



A Race for Space? How *Sphagnum fuscum* stabilizes vegetation composition during long-term climate manipulations

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A Race for Space? How *Sphagnum fuscum* stabilizes vegetation composition during long-term climate manipulations

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Complete List of Authors:	Keuper, Frida; VU University Amsterdam, Department of Systems Ecology Dorrepaal, Ellen; Climate Impacts Research Centre, Umeå University, Department of Ecology and Environmental Science van Bodegom, Peter M; VU University Amsterdam, Department of Systems Ecology Aerts, Rien; VU University Amsterdam, Dept of Systems Ecology van Logtestijn, Richard; VU University Amsterdam, Department of Systems Ecology Callaghan, Terry; Sheffield Centre for Arctic Ecology, University of Sheffield, Department of Animal and Plant Sciences; Abisko Naturvetenskapliga Station, Royal Swedish Academy of Sciences Cornelissen, Johannes HC; VU University Amsterdam, Department of Systems Ecology
Keywords:	climate change, long-term manipulation, peatland, vascular vegetation composition, resistance, bryophyte, diversity
Abstract:	Strong climate warming is predicted at higher latitudes this century, with potentially major consequences for productivity and carbon sequestration. Although northern peatlands contain one-third of the world's soil organic carbon, little is known about the long-term responses to experimental climate manipulations of vascular plant communities in these <i>Sphagnum</i> -dominated ecosystems. We aimed to see how long-term experimental climate change in and outside the growing season affects total vascular plant abundance and species composition when the community is dominated by mosses. During 8 years, we investigated how the vascular plant community of a <i>Sphagnum fuscum</i> -dominated subarctic peat bog responded to six experimental climate scenarios, including factorial combinations of summer as well as spring warming and a thicker snow cover. Vascular plant species composition in our peat bog was more stable than is typically

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	<p>observed in (sub)arctic experiments: neither changes in total vascular plant abundance, nor in individual species abundances, Shannon's diversity or evenness were found in response to the climate manipulations. For three key species (<i>Empetrum hermaphroditum</i>, <i>Betula nana</i> and <i>S. fuscum</i>) we also measured whether the treatments had a sustained effect on plant length growth responses and how these responses interacted. Contrasting with the stability at the community level, both key shrubs and the peatmoss showed sustained positive growth responses at the plant level to the climate treatments. However, a higher percentage of overgrown <i>E. hermaphroditum</i> shoots and a lack of change in <i>B. nana</i> net shrub height indicated encroachment by <i>S. fuscum</i>, resulting in long-term stability of the vascular community composition: in a warmer world, vascular species of subarctic peat bogs appear to just keep pace with growing <i>Sphagnum</i> in their race for space. Our findings contribute to general ecological theory by demonstrating that community resistance to environmental changes does not necessarily mean inertia in vegetation response.</p>

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A Race for Space? How *Sphagnum fuscum* stabilizes vegetation composition during long-term climate manipulations

Peatland community resists climate change

**Frida Keuper^{1,*}, Ellen Dorrepaal^{1,2}, Peter M. van Bodegom¹, Rien Aerts¹,
Richard S. P. van Logtestijn¹, Terry V. Callaghan^{3,4}, Johannes H. C. Cornelissen¹**

¹*Department of Systems Ecology, Institute of Ecological Science, VU University Amsterdam, De Boelelaan 1085, NL-1081 HV Amsterdam, The Netherlands;* ²*Climate Impacts Research Centre, Umeå University, Department of Ecology and Environmental Science, S-981 07 Abisko, Sweden.* ³*Abisko Naturvetenskapliga Station, Royal Swedish Academy of Sciences, SE-981 07 Abisko, Sweden.* ⁴*Sheffield Centre for Arctic Ecology, Department of Animal and Plant Sciences, University of Sheffield, 26 Taptonville Road, Sheffield S10 5BR, UK.*

* *Corresponding author. Tel. +31 20 598 6970; fax: +31 20 598 7211*

E-mail address: frida.keuper@ecology.falw.vu.nl

Keywords

Bryophyte, climate change, diversity, long-term manipulation, peatland, resistance, snow addition, spring warming, summer warming, vascular vegetation composition

Abstract

Strong climate warming is predicted at higher latitudes this century, with potentially major consequences for productivity and carbon sequestration. Although northern peatlands contain one-third of the world's soil organic carbon, little is known about the long-term responses to experimental climate manipulations of vascular plant communities in these *Sphagnum*-dominated ecosystems. We aimed to see how long-term experimental climate change in and outside the growing season affects total vascular plant abundance and species composition when the community is dominated by mosses. During 8 years, we investigated how the vascular plant community of a *Sphagnum fuscum*-dominated subarctic peat bog responded to six experimental climate scenarios, including factorial combinations of summer as well as spring warming and a thicker snow cover. Vascular plant species composition in our peat bog was more stable than is typically observed in (sub)arctic experiments: neither changes in total vascular plant abundance, nor in individual species abundances, Shannon's diversity or evenness were found in response to the climate manipulations. For three key species (*Empetrum hermaphroditum*, *Betula nana* and *S. fuscum*) we also measured whether the treatments had a sustained effect on plant length growth responses and how these responses interacted. Contrasting with the stability at the community level, both key shrubs and the peatmoss showed sustained positive growth responses at the plant level to the climate treatments. However, a higher percentage of overgrown *E. hermaphroditum* shoots and a lack of change in *B. nana* net shrub height indicated encroachment by *S. fuscum*, resulting in long-term stability of the vascular community composition: in a warmer world, vascular species of subarctic peat bogs appear to just keep pace with growing *Sphagnum* in their race for space. Our findings contribute to

general ecological theory by demonstrating that community resistance to environmental changes does not necessarily mean inertia in vegetation response.

