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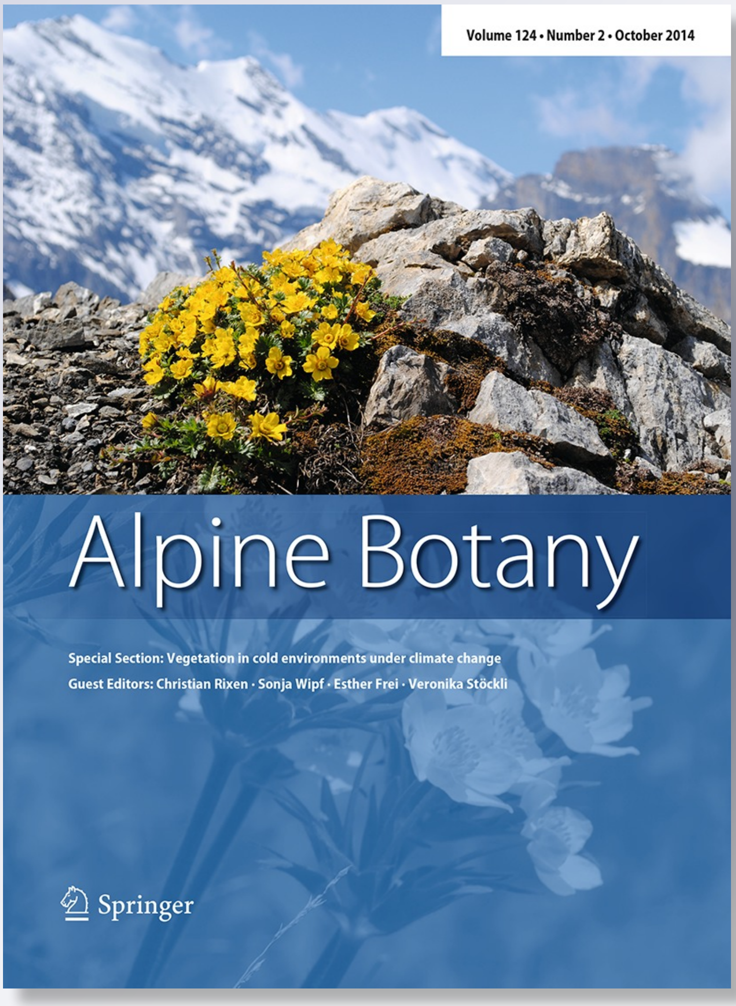

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VEGETATION IN COLD ENVIRONMENTS UNDER CLIMATE CHANGE

Snow cover consistently affects growth and reproduction of *Empetrum hermaphroditum* across latitudinal and local climatic gradients

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Abstract Arctic ecosystems face strong changes in snow conditions due to global warming. In contrast to habitat specialists, species occupying a wide range of microhabitats under different snow conditions may better cope with such changes. We studied how growth and reproduction of the dominant dwarf shrub *Empetrum hermaphroditum* varied among three habitat types differing in winter snow depth and summer irradiation, and whether the observed patterns were consistent along a local climatic gradient (sub-continental vs. sub-oceanic climates) and along a latitudinal gradient (northern Sweden vs. central Norway). Habitat type explained most of the variation in growth and reproduction. Shoots from shallow snow cover and high summer irradiation habitats had higher numbers of flowers and fruits, lower ramet heights, shorter shoot segments, lower numbers of lateral shoots and total biomass but higher leaf density and higher relative leaf allocation than shoots from habitats with higher snow depth and lower summer irradiation. In addition, biomass, leaf allocation and leaf life expectancy were strongly affected by latitude, whereas local climate had strong effects on seed number and seed mass. *Empetrum* showed high phenotypic trait variation, with a consistent match between local habitat conditions and its growth and reproduction. Although study areas varied strongly with respect to latitude and local climatic conditions, response patterns of growth and reproduction to habitats with different environmental conditions were consistent. Large elasticity of traits suggests that *Empetrum* may have the potential to cope with changing snow conditions expected in the course of climate change.

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Introduction

Temperature increase due to climate change alters the abiotic and biotic conditions of plants (e.g., ACIA 2004; IPCC 2013), which may respond though (a) shifts in phenology (b) range shifts and/or (c) in situ changes of morphological or physiological traits (Bellard et al. 2012). To better understand and predict the potential responses of plant species to these rapidly changing conditions, we need more knowledge concerning the effects of driving environmental factors on plant growth, distribution and abundance.

Ecosystems at high latitudes and altitudes are characterized by a cold and relatively short growing season (Bliss 1971). However, the Arctic is experiencing an increase in temperature, most pronounced in winter and spring, causing an earlier onset of snowmelt (Callaghan et al. 2011) and an earlier start of the growing season (Shabanov et al. 2002). Snow cover, which may last for over 8 months, represents an especially strong selection factor (e.g., Haapasaari 1988; Tybirk et al. 2000; Körner 2003) with significant effects on the distribution and abundance of plant species and communities (e.g., Sandberg 1958; Virtanen and Eurola 1997). Spatial variation in snow depth in Arctic ecosystems, created by a combination of topography and wind, ranges from snow-free wind-exposed ridges to sheltered depressions with deep snow accumulation (Saarinen and Lundell 2010). Usually, these habitat types are inhabited by plant communities with contrasting species composition (e.g., Jonasson 1981; Haapasaari 1988; Odland and Munkejord 2008) characterized by chionophilous (species preferring winter snow cover; phytosociological alliance: *Phyllodoco-Vaccinion*, Dierßen 1996) or chionophobous species (snow-avoiding species; phytosociological alliance: *Arctostaphylo-Cetrarion*, Dierßen 1996). However, some species occupy a wide range of habitats, and intraspecific differences in responses to variation in snow depth and duration can then be found in terms of growth, phenology and reproduction (McGraw and Antonovics 1983; Kudo et al. 1999; Bokhorst et al. 2008; Crawford 2008; Bokhorst et al. 2009; Wipf et al. 2009; Saarinen and Lundell 2010; Wipf 2010). For instance, individuals growing on wind-exposed ridges usually have smaller leaves (McGraw and Antonovics 1983) and a compact growth with shorter internodes (Lid and Lid 1994) compared to individuals on sites where snow accumulates. Besides local snow cover patterns, which influence species composition (Sandberg 1958; Virtanen and Eurola 1997), there are also general changes in snow depth in Arctic ecosystems. While snow depth has increased since the 1980s (Kohler et al. 2006; AMAP 2012), the duration of snow cover has decreased, probably owing to increasing winter and spring temperatures (Callaghan et al. 2011). Plants in Arctic ecosystems thus face profound changes in winter snow conditions. These may also influence nutrient availability and water supply, since snow cover has cascading feedback effects on the conditions during spring and summer. Thus, also the quantity and quality of solar radiation will co-vary with vegetation composition and structure along a snow cover gradient.

