many reasons. Firstly, there are many drivers of change and each driver, for example increasing temperature, has numerous interacting facets such as diurnal, seasonal and extremes. Secondly, there are practical issues that hinder research, such as difficult species groups and winter research. In this paper, we focus on a cryptogam (an understudied group), the winter period (underrepresented in field studies) and extreme warming events, that are both difficult to observe and even more difficult to predict (Bokhorst et al. 2016; Phoenix & Bjerke 2016).

Climate in northern ecosystems is changing more than the global average and more abruptly during winter than during summer (Walsh et al. 2011). Despite this, there are far fewer reports on moss responses to winter climate change than to summer warming. A recent literature search and review of ecosystem responses to winter climate change (Cooper 2014) found only four reports related to cryptogams, only two of these (Dorrepaal et al. 2004; Bjerke et al. 2011) dealt with mosses, and only the latter treated effects of stochastic warm periods (winter warming events).

Warm winters are often characterized by one or several warming events of variable duration preceded and followed by naturally cold, freezing periods (Putkonen & Roe 2003; Bokhorst et al. 2008; Bjerke et al. 2014; Hansen et al. 2014). During warming events, snow cover melts completely or partly, exposing the ground vegetation to subsequent ambient temperatures, which may be 15-30 degrees below freezing and fluctuate much more than in the subnivean environment (Pauli et al. 2013). The dehardening of vascular plants during such
events leads to increased susceptibility to freezing on the return of ambient sub-zero winter
temperatures. Therefore, many vascular plants are severely damaged after winter warming
events, as shown both by analyses of natural events and field experiments (Bokhorst et al.

The clonal mat-forming feathermoss Hylocomium splendens (Hedw.) Schimp. is the
only moss that has been studied in relation to winter warming events (Bjerke et al. 2011). It is
one of the most common and widespread mosses of the circumboreal forest and Arctic tundra,
and it has scattered occurrences elsewhere, for instance at high altitudes close to the Equator
(Rohrer 2004; GBIF 2015). It is probably one of the most abundant moss species in the world.
As other mat-forming mosses, it plays a crucial functional role in its ecosystems. It
contributes to soil insulation and stability, preservation of permafrost, sheltering for small
organisms, carbon balance, nitrogen fixation, and ecosystem conservation through hampering
of seed establishment (Chapin & Bledsoe 1992; Hörnberg, Ohlson & Zackrisson 1997;
Beringer et al. 2001; Heijmans, Arp & Chapin 2004; Cornelissen et al. 2007; Bjerke et al.
2011, 2013; Yoshikawa et al. 2002; Lang et al. 2012; Bokhorst et al. 2014). It is therefore of
major functional importance in its ecosystems.

Segment growth and photosynthetic activity of H. splendens was severely reduced (up
to 52 %) after three consecutive winters with short-lasting warming events that exposed the
moss to ambient temperatures (Bjerke et al. 2011, 2013). Negative effects were evident
already during the summer following the first winter warming event. Photosynthetic rates and
segment growth rates of previously winter-warmed mosses were 48 % to 52 % lower than in
control plots. During the winter warming events, photosynthetic rates were at optimal rates,
viz. similar to or higher than the rates achieved in summer. This clearly shows that the moss
was activated during the winter warming events. Hylocomium splendens and other mosses
initiate the growth of young, freeze-susceptible shoot apices in the early growing season
(Clausen 1964; Hudson & Brustkern 1965). Temperatures at −7.6 °C within 24 h after warming was ceased in the winter warming study, followed by temperatures as low as −18 °C two weeks later (Bokhorst et al. 2008, 2009, 2010) probably caused freezing damage to the moss shoot apices, which resulted in reductions in growing season photosynthesis and segment growth far beyond the year-to-year variation found in populations with stable winter climates (Bjerke et al. 2011). Death of apices promotes the sympodial growth form over the monopodial form. Although the two growth forms are genetically determined to some extent, they are both found in the same area and respond to environmental cues (Ross et al. 2001). This shows that mosses are under threat from winter warming events. However, impacts of winter warming beyond the immediate short-term responses reported above (Bjerke et al., 2011) remain unknown.