For Review Only

Introduction

Growth and survival of plants in high-latitude ecosystems are limited by harsh environmental conditions, such as low nutrient availability, low temperatures and low irradiance during a large part of the year. Increases in both summer and spring temperatures and in winter snowfall have been recorded in these areas over the past decades and are predicted to continue in this century (IPCC, 2007). It is currently widely recognized that these climatic changes will have immediate and persistent effects on composition and structure of Arctic vascular plant communities (Wullschleger *et al.*, 2010). This notion is primarily based on the results of meta-analyses showing rapid and consistent responses to experimental climate warming in general across plant communities. Indeed, Walker *et al.* (2006) showed that across many sites, experimental warming of tundra ecosystems not only increased height and cover of deciduous and evergreen shrubs and graminoids, but also decreased species diversity and evenness. However, it is important to realize that these meta-analyses did not address climatic changes other than summer warming, nor have they included all predominant tundra ecosystem types, with strong underrepresentation of *Sphagnum*-dominated peatlands.

Few studies so far accounted for the impact of climatic changes both inside and outside the growing season, even though increased snow in winter and increased spring temperatures are expected to strongly affect plant performance in the Arctic. Indeed phenological responses to short-term spring warming have been reported (Aerts *et al.*, 2006). Changes in the winter climate and increases in snow cover in particular have been linked with observed changes in Arctic shrub growth, possibly because overwintering shoots benefit from increased protection of a thicker snow layer and a

concomitantly higher nutrient availability due to higher winter soil temperatures (Sturm *et al.* 2001b; Sturm *et al.*, 2005; Tape *et al.*, 2006). Most experiments on impacts of a thicker snow cover so far have, however, made use of snow fences, which often cause an extreme and highly unrealistic increase in snow thickness (but see Johansson (2009)).

In addition to the paucity of data on the impact of realistic climatic changes outside the growing season, a distinction between peatland versus non-peatland vegetation responses is largely missing. Peatlands are important in the light of climate change because of their relatively large carbon storage capacity (one-third of the world's terrestrial carbon) (Gorham, 1991). In northern peatlands, vascular plant life is more controlled by the often dominant presence of peat mosses (*Sphagnum spp.*) than in other northern ecosystem types. By efficiently accumulating nutrients from atmospheric deposition and by slowing down soil organic matter decay and nutrient mineralization, *Sphagnum* mosses strongly reduce the availability of nutrients to vascular plants (Aerts *et al.*, 1992; Rydin *et al.*, 2006). In addition, the progressively increasing height of the *Sphagnum* forces vascular plants to keep pace in order not to become buried (Van Breemen, 1995; Rydin *et al.*, 2006; Dorrepaal *et al.*, 2006). Thus, both the abiotic as well as the biotic environment places extreme demands on vascular plant growth in high-latitude peatlands.

In non-*Sphagnum*-dominated ecosystems, monitoring studies have shown an increase in shrub abundance over the last decades (Tape *et al.*, 2006, but see Olofsson *et al.*, 2009.) Moreover, changes in vegetation composition in response to experimental summer warming (Walker *et al.*, 2006) and winter snow addition (Wipf *et al.*, 2010)

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were largely dominated by changes in cover of the dominant shrubs. This strong impact of climate change is often attributed to a positive nutrient feedback favouring shrubs (Wookey *et al.*, 2009). A general negative correlation between vascular and non-vascular species biomass has been observed in studies which addressed responses of both plant types to warming (Press *et al.*, 1998; Cornelissen *et al.*, 2001; van Wijk *et al.*, 2004; Walker *et al.*, 2006). However, these studies were all performed in non-*Sphagnum*-dominated ecosystems. Moreover, this negative correlation between the responses of vascular and non-vascular species was largely dominated by a decrease in lichen biomass. Hence, extending these findings to *Sphagnum*-dominated peat bogs is not self-evident.

There are several reasons to expect that a dominant presence of the peat moss *Sphagnum* in an ecosystem will counteract the abovementioned effects of climate on plant community composition. In addition to its influences on nutrient dynamics and vascular plant growth, a positive growth response to climatic changes of *Sphagnum fuscum* itself might negatively impact shrub growth (Dorrepaal *et al.*, 2006), especially in the long term. Hence, in contrast with responses in other Arctic ecosystems (Walker *et al.*, 2006; Wipf *et al.*, 2010), climatic changes might not result in increased height or closure of the vascular canopy above thick *Sphagnum* carpets, despite positive effects of increased temperatures on shrub growth. Yet, no long-term data on responses of vegetation composition to climate manipulations in northern *Sphagnum*-dominated peatlands have been published thus far.

Here, we present, to our knowledge, the first long-term experimental climate change study to take into account both realistic and independent climate changes inside and

outside the growing season as well as peatland-specific vascular plant community responses. Our aims were: (1) to quantify, over the course of 8 years, how the vascular plant community of a subarctic peat bog changed in species composition, diversity and evenness in response to six different experimental climate scenarios (summer warming, increased winter snow, increased winter snow plus spring warming and combinations thereof); and (2) to clarify how interactions between dominant growth forms at the plant level may affect community responses and community resistance or resilience to induced climate change, by measuring growth responses of the two dominant shrubs (*Empetrum hermaphroditum* and *Betula nana*) and the dominant peatmoss (*Sphagnum fuscum*).