A high degree of phenotypic trait variation within one species regarding contrasting environmental conditions broadens the range of habitats in which a species can survive (Crawford 2008). Due to the broader habitat range, we expect that these species may better cope with the on-going changes in the Arctic (Jonasson 1981). One such species is *E. hermaphroditum* Hagerup (*Empetrum nigrum* agg., Jäger and Rothmaler 2011; hereafter, denoted as *Empetrum*), a prominent evergreen dwarf shrub in several subarctic heath and mountain birch forest communities (Sonesson and Lundberg 1974; Nilsson and Wardle 2005). Owing to its ability to build up dense mats through clonal growth and by the release of allelochemicals (batatasin-III; Nilsson and Wardle 2005), the species gains dominance in various habitats and controls community and ecosystem processes such as species recruitment, microbial activity, decomposition and nutrient cycling (Tybirk et al. 2000). Although *Empetrum* mostly reproduces vegetatively and expands clonally, fruits may be abundant (Bell and Tallis 1973; Callaghan and Emanuelsson 1985). Despite its pivotal role in Arctic ecosystems its response to snow cover variation is equivocal. Thus, the species is considered to prefer either habitats with shallow (Jonasson 1981; Jonasson and Sköld 1983; Virtanen and Eurola 1997; Kudo et al. 1999; Odland and Munkejord 2008; Fletcher et al. 2010) or with relatively deep snow cover (Kudo et al. 1999; Tybirk et al. 2000; Fletcher et al. 2010), but *Empetrum* does not occur in the late-melting snowbed communities (phytosociological class *Salicetea-herbaceae*, Dierßen 1996).

In the context of the International Tundra Experiment (ITEX), the immediate response of circumpolar plant species to climate change in terms of growth and reproduction has been monitored within the tundra biome worldwide (Walker et al. 2006). The most important climate manipulation of ITEX is passive warming of small tundra plots using open top chambers (Walker et al. 2006), whereas the effects of variation in snow depth and snow cover duration are only examined in single-site experimental snow cover manipulations (e.g., Wipf et al. 2006; Bokhorst et al. 2008, 2009; Wipf et al. 2009; Wipf 2010; Gerdol et al. 2013). The results of these snow manipulation experiments, which artificially add or remove snow from local plots, have been summarized recently in a meta analysis (Wipf and Rixen 2010); the meta analysis shows that the growth response in snow manipulation experiments depends on plant growth form, habitat type and the type and degree of snowmelt manipulation. In contrast, studies on intraspecific variation in growth and morphology to snow cover using natural gradients of snow depth are scarce (e.g., McGraw and Antonovics 1983; Kudo et al. 1999). The assumption of this gradient approach is that plants will respond to temporal changes of environmental conditions in the same way that they now vary with different conditions over space (Dunne et al. 2004). A comparative multi-site gradient approach using natural site variation (a) allows the analysis of the response of species in terms of growth, morphology and reproductive traits to natural, long-term variation of conditions and (b) allows the evaluation of the relative importance of local habitat conditions versus regional drivers such as climate and latitude. This analysis may thus shed new light on elasticity and phenotypic trait variation of *Empetrum*—a keystone species of boreal and arctic ecosystems—in response to snow cover changes in the course of global change.

Therefore, the present paper compares intraspecific performance of *Empetrum* in habitats with contrasting winter snow cover and growing season light availability among regions differing in climate (continentality) and latitude. Assuming that snow cover represents a strong selection force, we expect larger differences in terms of growth and reproduction among habitats, than between climates and latitudes.

The following questions were addressed.

> **Q1**: Do shoot growth and morphology of *Empetrum* vary significantly among habitats defined according to their winter snow cover regimes? How large is the effect of habitat type in comparison with latitudinal and climatic variation?
>
> **Q2**: Do fruit and seed production of *Empetrum* vary significantly among habitats differing in winter snow cover regimes? Which habitat type is most suitable for seed production of *Empetrum*? How large is the effect of habitat type in comparison with climatic variation?

Materials and methods

Study regions and habitats

The study is based on data from four regions, two of which are located at latitudes of about 68°N (abbreviated 'North-'; regions: Abisko and Vassijaure in northern Sweden) and two are situated at 62–63°N (abbreviated 'South-'; regions: Kongsvold and Samsjøen in central Norway). Within each latitude, one study region represented sub-continental climate (abbreviated 'SC'; regions: Abisko and Kongsvold) and one region sub-oceanic climate (abbreviated 'SO'; regions: Vassijaure and Samsjøen), i.e., relatively low or high winter precipitation patterns, respectively (Table 1). Altitudes varied between 420 and 720 m a.s.l. at higher latitudes (North-SC, North-SO) and between 590 and 1,140 m a.s.l. at lower latitudes (South-SC, South-SO) and thus cover the sub-alpine and low alpine zone, i.e., forest–tundra ecotone.

We distinguished three habitats differing in snow depth and co-varying abiotic factors based on topography, community type and indicator species of contrasting snow cover conditions (Jonasson 1981; Odland and Munkejord 2008).

- Birch forest with deep snow cover (abbreviated by ***b***): sub-alpine birch forest with *Betula pubescens* ssp. *czerepanovii*.
- Alpine tundra with deep snow cover (***d***): wind-sheltered depressions in low alpine heath with tall and dense *Betula nana* as characteristic chionophilous species (Jonasson 1981; Odland and Munkejord 2008).
- Alpine tundra with shallow snow cover (***s***): wind-exposed ridges on low alpine heath. Characteristic chionophobous species for identifying this habitat type were *Arctostaphylos alpina*, *Loiseleuria procumbens*, *Cetraria nivalis* and *Cetraria cucullata* (Jonasson 1981; Odland and Munkejord 2008).

Thus, ***b*** + ***d*** habitats differ from ***s*** habitats with respect to winter snow cover, whereas, within the habitats with deep winter snow cover, ***b*** differs from ***d*** with respect to canopy shade during the growing season.

Plot selection

During summer 2012, we selected and permanently marked 10 1 × 1 m plots per habitat type in each of the 4 study regions for analyses of shoot growth and vegetation surveys along elevation transects from the sub-alpine birch forest to the low alpine heath zone with wind-sheltered depressions or wind-exposed ridges. The plots in North-SC and North-SO were located in south–north direction across a distance of 4,500 and 3,900 m, respectively. Plot arrangement in South-SC and South-SO was in west–east direction across a distance of 1,100 and 600 m, respectively. Plot selection was conditional on the criteria for habitat type selection above and the presence of *Empetrum*. Distance between individual plots depended on habitat affiliation and relief structures in the landscape.

Site characteristics

To describe and quantitatively compare the environmental conditions of the different habitat types, we conducted vegetation surveys, estimated snow depth, and measured

Table 1 Climate data of the four study regions North-SC, North-SO, South-SC and South-SO (period 1961–1990; based on data by Swedish meteorological institute (SMHI www.smhi.se/klimatdata) and Norwegian meteorological Institute (MET www.eklima.met.no)

Region	Coordinates	Altitude of plots (m.a.s.l.)	Climate	Mean annual precipitation (mm)	Mean annual temperature (°C)	Monthly temperature maxima (°C)	JJA mean temperature (°C)	Monthly precipitation maxima (mm)	Monthly temperature minima (°C)	Precipitation as snow (mm) (Nov–Mar)	Growing season length (days) (mean 2009–2011)
Abisko North-SC	68°2′N18°49′E	420–720	Sub-continental	304	−0.8	Jul (11.0)	9.7	Jul (54)	Jan (−11.9)	107	140
Vassijaure North-SO	68°2′N18°10′E	480–680	Sub-oceanic	844	−1.7	Jul (10.4)	8.9	Oct (109)	Jan (−11.9)	349	128
Kongsvold South-SC	62°18′N09°36′E	980–1140	Sub-continental	450	−0.4	Jul (9.6)	8.9	Jul (68)	Jan (−9.4)	135	155
Samsjøen South-SO	63°05′N10°38′E	590–650	Oceanic	830	3.9	Jul (14.0)	13.2	Sep (101)	Jan (−6.0)	331	172