Here, we follow up on the short-term responses in the experimental period reported in Bjerke et al. (2011) with a longer-term assessment of the moss growth and photosynthesis responses in the four years after the warming simulations, to determine the persistence of the observed negative effects arising from the events. We also studied in more detail the morphology of moss segments by resurveying all moss samples taken from the experimental years and following years to test whether declining vitality is associated with developmental instability. Fluctuating asymmetry (FA), as a measure of developmental instability, is widely used as a symptom of stress in vascular plant leaves and animals (Palmer & Strobeck 1992, 2003; Kozlov et al. 1996). However, FA in mosses is a poorly studied subject; to our knowledge, the applicability of FA as a stress signal in mosses has not been assessed previously.

We hypothesized that surviving individuals of H. splendens from three consecutive winter warming events (Bjerke et al. 2011) would increase photosynthetic and segment growth rates and reach the same level as in control plots within the first years after the last
winter warming event. Furthermore, we hypothesized that retarded growth also would be associated with increasing FA of moss segments, and that this trait would disappear during recovery of normal segment growth rates.

During the recovery years of 2012 and 2013, our study site and the entire Abisko region (Swedish sub-Arctic) was affected by a caterpillar outbreak of the geometrid moth Epirrita autumnata (Bjerke et al. 2014; Bokhorst et al. 2015). The caterpillars defoliated many vascular plants, and this led to a decline in the cover of dwarf shrubs and an increase of moss cover in the years of 2012 and 2013 (Bokhorst et al. 2015). These summers were also much wetter than the summers during the experimental period (Table 1; see also Bokhorst et al. 2015). Since these environmental changes took place after the study was initiated, we did not phrase any a priori hypotheses of their impacts on the ecophysiology of H. splendens. However, knowing that summer rainfall stimulates moss growth (Potter et al. 1995, Sonesson et al. 2002), that more space would be available for horizontal growth due to vascular plant damage, and that more throughfall of nutrients would reach the cryptogam layer (Bokhorst et al. 2015); we hypothesized a posteriori that the ecophysiological performance of H. splendens would benefit from the caterpillar outbreak and the increasing precipitation rates.

Material and methods

FIELD SITE AND EXPERIMENTAL SIMULATIONS

Simulations of winter warming events in the field were conducted on a sub-Arctic heathland in open mountain birch (Betula pubescens) forest close to the Abisko Scientific Research Station (ANS) in northern Sweden (68° 21’ N, 18° 49’ E) during March 2007, 2008 and 2009. Details of the research site and experimental design are described in Bokhorst et al. (2008, 2009) and Bjerke et al. (2011). In brief, the experiment consisted of 18 plots (2.1 m × 1.0 m),
consisting of 6 control plots that remained under their natural snow cover throughout the winter; 6 that were exposed to a week-long winter warming event called ‘canopy warming’, using infrared heating lamps (800 W emitting at 3 \( \mu \)m; HS 2408, Kalglo Electronics Co., Bethlehem, USA); and 6 where warming from infrared heating lamps was combined with soil warming from cables at 5 cm soil depth called ‘canopy and soil warming’. Soil warming cables (LS-TXLP, Nexans, Norway, producing 120 W m\(^{-2}\)) were switched on two days after the lamps to simulate the delay in soil thaw during a real event. Complete snow melt and exposure of the vegetation was achieved within two to three days.

Temperature was monitored with thermistors placed in each plot at canopy height and at the soil surface, with logging at 6-h intervals recorded on a data logger (CR10 X, Campbell Scientific, UK). Details on the temperature effects of the treatments are provided in Bokhorst et al. (2011, 2012b). In summary, temperatures rose on average to 5 °C during the events, while for the remainder of winter, temperatures fluctuated concurrently with the ambient conditions (ranging from −17 °C to 4 °C) due to the reduced snow cover (initially none, and then thin coverage as new snow covered the exposed vegetation), meaning there was little to no insulation from air temperatures. In contrast, control plots remained well insulated under snow and experienced temperatures between −7 °C and 0 °C until snowmelt. Weather data presented are from the meteorological station at ANS, ca. 200 m from our study site.