Methods

STUDY SITE

The study was performed on a slightly sloping sub-arctic bog on the southern shore of Lake Torneträsk, near the Abisko Scientific Research Station in northern Sweden (68°21'N, 18°49'E, alt. 340 m). The recent decade (1999–2008) showed a mean annual rainfall of 352 mm and mean monthly January and July temperatures of -9.7°C and 12.3°C, respectively, (meteorological data Abisko Scientific Research Station, Freschet *et al.*, 2010). The length of the growing season is 130 days (Karlsson *et al.*, 1996), and the site is permafrost underlain with an active layer thickness of approx. 55 cm. The dominant component of the bog vegetation is the peat moss *Sphagnum fuscum* (Schimp.) H. Klinggr. The vascular plant community is low-statured and open (maximum shrub height 15 cm, average cover 25%) and mainly consists of the evergreen dwarf shrubs *Empetrum hermaphroditum* Hagerup (41%) and *Andromeda polifolia* L. (5%), the deciduous dwarf shrubs *Betula nana* L. (22%) and *Vaccinium uliginosum* L. (6%), the grass *Calamagrostis lapponica* (Wahlenb.) Hartm. (5%) and the forb *Rubus chamaemorus* L. (10%).

EXPERIMENTAL DESIGN OF THE CLIMATE CHANGE EXPERIMENT

Six climatic regimes were established in June 2000, relevant to different possible future climate scenarios in the Arctic (Sælthun, 2003; ACIA, 2004; Kohler *et al.*, 2008) and allowing to study separate and interactive effects of climate change in different seasons (Dorrepaal *et al.*, 2004). Our experimental manipulations led to full-factorial combinations of two summer treatments (ambient, warming) and three treatments during winter and spring (ambient, snow addition, snow addition plus spring warming). For brevity, the latter are referred to as winter treatments ($n=5$; Table

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3 1). Warming treatments were imposed by passive warming using a modified, larger
4 version of the transparent, hexagonal ITEX Open Top Chambers (OTCs; 50 cm high,
5 2.2-2.5m bottom diameter; cf. Marion *et al.* 1997). Average daily mean air temperature
6 in the OTCs increased by 0.3-1.0 °C in spring (late-April- 1 June) and by 0.2-0.9 °C in
7 summer (for treatment codes see Table 1). Soil temperature responses generally
8 tracked those of air temperatures, with an increase in spring soil temperature of about
9 1.0 °C, and a summer increase of 0.6-0.9 °C. During winter (October-April) the OTCs
10 passively accumulated snow, thereby increasing the average temperatures by 0.5-2.8
11 °C and 0.5-2.2 °C at +5 and -5 cm respectively, and doubling the ambient snow-cover
12 thickness (max. approx. 15 cm). Full details of the experimental procedures and their
13 effects on summer and winter microclimate were presented by Dorrepaal *et al.* (2004,
14 2009).

VEGETATION ABUNDANCE MEASUREMENTS

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17 In the first two weeks of August 2000, 2002, 2006 and 2008, i.e. 0, 2, 6 and 8 years
18 after the start of the experiment, vegetation cover was measured by means of the point
19 intercept method (Jonasson, 1988). We used a 60*60cm metal frame with adjustable
20 legs and a metal mobile double-strip with 11 holes in a row. By moving the double-
21 strip 5 cm horizontally each time, a grid with 121 holes was created. The position of
22 the frame was marked permanently and chosen at a minimum of 65cm from the plot
23 edge to prevent edge effects like reduced precipitation or clonal connections beyond
24 the plots. A metal pin 5 mm in diameter was lowered through each hole in the strip and
25 each contact of the pin with green living vegetation was recorded by species until the
26 pin reached the moss substrate. Depending on the species, a hit related to a single
27 bigger leaf (of e.g. *R. chamaemorus*, *C. lapponica*, *V. uliginosum*, *B. nana*) or to a
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single stem or branch with several smaller leaves (e.g. *E. hermaphroditum*, *A. polifolia*, *V. microcarpum*). Earlier studies have shown that point intercept measurements are a good estimator of plant biomass (Jonasson, 1988; Hobbie *et al.*, 1999; Aerts, 2009) .

SHRUB LENGTH GROWTH, SHRUB HEIGHT ABOVE *SPHAGNUM* AND *SPHAGNUM* VERTICAL GROWTH MEASUREMENTS

To assess the effects of changes in summer and winter climate on shrub growth and on interactions between shrubs and their living *S. fuscum* substrate, we performed additional measurements on *E. hermaphroditum*, *B. nana* and *S. fuscum*. Because the shrubs are long-lived perennials, the ramets of which are connected below the moss layer through overgrown stems, we defined a shoot as a stem that emerged above the moss layer (Chapin *et al.*, 1985).

Annual stem-length increments of ten randomly selected *E. hermaphroditum* shoots per plot were measured for years 7 and 8. Current-year growth was identified using colour differences of the stem, bud scars and changes in leaf length between the growth segments of the different years. Annual stem-length increment data for years 1 and 2 were taken from Dorrepaal *et al.* (2006). In addition, from a random subsample of 10 shoots per plot the percentage of shoots of which fewer than two year-segments or less than one year-segment was visible above the moss-layer was counted in year 8 (as an estimate of overgrowth by *S. fuscum*).