Climate data for the region around North-SO are available from Katterjåkk at a distance of 3 km to North-SO. Climate data for the region around South-SO are available from Melhus at a distance of 30 km to South-SO. Growing season starts when at least 5 consecutive days reached a threshold temperature of at least 5 °C and ends when the mean daily temperature of 5 consecutive days is below the 5 °C threshold. Calculation of growing season length in Norway is based on data from Dombås in 35 km distance to South-SC and Selbu in 25 km distance to South-SO

Jan January, *Mar* March, *Jul* July, *Sep* September, *Oct* October, *Nov* November, *JJA* June, July and August

humus depth, site openness, vegetation cover and *Empetrum* cover for each plot. Furthermore, we measured temperature at the soil surface with data loggers (micro-T, DS1922L; NexSens Technology, Alpha, Ohio, USA) from September 2012 to July 2013 every 3 h. We summed temperatures from the 1st of April to the 27th of June 2013 for all habitats and study regions. For statistical analyses, we calculated daily mean temperatures for each plot and summed up monthly temperature sums for April, May and June. The temperature curves (see Electronic Supplementary Material S1) of the habitat types showed almost the same patterns in all four regions during the analyzed time period. From early- to mid-April temperature curve of ***s***-habitats fluctuated around −5 °C, whereas temperature of ***b***-habitats was around 0 °C; ***d***-habitats took an intermediate position. Only in South-SC, temperatures of all habitats were slightly higher, but not above 0 °C. From mid-April to early-May, temperature curves of all habitats fluctuated around 0 °C. From mid-May to late-June, the temperature curve of ***s***-habitats was significantly higher than those of ***b***–and ***d***-habitats, which had nearly the same temperature. Higher temperatures in ***b***-than in ***s***-habitats in North-SO might be due to lower canopy closure as a consequence of leaf damage due to a caterpillar outbreak. Independent of altitude, temperatures were very similar. Therefore, we assume that altitudinal differences between sites (especially high altitudes in South-SC) were compensated by a latitudinal effect.

Vegetation surveys were carried out in the northern study regions between the 19th of June and the 8th of July 2012 and in the southern study regions between the 9th and 17th of July 2013. To characterize the vegetation within the 1 × 1 m plots, we recorded the cover of all species in the tree-, shrub-, herb- and cryptogam-layer. Cover was estimated on an ordinal scale, ranging from 1 to 9: 1 = <5 % cover, only 1 individual, 2 = <5 % cover, 2–5 individuals, 3 = <5 % cover, 6–50 individuals, 4 = <5 %, >50 individuals, 5 = >5–12.5 %, 6 = >12.5–25 %, 7 = >25–50 %, 8 = >50–75 %, and 9 = 76–100 % cover (cf. Tremp 2005). Nomenclature follows Mossberg and Stenberg (2008) for vascular plants and Skytte Christiansen et al. (1996); Ursing (1953); Hallingbäck et al. (2006); Moberg and Holmasen (1999) for cryptogams.

In the birch forest, we used the height of *Parmelia olivacea* on birch stems to estimate the maximum winter snow depth (Sonesson et al. 1994), whereas in the alpine tundra, the height of the tallest but vital dwarf shrub or herb was used to estimate the minimum snow depth (Grogan and Jonasson 2006; Sturm et al. 2001).

Furthermore, at each plot, we measured the depth of the organic layer (from ground surface down to the mineral layer) and estimated total vegetation cover (proportion of vegetation-covered ground within the plot) and *Empetrum* cover (proportion of total plot area covered by crowberry, with 5 % accuracy).

To measure site openness, hemispherical images were taken with a Nikon Coolpix 4500 digital camera equipped with a 180° fisheye lens. The camera was installed on a tripod within the center of each plot at a height of 15 cm (due to technical errors during fieldwork at 30 cm in South-SO). Incidentally, in North-SC and North-SO, fisheye images were taken after the start of a caterpillar outbreak, which damaged birch leaves and thus influenced the estimates of site openness especially in birch forest plots. Color images were transformed into black and white images with the program Sidelook 1.1 (Nobis 2005). Afterwards, the software Gap light analyzer 2.0 (Frazer et al. 1999) was used to extract site openness of each individual plot as an indicator of habitat light conditions.

Shoot growth

To analyze shoot growth and morphology, three individual *Empetrum* ramets were randomly selected and harvested, in each plot in the northern and southern study regions in mid-June 2012 and September 2012, respectively. Before harvesting, ramet height was determined as height from soil surface to the top of the current year's shoot. The harvested ramets were stored in labeled plastic bags with a wet tissue in a cold room (5 °C) for a maximum of 3–4 days before further analysis.

Shoot morphology of *Empetrum* was measured according to Shevtsova et al. (1997) for the last four shoot generations ($C = 2012$, $C_{+1} = 2011$, $C_{+2} = 2010$, $C_{+3} = 2009$) of the main stem and of the lateral shoots. For further analyses, the current year's shoots were discarded because of different harvest periods at the two latitudes. For the three remaining shoot generations (C_{+1}, C_{+2}, C_{+3}), the following variables were recorded: length of the main shoot, number of lateral shoots, number of living green leaves, dead brown leaves, leaf scars (shed leaves) and leaves per mm stem length (hereafter, denoted as leaf density). We measured total biomass, total leaf dry mass and total stem dry mass after drying for 48 h at 65 °C. Furthermore, we calculated leaf life expectancy of shoots for each plot according to Krebs (1985), using the average number of vital leaves during the age interval C_{+1} to C_{+2} (=leaf life expectancy C_{+1}).

To obtain robust data integrated over years and to avoid pseudoreplication, for all statistical analyses, the three shoot generations C_{+1}, C_{+2} and C_{+3} were averaged per individual and data of the three selected ramets were averaged per plot. Thus, N equals 120 for data on environmental characteristics of plots and shoot growth.

Reproduction

In September 2012, we analyzed flower and fruit production of *Empetrum* shoots. For logistic reasons, this could only be done in the northern study regions (North-SC and North-SO; thus $N = 60$). We wanted to use the same plots like in the shoot growth study, but the caterpillar outbreak during the spring and summer of 2012 led to almost total defoliation of shoots in 5 plots in North-SO. Therefore, we replaced the previous 5 birch forest plots with 5 new plots with intact shoots at a distance of maximum 3.5 km away from the old ones, in birch forests with similar conditions. We used a wooden frame of 50 × 50 cm with a 7 × 7 grid of elastic threads, resulting in 49 intersection points. Within a maximum distance of 5 m of each study plot, we randomly selected five frame positions that contained *Empetrum*. At each intersection point within the frame, we recorded the presence of *Empetrum* shoots and counted the number of berries on that particular shoot. Furthermore, we randomly sampled 20 berries per plot. Seeds were extracted from berries and counted. We tested the floatability of seeds to separate filled (=alive; sinking) and empty (=dead; floating) seeds (Baskin et al. 2002) and measured the mass of sunken seeds after drying at 60 °C for 24 h.

Additionally, we counted the number of flower buds on *Empetrum* shoots that were collected for a common garden experiment. For each plot in North-SC and North-SO, one clone was sampled in autumn 2012 and from each clone between 30 and 60 ramets were cut and planted into a mixture of peat and sand. After 8 weeks in a greenhouse (day temperature 26 °C; night temperature 18 °C; air humidity 80 %), all visible flower buds were counted, and the percentage of flower buds for each clone (one plot) was calculated. Since flower buds are fully developed by September in the season before flowering (Bell and Tallis 1973), we assume that greenhouse conditions did not influence number of flower buds.