PHOTOSYNTHESIS AND CHLOROPHYLL FLUORESCENCE

Gas exchange (CO\(_2\)) was measured in June or July during the summers following the experimental years from 2007 to 2009 and during the summers of 2012 and 2013. Measurements were made with a portable gas exchange fluorescence system (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany) using moss segments with optimal water content, as described in Bjerke et al. (2011). Only first-year and second-year segments of H. splendens
were used, as older segments have reduced photosynthetic rates (Callaghan et al. 1978, 1997).

Each moss sample consisted of c. 5 cut shoots. Assimilation rates were calculated on a per-
dry-weight basis. One sample was analysed from each plot at each occasion. A saturating
photosynthetic photon flux density (PPFD) of 800 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) was used during
measurements of net photosynthesis. \( \text{CO}_2 \) concentration was set to 380 ppm and cuvette
humidity to 9000 ppm \( \text{H}_2\text{O} \). Cuvette temperatures were adjusted to ambient noon
temperatures at the time of measurement.

Using the PAM-fluorometer of the GFS-3000, chlorophyll fluorescence, as maximal
quantum efficiency of photosystem II, i.e. \( \text{F}_v/\text{F}_m \) (Maxwell & Johnson 2000), was measured
on dark-adapted, naturally moist or wetted samples consisting of first- and second-year
segments.

SEGMENT GROWTH AND ASYMMETRY

Segments were collected at one point in time during the growing seasons following the winter
warming events of 2007, 2008 and 2009, and also during the growing seasons of 2010, 2011
and 2013. These were air-dried, and lengths of second-year segments were measured with
digital callipers along the main stem. Total width, i.e. left (L) plus right (R) sides of the
segment, was measured on the same second-year segments at the place where the shoot
segment was widest, typically near the segment base, perpendicular to the stem. Samples were
collected in June or early July, except for in 2010, when they were collected in late August.

Width of each side (i.e. R and L separately) was subsequently measured on samples
from 2007, 2008, 2009 and 2011. This latter dataset was first tested for directional
asymmetry, i.e. when one side is consistently larger than the other in the same direction
(Palmer & Strobeck 2003). Thereafter, we tested for treatment effects on fluctuating
asymmetry (FA). As FA has not been tested on mosses previously, we screened the utility of
various FA indices. The most commonly used indices all rendered similar results, and we here present results for the index for trait difference divided by trait mean $[|R-L|/((R+L)/2)]$.

DATA PUBLISHED PREVIOUSLY

The ecophysiological data from the experimental years and the shoot segment lengths from the years 2008-2010 were first reported in Bjerke et al. (2011), there with separate values for the two types of warming treatment data, while we here pool these data (see below). The following data have not been reported previously: the ecophysiological data from 2012 to 2013, segment lengths from 2011 and 2013, all data on segment width, length-to-width ratios and FA.

DATA ANALYSES

All tests were run with SPSS Statistics 22 (IBM Corporation, Armonk, NY, USA).

Differences between the two warming treatments were first tested with a series of Student’s t-tests. For most of the measured parameters (except FA), there were no significant differences between the two treatments, and the two types of warming treatment data could be pooled (canopy warming, and canopy and soil warming), here called ‘winter warming’. Time differences, overall treatment differences and their interactions, and pairwise comparisons of specific years were tested with the repeated-measures ANOVA procedure of SPSS. The Tukey HSD test was used for multiple comparisons of treatment effects. Year-to-year comparisons from the repeated-measures ANOVA were also checked with paired student’s t-tests, and these two tests rendered almost identical results. Student’s t-tests were also applied to test for differences between left and right segment widths.

Data sets containing more than one randomly chosen data point per replicate (plot) were first surveyed using a nested ANOVA design in order to check whether the variation within the replicates was larger than between replicates. As the variation within plots in all cases was
very low as compared to the variation between plots, the mean value per replicate was used in
further ANOVA analyses. Data were tested for normality and heterogeneity of variance prior
to ANOVAs and correlations. No transformation of data was necessary.