For *B. nana*, the length of the current-year growth of the main axis of 10 randomly selected shoots per plot was measured in year 8. Current-year growth was identified using colour differences of the stem and scars of the terminal bud. Additionally, current-year stem-length growth data for years 1 and 2 were taken from Dorrepaal *et al.* (2006). Unlike *E. hermaphroditum* shoots, *B. nana* shoots in our plots do not grow

perpendicular to the moss substrate. Therefore, *B. nana* shrub height after 9 years was measured as the vertically projected distance from the top of the shoot to the *S. fuscum* surface (five shoots per plot). *S. fuscum* length growth was measured in all plots in year 9 using a modification (Dorrepaal *et al.*, 2004) of the cranked wire technique (Clymo, 1970), with five wires per plot. In addition, *S. fuscum* length-growth data for year 1 and 2 for the same plots were taken from Dorrepaal *et al.* (2004).

STATISTICAL ANALYSIS

Prior to statistical analysis, plot means were calculated for all parameters. All plot mean data were tested for normality and homogeneity of variances by visual estimation of residual and probability plots. For the vegetation cover data ln-transformation improved the homogeneity of variances considerably. Transformation did not improve the distribution of *E. hermaphroditum* length increment data for years 7 and 8. As ANOVA is robust to considerable heterogeneity of variances as long as sample sizes are nearly equal (Zar, 1999), we included these data untransformed. All other data approximated normal distributions and homogeneous variance. All analyses were performed with SPSS 15.0 for Windows.

The effects of the summer and winter climate manipulations on vegetation cover (number of hits) over years 0-8 were analysed using repeated measures (RM-)ANCOVAs. 'Year' was the within-subject factor, 'initial cover' the covariate (to account for differences in initial cover), and 'summer treatment' and 'winter treatment' were the between-subject factors. 'Winter treatment' was ambient, snow addition or snow plus spring warming, the effects of which were separated by a Tukey's HSD post hoc test on data corrected for the covariate to allow post hoc testing. This analysis was

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performed for the total cover as well as for individual cover of each of the six most abundant species.

Likewise, the effects of the summer and winter climate manipulations on *E. hermaphroditum* annual stem-length increments over years 1, 2, 7 and 8 were analysed with RM-ANOVAS, with year as the within-subject factor, and summer treatment and winter treatment as between-subject factors. This same RM-ANOVA was also applied to *S. fuscum* vertical growth over years 1, 2 and 9. The data for *B. nana* growth year 8, and shrub height *B. nana* in year 9 were analysed using an ANOVA with summer treatment and winter treatment as fixed factors. Treatment effects on the percentage of *E. hermaphroditum* shoots that had fewer than two year-segments or fewer than one year-segment visible above the moss in year 8 were analysed with the χ^2 -test.

Results

COMMUNITY PARAMETERS

ABOVEGROUND VASCULAR PLANT ABUNDANCE

There were no significant main treatment effects of the climate manipulations on total vascular plant abundance in the course of 8 years. The interaction between the effects of the summer and winter treatments (Fig. 1; Table 2) was most likely caused by the contrasting effects of summer warming in winter ambient vs. snow addition plus warming treatments. Correspondingly, no change in abundance in response to any climate manipulation was observed at the species level, as no changes were detected in the abundances of the main representatives of the growth forms in our system: evergreen shrubs (*E. hermaphroditum*, *A. polifolia*), deciduous shrubs (*B. nana*, *V. uliginosum*), graminoids (*C. lapponica*) and forbs (*R. chamaemorus*) in the course of 8 years (Table 2). Apparent trends ($P < 0.1$) of winter and winter x summer treatments affecting the abundance of *C. lapponica* and *R. chamaemorus* respectively seem to be statistical artefacts caused by the low number of hits for these individual species, which made them particularly sensitive to variance in initial cover. Indeed, these apparent trends disappeared when cover was analysed as differences compared to initial cover in a RM-ANOVA. However, the apparent trend towards interaction between year and summer treatment for *E. hermaphroditum* was consistent in both analyses. *E. hermaphroditum* abundance increased under ambient conditions in the last 2 years of the experiment, but remained unchanged in any of the other year-treatment combinations.

DIVERSITY & EVENNESS

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The unaltered total vascular plant abundance and individual species abundances were reflected in the diversity indices, as none of the treatments affected the Shannon's diversity index (Table 2). Similarly, Shannon's evenness index remained unchanged in response to the treatments, although the higher order interaction between year, summer treatments and winter treatments indicated a minor influence caused by the combination of treatments in some years (Table 2).

GROSS GROWTH PARAMETERS

Apical growth of *E. hermaphroditum* showed a positive trend in response to the winter treatments, in particular to spring warming (Tukey's HSD, AS+/WS+ vs AS/WS, $P = 0.053$) (Fig. 2; Table 2) and this effect became more pronounced in the later years of the experiment. Summer warming did not affect *E. hermaphroditum* stem growth. In contrast to the positive effect of spring warming on *E. hermaphroditum*, the winter treatments did not affect *B. nana* stem length growth. However, summer warming had a sustained positive effect on *B. nana* stem growth (Fig. 2; Table 2). *S. fuscum* vertical growth was higher in response to summer warming, but was not affected by the winter treatments (Fig. 3; Table 2), except for a higher order interaction effect with time.

NET GROWTH PARAMETERS (YEAR 8)

In year 8 of the treatment, more *E. hermaphroditum* branches were partly overgrown (*i.e.* a higher percentage of branches had less than one or two year segments above the moss) by *S. fuscum* in the manipulation treatments than in the ambient plots (χ^2 -test, all six treatments, $P < 0.01$). In particular, the summer warming treatment increased the percentage of partly overgrown branches (χ^2 -test, AA/AS/AS+ vs WA/WS/WS+, $P < 0.001$) (Fig. 4; Table 2).