The following reproductive traits were recorded: number of berries per *Empetrum* shoot, mean number of seeds per berry, seed mass per filled (=sinking) seed (mg) (field data) and number of flower buds per shoot (data from clones in the greenhouse).

Statistical analysis

We used a hierarchical analysis of variance (ANOVA) with sequential sums of squares (Quinn and Keough 2002) to test the effect of latitude (factor levels [k] = 2: North, South), climate (k = 2: sub-atlantic (North-SO, South-SO), sub-continental (North-SC, South-SC), nested within latitude) and habitat (k = 3: ***b***, ***d*** and ***s***, nested within climate and latitude) on environmental variables and shoot growth of *Empetrum*. All factors were treated as fixed effects. ANOVA assumptions, such as normality, were visually checked using diagnostic plots and homogeneity of variances was tested by Cochran's test. Variables were log-, ln- or arcsine-transformed when necessary to improve homogeneity of variances. As a simple measure of the relative effect of each factor on each of the dependent variables, we divided the sums of squares of each factor by the total sums of squares and expressed this ratio as a percentage (cf. Welden and Slauson 1986).

To compare means between habitat types, we employed two orthogonal planned contrasts (Quinn and Keough 2002). First, we tested whether plots with high winter snow accumulation (habitat types: ***b*** plus ***d***) differed from plots with shallow snow cover (habitat type: ***s***), and second, whether the two habitat types with high snow accumulation but contrasting canopy shade during the growing season differed from each other (i.e., ***b*** vs. ***d***).

The vegetation survey data were analyzed by detrended correspondence analysis (DCA) to analyze environmental gradients and compositional similarity between plots.

Ordinations were performed using PC-ORD 5.32 (McCune and Mefford 2006), all other analyses were done with STATISTICA 10.0 (StatSoft 2010).

Results

Site characteristics

Both environmental variables differed significantly among the three habitat types (Table 2; Fig. 1). As expected, snow depth decreased significantly within all study regions from the ***b***- (mean ± standard error 103.0 ± 8.5 cm) and ***d***- (36.3 ± 2.2 cm) to the ***s***-habitats (10.1 ± 0.7 cm). Along the climatic gradient, there was a significantly higher snow depth in the sub-oceanic (64.4 ± 8.4 cm) than the sub-continental study regions (35.1 ± 3.0). The factor habitat explained 83.7 % of the observed variation in snow depth, whereas climate explained only 1.8 %. The effect of latitude on snow depth was not significant.

Table 2 The effect of habitat type, latitude and climatic region on site characteristics (hierarchical ANOVA)

Factor	*df*	Snow depth (log) SQ	% ev	Site openness SQ	% ev
Latitude	1	0.028^{ns}	0.1	3077.7***	6.5
Climate (latitude)	2	0.454**	1.8	3384.1***	7.1
Habitat [climate (latitude)]	8	21.279***	83.7	36468.4***	77.0
Contrasts					
b + ***d*** vs. ***s***	1	15.722***		13784.0***	
b vs. ***d***	1	3.346***		15478.0***	
Residuals	108	3.648	14.4	4454.9	9.4

ANOVA was performed on log-transformed data for estimated snow depth. Residual df was 107 for site openness

b birch forest, *d* deep snow cover sites, *ns* not significant, *s* shallow snow cover sites. *% ev* percent of explained variance

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

We found highest site openness in the ***s***-habitats (86.0 ± 0.4 %), followed by ***d***-habitats and ***b***-habitats which were characterized by lower site openness (77.0 ± 1.7 and 49.2 ± 2.9 %, respectively). Along the climatic gradient, site openness (SC 67.0 ± 3.0; SO: 74.4 ± 2.0 %) was higher in the sub-oceanic study regions. Furthermore, along the latitudinal gradient, site openness decreased from North to South (North 75.7 ± 1.3; South 65.5 ± 3.3). The factor habitat explained 77.0 % of the total variation in site openness, whereas climate and latitude explained only 7.1 % and 6.5 %, respectively.

The ordination of the vegetation survey data showed a clear differentiation of habitats along the first axis (Fig. 2) with ***b***-habitat plots in the left part, ***d***-habitat plots in the center, and ***s***–habitat plots in the right part of the diagram. Environmental characteristics correlated with the first axis as follows: estimated snow depth ($r = -0.616$), temperature sum May ($r = 0.529$), leaf density ($r = 0.590$), humus depth ($r = -0.485$), vegetation cover ($r = -0.318$) and *Empetrum* cover ($r = -0.244$). Furthermore, there was a clear differentiation of the latitudes along the second axis, with North-SO in the lower part, North-SC and South-SC in the center and South-SO in the upper part. Environmental characteristics correlated with the second axis as follows: total biomass ($r = 0.676$), temperature sum April ($r = 0.577$), length of shoot segment ($r = 0.554$), leaf dry mass ($r = -0.508$), no. of lateral shoots ($r = 0.494$) and site openness ($r = -0.484$).

Vegetative growth

For all vegetative traits, except leaf life expectancy, habitat explained the highest percentage of variation (38–80 %, Table 3; Fig. 3, Electronic Supplementary Material S2). Ramet height (***b***: 15.0 ± 0.8; ***d***: 11.7 ± 0.5; ***s***: 4.6 ± 0.2 cm), length of annual shoot segments (***b***: 32.3 ± 1.9; ***d***: 24.2 ± 1.5; ***s***: 10.4 ± 0.5 mm), number of lateral shoots (***b***: 3.9 ± 0.3; ***d***: 3.1 ± 0.2; ***s***: 1.8 ± 0.1) and total biomass (***b***: 32.3 ± 4.6; ***d***: 21.7 ± 3.2; ***s***: 5.7 ± 0.4 mg) showed lowest values in ***s***-habitats, intermediate values in ***d***-habitats and highest values in ***b***-habitats. In contrast, leaf density and relative leaf mass were highest in ***s***-habitats, intermediate in ***d***- and lowest in ***b***-habitats (leaf density ***b***: 1.4 ± 0.0; ***d***: 1.6 ± 0.1; ***s***: 2.5 ± 0.1 leaves per mm stem; relative leaf mass: ***b***: 6.0 ± 0.6; ***d***: 9.0 ± 0.8; ***s***: 19.0 ± 1.3 % of total biomass). Leaf life expectancy of the C_{+1} shoot generation was higher in the ***s***-habitats (1.2 ± 0.1 years) than in the ***b***-plus ***d***-habitats (***b***: 1.1 ± 0.1; ***d***: 1.0 ± 0.1 years).