Results

Negative effects of the simulated winter warming events on net photosynthesis (NP) were still
evident in Hylocomium splendens in the summers 3-4 years after the last simulated event, i.e.
in 2012 and 2013 (Fig. 1a). The average reduction from controls was 32% in 2012 and 30%
in 2013, whilst in 2009, the summer after the last winter warming event, the reduction was 44%
%
Even if NP of both treatments (warming and control) reached minimum rates in 2009
(Fig. 1a), pairwise comparisons show that NP in controls did not vary in time, except for the
pair 2009 and 2012 (P = 0.010). The only between-year differences for NP in warmed plots
were that 2009 had lower values than the other years (P < 0.033).

The warming events did not affect chlorophyll fluorescence in any of the years, but
fluorescence increased steadily with time (P < 0.001) and was 26% higher in 2013 than in
2007 (Fig. 1b).

In the years following the experimental period, second-year segments of the warmed
plots were significantly smaller than segments from the controls (Fig. 2). In 2013, segments
from the warmed plots were 36% shorter (Fig. 2a) and 25% narrower (Fig. 2b) than the
control samples. The highest relative reduction was found in 2009 after the third winter
warming event when segments were 43% shorter and 38% narrower.
Segment length in the warmed plots increased by 27-52 % from the two last years of manipulation (2008-2009) to the recovery years of 2011 and 2013 and became more similar to the length of controls (Fig. 2a). However, segments were still 25 % shorter in the last recovery year than in the first year of manipulation (2007 vs. 2013: P = 0.001). Segment size also varied in control plots, but with few significant between-year differences (Fig. 2).

The length-to-width ratio varied much between years (Fig. 2c). Treatment effects on this ratio were minor and only significant in two of the six years (2008 and 2013). Width and length were correlated both for controls and warmed plot samples, and regression lines have almost identical slopes and intercepts, but many samples deviated much from the general trend, rendering relatively low correlations (Fig. 3).

The right sides of segments were 3.8 % narrower than the left sides (paired samples from all years and treatments: t =3.65, P < 0.001). There was no treatment effect on R−L (repeated-measures ANOVA: treatment: F = 1.26, P = 0.280; time: F = 0.37, P = 0.772; time × treatment: F = 0.43, P = 0.733; data not shown).

The FA index varied between years and treatments (Fig. 4). The canopy and canopy+soil warming treatments showed contrasting trends and were therefore not pooled. In 2007, moss segments from the canopy warming treatment had higher asymmetry than from the soil and canopy warming treatment, but none of those differed from controls. The only time when one of the warming treatments differed from controls was in 2009 when mosses from the soil and canopy warming treatment were 44 % more asymmetric than mosses from the controls.
This is the first study to determine the effects of winter warming events on a common and important moss species, both immediately after the events and in the recovery years that followed. We did not find support for the hypothesis that the negative effects of the warming treatment would disappear in the years following the experimental period, as photosynthesis and segment growth rates remained lower compared to control plots even four years after the final winter warming event simulation. These persistent impacts on physiology and segment growth following the extreme winter warming events suggest that H. splendens may be disadvantaged in a future sub-Arctic climate where high frequency of winter warming events may become the norm. More broadly, this suggests the potential for large consequences for high-latitude systems where bryophytes are often a major component and where the greatest increases in extreme winter events may be expected (Bjerke et al. 2014), and where they can have a strong influence on ground temperature and moisture, evapotranspiration, cycling of nutrients and water, permafrost thaw and ecosystem carbon balance (Turetsky et al. 2012).

Size of new clonal shoots and segments of H. splendens is strongly size-dependent (Økland 1995); viz. developing shoots and segments receive limited nutrients from small mother individuals. Hence, new shoots and segments have limited abilities to grow larger than their mother shoots/segments. This may be a primary reason for the persistent difference between size and photosynthetic rates of previously damaged shoots in warmed plots and undamaged shoots in control plots.