Despite its increased apical growth rate in response to summer warming, net shrub height of *B. nana* (vertical distance from the shoot tip to the *S.fuscum* moss layer) remained the same under all climate manipulations (Fig. 4), as did the average stem inclination towards the moss-surface (results not shown).

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Discussion

Vascular plant community composition in our peat bog was more resistant to climate manipulations than is typically observed in other (sub)arctic ecosystems: vascular plant abundance, individual species abundances, Shannon's diversity or evenness did not change across any growth form in response to 8 years of either winter snow addition or experimental spring or summer warming. This resistance occurred despite the fact that growth rates of *B. nana* and *E. hermaphroditum* responded strongly and significantly and sustained this response over 8 years of treatments. This paradox of no effects of the climate manipulations at the community level *versus* significant individual growth responses may be explained by the role of *S. fuscum* in modifying effects of climate change at the community level.

CLIMATE CHANGE EFFECTS ON THE VASCULAR PLANT COMMUNITY

Winter snow addition did not change our vascular plant community, which contrasts with the generally found pattern of increasing deciduous shrub abundance and decreased species richness in response to thicker snow cover (Sturm *et al.*, 2005; Tape *et al.*, 2006; Wipf *et al.*, 2010). A hypothesized mechanism behind observed increases in shrub abundance is a positive feedback loop leading from more shrubs to thicker snow cover to higher subnival temperatures, with associated increases in decomposition and nutrient mineralization (Sturm *et al.*, 2001a). This mechanism seems a plausible explanation for systems with relatively large shrubs (e.g. *B. nana* up to approx. 0.3 m in Alaska, Happy Valley, and in Siberia, Kytalyk Reserve (F. Keuper, data unpublished)), as compared to the shrubs in our system (*B. nana* up to approx. 0.15 m). Moreover, the vascular plant community on *S. fuscum* dominated peatlands is generally low and open due to competition between the vascular community and the peatmoss (e.g. 25% vascular plant cover in the current study). Accordingly, the

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3 experimental increase in snow thickness was much lower in our experiment than in
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5 most experimental snow increase studies so far (Wahren *et al.*, 2005; Borner *et al.*,
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7 2008; but see Johansson *et al.*, 2009). The unresponsiveness of the vascular
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9 community and in particular of the dwarf shrubs to our moderate snow treatment may
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11 thus be explained by a combination of low initial shoot density and a rather moderate
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13 increase in insulation, insufficient for initiating a positive feedback loop as
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15 hypothesized by Sturm (2001a).
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21 Furthermore, eight years of experimental warming in spring and/or summer did not
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23 change the vegetation community composition either. This also contrasts with previous
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25 findings of increased shrub abundance in response to (experimental) climate warming
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27 (Tape *et al.* 2006; Walker *et al.* 2006; but see van Wijk *et al.* 2004; Olofsson *et al.*
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29 2009), and with the commonly observed decrease in subarctic species diversity and
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31 evenness (Press *et al.*, 1998; Walker *et al.*, 2006) as a result of such changes. The most
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33 likely explanation for these discrepancies is that our study is the first study looking
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35 closely at long-term effects of experimental warming on the vascular plant community
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37 of a *Sphagnum*-dominated peatland.
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46 EFFECTS OF SUMMER AND WINTER TREATMENTS ON PLANT GROWTH RATES

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48 Even in the absence of changes at the community level, we did expect to find positive
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50 effects of the treatments at the plant level. Indeed, apical growth of *E. hermaphroditum*
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52 increased in response to the spring warming treatment in year 7 and 8 of the
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54 experiment, while it did not increase in response to summer warming. *Empetrum* is
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56 somewhat drought sensitive (Tybirk *et al.*, 2000) and our summer warming treatment
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58 slightly affected summer soil moisture (mean summer soil moisture by volume 26% in
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the summer warmed plots vs. 34 % ambient; $P < 0.05$; Dorrepaal *et al.* 2009). The direct effect of warming on *E. hermaphroditum* apical growth might thus have been compensated by a negative growth response to drying of the peat. In contrast to *Empetrum*, length growth of *B. nana* showed a sustained increase to summer warming at the plant level, which is in line with previous reports (Bret-Harte *et al.*, 2001; Dorrepaal *et al.*, 2006). Unlike summer warming, snow addition did not affect the length growth of *B. nana*, *E. hermaphroditum* or *S. fuscum*, which again may be explained by the modest increase in snow cover in our winter treatment. This indicates, in addition to the absence of snow cover effects on the vascular plant community, that in this experiment summer warming seems to be a more likely driver behind possible future changes than increases in snow cover.

The average difference in annual apical growth rates between the warmed and the ambient treatments would add up to a cumulative difference over 8 years of 12 mm for *E. hermaphroditum* and 64 mm for *B. nana*. These differences are remarkable, as the ambient average height of the shoot tip above the moss is roughly 20 mm for *E. hermaphroditum* and 60 mm for *B. nana* (with an average branch length of 90 mm, but an inclination of approx. 45°). This 60% increase in shoot length of the two most abundant vascular species should have been detected by the point-intercept data, if these increased growths had not been masked by a persistent increase in *S. fuscum* growth under warmed conditions.