Additionally, most vegetative traits differed significantly among latitudes (Fig. 3), although latitude mostly explained less of the total variation than habitat type. Relatively high

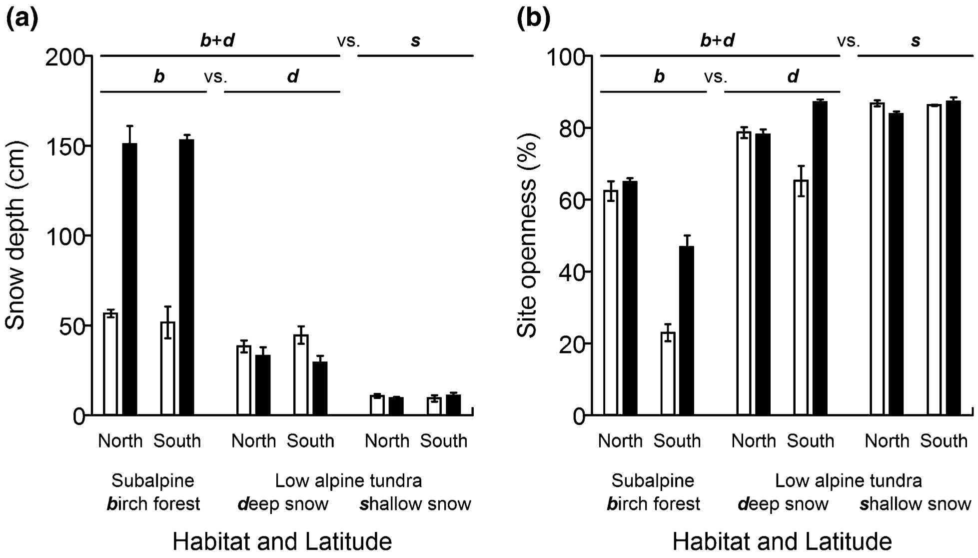

Fig. 1 Estimated snow depth (cm) (**a**), and site openness (%) (**b**) in different habitats with *Empetrum* along the climatic and latitudinal gradient. Values represent untransformed mean ± SE, $n = 10$. *White bars* represent sub-continental climate and *black bars* sub-oceanic climate. *Lines* above the *bars* depict the planned contrasts between $b + d$ vs. s and b vs. d, respectively. A break between the *lines* indicates significant differences between groups

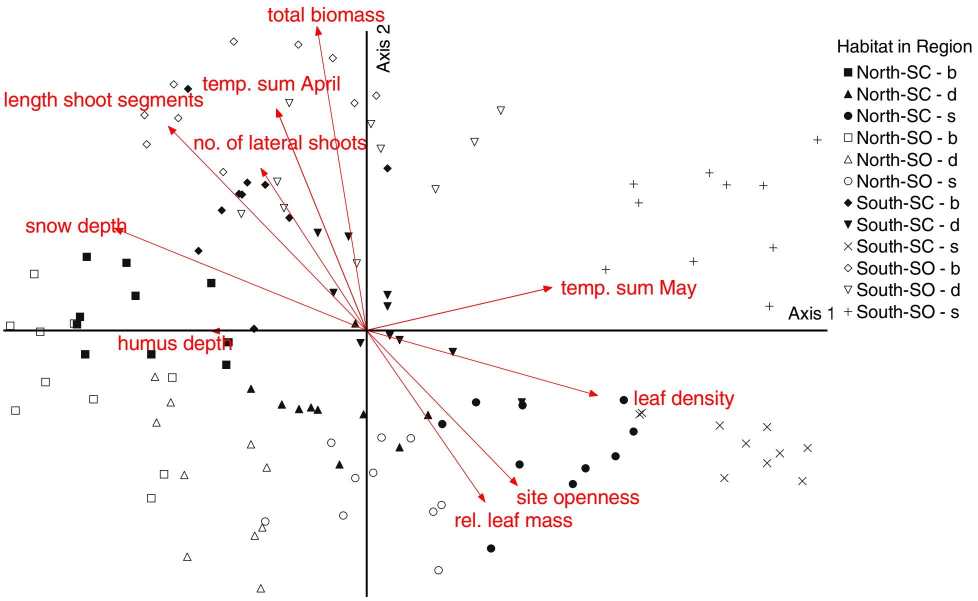

Fig. 2 DCA ordination of 120 vegetation surveys from habitats with deep snow cover and low (***b***) and intermediate site openness, respectively (***d***) and from habitats with shallow snow cover and higher site openness (***s***) in North and South with post hoc correlation of the ordination axes with environmental data and growth variables. Eigenvalue axis 1/axis 2: 0.44/0.23; length of gradient: 3.16/2.14

percentages of explained variation were found for leaf allocation (26.3 %) and total biomass (30.9 %), and the importance of latitude exceeded that of habitat type in the case of leaf life expectancy (31.2 %). Ramet height (North 9.1 ± 0.5; South 11.7 ± 0.9 cm), length of annual shoot segments (North 18.9 ± 0.10; South 25.5 ± 2.0 mm), number of lateral shoots (North 2.4 ± 0.1; South 3.4 ± 0.2) and total biomass (North 8.5 ± 0.6; South 31.0 ± 3.6 mg) were generally higher at lower latitudes. In contrast, leaf density (North 2.0 ± 0.1; South 1.7 ± 0.1 leaves per mm stem), relative leaf mass (North 15.1 ± 1.1; South 7.7 ± 0.8 % of total biomass) and leaf life expectancy of the C_{+1} shoot generation (North 1.3; South 0.9 years) were significantly lower at lower latitudes.

Although climate explained only between 1 and 14 % of the total variation, most traits differed significantly among climates within latitudes. Along the climatic gradient, relative leaf mass (SC 12.6 ± 1.1; SO 10.2 ± 1.0 % of total biomass) and leaf life expectancy were lower in the sub-oceanic study regions (SC 1.2 ± 0.0; SO 1.0 ± 0.0 years). In contrast, number of lateral shoots (SC 2.6 ± 0.2; SO 3.2 ± 0.2) and total biomass (SC 14.3 ± 1.6; SO 25.5 ± 3.8 mg) were significantly higher in the sub-oceanic

Table 3 The effect of habitat type, latitude and climatic region on shoot growth variables of *Empetrum* (hierarchical ANOVA)

Factor		Ramet height (log)		Shoot length (log)		# Lateral shoots		Total biomass (log)	
	df	SQ	% ev	SQ	% ev	SQ	% ev	SQ	% ev
Latitude	1	0.216***	3.0	0.213***	2.9	32.661***	11.5	6.149***	30.9
Climate (latitude)	2	0.090*	1.3	0.075^{ns}	1.0	13.354**	4.7	0.690***	3.5
Habitat [climate (latitude)]	8	5.722***	79.6	5.285***	71.2	108.798***	38.2	9.850***	49.4
Contrasts									
b + ***d*** vs. ***s***	1	5.345***		4.522***		75.561***		8.230***	
b vs. ***d***	1	0.181***		0.323***		10.691**		0.417***	
Residuals	107	1.160	16.1	1.846	24.9	130.131	45.7	3.238	16.3

Factor	*df*	Leaf density (log)		Relative leaf mass (log)		Leaf life exp. C_{+1}	
		SQ	% ev	SQ	% ev	SQ	% ev
Latitude	1	0.143***	6.3	4.254***	26.3	4.788***	31.2
Climate (latitude)	2	0.146***	6.4	0.693***	4.3	2.165***	14.1
Habitat [climate (latitude)]	8	1.349***	59.4	7.548***	46.5	1.990***	13.0
Contrasts							
b + ***d*** vs. ***s***	1	1.184***		5.671***		0.767***	
b vs. ***d***	1	0.071***		0.729***		0.213^{ns}	
Residuals	107	0.634	27.9	3.732	23.0	6.404	41.7

ANOVA was performed on log-transformed data for ramet height, shoot length, total biomass, leaf density and relative leaf mass. Residual df was 103 for leaf life exp. C_{+1}

b birch forest, *d* deep snow cover sites, *ns* not significant, *s* shallow snow cover sites. *% ev* percent of explained variance

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

than in the sub-continental regions. For ramet height and leaf density, there was no clear trend.