High chlorophyll fluorescence rates in the warmed plots during all study years show that intact photosynthesizing cells were highly active, even in shoots with retarded growth and reduced photosynthesis. The decoupling of photosynthesis and chlorophyll fluorescence indicates that only certain parts of the segments were stressed, and that the unaffected parts
continued to photosynthesize at normal rates. This suggests an on-or-off mechanism whereby in affected cells, the photosynthetic apparatus is badly damaged and turned off thereby not emitting any chlorophyll signal, while in unaffected cells, photosynthesis continues as normal and makes up the entire chlorophyll signal detected by the fluorometer. The observed decoupling of photosynthesis and fluorescence rates has been seen in other stress studies, though these are not well understood (e.g. Taulavuori et al. 2000; Nabe et al. 2007; Granath, Wiedermann & Strengbom 2009). Chlorophyll fluorescence imaging (Chen et al. 2015) could render further insight into this decoupling.

We did not find support for the hypothesis that retarded segment growth would be associated with increasing asymmetry, as even the most stressed shoots of H. splendens showed only modest developmental instability, as measured by the FA index. This may largely be due to the directional asymmetry of segment width, with left sides being inherently wider than right sides. Instead of increasing asymmetry with increasing stress, both width and length were equally reduced in stressed shoots. It may be that FA indices developed for vascular plant leaves and other organisms (Palmer & Strobeck 1992, 2003; Kozlov et al. 1996) do not work well for mosses. More moss species under variable stress regimes should be studied to test if FA is a useful indicator of stress for mosses. It is unknown if different structures of a moss show contrasting symmetry responses to stress. Traits not showing directional asymmetry should in such case be searched for (Palmer & Strobeck 2003). In addition, the ratio of monopodial to sympodial segments could be studied to detect the environmental effects on these two contrasting growth forms that co-occur but vary in ratios between sub- and high-Arctic areas (Ross et al. 2001).

Despite the adverse effects of experimental winter warming, the abundance of H. splendens did not change during the years of manipulations (Bokhorst et al. 2011), but increased during the recovery years by 50 % compared to the starting conditions of 2007.
The increase in moss cover was assumed to be driven by optimal moisture conditions due to increased rainfall during the growing seasons, nutrient input from frass from the large caterpillar outbreak and increasing open space following the severe caterpillar-induced dieback of dwarf shrubs (Bokhorst et al. 2015). Chlorophyll fluorescence and segment length in both warmed and control plots increased from the years of manipulation (2008-2009) to the last recovery year (2013). Although the difference between NP of controls and warmed plots was high in all years, absolute values varied much between years, which probably was caused by variation in moisture and temperature in the days prior to analysis (Bjerke et al. 2011, 2013). NP measured once per season may therefore not be a good trait for between-year comparisons, but still, it is likely that the increase from 2009 to 2012 for both treatments was driven by increasing precipitation rates. We conclude that our a posteriori hypothesis that the ecophysiological performance of H. splendens would benefit from the caterpillar outbreaks and the increasing precipitation rates was partly supported. It is also noted though, that while the shrub damage from E. autumnata should create conditions conducive to H. splendens recovery, the recovery in segment growth was relatively modest and may well have been even weaker had the shrub canopy not been removed by the caterpillar outbreak.

Other multi-year studies also report on recent increases in H. splendens, and these studies may contribute to elucidate the drivers of increasing cover, chlorophyll fluorescence and segment length. At another birch forest site near our field study, H. splendens showed some indications of increases in cover from 1991 to 2009 (Callaghan et al. 2013), while mat-forming mosses show an increasing trend at Norwegian forest monitoring sites (Aarrestad et al. 2014; Framstad 2015). This has been assumed to be due to delayed onset of snow season, which provides opportunity for moss growth in autumn after vascular plant growth has ceased (Framstad 2015). Hylocomium splendens shows high photosynthetic activity at temperatures
between 0 and 5 °C at relatively low light intensities (Sonesson, Gehrke & Tjus 1992; Bjerke et al. 2013). Other cryptogams also take advantage of mild autumns (Bjerke et al. 2013; Lund et al. 2014). Thus, warmer and longer autumns may in fact stimulate cryptogams more than vascular plants, and this may drive vegetation changes that contrast to what is expected based on the results of summer warming simulations that do not extend into the autumn. In Abisko, September was 1.5 °C warmer during the years from 2011 to 2013 than during the experimental years. Thus, it may be that autumn weather in the years after the simulated winter warming events also contributed to the increases in segment growth, chlorophyll fluorescence and cover.