THE ROLE OF *SPHAGNUM FUSCUM* IN STABILIZING VEGETATION COMPOSITION DURING
LONG-TERM CLIMATE MANIPULATIONS

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3 The cumulative difference in vertical growth of *S. fuscum* in warmed versus ambient
4 plots was approximately 18 mm over 8 years. Direct evidence for a 'race for space' is
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6 provided by the enhanced encroachment of *E. hermaphroditum* by *S. fuscum* in the
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8 summer warmed plots (Fig. 4), in correspondence to the higher growth of *S. fuscum*
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10 upon summer warming. Also for *B. nana*, the advancement of *S. fuscum* on the shrubs
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12 as a result of summer warming masked the increased apical growth of the shrub (Fig.
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14 2) as a consequence of which no changes in height (i.e. vertical distance of the shoot
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16 tips to the moss) were detected (Fig. 4). Hence, the long-term absence of changes in
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18 net shrub height in response to the summer warming treatment exemplifies the role of
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20 the elevating moss surface: *S. fuscum*-mediated effects are long-term and strong
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22 enough to prevent vascular plant growth responses from becoming apparent at the
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24 community level.
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34 In other, non-*Sphagnum*-dominated ecosystems, strong responses of *B. nana*
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36 abundance to either increased winter snow or summer warming have been ascribed to
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38 its high biomass production at a relatively low nitrogen investment, by which it may
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40 outcompete other species when subject to increased nitrogen availability (Shaver *et al.*,
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42 2001; Sturm *et al.*, 2005). Reasons for the absence of this response to climatic changes
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44 in our *S. fuscum*-dominated system may be twofold: firstly, inorganic nitrogen pool
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46 sizes do not differ among our treatments, whereas the microbial-nitrogen pool is
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48 significantly higher in the warming (WA) and snow addition (WS+) treatment (J.T.
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50 Weedon, unpublished results). Hence, nutrient availability may not increase in
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52 response to climatic warming or snow addition because *Sphagnum* itself is a strong
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54 competitor for (and immobilizer of) nutrients, or because of a strong microbial sink for
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56 nutrients in organic (sub)arctic soils (cf. Jonasson *et al.* 1996; Schmidt *et al.* 1999).
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Secondly, and crucial to our findings, while greater biomass production by *B. nana* in non-*Sphagnum*-dominated systems often gives it competitive superiority through out-shading neighbouring plants, in a *Sphagnum*-dominated system the shrubs appear to only just keep pace with *Sphagnum* in their race for space.

Although some other studies also found discrepancies between responses at the plant-level and at the community level, these seemed idiosyncratic and have so far lacked a clear mechanistic explanation (Wahren *et al.*, 2005; Hudson *et al.*, 2010). In our system, we have provided mechanistic evidence that the overall unaltered vascular species composition may be a consequence of the dominant positive growth responses of *S. fuscum* (the 'living soil') to experimental warming. This key finding adds another important new contributor to the list of mechanisms by which mosses, as key ecosystem engineers (*sensu* Lawton 1994), tightly regulate soil hydrology, biogeochemical cycling and climate (Van Breemen, 1995; Beringer *et al.*, 2001; Gornall *et al.*, 2007; Cornelissen *et al.*, 2007; Gavazov *et al.*, 2010,)

NORTHERN *SPHAGNUM* PEATLANDS RESISTANT TO CLIMATE CHANGE?

Our key finding, that the vascular plant community composition of a *S. fuscum*-dominated peatland was resistant to the imposed climatic changes, does not imply that these northern peatlands are dormant players in the global carbon cycle under a changing climate. First, the observed growth responses of both the predominant vascular plants and *S. fuscum* itself indicate that carbon sequestration must have increased in response to warming. Secondly, the unaltered aboveground vascular community does not reflect responses of belowground processes, which were shown to be significant and of great relevance in the light of climate change (*e.g.* total ecosystem respiration rates accelerated by up to 60 % in response to 1°C warming in our

experiment) (Dorrepaal *et al.*, 2009). Finally, the resistance of the vegetation composition in direct response to different climate change scenarios imposed in this study does not mean that climate change does not threaten *S. fuscum*-dominated peatlands. Disturbances invoked by climate change, such as thawing permafrost and subsequently altered hydrology, may severely threaten these systems, as has already been observed in various peatlands in northern Sweden during this decade (Christensen *et al.*, 2004; Johansson *et al.*, 2006; Akerman *et al.*, 2008; Limpens *et al.*, 2008). Moreover, if the structure of the faster growing moss changes (Dorrepaal *et al.*, 2004), this may also affect small-scale local hydrology in the longer term. As local hydrology is in this type of ecosystem a strong determinant of moss survival (Granath *et al.*, 2010), moss species interactions (Sonesson *et al.*, 2002) and of vascular plant composition (Lang *et al.*, 2009), climate change induced changes in hydrology may have a more pronounced effect on the vascular plant community than was observed under the experimentally altered climatic conditions in the current study. However, paleo records show that ombrotrophic bogs in general have been persistent in their presence ever since the Holocene (*e.g.* Kuhry, 1998; Sannel *et al.*, 2008). Furthermore, we know that our bog has undergone changes in mean annual temperature of 2.5°C over the last 100 years without major shifts in vegetation (Sonesson, 1974; Callaghan *et al.*, 2010). Our study might very well be a step forwards in explaining the resistance of subarctic *S. fuscum*-dominated peat bogs and their vascular plant community to the prevailing climatic changes. In a still broader context, by revealing the mechanisms of peatland species interactions in response to climate change, our findings also contribute to fundamental ecological theory, revealing important new insights into the mechanisms of ecosystem resistance and resilience to global changes. Specifically, we show that resistance to climate change, here in terms of stable community composition,

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does not necessarily mean vegetation inertia (*cf.* Grime *et al.*, 2000, Hudson *et al.*, 2010), but that community stability can also be achieved in a dynamic ecosystem, in our case with strong growth response to warming.