Reproduction

Fruit and flower production differed significantly (except number of berries and seed mass in North-SC) among habitat types (Table 4; Fig. 4). Number of berries per shoot (***b***: 0.02 ± 0.00; ***d***: 0.04 ± 0.01; ***s***: 0.07 ± 0.01), seed mass (***b***: 0.8 ± 0.0; ***d***: 0.9 ± 0.0 ***s***: 1.0 ± 0.0 mg) and number of flower buds (***b***: 6.3 ± 2.4; ***d***: 16.0 ± 4.7; ***s***: 26.9 ± 6.3) increased from ***b***- and ***d***- to ***s***-habitats. For the mean number of seeds per berry, there was no effect of habitat type. However, the number of seeds per berry (North-SC 7.5 ± 0.1; North-SO 8.0 ± 0.1) was significantly higher, and seed mass (North-SC 1.1 ± 0.0; North-SO 0.8 ± 0.0 mg) was significantly lower in the sub-continental study region. The number of berries and number of flower buds showed no significant effect of climate.

The factor habitat explained 31.4 and 24.9 % of variation in number of berries per shoot and number of flower buds per clone, whereas the factor climate had no significant influence on these two variables. In contrast, climate explained 34.6 and 39.1 % of the variation in number of seeds per berry and seed mass, respectively, whereas habitat explained only 5.6 and 25.0 %, respectively.

Discussion

Our data clearly show that vegetative growth and reproduction of *Empetrum* varied significantly among habitats defined according to winter snow depth. The relationship appears to be strong, as habitat effects were mostly larger than the effects of latitude and climate. This allows a novel multi-scale perspective on the geographic variation of morphological traits in *Empetrum*. Additionally, consistently different performance in terms of growth and reproduction between contrasting habitat types suggests that there may be local adaptation (Kawecki and Ebert 2004) to habitats with different winter snow cover (and co-varying abiotic conditions during the growing season) in this keystone species despite more or less continuous populations. Local adaptation, despite gene flow, has been recently demonstrated in the alpine grass *Festuca eskia* (Gonzalo-Turpin and Hazard 2009). For *Empetrum*, on-going landscape genetic studies will show whether observed

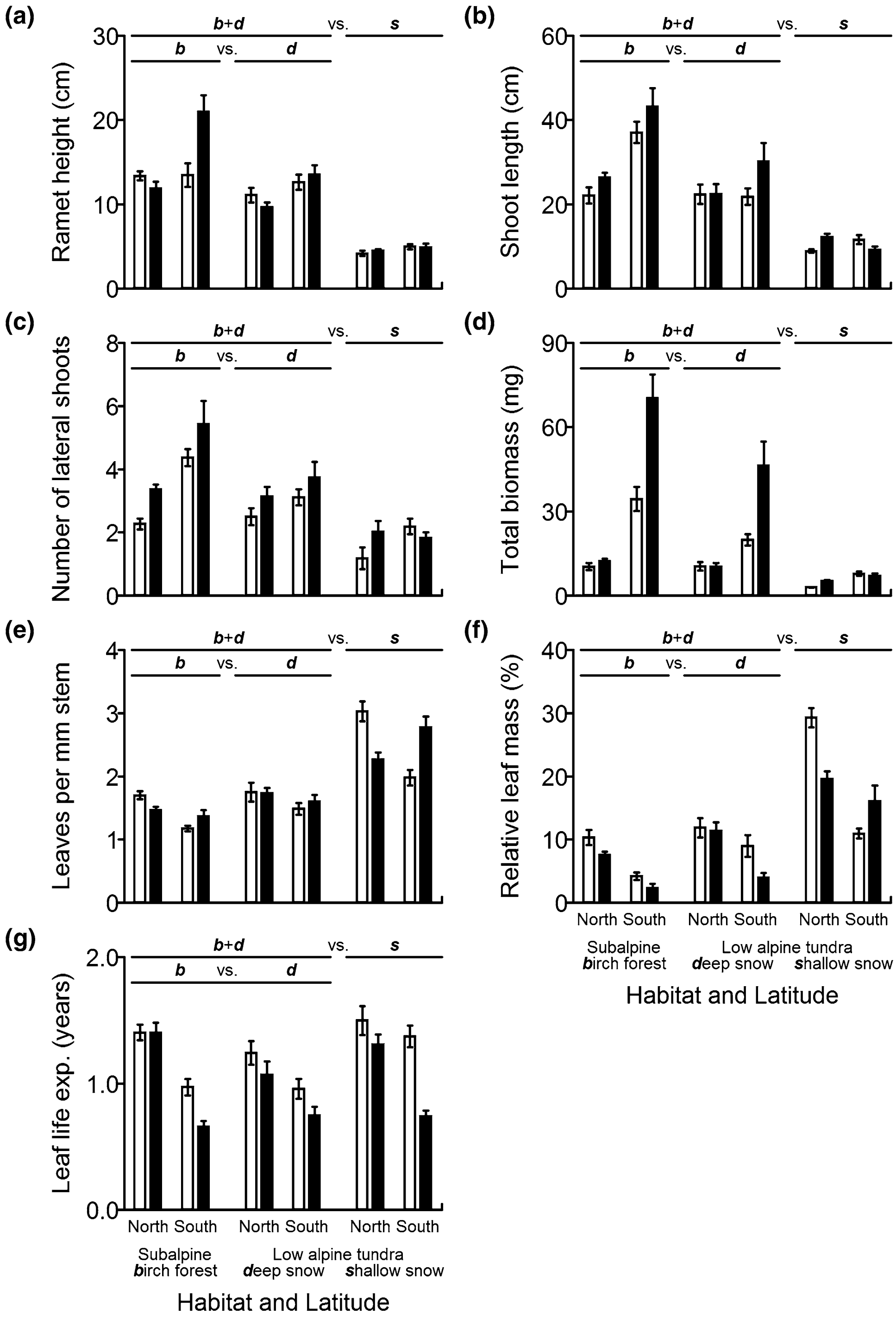

Fig. 3 Ramet height above ground (cm) (**a**), length of shoot segment (mm) (**b**), number of lateral shoots (**c**), total biomass (mg) (**d**), leaves per mm stem length (**e**), relative leaf dry mass (% of total biomass) (**f**), and leaf life expectancy (C_{+1}) (**g**) of *Empetrum* in different habitats along the climatic and latitudinal gradient. Values represent untransformed mean ± SE, $n = 10$. *White bars* represent sub-continental climate and *black bars* sub-oceanic climate. *Lines* above the *bars* depict the planned contrasts between ***b*** + ***d*** vs. ***s*** and ***b*** vs. ***d***, respectively. A break between the *lines* indicates significant differences between groups

phenotypic trait variation is genetically fixed or rather owing to phenotypic plasticity (Bienau et al. in progress).