Framstad (2015) also hypothesizes that rodent outbreaks facilitate moss growth through thinning of the vascular plant cover and denudation of soil. Near our experimental field site, there have been recent outbreaks of rodents (Callaghan et al. 2013). However, we have not observed rodent activity within our field plots, thus rodents do not seem to have played a role in the increase of cryptogams there.

Overall, this study has demonstrated that the widespread and important moss H. splendens is likely to be significantly impacted by winter warming events. Moreover, it is of concern that the damage to photosynthesis and segment growth persisted even four years after the last event and that these legacy effects remained of similar magnitude to the responses immediately after the events. Such impacts may ultimately affect important ecosystem functions given the importance of mosses for these, including ecosystem carbon balance, in high-latitude regions.

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Data accessibility

All data used in this manuscript are present in the main article and in the supporting information.

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Tables and Figures

Legends

Table 1. Monthly precipitation rates (mm) of summers (June-July) during the experimental period (2007-2009) and during the following years (2010-2013).

Fig. 1. Ecophysiological performance of Hylocomium splendens in the growing seasons following the simulated winter warming events (2007-2009) and during the summers 3-4 years after the last winter warming event (2012-2013). (a) Net photosynthetic rates at optimal water content (treatment: $F = 38.08$, $P < 0.001$, time: $F = 3.75$, $P = 0.008$, treatment × time: $F = 0.45$, $P = 0.771$); (b) photosystem II efficiency of dark-adapted samples (treatment: $F = 3.66$, $P = 0.077$, time: $F = 26.56$, $P < 0.001$, treatment × time: $F = 0.225$, $P = 0.923$), $n = 4–6$ per treatment and time combination (some plots with low abundance and hence not sampled in all occasions). Treatment years are left and recovery years right of the dashed vertical line. Error bars are ±1 SE. Asterisks indicate treatment effects: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Letters placed on bars reflect time differences within the control (black letters) and warming (white letters) treatments, respectively. Bars sharing the same letter are not significantly different.

Fig. 2. Size of second-year shoot segments of Hylocomium splendens measured in the growing seasons following the winter warming events (2007-2009) and during the summers 1, 2 and 4 years after the last winter warming event (2010, 2011 and 2013). (a) Segment length (treatment: $F = 53.78$, $P < 0.001$, time: $F = 11.98$, $P < 0.001$, treatment × time: $F = 3.23$, $P = 0.011$). (b) Segment width (treatment: $F = 51.42$, $P < 0.001$, time: $F = 7.77$, $P < 0.001$,
treatment × time: $F = 2.30, P = 0.052$). (c) Length-to-width ratio (treatment: $F = 0.51, P = 0.485$, time: $F = 8.69, P < 0.001$, treatment × time: $F = 1.67, P = 0.151$). $n = 4–6$ per treatment and time combination (some plots with low abundance and hence not sampled in all occasions). Treatment years are left and recovery years right of the dashed vertical line. Error bars are ±1 SE. Asterisks indicate treatment effects: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Letters placed on bars reflect time differences within the control (black letters) and warming (white letters) treatments, respectively. Bars sharing the same letter are not significantly different.

Fig. 3. Relationship between length and width of second-year shoot segments. Shoots from (a) control plots ($r^2 = 0.38, P < 0.001$), and (b) winter warming simulation plots ($r^2 = 0.37, P < 0.001$).

Fig. 4. Fluctuating asymmetry of second-year shoot segments of Hylocomium splendens measured on dried samples from the growing seasons following the winter warming events (2007-2009) and from the growing season 2 years after the last winter warming event (2011) (treatment $F = 2.20, P = 0.150$, time: $F = 1.27, P = 0.297$, time × treatment: $F = 2.59, P = 0.033$). $n = 6$ for each treatment. Treatment years are left and recovery years right of the dashed vertical line. Error bars are ±1 SE. Different letters indicate significant differences ($P < 0.05$) between treatments. n.s. = not significant.
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<td>76</td>
<td>116</td>
</tr>
<tr>
<td>Mean 2011-2013</td>
<td>44</td>
<td>76</td>
<td>116</td>
</tr>
</tbody>
</table>

Increase from 2007-2009 to 2011-2013 (%) | 55 | 121 | 91 |