For Review Only

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Tables

Table 1. Experimental design and treatment codes used for the climate manipulations

Winter treatment	Summer treatment	
	Ambient	Warming
Ambient	AA	WA
Snow addition	AS	WS
Snow addition plus spring warming	AS+	WS+

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Table 2. *F*- statistics for repeated-measures ANCOVAs for the effects of summer (ambient, warming: SUM) and winter treatments (ambient, snow addition, snow addition plus spring warming: WIN) and initial values (INI) on the **community parameters**: abundance (number of point-intercept hits), Shannon's diversity and Shannon's evenness; and on the **gross growth parameters**: annual stem length increments of *Empetrum hermaphroditum* and *Betula nana*, and vertical growth of *Sphagnum fuscum*. The summer and winter treatments (SUM & WIN) were taken as between-subject factors, year as within-subject factor and initial densities (INI) as a covariate

Variable and species	Source								
	SUM	WIN	INI	SUM x WIN	Year	Year x SUM	Year x WIN	Year x SUM x WIN	Year x INI
Community parameters									
Years (0), 2, 6 & 8									
Abundance^a									
Total number of hits	0.769	0.444	25.9	3.42 *	1.25	2.32	0.434	0.691	1.16
<i>Empetrum</i>	0.259	0.924	9.53	0.544	0.041	2.88 +	0.334	0.855	0.029
<i>Betula nana</i>	1.14	0.737	54.0	0.081	1.26	0.293	0.775	1.04	0.760
<i>Calamagrostis lapponica</i>	1.24	3.21	62.0	0.150	1.52	0.638	1.01	0.101	0.173
<i>Rubus chamaemorus</i>	1.28	0.686	32.5	2.90 +	1.12	2.49	1.35	0.732	1.11
<i>Vaccinium uliginosum</i>	0.003	0.509	92.9	1.01	4.01 *	1.16	0.479	0.141	3.79 *
<i>Andromeda polifolia</i>	1.16	0.248	36.6	1.16	0.933	1.61	1.69	1.18	2.00
Diversity & Evenness^b									
Shannon's Diversity (H)	0.410	1.44	33.6	0.759	1.94	0.356	0.362	1.08	
Shannon's Evenness (J)	0.314	1.21	18.7	2.50	1.34	0.040	0.679	2.59 *	
Gross growth parameters^{a, c}									
Apical growth^{a, c}									
<i>Empetrum</i>									
Years 1, 2, 7 & 8	2.61	3.13	-	0.071	16.5	0.959	1.33	0.480	-
Years 1 & 2	2.50	0.550	-	0.060	44.7	0.530	0.892	0.639	-
Years 7 & 8	1.57	4.24	-	0.110	11.6	2.00	0.310	1.02	-
<i>Betula nana</i>									
Years 1, 2 & 8	12.1	0.559	-	0.019	4.82	0.211	0.199	0.864	-
Years 1 & 2	7.77	0.850	-	0.139	1.26	0.137	0.235	1.28	-
Year 8 ^d	6.04	0.021	-	0.510	-	-	-	-	-
Vertical growth^{b, c}									
<i>Sphagnum fuscum</i>									
Years 1, 2, 9	6.42	0.235	-	1.69	24.8	1.59	1.21	2.78 *	-

Years 1 & 2	7.11	0.132	-	2.00	41.4	0.037	2.53	1.19	-
Year 9 ^d	2.03	0.391	-	2.41	-	-	-	-	-

Notes indicate: ^a: data ln-transformed; ^b: data untransformed; ^c: RM ANOVA; ^d: Two-way ANOVA. Asterisks indicate significance level of treatment effects: ⁺: $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

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9 Figures

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11 **Fig. 1** Mean (\pm 1SE) abundances (expressed as mean number of hits) of all vascular
 12 plants and three important individual species after 2, 6 and 8 years of simulated climate
 13 change compared to initial abundances (data from year 0 are without SE since these
 14 values were used as a covariate). There were no significant main effects of summer or
 15 winter treatments or year of sampling (Table 2). For treatment codes see Table 1.

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17 **Fig. 2** Apical annual growth (mean \pm 1SE) of *Empetrum hermaphroditum* and *Betula*
 18 *nana* in response to simulated environmental change after 1, 2, 7 and 8 years of
 19 simulated climate change. Tukey's post-hoc test at $P < 0.05$ on RM-ANOVA with
 20 between subjects-factors: summer (A, W) and winter (A, S, S+) indicated that
 21 AS+/WS+ vs. AS/WS differed significantly for *E. hermaphroditum*. *B. nana* growth
 22 was significantly affected by summer warming (Table 2). For treatment codes see
 23 Table 1.

24

25 **Fig. 3** *Sphagnum fuscum* vertical annual growth (mean \pm 1SE) after 1, 2 and 9 years
 26 of simulated climate change. Only summer warming affected growth significantly
 27 (RM-ANOVA with between subjects-factors: summer (A, W) and winter (A, S, S+)
 28 followed by a Tukey's post-hoc test at $P < 0.05$). For treatment codes see Table 1.