Shoot growth

Statistical analysis confirmed that habitat types across latitudes and climates differed significantly in snow depth and snow data are quantitatively in line with the long-term snow depth records for Abisko (North-SC) of 51.5 cm in March (Kohler et al. 2006). The performance of *Empetrum* in habitats with deep winter snow cover with higher ramets, longer shoot segments, more lateral shoots and higher total biomass could, first, be a consequence of physical protection from wind damage and ice abrasion in winter. Shoot height of most dwarf shrubs is probably controlled by snow depth since shoots protruding above the protective snow layer will

Table 4 The effect of habitat type, latitude and climatic region on reproduction variables of *Empetrum* (hierarchical ANOVA)

Factor		Berries per shoot (ln)		Seeds per berry		Seed mass		# Flower buds (arcsine)	
	df	SQ	% ev	SQ	% ev	SQ	% ev	SQ	% ev
Climate	1	0.001^{ns}	0.2	4.564***	34.6	0.818***	39.1	0.282^{ns}	4.4
Habitat (climate)	4	0.192***	31.4	0.743^{ns}	5.6	0.522***	25.0	1.581**	24.9
Contrasts									
b* + *d* vs. *s	1	0.098***		0.341^{ns}		0.225***		0.795**	
b* vs. *d	1	0.039*		0.121^{ns}		0.158**		0.231^{ns}	
Residuals	54	0.419	68.4	7.871	59.7	0.751	35.9	4.499	70.7

ANOVA was performed on ln-transformed data for berries per shoot and on arcsine-transformed data for number of flower buds

b birch forest, *d* deep snow cover sites, *ns* not significant, *s* shallow snow cover sites. % *ev* percent of explained variance

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

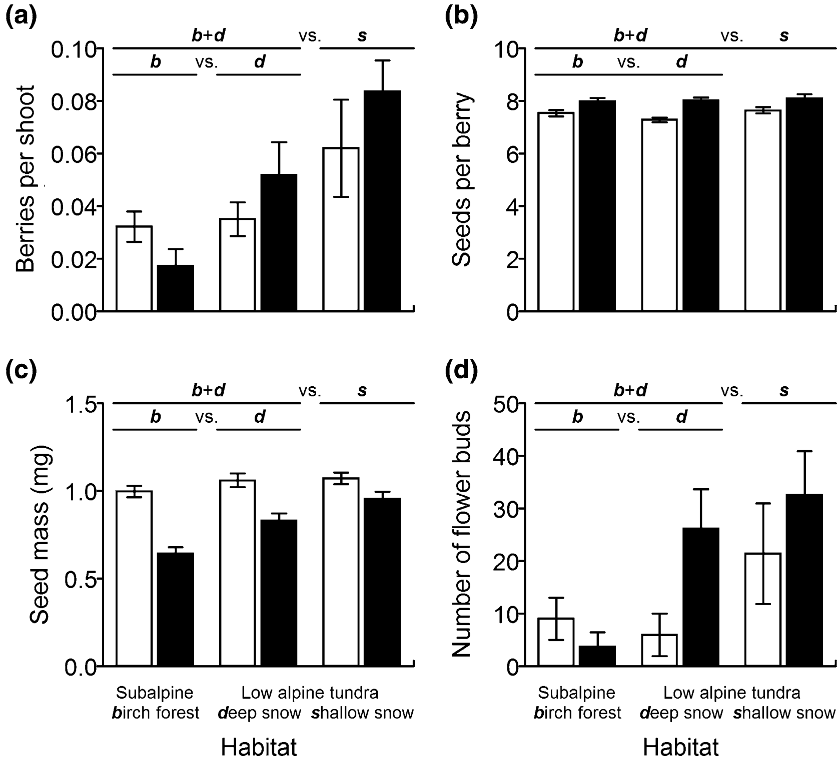

Fig. 4 Number of berries per shoot (**a**), mean number of seeds per berry (**b**), seed mass (mg) (**c**), and number of flower buds (**d**) of *Empetrum* in different habitats along the climatic and latitudinal gradient. Values represent untransformed mean ± SE, $n = 10$. *White bars* represent sub-continental climate and *black bars* sub-oceanic climate. *Lines* above the *bars* depict the planned contrasts between ***b* + *d*** vs. ***s*** and ***b*** vs. ***d***, respectively. A break between the *lines* indicates significant differences between groups

be damaged (Sonesson and Callaghan 1991; Callaghan et al. 2011). Second, snow has an insulating effect (Kelley and Weaver 1969). Thus, a snow layer of >20 cm will protect plant tissues from extreme temperatures and also reduce the potential damage of frost spells early in the season (Körner 2003). Finally, the performance of *Empetrum* in habitats with deep snow may be caused by facilitation through co-occurring erect shrubs such as *Betula nana* (Fletcher et al. 2010), which acts as a snow trap in winter, but also presents wind protection during the snow-free period (Sturm et al. 2001). Furthermore, water and nutrient availability during summer are higher in sheltered habitats (Billings and Bliss 1959; Hadley and Smith 1987; Sturm et al. 2001; Fletcher et al. 2010). In Arctic ecosystems with extreme abiotic conditions, facilitative effects of neighbors may be stronger than negative effects of competition (Carlsson and Callaghan 1991; Shevtsova et al. 1995; Callaway et al. 2002; Wipf et al. 2006; Olofsson et al. 2011).

In wind-exposed ***s***-habitats, with low or lacking snow cover during winter, *Empetrum* has a more procumbent growth form with lower ramet height, shorter shoot segments and lower numbers of branches, but higher leaf density. As a result of an unstable, shallow snow cover during winter, soil temperature is lower and frost can penetrate more deeply into the soil than on sites with a protecting snow cover during winter (Sjögersten and

Wookey 2005). Consequently, a denser leaf packing probably presents an adaptation to cold winter temperatures and the prevailing strong winds, reducing freezing and desiccation (Körner 2003). Furthermore, the present study revealed significantly higher leaf life expectancy of the C_{+1} generation for *Empetrum* in the ***s***-than in ***b***-and ***d***-habitats. In the latter habitats with deep snow, leaf mortality may increase as a consequence of higher abundance of pathogens beneath the long-lasting snow cover (e.g., Olofsson et al. 2011). Specifically, *Arwidssonia empetri*, a host-specific fungal pathogen of *Empetrum*, may cause dramatic declines of its abundance (Olofsson et al. 2011). Deeper snow cover may also promote the development of other plant pathogens such as snow molds (fungi: Ascomycetes, Basidiomycetes, Zygomycetes; and fungi-like micro-organisms: Oomycetes), which damage plants at low temperatures under snow cover (Hoshino et al. 2009; Tojo and Newsham 2012). Generally, estimated leaf life expectancies are in line with observed leaf life spans of between 1 and 4 years for evergreen species, depending on species and habitat (Bliss 1971; Karlsson 1992).

Deeper snow cover may also lead to higher nutrient availability which might promote the growth of *Empetrum*. Generally, snowpack may act as a reservoir of atmospherically deposited inorganic nitrogen which leads to greater nitrogen inputs during snowmelt on sites with higher snow accumulation (Bowman 1992; Weih 1998) in ***b***-and ***d***-habitats as well as in sub-oceanic compared to sub-continental study sites. Furthermore, mineralization of organic matter as a source of soil inorganic nitrogen before and during snowmelt in spring is higher under deep snow packs (Brooks et al. 1996). In fertilizer experiments, *Empetrum* responded to artificially increased nutrient availability with an increase in leaf number and leaf mass per shoot, a greater shoot mass, an increase in shoot extension growth and stem length, an increase in height and production of more lateral branches (Chapin and Shaver 1985; Wookey et al. 1993; Parsons et al. 1994; Campioli et al. 2012; but see Press et al. 1998).

During the growing season, the amount of solar radiation is an important abiotic factor for *Empetrum* growth. Due to the low vegetation height, plants on wind-exposed ridges experience almost full illumination. In contrast, the ***b***-habitat showed the lowest site openness, caused by the presence of trees whose leaf canopies reduce solar radiation and light quality.