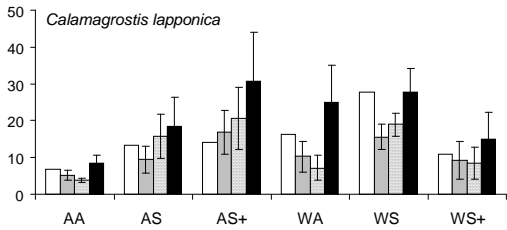
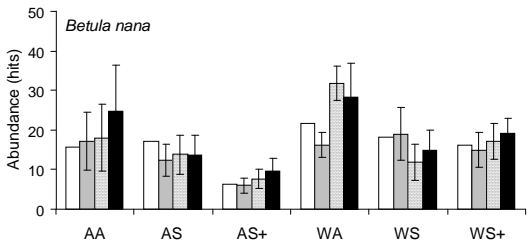
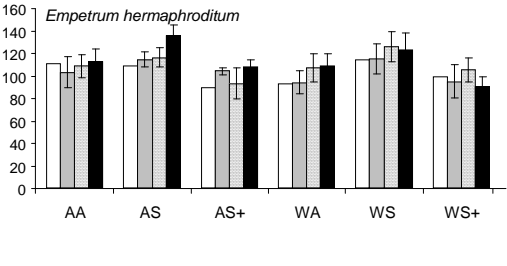
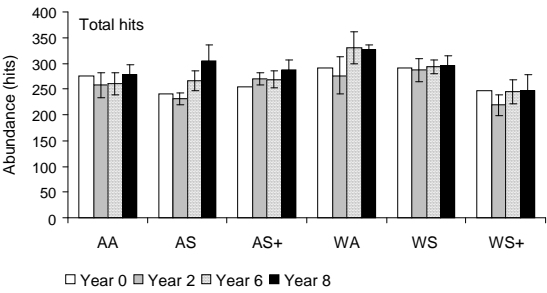
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30 **Fig. 4** Measures of overgrowth by *S. fuscum* of two key species after 8 years of
 31 simulated environmental change. a) *E. hermaphroditum*: percentage of branches with
 32 less than one or than two year-segments visible above the moss-surface. Summer
 33 warming increased the percentage of overgrown branches (χ^2 -test, AA/AS/AS+ vs

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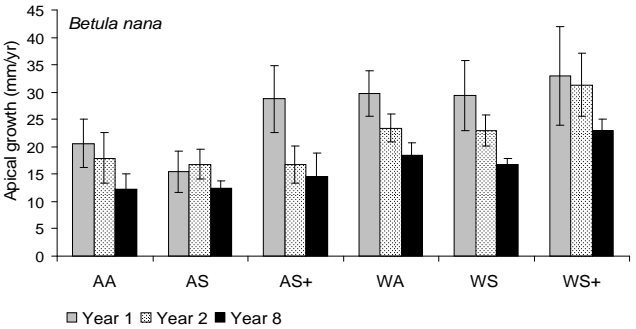
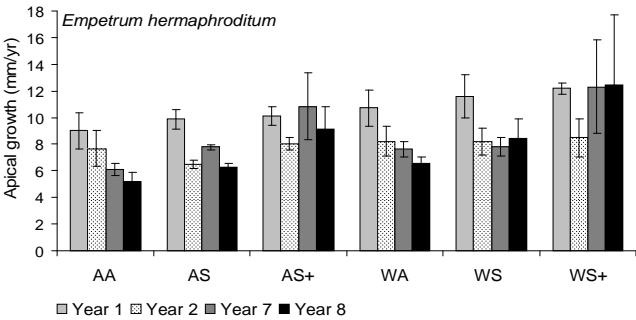
34 WA/WS/WS+, $P < 0.001$) and b) *B. nana* net shrub height above the moss-surface
35 remained unaltered in response to all treatments. Error bars indicate SEM. For
36 treatment codes see Table 1.

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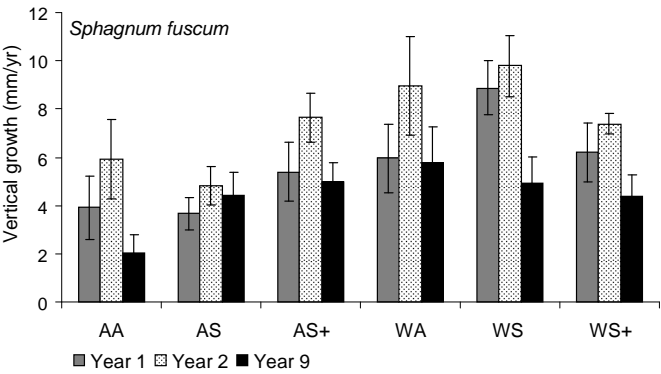


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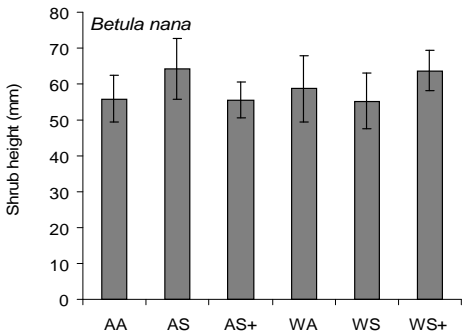
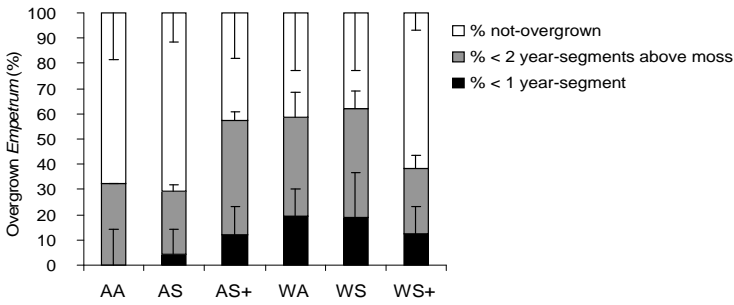
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