Higher relative allocation to leaves and higher leaf density might ensure sufficient assimilation and biomass production in the ***s***-habitats with high solar radiation and a long growing season, despite less favorable resource conditions. However, high solar radiation may lead to water stress in spring and summer through stomatal limitation of photosynthesis. Therefore, photosynthetic capacity of plants is higher in plots with late snow melt (Kudo et al. 1999; Fletcher et al. 2010). Furthermore, the longer shoot length in the more shaded ***b***- and ***d***-habitats may be related to shade avoidance. In general, plants show elongated stems and petioles and suppressed branching in darker environments to reach solar radiation (Schmitt and Wulff 1993; Stuefer and Huber 1998; McConnaughay and Coleman 1999; Callaway et al. 2003; Semchenko et al. 2012).

Owing to higher amounts of winter precipitation, our sub-oceanic study regions featured higher snow depths than sub-continental regions (Table 1). Also, *Empetrum* performance, in terms of shoot growth and morphology, varied significantly between climates, although the amount of variance explained by climate was relatively low.

The results showed higher relative leaf mass and leaf life expectancy and lower number of lateral shoots and total biomass in the sub-continental study regions. This is consistent with the response of *Empetrum* to different habitats and might be forced by greater nitrogen inputs during snowmelt on sites with higher snow accumulation (Bowman 1992; Weih 1998) as well as higher physical protection from wind and ice abrasion in winter (Sonesson and Callaghan 1991; Callaghan et al. 2011).

Furthermore, ramet height, length of annual shoot segments, number of lateral shoots and total biomass were higher at lower latitudes. This is probably related to relatively milder climate at more southern latitudes, e.g., indicated by c. 30 days (means of 2009–2011) longer growing season in the south, allowing prolonged growth (Jonas et al. 2008). Longer and more accelerated growth at southern latitudes can only be achieved through high assimilation rates, leading in turn to higher tissue turnover and lower leaf life expectancy. This is in line with Karlsson (1992), who found a positive relationship between leaf longevity and latitude.

Higher site openness in birch forest habitats in North-SC and North-SO than in South-SC and South-SO may be caused by the caterpillar outbreak during the summer of 2012 reducing the birch canopy in North-SC and North-SO. There is a 9- to 10-year cyclicity of caterpillar outbreaks (*Epirrita autumnata* and *Operophtera brumata*) in the Scandes (Tenow 1996; Bylund 1999; Ruohomäki et al. 2000). During these outbreaks, either limited areas might become totally defoliated or areas of hundreds of square kilometers might be damaged (Ruohomäki et al. 2000). The caterpillars do not only damage the birch leaves, but larvae dropping from the trees may defoliate the ground vegetation, in particular *Betula nana*, *Empetrum*, *Vaccinium myrtillus* and *V. vitis-idaea* (Tenow 1996).

Reproduction

Increasing numbers of berries per shoot, numbers of flower buds and seed mass from ***b***- and ***d***- to ***s***-habitats might be an effect of the open habitat. Due to earlier snow melt, the growing season starts earlier which promotes flowering (Kudo and Suzuki 1999). Additionally, higher average temperatures in ***s***-habitats during the growing season (Electronic Supplementary Material S1) will probably benefit fruit maturation and seed quality (Graae et al. 2008). *Empetrum* seeds need warm stratification after cold stratification to break dormancy (Baskin et al. 2002; Graae et al. 2008). Consequently, germination of *Empetrum* may be promoted by soil disturbance, which removes the insulating cover over seeds and enables warm stratification (Baskin et al. 2002) and by reduced competition from surrounding vegetation and other *Empetrum* individuals (Szmidt et al. 2002). A similar effect might be active in open habitats with earlier snowmelt. Therefore, the ***s***-habitat seems to be the most favorable habitat for seed production and seedling establishment of *Empetrum.* Once *Empetrum* has established, clonal growth will be more important for determining site occupancy and population structure (Szmidt et al. 2002; Boudreau et al. 2010).

North-SC had lower seed numbers but heavier seeds than North-SO. Due to the later start of the growing season, seeds had less time to ripen and were therefore smaller. However, the significantly lower number of flower buds and berries and the production of lighter seeds in the ***b***-habitat of North-SO might partly be related to the effects of herbivory of caterpillars, which showed much higher abundances in the birch forest habitat in North-SO than in North-SC (personal observation). The caterpillars damaged *Empetrum* to a high degree which likely had a negative influence on reproductive variables of *Empetrum*.

Implications for the response of *Empetrum* to climate change

Expected changes in snow depth and timing of snow melt may have strong effects on Arctic ecosystems (Bokhorst et al. 2012). Snow manipulation experiments showed that earlier snowmelt resulted in a longer growing season (cf. Wipf et al. 2006). On the other hand, earlier snowmelt may also lead to increased frost damage because of a high probability and frequency of frost spells early in the year (Wipf et al. 2006, 2009). However, although higher elevation and earlier snow melt habitats had a higher risk of spring freezing exposure, spring freezing resistance of four shrub species did not differ significantly along elevational and snow melt gradients (Wheeler et al. 2014). Shoot growth, flower bud break and flowering in *Empetrum* were advanced when snowmelt occurred earlier (Wipf et al. 2009; Wipf 2010), whereas even short-term events like a 1-week episode of winter warming may have strong effects such as delayed bud burst in *Empetrum* and reduced shoot growth (Bokhorst et al. 2008, 2009).

The present study investigated the response of a plant species to natural variation of snow cover in the field across latitudinal and local climatic gradients. This comparative multi-site analysis along a steep natural environmental gradient, encompassing the range of climate change predictions, is more likely to give a realistic picture concerning extent of intraspecific phenotypic trait variation, which may determine the long-term adaptive potential of *Empetrum* to climate change (Körner 2003; Dunne et al. 2004; Kudo and Hirao 2006).

We found consistent variation among habitat types across latitudes and climatic gradients underlining that snow cover potentially represents a strong force of selection. Additionally, differences in the timing of snow melt may affect flowering phenology, restrict gene flow between habitats and lead to genetic isolation of microhabitats. Clear and consistent differences in growth and reproduction may suggest local adaptation of *Empetrum* to habitats differing in snow depth (Kawecki and Ebert 2004; Gonzalo-Turpin and Hazard 2009). However, shoots of *S. herbacea* from phenologically isolated microhabitats were not genetically differentiated (Cortés et al. 2014), but owing to asymmetric gene flow towards snow beds, these late-melting microhabitats were genetically more diverse than early melting ridge sites.

The present study demonstrates that *Empetrum* has a broad ecological niche and shows a consistent match between its growth and morphology and the prevailing local habitat conditions. The high morphological plasticity of *Empetrum* supports findings of climate change experiments, and suggests that the species has the potential to cope with changing snow conditions in the course of climate change. However, while phenotypic plasticity will allow individuals to immediately adapt to changing conditions, locally adapted populations may locally go extinct. The latter will offer the possibility for seedling recruitment of adapted genotypes, but possibly also for replacement of *Empetrum* by other species with cascading effects on ecosystem functioning. Therefore, it will be crucial to understand how much of the habitat-specific variation in growth and reproduction is driven by phenotypic plasticity or genetic variation before predictions concerning the effects of climate change on fitness and distribution of this ecosystem driver can be made.

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